PONTIFICIAE ACADEMIAE SCIENTIARVM SCRIPTA VARIA

54

STUDY WEEK

ON:

PATTERN RECOGNITION MECHANISMS

April 25-29, 1983

EDITED BY

CARLOS CHAGAS - RICARDO GATTASS - CHARLES GROSS

PONTIFICIA
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SCIENTIARVM

EX AEDIBVS ACADEMICIS IN CIVITATE VATICANA

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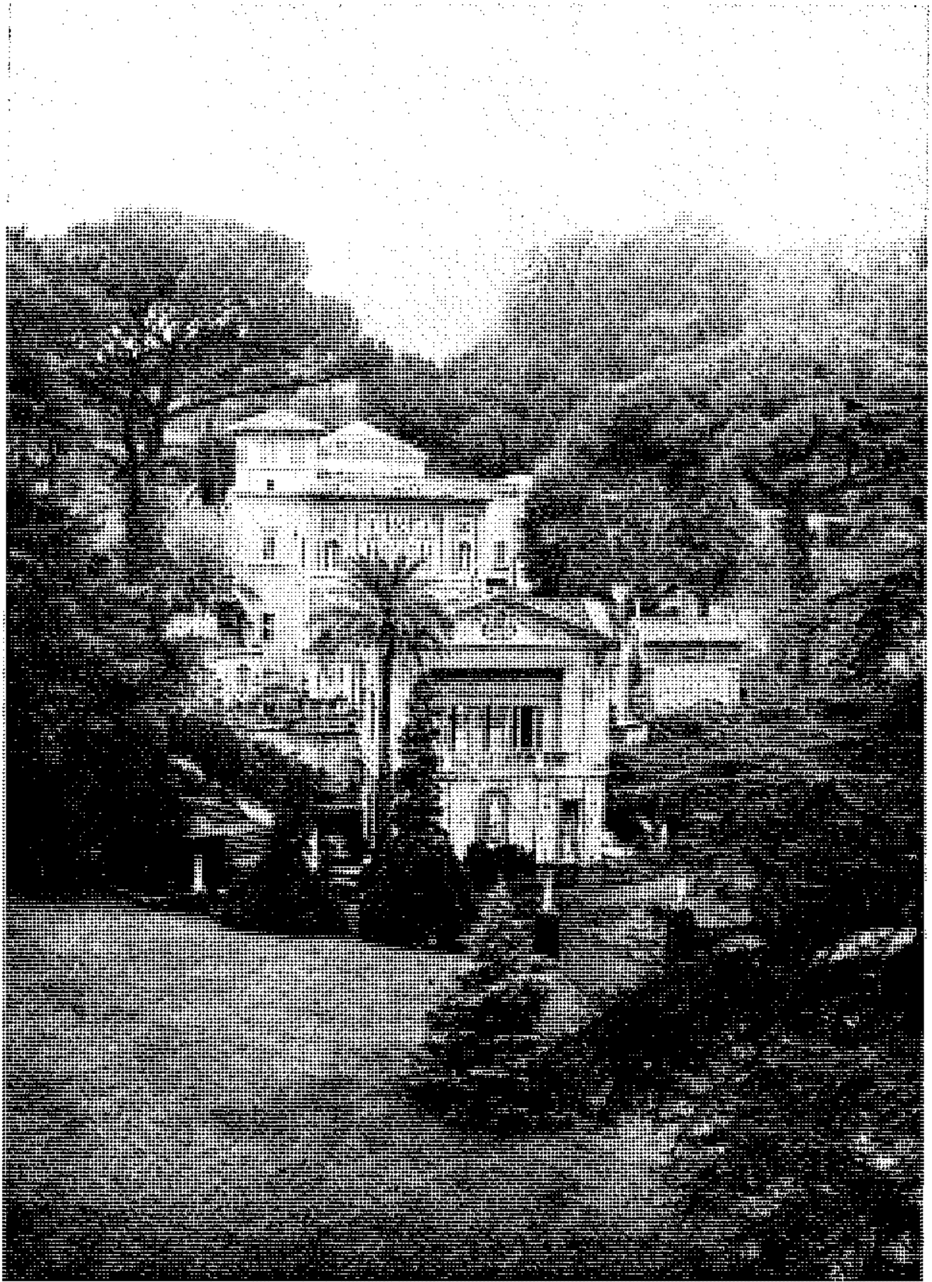

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SCIENTIFIC PAPERS

FOREWORD

The Meeting held at the Pontifical Academy of Sciences on “Pattern Recognition Mechanisms” *had its origin from a talk I had in Rio de Janeiro with Charles Gross and my colleagues of the Instituto de Biofisica, one of whom, C.E. Rocha Miranda, had worked with him at his earlier days at the Massachusetts General Hospital in Boston.*

Form recognition by some neurons of the optical patterns, was the subject discussed in at least one seminar during the stay of Dr. Gross in Rio. From the data presented emerged the idea of a Study Week in which the subject of how information gained by the optical system is received and can be treated. The idea was an ambitious one, but I believe that our scientific guests have advanced our knowledge on the subject, thus opening new perspectives for research.

The knowledge of how our brain works for the performance of actions which are not realized by other animals, is a constant subject of exposés, meetings and discussions and for three times has been the subject of our work.

Sir John C. Eccles, a Member of the Pontifical Academy of Sciences since 1961, was one of the scientists who has taken a great part in the criticism of many of the theories presented in this area and has exposed in a very incisive way his own ideas, with the forcefulness and the charm which are his. His contribution to neurobiology is admired by both those who follow his ideas and those who diverge from them. His participation in the work of the Academy has been extremely fruitful. It was Eccles who organized in 1964 our first Meeting on Brain Sciences. The work done then by the Study Week on Neurobiology was published under the title of “Brain and Conscious Experience” (Scripta Varia No. 30). *As always he took a very active part in this Study Week.*

It was for me a joy to honour John Eccles at his 80th anniversary.

I wish to express my profound thankfulness to Charles Gross and R. Gattass for helping the Academy to organize this meeting.

I wish also to express my thanks to all the Participants. They left their homes and laboratories to come here, not to see the beauties of Rome, but to work extremely hard from 9 a.m. to 6 p.m. during 5 days, and this, I believe, will bring new perspectives to brain research.

Finally it is my wish to express my deep thanks to Father Enrico di Rovasenda, to Mrs. Michelle Porcelli, Mrs. Gilda Massa and Mr. Silvio Devoto for the help they have given to me during the meeting, a help which is just the continuation of the splendid work they have accomplished for the Academy, sometimes in very exhausting conditions.

CARLOS CHAGAS
President of the Pontifical Academy of Sciences

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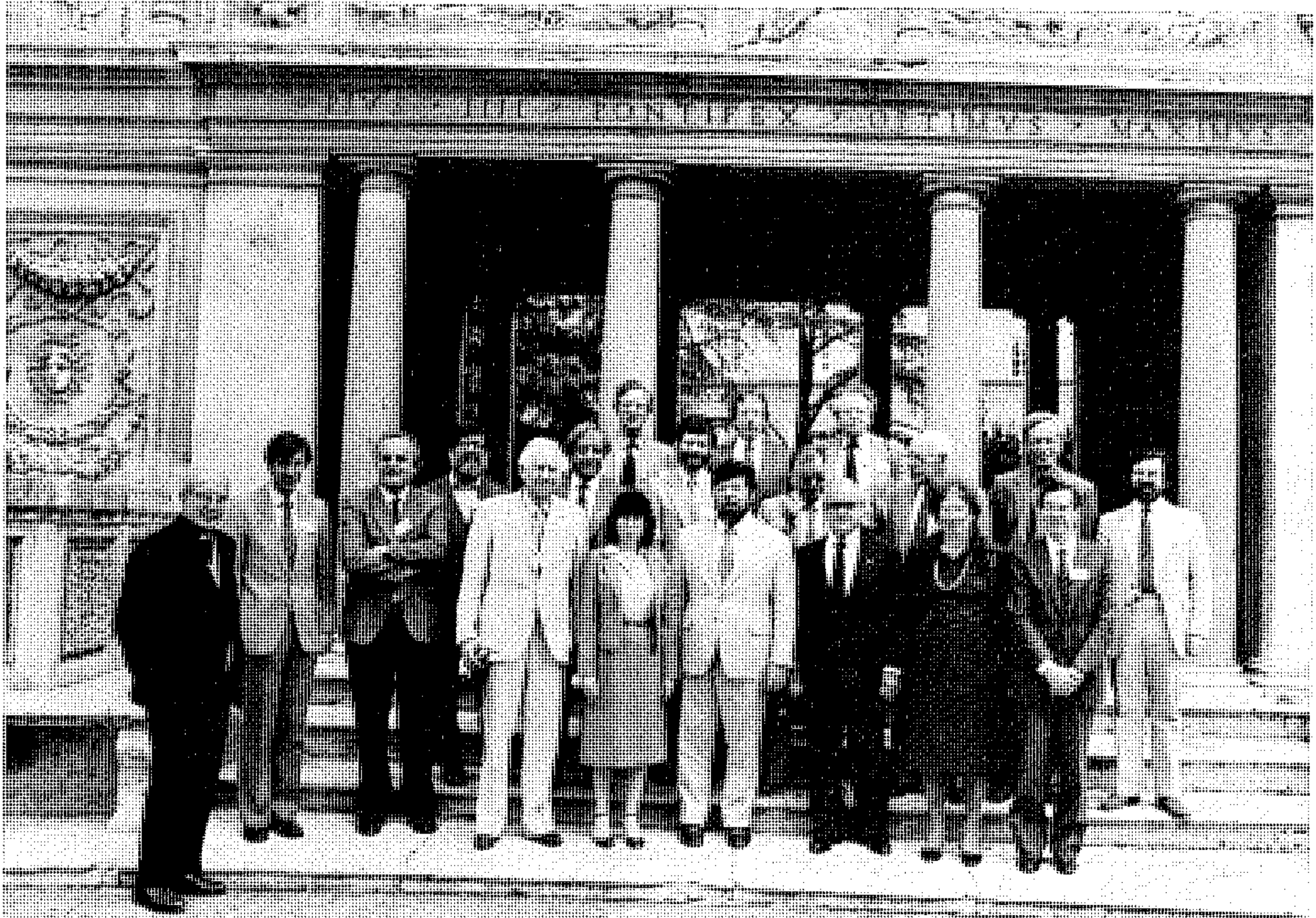

SCIENTIFIC PAPERS

CORTICAL VISUAL AREAS OF THE MACAQUE: POSSIBLE SUBSTRATES FOR PATTERN RECOGNITION MECHANISMS

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INTRODUCTION

In primates, a large proportion of the posterior cortical mantle is visual in function. The prestriate cortex in these animals is composed of multiple topographically organized representations of the visual field. In the owl monkey, a relatively lissencephalic New World primate, Allman and Kaas have described nine such areas (see Allman, 1981). In the macaque, an Old World primate with a highly convoluted cortex, this organization is not well understood. Based on anatomical and electrophysiological evidences Zeki suggested that there are two visuotopically organized areas anterior to striate cortex which he named V2 and V3 (Zeki, 1977). He also described a motion sensitive area in the superior temporal sulcus (Zeki, 1974) and a color sensitive V4 complex in the prelunate gyrus (Zeki, 1973). Van Essen and Zeki (1978) have also described an additional dorsal visual area, V3A. However, they neither defined the extent nor described the topographic organization of any of these extra-striate visual areas.

We have been mapping the organization of extrastriate cortex in the macaque by recording from clusters of neurons on successive electrode penetrations. Each animal was recorded from on several occasions yielding information about receptive field location of neurons in hundreds of systematically located sample sites. On the basis of these data we have reported on the visual organization of V2 (Gattass *et al.*, 1981), MT (Gattass and Gross, 1981), V3 and V4 (Sousa *et al*, 1981); and PO (Covey *et al.*, 1982). The purpose of this paper is to review the evidence for topographic organization in extrastriate visual cortical areas of the macaque. We discuss receptive field size and cortical magnification and the use of these measures as criteria for assessing the possible role of each area in pattern recognition.

THE PRESTRIATE VISUAL AREAS: LOCATION AND ORGANIZATION

The location and extent of the cortical visual areas of the macaque are shown in figure 1.

V2

In New World monkeys, the existence of V2 was first suggested by Covey (1964) in the squirrel/monkey. It was subsequently mapped in detail by Allman and Kaas (1974) in the owl monkey. In Old World monkeys, V2 was first demonstrated by Zeki and his colleagues (Zeki and Sandeman, 1976; Van Essen and Zeki, 1978), who mapped an area of about 10° of the lower visual field adjacent to striate cortex in the macaque. We have subsequently mapped the topographic organization of V2 in detail and defined its boundaries in this species (Gattass *et al.*, 1981).

V2 is larger tban any other prestriate area. It is myeloarchitectonically distinct from the surrounding cortex and, in sections stained for myelin by the Heidenhain-Woelke method, it is characterized by a broad homogeneous dark band of fibers extending from layer 6 through layer 4 and fading out in layer 3 (Gattass *et al.*, 1981). V2 forms a belt around striate cortex, which is continuous except for a small interruption at the anterior portion of the calcarine fissure (Fig. 1). V2 appears to be coextensive with Von Bonin and Bailey's (1947) cytoarchitectonic area OB, except at the extreme rostral end of the calcarine fissure, anterior to striate cortex. V2 contains a topographically organized representation of the contralateral visual field up to an eccentricity of at least 80°. The representation of the vertical meridian is adjacent to that of V1 and forms the posterior border of V2. The representation of the horizontal meridian in V2 is split and forms its anterior border. The lower visual field representation is located dorsally and that of the upper field ventrally. As in V1, the representation of the central visual field is magnified relative to that of the periphery (Gattass *et al.*, 1981).

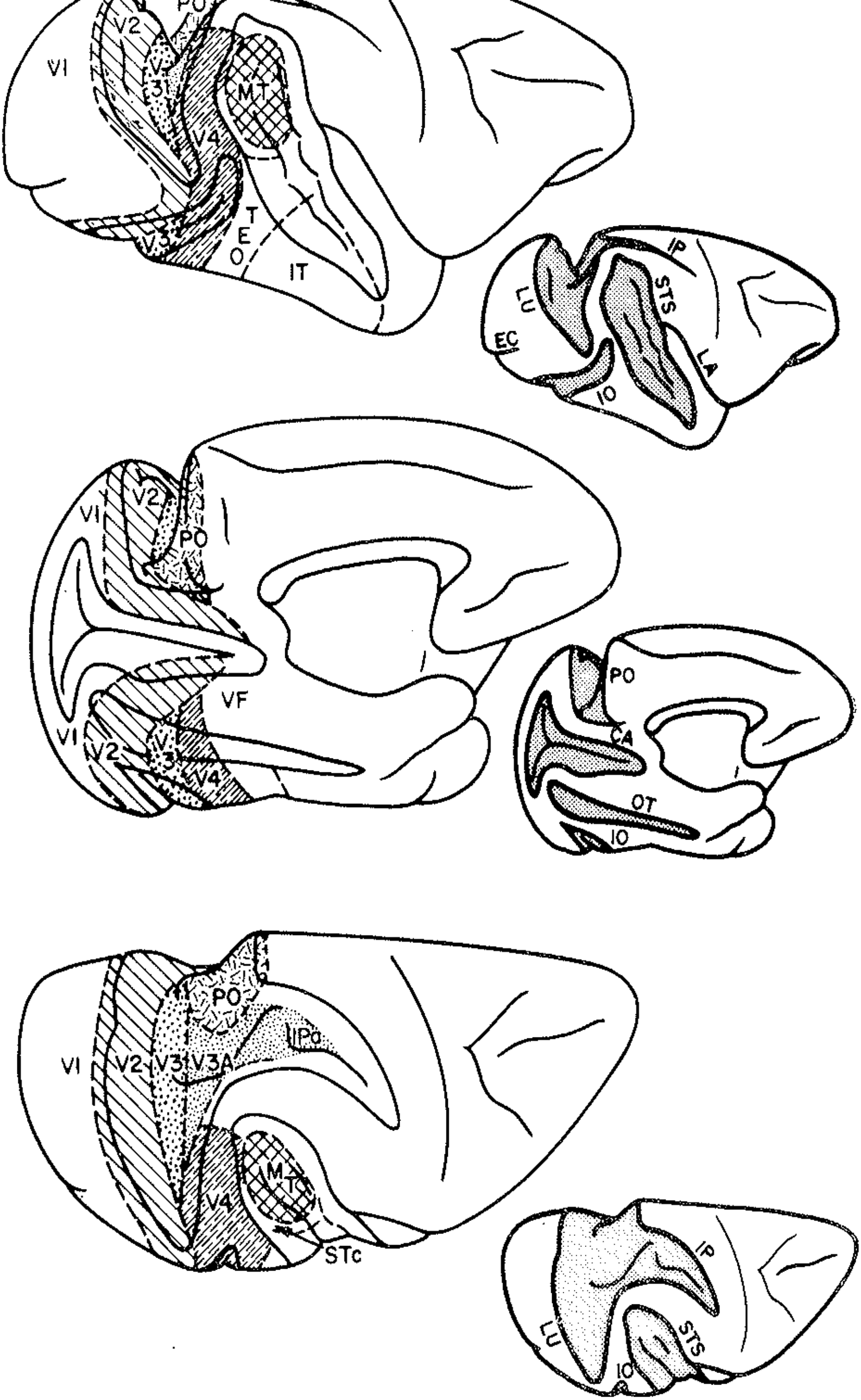

Fig. 1. Lateral (upper), medial (middle) and dorsal (lower) views of a brain with the sulci partially opened (stippled areas in right drawings). Left drawings show the location of the prestriate visual areas. In this and subsequent figures V3A refers to visual areas in the annectant gyrus, and STc refers to STS color area. In right: CA, calcarine sulcus; EC,

The area described electrophysiologically as V2 appears to correspond closely to a zone that receives a topographically organized projection from striate cortex (Cragg, 1969; Zeki, 1969; 1977; Zeki and Sandeman, 1976; Ungerleider and Mishkin, 1979b; Rockland and Pandya, 1981).

Allman and Kaas (1974) have theorized that the visuotopic organization in V1 and V2 represents the optimal configuration to provide efficient anatomical connections between corresponding points. They have further suggested that V1 and V2 may form a functional dyad. There is physiological evidence for a high degree of interaction and interdependence between V1 and V2 (e.g., Schiller and Malpeli, 1977; Sandell and Schiller, 1982). The idea of a cooperative interaction between V1 and V2 is compatible with our finding of similar cortical magnification, surface area, and extent of the visual field represented in V1 and V2 (Gattass *et al.*, 1981).

MT

Several studies in the macaque have demonstrated a projection from striate cortex to a limited area in the posterior portion of the superior temporal sulcus (STS). Zeki (1974; 1978) has termed this area the motion-sensitive area of STS, because its neurons are particularly sensitive to the direction of stimulus movement. We avoid using this name because there are other motion-sensitive areas in STS (Bruce *et al.*, 1981; Van Essen *et al.*, 1981). Like Weller and Kaas (1981) and Van Essen *et al.* (1981) we have called it MT (Gattass and Gross, 1981) because it seems to be homologous to the middle temporal visual area of the owl monkey (see Allman, 1981).

MT is a roughly oval-shaped area in the lower bank and floor of the posterior portion of STS (Fig. 1). It contains a representation of virtually the entire visual hemifield. The representation of the vertical meridian lies near the bottom of the lower bank of STS and forms the ventrolateral border of MT. The horizontal meridian representation runs obliquely and anteriorly across the floor of STS. The upper visual field is located anteriorly and ventrally and the lower visual field posteriorly and dorsally (Fig. 2). The medial border of MT lies slightly above the junction of the floor of STS and its upper bank.

MT is heavily myelinated, but its myeloarchitecture is not homogeneous throughout its extent. There is a more heavily myelinated region at the representation of the central visual field; within this region the pattern of fibers extending from the bottom of layer 3 to layer 6 almost totally

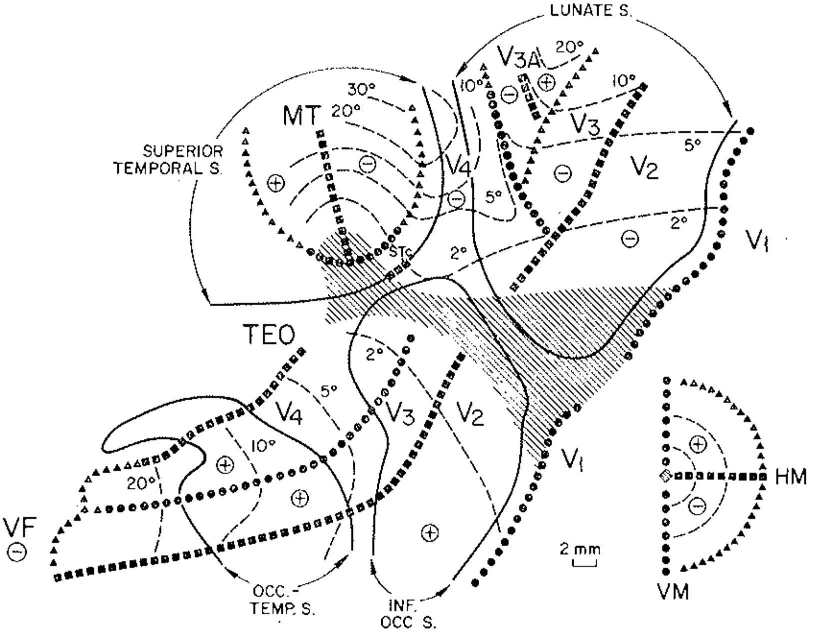

FIG. 2. Flattened reconstruction of the lateral prestriate showing the visual topography of V3, V4 and surrounding areas. Insert is a representation of upper (+) and lower (−) visual field with vertical meridian (dots), horizontal meridian (squares), periphery (triangles), center of gaze (hatched area) and isoeccentricity lines (dashed lines). In the flattened reconstruction the meridians and isoeccentricity lines were drawn based on the coordinates of the receptive field centers. The borders of the lunate, inferior-occipital (inf. occ.), occipital temporal (occ. temp.) and superior temporal sulci are represented by heavy lines.

obscures the two bands of Baillarger. In more peripheral portions, MT is less heavily myelinated and the bands of Baillarger become more visible. Dorsally and posteriorly (in V4), the density of myelination is similar to that in adjacent MT, but the inner band of Baillarger is thicker and layer 6 paler (Gattass and Gross, 1981).

Using visual topography as our criterion, we have defined MT as including both the heavily myelinated area called MT by Van Essen *et al.* (1981) and the less heavily myelinated region extending posteriorly and laterally.

This proposed map of MT is compatible with data shown by Weller and Kaas (1981), Montero (1980) and Rockland and Pandya (1981) using anterograde transport of labelled amino acids from V1, and with anterograde degeneration after lesions that collectively included all of striate cortex (Ungerleider and Mishkin, 1979a).

At a given eccentricity, MT has larger receptive fields and a cruder topography than V1 and V2. Similar to V1 (Hubel and Wiesel, 1974), the scatter of receptive field positions at a given point in MT is proportional to receptive field size (Gattass and Gross, 1981). MT is much smaller than striate cortex, occupying about 1/10 as much cortical area. In MT, as in V1, the representation of the central field is greatly magnified.

If one plots magnification factor versus eccentricity for V1 and MT, the slopes of the power functions for the two areas are not statistically different (Fig. 7A). Thus, the visual topography of MT can be seen as a compression of the map in V1.

V3

Zeki (1977) first reported the presence of another topographically organized area anterior to V2 in which he mapped a representation of the central lower visual field; he called this area V3. Gattass *et al.* (1984) subsequently mapped in detail an area which consists of a narrow strip (4-5 mm wide) of myeloarchitectonically distinct cortex located anterior to V2 on the dorsal and ventral cortical surfaces. We call this area V3 because it appears to correspond to the area so named by Zeki.

Dorsally, V3 occupies the floor of the lunate sulcus and the posterior portion of the annectant gyrus. Ventrally, V3 extends across both banks of the inferior occipital and occipito-temporal sulci (Fig. 1). In sections stained for myelin by the Heidenhain-Woelke method V3 is characterized by a rich pattern of fibers from layer 6 to layer 3, showing a prominent inner band of Baillarger. It is myeloarchitectonically distinct from the surrounding areas, except from one area located medially in the annectant gyrus (Gattass *et al.*, 1984) apparently corresponding to Zeki's area V3A (see Figs. 1 and 2).

The dorsal portion of V3 contains a systematic representation of the lower visual field, while the ventral portion contains a systematic representation of the upper visual field (Fig. 2). The horizontal meridian representation is adjacent to that of V2 and forms the posterior border of V3 both dorsally and ventrally. On the dorsal surface, V3 is bordered anteriorly by V4, V3A in the annectant gyrus and, in some animals, by Area PO. Dorsally, the border of V3 with V4 lodges the representation of the vertical meridian, while the peripheral field representation lies within the annectant gyrus and in the neighborhood of area PO. Ventrally, the border of V3 with V4 coincides with the representation of the vertical meridian. In animals in which V3 borders VF (see below) this border coincides with the representation of the periphery. Our data suggest that V3 may not contain a complete representation of the visual field, because we have only recorded receptive fields extending up to 40° eccentricity.

Zeki (1977) reported a direct projection from striate cortex to both the dorsal and ventral portions of V3. In contrast, Van Essen *et al.* (1982) found only the dorsal portion to he striate recipient. On the basis of these results, Van Essen and his colleagues retained the name V3 for the dorsal portion, but renamed the ventral portion as VP, assuming that it was a separate area. Injections of 3H-amino acids in V2 result in two separate patches of anterograde label anterior to V2, both dorsally and ventrally (Ungerleider *et al.*, 1983). These two zones appear to correspond to dorsal and ventral V3 and V4 as we have defined them electrophysiologically. According to Ungerleider (1983) the main projection field of V1 is V2, which in turn projects to V3 and V4.

Thus the available evidence suggests that what we call dorsal V3 probably corresponds to the area described as V3 by Zeki (1977) and by Van Essen *et al.* (1982); and what we call ventral V3 probably corresponds to the ventral part of V3 as proposed by Zeki (1977) and to area VP as described by Newsome *et al.* (1980).

V4

Zeki (1973) and Van Essen and Zeki (1978) have described a color sensitive complex in the prelunate gyrus which they named V4. We studied tbe topographic organization of V4 (Sousa *et al.*, 1981) both on the dorsal and ventral surfaces (Fig. 1 and 2). V4 is a strip (5-8 mm wide) of myeloarchitectonically distinct cortex characterized by prominent inner and outer bands of Baillarger. Dorsally it occupies the prelunate gyrus, extending posteriorly onto the anterior bank of the lunate sulcus and anteriorly onto the posterior bank of the superior temporal sulcus. Along the prelunate gyrus, the medial border of V4 always lies a few millimeters below the posterior tip of the superior temporal sulcus. V4 extends laterally and ventrally to occupy both banks of the inferior occipital and occipital temporal sulci. Dorsomedially V4 borders area PG (area 7); posteriorly it abuts against V3A in the annectant gyrus, as well as V3 and V2; anteriorly V4 borders MT, the STS color area, described by Zeki (1973) and the areas described by Von Bonin and Bailey as TEO and TF.

V4 contains a coarse but systematic representation of the contralateral visual field. The representation of the lower visual field is dorsal, while that of the upper field is ventral (Sousa *et al.*, 1981). The vertical meridian of V4 forms its posterior border, adjacent to V3 and V3A. The representation of the horizontal meridian lies laterally on the border with the STS color area. The representation of the periphery forms the dorsal and anterior border of V4, adjacent to MT. The foveal representation of V4 is located in the lateral surface. Ventrally, the vertical meridian of V4 is adjacent to that of V3 and forms its posterior border. The horizontal meridian forms its anterior border adjacent to area TEO. The representation of the periphery forms the border of V4 with another visual area located in TF cortex, labeled VF in figures 1 and 2.

Our data suggest that V4 does not include an entire representation of the visual field. We only recorded receptive fields in V4 extending up to 50° eccentricity. The representation of the central portion of the visual field in V4 is greatly expanded with respect to the periphery (Sousa *et al.*, 1981).

Our description of V4 corresponds closely to the more anteriorly located V2 projection zone described by Ungerleider *et al.* (1983) both dorsally and ventrally. V4 as described by Zeki (1978) and by Van Essen and Zeki (1978) correspond to part of the area that we have described as dorsal V4 (Sousa *et al.*, 1981).

Area PO

While studying the visual topography of the lower field representation of V2 we discovered an upper field representation bordering V2 on the medial cortical surface. This finding constituted evidence for an additional visual area which we provisionally called Area PO (Covey *et al.*, 1982), because of its location in the parieto-occipital sulcus. Area PO lies on the anterior bank of the parieto-occipital sulcus and extends onto adjacent portions of the precuneate gyrus and onto the adjacent portion of the medial bank of the intraparietal sulcus (Fig. 1). Area PO can be distinguished from surrounding areas in fiber-stained sections. It has the myeloarchitectonic pattern typical of area OA with prominent inner and outer bands of Baillarger. Area PO borders V2 medially, area 5 dorsally, V3 ventrally and posteriorly, and a myeloarchitectonically distinct area in the annectant gyrus, ventrolaterally (Covey *et al.*, 1982).

Area PO contains a complete representation of the contralateral visual field, with the representation of the upper field located medially and that of the lower field laterally (Fig. 3). The representation of the horizontal meridian lies along the ventromedial border of Area PO, separating it from V2. More laterally it splits and extends along the anterior bank of the parieto-occipital sulcus, separating upper and lower visual fields within Area PO.

The representation of the visual periphery is extremely large compared to that of the central 30°, and often appears to be discontinuous. Because of these discontinuities and the seemingly complex topography of the area we cannot rule out the possibility that what we call Area PO may be more than one visual area.

Colby *et al.* (1983) injected retrograde tracers in this area. They found that PO receives substantial projections from parts of V1 and V2 representing the visual periphery. They also found substantial labeling in the posterior part of the superior temporal sulcus and in the intraparietal sulcus.

The location, pattern of connections and the basic topographic arrangement of Area PO suggest that it is homologous to area M described by Allman and Kaas (1976), in the owl monkey.

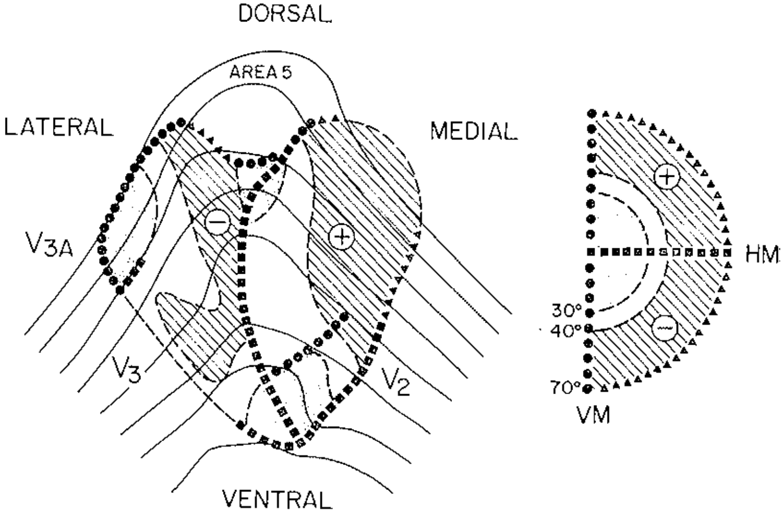

FIG. 3. Visual topography of Area PO. *Left*: Flattened reconstruction of PO, from coronal sections (continuous lines). *Right*: Contralateral hemifield representation subdivided into central (stippled), intermediate (clear) and peripheral (dashed) regions. Vertical meridian (dots) and horizontal meridian (squares). Upper (+) and lower (−) fields.

EVIDENCE FOR ADDITIONAL VISUAL AREAS

In the course of studying the topography of V2, V3 and V4, we obtained evidence for the existence of additional outlying cortical visual areas. The presence of an inferior visual field representation in ventral prestriate cortex was an evidence for an additional visual area which we provisionally term VF. VF is located within the posterior portion of cytoarchitectonic area TF (Von Bonin and Bailey, 1947), anterior to V3 and V4 and lateral to V2. The lower field representation of VF borders the upper field representations of V2, V3 and V4 and it is part of a hemifield representation located within a myeloarchitectonic area distinct from V2, V3, V4 and TEO. It is much less myelinated than V2 and V4, with a pale band in the lower cortical layers. The receptive fields recorded in this area are larger than those of V4 at a given eccentricity. Figure 4

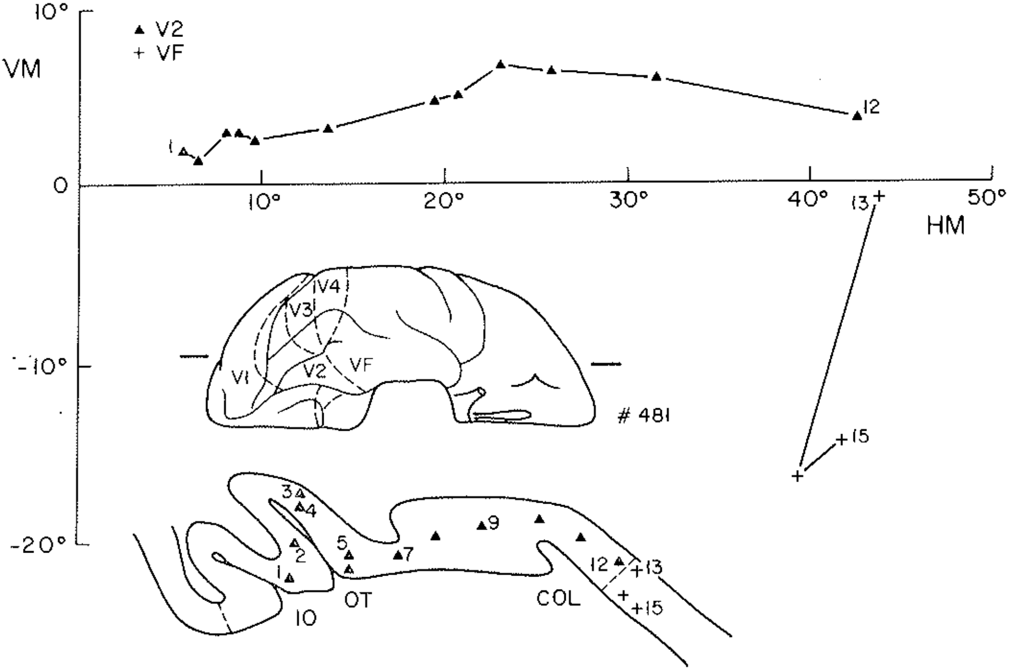

FIG. 4. Receptive field centers in V2 and VF, recorded in a series of penetrations in the parassagital plane. Upper: Receptive field centers recorded at sites shown in lower. Middle: Ventral view of the brain showing the level of the section. Lower: Enlarged view of the posterior half of the ventral surface of the sagittal section showing the position of recording sites.

shows receptive field centers from clusters of neurons recorded across the transition between V2 and VF. Moving within V2 from site 1 to 12 the field centers move parallel to the horizontal meridian in the upper field. On crossing into VF the field centers move into the inferior visual field, away from the horizontal meridian, into the periphery.

There are several myeloarchitectonic distinct areas within the intraparietal sulcus and on the annectant gyrus. The morphology of the annectant gyrus in the macaque is variable from animal to animal and its topology is rather complex (see Van Essen *et al.*, 1982). However, we have seen evidence for reversals in receptive field progressions which coincide with the myeloarchitectonic transitions. There are both upper and lower field representations on the annectant gyrus and in the intraparietal sulcus. The visual topography of the annectant gyrus suggests the presence of at least two different visual areas in this region, one of which probably corresponds to part of the area called V3A by Van Essen and Zeki (1978), and may also correspond to the MT projection zone, IP1, described by Ungerleider *et al.* (1982). More anteriorly, in the intraparietal sulcus, there are upper and lower field representations which we provisionally term IPa (anterior intraparietal area). This area may correspond to the MT projection zone described as IP2 by Ungerleider *et al.* (1982) and as VIP by Van Essen and Maunsell (1983).

Cortical Organization in Primates

How is the organization of the cortical visual areas of the macaque related to that of the owl monkey? Figure 5 shows the organization of the cortical visual areas in both species and illustrates the meridians and the relationships between the areas. A simplified version of the flattened map of the visual areas of the owl monkey as proposed by Allman and Kaas (1975) is shown in the upper part of the figure. The lower part is a schematic representation of the visual areas of the macaque.

At the time we began to study the visual topography of the prestriate areas of the macaque, Zeki had already proposed a scheme for the organization of the prestriate areas in which areas V2, V3 and V4 formed concentric rings around V1. Zeki emphasized the differences in cortical organization between these two species of primates; we prefer to emphasize the similarities. Both animals have similar visuotopic organizations for V1, V2, MT and probably Area PO. The ventral portion of V3 and V4 are similar

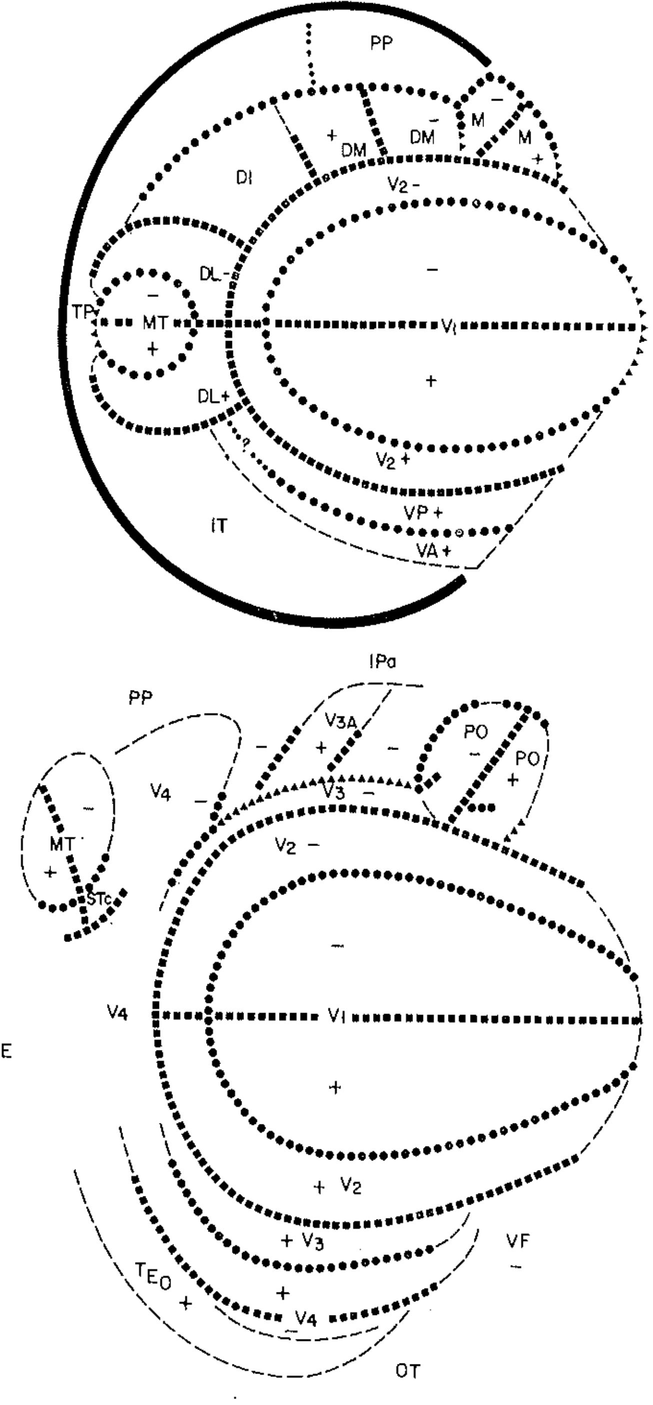

FIG. 5. Flattened representation of the striate and prestriate areas of New (upper) and Old (lower) World monkeys. Vertical meridian (dots), horizontal meridian (squares) and periphery (triangles). For details, see text.

to areas VP and VA in the owl monkey. The topography of one of the areas of the annectant gyrus, V3A, may correspond to that of DM (Allman, 1981). Thus, the differences in cortical organization of these monkeys, such as the apparent absence of V3 in the owl monkey may be exceptions to a general rule that applies to both species. Therefore, despite differences in phylogeny, habitat and behavior, there appear to be many homologies in the cortical areas of these two species.

Field Size and Cortical Magnification

In the prestriate areas, as in V1, receptive field sizes increase with eccentricity. Figure 6 shows plots of receptive field area versus eccentricity in several cortical visual areas. These functions were derived by the

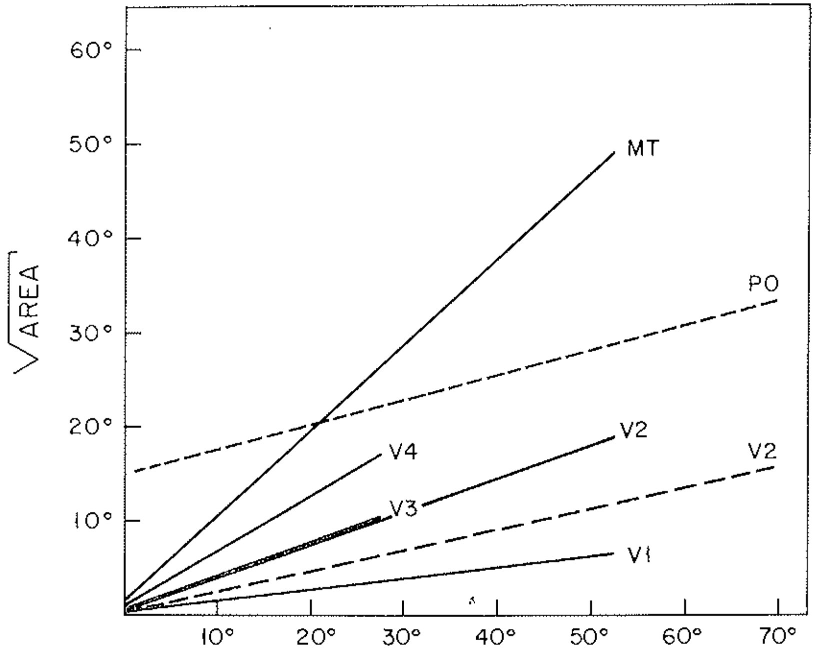

Fig. 6. Receptive field size (square root of receptive field area) as a function of eccentricity for V1, V2, V3, V4, MT and PO. The continuous regression lines were drawn based on data from one animal and the dashed regression lines, from another animal.

method of least squares. At a given eccentricity, receptive fields in MT are larger than in V4, which in turn are larger than in V3 and V2, which are also larger than those in V1. Two slightly different functions are shown for V2, based on data recorded from two animals using electrodes with different dimensions and impedances.

Figure 7 illustrates the magnification factors for several visual areas. Figure 7A shows the power functions, fitted by the method of least squares, which relate eccentricity with distance of cortex dedicated to one degree of visual field. Figure 7B shows the mean and standard deviation of magnification factors in Area PO and MT. Except for Area PO, the slopes of these functions, and thus the magnification factors, are virtually the same. In all of these areas there is an expanded representation of the central portion of the visual field relative to the periphery. In Area PO the situation is reversed, with the peripheral representation greatly expanded relative to that of the central part of the visual field. Thus the power function for Area PO appears as a positive exponential. These results suggest that the type of processing performed by Area PO may be different from that performed by other visual areas.

VISUAL AREAS AND PATTERN RECOGNITION

Do the topographic characteristics of the cortical maps we have described provide clues to their role in pattern recognition? Or, alternatively, how would the cortical maps be related to or facilitate the processing of visual pattern.

Hypothesis about neural mechanisms should ideally be substantiated by behavioral data. However, the descriptions of the visual areas in the macaque are relatively recent, and available behavioral data were obtained with lesions that often included several prestriate areas. For example, the so-called foveal prestriate lesions (Cowey and Gross, 1970), that produced a severe impairment of post-operative acquisition and retention of visual pattern discrimination tasks, included the foveal region of V4, V3 and V2. In the absence of data from lesions restricted to specific areas we shall have to limit our discussion to functional hypothesis concerned with pattern recognition based on the currently available data, which are concerned mostly with topographic mapping.

Scanning of the stimulus with the foveal vision is a frequent concomitant of pattern recognition. This may suggest that any neural

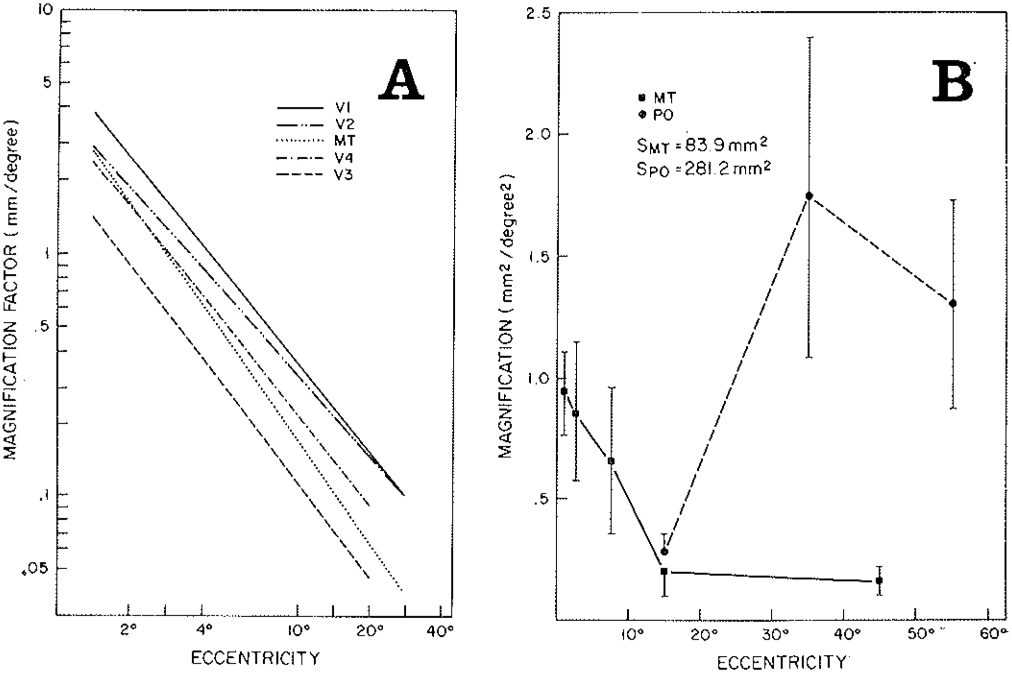

FIG. 7. A. Magnification factor in mm/degree versus eccentricity for V1, V2, V3, V4 and MT. B. Magnification factor in mm²/degree² versus eccentricity for MT and PO. Dots and squares are mean values and the vertical bars, the standard deviation. Mean area (S) and magnification data were derived from flattened maps of three (MT) and two (PO) animals.

mechanism that directly contributes to pattern recognition probably involves visual areas with large foveal representations. It is well known that the slope of the power function representing magnification correlates well with the deterioration of human visual acuity from foveal to peripheral retina. Cowey and Rolls (1974), using the data of Brindley and Lewin (1968) calculated the magnification factor of V1 and showed a good correlation between the reciprocal of the magnification factor and the minimal angle of resolution. A good correlation like the one just described applies to a wide range of power functions with the same slope and different intercepts. Thus, it would apply to several areas of extrastriate cortex such as V2, V3, V4 and MT. It would not apply to Area PO which has a smaller representation of the central visual field relative to that of the periphery. This excludes Area PO as a possible neural substrate for performing the computations necessary for normal acuity (and perhaps texture discrimination).

Visual acuity should also depend upon receptive field size. Areas with small receptive fields are more likely to contribute to visual acuity than those with large receptive fields. Thus, it is likely that V2, but not necessarily V4 or MT, would be involved in visual acuity.

On the other hand, the mechanisms underlying pattern recognition may be more complex than those underlying simple visual acuity. Form perception is achieved even in the absence of high frequency components of the visual scene. It could depend on an assembly of cells with large receptive fields in which the response of cells is determined by a large number of neighboring elements, which constitute the surround of the cells receptive field. Thus, areas with high foveal magnification and large receptive fields could perform both a fine and global analysis of visual stimuli. Cortical areas with these characteristics could thus extract visual information based on global comparison of local features. Both form and color perception depend on rather global analysis of visual stimuli; one candidate for this kind of processing is V4, an area with rather large receptive fields and large foveal magnification. Evidence for the participation of V4 in pattern and color perception was recently provided by Desimone *et al.* (1983). Ungerleider and Mishkin (1982) on the basis of anatomical connections and behavioral data proposed a division of the visual system into two functional "streams". One of these ultimately projects to the inferior temporal cortex (IT) and plays a major role in pattern vision and object recognition; the other projects to the parietal lobe and is related to spatial perception. Areas with high absolute values of foveal magnification factors, such as V2 and V4, compose the first stream; while areas with smaller values constitute the other stream.

Finally, pattern recognition may involve a more complex mechanism based on discrimination and storage of tracking eye movements during the analysis of a larger pattern. In this case the prestriate areas, particularly those sensitive to stimulus movement, like MT and the areas of the intraparietal sulcus, could also be involved in the circuitry performing pattern recognition.

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THE CORTICOCORTICAL PATHWAYS FOR OBJECT RECOGNITION AND SPATIAL PERCEPTION

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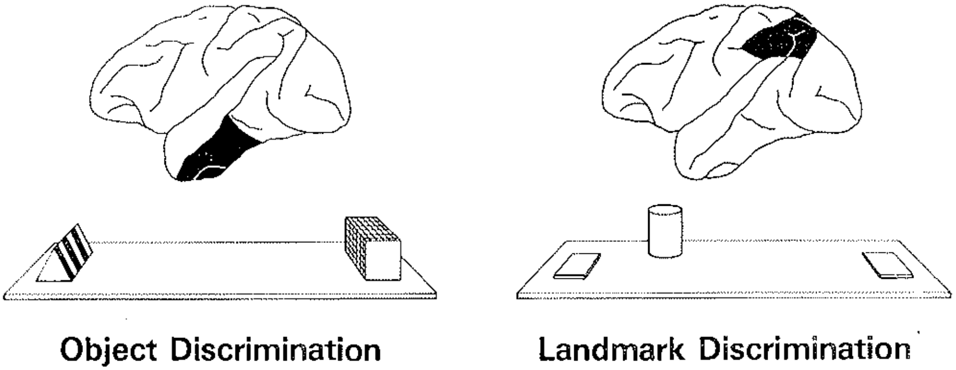
There is now converging evidence from anatomical, electrophysiological, behavioral, and metabolic mapping studies that visual cortex in the monkey extends far beyond the primary visual cortex, or striate cortex, to include prestriate cortex and parts of the temporal and parietal lobes (e.g., Desimone and Gross, 1979; Hyvärinen, 1981; Macko *et al.*, 1982; for reviews, see Gross, 1973; Dean, 1976; Zeki, 1978a; Ungerleider and Mishkin, 1982). This large expanse of cortex is not only structurally heterogeneous, being composed of at least five distinct cytoarchitectural areas — OC, OB, OA, TE, and PG (Bonin and Bailey, 1947), but functionally heterogeneous as well.

With the exception of the striate cortex itself, the two areas whose functions we probably know the most about are inferior temporal cortex and the posterior parietal area. Mishkin and his colleagues (for review, see Mishkin *et al.*, 1983) have demonstrated that the functions of these two higher-order visual areas can be distinguished by two behavioral tasks, which are shown in Figure 1. The first task in an object discrimination. In one version of this task, called one-trial object recognition, the monkey is first familiarized with a three-dimensional object presented over a central foodwell, which the monkey uncovers to obtain a concealed peanut reward. Then, on the test trial a few seconds later (Fig. 1, left panel), the monkey is shown that same object and a novel one, each over a lateral foodwell. To obtain its reward on the test trial, the monkey must avoid the familiar object and select instead the novel one. Thus, to perform the task, the monkey must recognize a recently seen object. The other task is called the landmark discrimination. In this task (Fig. 1, right panel), two blank



Object Discrimination

Landmark Discrimination

FIG. 1. Behavioral tasks sensitive to cortical visual lesions in monkeys. Left panel: Bilateral removal of area TE in inferior temporal cortex produces severe impairment on object discriminations. A simple version of such a discrimination is a one-trial object recognition task based on the principle of nonmatching to sample, in which monkeys are first familiarized with one object of a pair in a central location (familiarization trial not shown) and are then rewarded on the choice test for selecting the unfamiliar object. Right panel: Bilateral removal of posterior parietal cortex produces severe impairment on the landmark discrimination. On this task, monkeys are rewarded for choosing the covered foodwell closer to a tall cylinder, the "landmark", which is positioned randomly from trial to trial closer to the left cover or closer to the right cover, the two covers being otherwise identical.

plaques cover foodwells, and the monkey is rewarded for choosing the plaque located closer to a cylinder, the "landmark", which changes its left-right position randomly from trial to trial. Thus, to perform this task, the monkey must be able to judge which of two plaques is closer to the landmark, i.e., make a spatial discrimination. Monkeys with inferior temporal lesions are severely impaired on object discrimination tasks but not on the landmark task, while monkeys with posterior parietal lesions are impaired on the landmark task but not on object discrimination tasks (Pohl, 1973). These findings, and those from many related behavioral (Iwai and Mishkin, 1968; Mishkin, 1972; Mishkin and Oubre, 1977; Mishkin, 1982; Mishkin and Ungerleider, 1982; Mishkin *et al.*, 1982) and electrophysiological (Hyvärinen and Poranen, 1974; Mountcastle *et al.*, 1975; Lynch *et al.*, 1977; Rolls *et al.*, 1977; Robinson *et al.*, 1978; Desimone *et al.*, 1980a; Schwartz *et al.*, 1983) experiments led to the proposal that inferior temporal cortex is part of a system underlying the recognition of objects while posterior parietal cortex is part of a system involved in the appreciation of the spatial relationships among objects (Ungerleider and Mishkin, 1982; Mishkin *et al.*, 1983).

The pathway through which these two higher-order cortical areas receive their visual information was first suggested on the basis of early neuronographic data (Bonin *et al.*, 1942). It had been shown in both the monkey and chimpanzee that if strychnine is applied to striate cortex spike discharges can be recorded from a prestriate cortical belt, whereas if strychnine is applied to any part of this prestriate region spikes can be recorded in the inferior part of the temporal lobe. These neuronographic findings were later confirmed by the degeneration experiments of Kuypers *et al.* (1965) and Jones and Powell (1970) who found that striate cortex projects to a prestriate cortical belt, which, in turn, projects to the inferior temporal area. The implication of these studies was that information in striate cortex was transmitted to prestriate cortex and then to inferior temporal cortex for processing, and that probably a similar serial processing was going on for information destined for posterior parietal cortex as well.

This model of serial processing was called into question when Allman and Kaas (1971a, 1971b, 1974a, 1974b, 1975, 1976) described a multitude of visual areas in prestriate cortex of the owl monkey, a New World primate, on the basis of their physiological recording work. That prestriate cortex contained multiple visual areas, each — like the striate cortex itself — with a representation of the visual field, was a revolutionary idea. In the macaque, prestriate cortex was similarly found to be composed of several visual areas (Cragg and Ainsworth, 1969; Zeki, 1969, 1971a, 1976, 1978b). These findings suggested that visual information from striate cortex was not transmitted serially through prestriate cortex, but rather the information was distributed to multiple prestriate areas which processed the information in parallel with each other. Zeki (1978a) proposed that each area in the macaque analyzed a different aspect of the stimulus, e.g., orientation in V2, color in V4, and direction of motion in MT. Presumably, the output of all these different prestriate areas converged in inferior temporal and posterior parietal cortex, at which point a synthesis of the visual information took place.

Although this model of parallel processing was attractive, there was little evidence that the outputs of striate cortex were distributed to many different areas. Particularly in Old World monkeys, most of prestriate cortex remained unexplored. We did not know how many areas were located in prestriate cortex, how they were organized, or how they received their information. Therefore, building on the anatomical studies of Zeki and others (Kuypers *et al.*, 1965; Cragg and Ainsworth, 1969; Zeki, 1969, 1971a, 1971b, 1976, 1978b; Jones and Powell, 1970), we set out several years ago not only to delineate all the prestriate visual areas in the macaque, but also to trace the flow of information through them. Our results suggested that striate cortex is the source of two diverging pathways, each of which involves multiple prestriate areas. One pathway is directed dorsally into posterior parietal cortex, while the other is directed ventrally into inferior temporal cortex. As will be discussed later, elements of serial and parallel processing are evident in both of these pathways.

Projections of Striate Cortex

We began our anatomical studies with an investigation of the forward projections of the striate cortex itself. This was because the only information available at the time was on the projections from the lateral part of striate cortex (Kuypers *et al.*, 1965; Cragg and Ainsworth, 1969; Zeki, 1969, 1971a, 1976; Jones and Powell, 1970), which in the macaque represents only the central 7° of the visual field (Talbot and Marshall, 1941; Daniel and Whitteridge, 1961). To understand the complete organization of prestriate cortex, we needed to know the full extent of prestriate cortex that receives striate projections. To determine this extent, we prepared one series of monkeys with large lesions that covered, collectively, all of striate cortex and then processed the brains for anterograde terminal degeneration (Fink and Heimer, 1967). To determine the topographic organization of the striate projection fields within prestriate cortex, we prepared a second series of monkeys with tritiated amino-acid injections into selected sites throughout striate cortex and processed these brains for autoradiography (Cowan *et al.*, 1972). From the combined results of our degeneration and autoradiographic experiments, we were able to define the extent and organization of the two major projection fields of striate cortex: visual area 2, or V2, and an area called MT.

As shown in Figure 2, V2 forms a cortical belt that nearly surrounds the striate cortex. The total extent of this projection field corresponds closely to cytoarchitectonic area OB, and indeed the two may be equivalent (Ungerleider and Mishkin, 1979a). The topography of V2 mirrors that of striate cortex, with the representation of central vision in V2 located laterally in the hemisphere adjacent to the representation of central vision in striate cortex and with the representation of peripheral vision in V2 located medially in the hemisphere adjacent to the representation of peripheral vision in striate cortex (Ungerleider and Mishkin, 1980). Our work

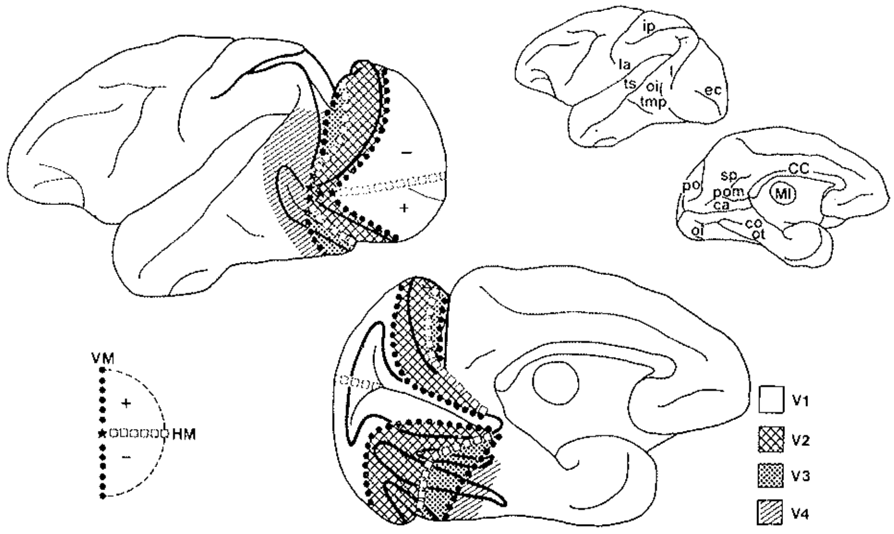


FIG. 2. Location and extent of striate cortex, V2, V3, and V4. Visual areas are shown on lateral and medial views of the hemisphere in which the sulci are partially opened (adapted from Gattass *et al.*, 1981). Names of sulci are indicated on small brain drawings. A plus sign (+) indicates the representation of the upper visual field, and a minus sign (−) indicates the representation of the lower visual field. The filled circles indicate the representation of the vertical meridian (VM), the squares the representation of the horizontal meridian (HM), and the stars the representation of the center of gaze. As in striate cortex (shown in white), in V2 (shown in crosshatch), V3 (shown in dots), and V4 (shown in stripes), the upper visual field is represented ventrally in the hemisphere and the lower visual field is represented dorsally. At the borders of V1, V2, and V3 there is a series of alternating representations of the vertical and horizontal meridians. Abbreviations: ca, calcarine fissure; CC, corpus callosum; co, collateral sulcus; ec, ectocalcarine sulcus; ip, intraparietal sulcus; l, lunate sulcus; la, lateral sulcus; MI, massa intermedia; oi, inferior occipital sulcus; ot, occipitotemporal sulcus; po, parieto-occipital sulcus; pom, medial parieto-occipital sulcus; sp, subparietal sulcus; tmp, posterior middle temporal sulcus; ts, superior temporal sulcus.

thus confirms previous studies on the location of V2's central visual field representation (Cragg and Ainsworth, 1969; Zeki, 1969), but extends those findings to include the location of V2's peripheral field representation as well. In V2, as in striate cortex, the lower visual field is represented dorsally in the hemisphere and the upper field is represented ventrally. The vertical meridian in V2 is represented at V2's posterior border, which it shares with striate cortex, and the horizontal meridian is represented at V2's anterior border. One interesting aspect of V2 that others have noted previously is that its horizontal meridian is doubly represented, with one representation located dorsally and the other ventrally (Cragg and Ainsworth, 1969; Zeki, 1969; Allman and Kaas, 1974a). Because of this double representation, a single injection into the horizontal meridian of striate cortex results in two patches of label in V2, one dorsally in the lower visual field representation and another ventrally in the upper visual field representation (e.g., Weller and Kaas, 1983). The full extent and topography of V2 that we have demonstrated anatomically match closely the results that Gattass *et al.* (1981) have obtained from electrophysiological mapping studies.

The second major projection field of striate cortex, MT, is located in cytoarchitectonic area OA along the caudal portion of the superior temporal sulcus (see Fig. 3). This area is called MT because in the owl monkey, in which it was first described by Allman and Kaas (1971a), the homologous

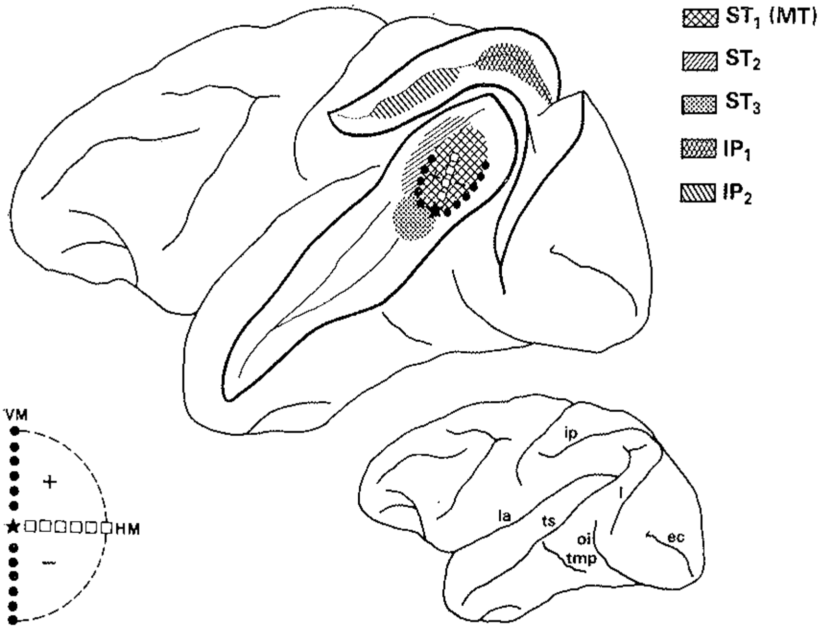


FIG. 3. Location and extent of MT and some of the areas to which MT projects. Areas are illustrated on a lateral view of the hemisphere in which the superior temporal and intraparietal sulci are opened to show their upper and lower banks. MT (ST1) projects to two areas in the superior temporal sulcus (ST2 and ST3) and two in the intraparietal sulcus (IP1 and IP2). Each of these areas, like MT, is characterized by a distinctive myeloarchitectural appearance. See also legend to Figure 2.

area is located in the middle part of the temporal lobe. Although a projection from striate cortex to MT in the macaque had been demonstrated previously by Zeki and others (Kuypers *et al.*, 1965; Cragg and Ainsworth, 1969; Jones and Powell, 1970; Zeki, 1971a, 1976), we found several years ago that the projection is topographically organized (Ungerleider and Mishkin, 1979b). The topography became apparent when we studied the projections from the parts of striate cortex representing peripheral vision. While lateral striate cortex projects to the lower bank of the superior temporal sulcus, where central vision is represented, medial striate cortex projects to the sulcal floor, where peripheral vision is represented. In MT, as in striate cortex, the representation of the vertical meridian forms the outer boundary of the area, and there is a single representation of the horizontal meridian that runs continuously across the area, such that the lower visual field is located posteriorly and the upper visual field is located anteriorly (Gattass and Gross, 1981; Van Essen *et al.*, 1981; Weller and Kaas, 1983). Allman and Kaas (1971a) first reported that MT in the owl monkey can be distinguished by its heavy myelination, and we have also found this to be the case in the macaque. Indeed, as will be described below, we have been able to use distinctive myeloarchitecture not only as a marker for MT, but also as a marker for a number of other areas in prestriate cortex that cannot be readily distinguished on the basis of their cytoarchitecture.

Projections from striate cortex to prestriate areas V2 and MT terminate predominantly in granular layer IV and the deep part of layer III but extend, though less densely, into the supragranular layers as well. The significance of this laminar pattern of termination will be discussed below, where we next examine the projections of both areas V2 and MT.

Projections of Area V2

Our approach to studying the projections of V2 was the same as that used in striate cortex and again employed both degeneration and autoradiographic tracing techniques. First, we determined the full extent of the projection fields by making large lesions that covered, collectively, all of V2. Second, the topographic organization of the fields was determined by injecting tritiated amino acids into selected V2 sites. In these experiments, the sites were identified electrophysiologically and included the center of gaze and positions ranging from about 2.5° to greater than 45° in both the upper and lower visual fields.

Our results showed that V2 projects to two areas located anterior to it, Zeki's (1978b) areas V3 and V4 (Ungerleider *et al.*, 1983). Together, V2, V3, and V4 are arranged in adjacent cortical belts throughout most of their extents (see Fig. 2). Like V2, both V3 and V4 appear to be topographically organized, with the upper visual field represented ventrally in the hemisphere, the lower visual field dorsally, the central visual field laterally, and the peripheral visual field medially. As Figure 2 indicates, the vertical and horizontal meridians are represented alternately at the successive borders of V1, V2, and V3, at least within the central visual field. The fact that injections of V2 beyond 40° result in label in V3 but not in V4 suggests that the representation of the visual field within V4 may not extend to the far periphery.

One question raised repeatedly is whether or not V3 receives a direct projection from striate cortex. While Zeki (1969) and Cragg and Ainsworth (1969) originally reported such a projection, several recent studies have failed to obtain conclusive evidence (Rockland and Pandya, 1981; Weller and Kaas, 1983). Van Essen *et al.* (1979) have found that striate cortex does project directly to V3, but the projection is limited to the lower visual field. For this reason, they regard dorsal and ventral V3 as separate visual areas, which they have termed V3 and VP, respectively. Because V2 projects to both the upper and lower visual field representations of V3, we regard V3 as a single visual area with V2 as the major source of its visual inputs.

In addition to projections to V3 and V4, there is a projection from V2 to MT. Zeki (1976) has shown, and we have confirmed, that this projection is in topographic register with the projection that MT receives directly from striate cortex. There is also a projection from V2 back to striate cortex. In contrast to the forward projections of V2 to areas V3, V4, and MT, which terminate predominantly in layer IV and the deep part of layer III and often appear as columns, the backward projection of V2 to striate cortex terminates in layers I, II, and V (Ungerleider *et al.*, 1983). This difference in the laminar organization of "forward" projections, i.e., those directed away from the striate cortex, and "backward" projections, i.e., those directed towards the striate cortex, has also been noted by other investigators (Kuypers *et al.*, 1965; Tigges *et al.*, 1973, 1974; Spatz, 1977; Wong-Riley, 1978; Rockland and Pandya, 1979). As described previously, the projections of the striate cortex itself to areas V2 and MT are characterized by the "forward" laminar pattern.

Projections of Area MT

To determine the projection fields of MT, we restricted ourselves to autoradiographic tracing methods, inasmuch as MT is contained within the superior temporal sulcus and is impossible to remove without inadvertent damage to the surrounding cortex. Our tritiated amino-acid injections covered, collectively, most of MT including the center of gaze and positions ranging from 8° to 25° in both the upper and lower visual fields. As in V2, the injection sites in MT were identified electrophysiologically.

Our results showed that MT has forward projections to four separate areas located dorsally in occipito-parietal cortex (Ungerleider *et al.*, 1982). There are two projection zones in the depth of the intraparietal sulcus and two in the cortex surrounding MT in the superior temporal sulcus (see Fig. 3). Maunsell and Van Essen (1983) have reported projections of MT that are essentially the same in location, though they have divided them into fewer zones. Each of the projection zones of MT that we have identified, like MT itself, has a distinctive myeloarchitecture, which we have been able to use to define the borders of these areas.

Within the intraparietal sulcus, a posterior projection zone (IP1) begins in the annectent gyrus caudally and extends along the fundus of the posterior third of the intraparietal sulcus. This zone, which may correspond to area V3A of Zeki (1978b), also appears to receive a sparse projection from striate cortex (Ungerleider and Mishkin, 1979a, 1982; Zeki, 1980a). The other projection zone of MT in the intraparietal sulcus (IP2) lies in the anterior two-thirds of the sulcus, extending from the fundus onto the posterior bank; this zone is located in cytoarchitectonic area PG. Both projection zones, anterior and posterior, receive input from all parts of MT, including upper and lower visual field representations.

Within the superior temporal sulcus, one projection zone (ST2) of MT is located on the anterior bank of the sulcus, bordering MT medially. A second projection zone in the superior temporal sulcus (ST3) is located in the sulcal floor, bordering MT anteriorly. We found a great deal of overlap in the projections to these medial and anterior zones from all parts of MT, indicating a convergence of inputs representing widely separated parts of the visual field. This result suggests that neurons within these two projection zones might have very large receptive fields.

The finding of multiple projection zones of MT in both the superior temporal and intraparietal sulci raises the question of what role these areas play in visual function. To explore this question, we have begun recording the electrophysiological properties of neurons within MT's projection zones and comparing these properties with those of neurons in MT itself. Our preliminary results indicate that, like MT (Zeki, 1974, 1980b; Baker *et al.*, 1981; Van Essen *et al.*, 1981; Albright *et al.*, 1984), the projection zone medial to MT in the superior temporal sulcus is characterized by a high proportion of directionally selective neurons (Ungerleider *et al.*, 1982). Thus, the analysis of direction-of-motion information in MT appears to be elaborated further in the projection zone medial to MT. By contrast, few neurons in the projection zone anterior to MT in the superior temporal sulcus are directionally selective. Interestingly, receptive fields of neurons recorded anterior and medial to MT are larger in size than those recorded within MT. This increase in receptive field size in the areas anterior and medial to MT is consistent with the convergent input that these two areas appear to receive from all parts of MT. For the area medial to MT, such convergence is presumably related to the large size of the receptive field over which information about direction of motion is analyzed. For the area anterior to MT, the neuronal properties are still unknown.

We speculate that MT and the areas to which MT projects are involved in visuospatial function rather than in detailed form perception. Consistent with a visuospatial function is, first, the location of these areas in occipitoparietal cortex, lesions of which produce visuospatial impairments (for review, see Ungerleider and Mishkin, 1982); second, the fact that neurons in at least some of these areas have large receptive fields that are directionally selective; and, third, the finding that the activity of neurons in the projection zone medial to MT is related to tracking eye movements (Newsome and Wurtz, 1981; Sakata *et al.*, 1983).

Two Corticocortical Pathways

A summary of the results of our anatomical findings are presented in Figure 4. We have found that striate cortex has two major projections, to areas V2 and MT, and both of these areas project back to striate cortex. V2, in addition to its projections to MT, projects forward to both V3 and

V4. Together, V2, V3, and V4 form cortical belts which partially surround the striate cortex, and all of these areas are topographically organized. We have additional data from Desimone *et al.* (1980b) and Dineen and Hendrickson (1982) that at least parts of V4 project to inferior temporal cortex, area TE. As indicated at the outset, area TE is known to play a crucial role in object recognition (for reviews, see Mishkin, 1982; Ungerleider and Mishkin, 1982).

Area MT, which projects back to striate cortex, V2, and V3, also projects forward to four separate visual areas in the superior temporal and intraparietal sulci. We have tentatively named these areas ST2, ST3, IP1, and IP2. In contrast to MT's backward projections, which are topographically organized, MT's forward projections are highly convergent. Both ST2 and IP2 are located in area PG of posterior parietal cortex, and there is suggestive data from Mesulam *et al.* (1977) that ST3 may also project to at least part of area PG. Area PG, as discussed above, is thought to play an important role in visuospatial function (for reviews, see Lynch, 1980; Ungerleider and Mishkin, 1982). The anatomical data therefore suggest that there is a divergence in the flow of visual information from striate cortex, beginning with the first prestriate areas, V2 and MT. These two diverging pathways may thus be the anatomical substrate for an occipito-temporal system, mediating object recognition, and an occipito-parietal system, mediating spatial perception.

The anatomical data are also relevant to the issue raised earlier of serial versus parallel processing. Figure 4 illustrates that there are elements of both kinds of processing operating within both pathways. In the ventral pathway into the temporal lobe, however, there are only a few areas — V2, V3, and V4 — and these areas are primarily organized in series. By contrast, MT distributes its outputs to multiple areas, suggesting that within the dorsal pathway into the parietal lobe parallel processing may be emphasized.

Although we have made great progress in understanding the general organization of extrastriate visual cortex, there are still large parts of this cortex that remain unexplored. For example, Covey *et al.* (1982) have described a new visual area, PO, which is located medially in prestriate cortex within the parieto-occipital sulcus. It was recently discovered that PO receives input from the peripheral visual field representations of both striate cortex and V2 (Colby *et al.*, 1983; Ungerleider *et al.*, 1983), but we

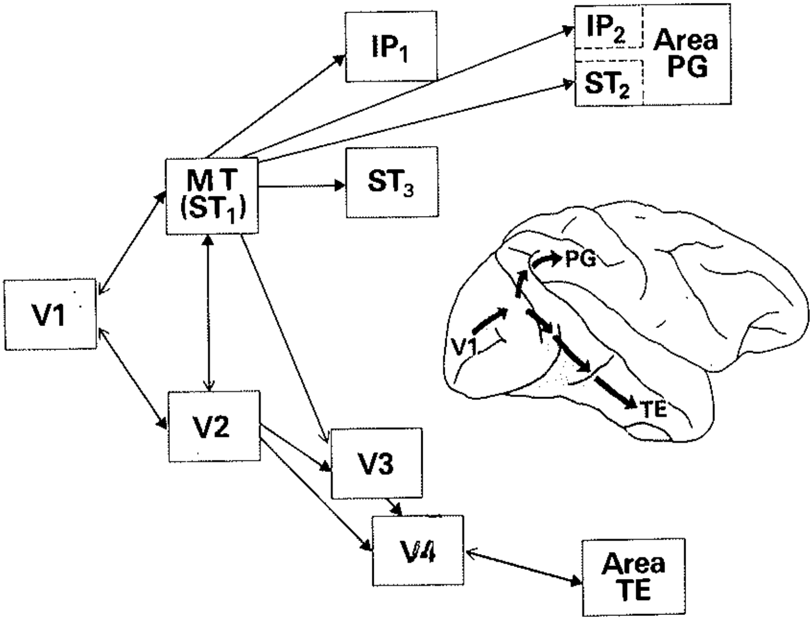


FIG. 4. Summary of visual cortical areas and their known connections. Heavy arrowheads indicate "forward" projections, which terminate predominantly in layer IV and the deep part of layer III, and light arrowheads indicate "backward" projections, which avoid layer IV and terminate instead in the supragranular and infragranular layers. The data suggest a divergence in the flow of visual informatoin from striate cortex (V1), beginning with areas V2 and MT. One pathway is directed dorsally into posterior parietal cortex and the other is directed ventrally into inferior temporal cortex. We speculate that these two diverging pathways mediate spatial perception and object recognition, respectively. Not shown in the figure are the projections from striate cortex to either V3, which appear to be limited to the representation of the lower visual field (Van Essen *et al.*, 1979; Ungerleider, unpublished observations), or PO and IP1, which may be limited to the representation of the peripheral visual field (Zeki, 1980a; Colby *et al.*, 1983; Ungerleider *et al.*, 1983).

do not yet know how PO fits into our "wiring diagram" of extrastriate cortex. In addition to identifying the visual areas within unexplored regions of extrastriate cortex, we still have to unravel the complexities of areas PG and TE. Our data suggest that PG cortex may contain a mosaic of visual areas, and this could also be true for area TE. Indeed, Weller and Kaas (1982) have found that inferior temporal cortex in the owl monkey contains at least three separate areas. Finally, an important question for the future will be how information about object features carried in the occipitotemporal pathway is subsequently integrated with information about the spatial relationships among objects carried in the occipito-parietal pathway to give a unified visual percept.

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FUNCTIONAL ANATOMY OF THE VISUAL CENTERS AS CUES FOR PATTERN RECOGNITION CONCEPTS

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INTRODUCTION

It has been a general assumption among the neuroscientists that the "raw sensory pattern" picked up by the receptors would be processed, while being conducted over the afferent sensory pathway towards the sensory cortical areas, in a way that various crucial features of the pattern would be extracted gradually. The logical process of such feature extraction would be a stepwise progress from the general towards the specific, so that the raw pattern would be decomposed in a mosaic of more and more specific details. The obvious difficulty of such a mental picture being that an opposite strategy of processing had to be assumed by which this mosaic of details would eventually be assembled into something global of the "Gestalt" type or, else, there had to be made the absurd assumption of an infinite regression towards individual cells or even smaller units for each percept. The physiological study of the sensory pathways appeared to support initially the notion of gradual feature extraction — at least for the higher vertebrates. This was most obvious in the two most studied sensory systems the somatosensory and particularly the visual. The receptive fields in the latter were found to be radially symmetric, primarily geared for sharpening the focus and the contrast for each individual spot of the visual field. The anatomy of the retina seemed to correspond exactly to this notion, the horizontal cell system in the outer plexiform layer and the amacrine cell system in the inner seemed to be ideally suited for such a simple type of processing. The much more sophisticated performance of the retina in some of the lower vertebrates, notably in the amphibia, had their substrates in some specific cell types and some other characteristics of the circuitry that could be held responsible for such functions. An essentially similar role was assigned to the main subcortical relay nucleus, the lateral geniculate body (in the higher vertebrates), while in the lower the sophisticated neuron circuitry of the optic lobe of the tectum and a number of highly specific detectors for calculating size, speed, velocity, direction, distance, etc., of the potential prey seemed and still appear to be in good agreement.

The anatomist went along happily with this mental strategy, because divergence, convergence, local inhibitory neurons or circuits — both of the feedforward and feedback type — seemed to be well in accord with the earlier simplistic notions about the steps of feature analysis experienced by the physiologist. This appeared simple enough as long as neuron circuitry could be assumed to obey the simple laws of histodynamically polarized neurons as so beautifully illustrated in the ingenious classical drawings of Ramón y Cajal, with their little arrows indicating the direction of the flow of excitation. This simplistic interpretation of neuron connectivities soon came to an end when unfamiliar types of synapses between dendrites, cell bodies and dendrites, serial synapses, etc., were found in infinite variety by aid of the electron microscope in the olfactory bulb, in the lower relay centers and particularly in the thalamus and the geniculate nuclei. A whole new world of micro-circuitry became known from the end of the sixties over most part of the seventies, culminating in a new generalized concept of local neuron circuits (Rakic, 1975; Schmitt *et al.*, 1976). Many speculations soon came forward and we are still struggling with the functional interpretation of the unconventional synaptic arrangements, although very elegant models were developed by Láhos (1977a) and Koch *et al.* (1982), leaning strongly on purely theoretical considerations. Physiology was rather late in catching up with the corresponding direct observations (Vidyasagar and Urbas, 1982).

The development was rather different in the neocortex, where the basic observations on the "columnar arrangement" of cells having similar receptive fields (Mountcastle, 1957; Hubel and Wiesel, 1959) offered ample opportunity for the anatomist to try to find the structural substrates for such a highly specific spatial distribution of various functional phenomena, especially like orientation sensitivity in the visual cortex. This author has devoted much of his time over the last fifteen years struggling with neuron circuit models (Szentágothai, 1967, 1969, 1970, 1973, 1975, 1978a, 1981) that might he considered as acceptable structural substrates for the physiological observations. A recent review made on another occasion to honour Sir John Eccles on the occasion of the 80th anniversary of his birth (Szentágothai, 1984) of the earlier circuit models as confronted with the recent explosive development of cortical histology, gave reason to ambivalent feelings. Although the models did stand up reasonably well to the later test by new and better information about various cell types and connexions, we do not seem to be nearer to a solution of the question of how the brain migbt recognise patterns in terms of neuronal activities. Let me raise on this occasion the question: were we on the wrong track, was our mental strategy wrong to look for the cues?

Lateral Geniculate Nucleus

The main subcortical relay nucleus of the visual system is used as a paradigm for subcortical pattern processing for purely practical reasons, because this is probably the most studied by physiological methods, and the author has most direct experience with this nucleus in the cat and the monkey. The ventrobasal nucleus of the thalamus, or the medial geniculate nucleus could be taken with the same justification because their synaptic architecture is basically similar.

As already mentioned in the Introduction, both structure and function of the lateral geniculate were looked at as a simple almost one-to-one relay station with some divergence and some convergence combined mainly with feedforward and possibly also with some feedback inhibition by local inhibitory interneurons built into the network. An early circuit model proposed on the basis of electron microscope level degeneration studies (Szentágothai *et al.*, 1966) soon proved to be inadequate by not taking proper account of what appeared first by the axo-axonic synapses. When it was recognized (Famiglietti and Peters, 1972; Pasik *et al.*, 1973a) that many of the apparently presynaptic profiles were in fact dendritic, the models had to be reconstructed radically (Hámori *et al.*, 1974). Using serial reconstructions of the glomerular (or encapsulated) synaptic zones, it soon became apparent, that presynaptic dendrites become engaged with one another in mutual synaptic contacts of reverse polarity; a chain like (or possibly network like) continuity of inhibitory interneuron dendrites had to be envisaged (Pasik *et al.*, 1976). A complication is introduced by the fact that after complete separation from tbe cortex in non-primates many projective (geniculo-cortical) cells show certain changes (dedifferentiation) towards assuming characteristics of the local interneurons (Hámori and Silakov, 1980).

In spite of these uncertainties and inconsistencies it became imperative to give some explanation for the standard triadic synaptic arrangement of virtually all specific thalamic nuclei of one specific afferent profile (labeled R for "retinal" in Fig. 1), presynaptic to a projective cell dendrite (or body) and to a Golgi II cell dendrite profile (labeled P for projective and G for Golgi type II cell), from which the Golgi dendrite profile is invariably postsynaptic to the specific retinal afferent and presynaptic to the projective cell dendrite. Besides such classical triads a number of other "triadic" combinations are also found, but they will not be considered here. Physiological speculations offered practically no cues for the functional interpretation of such a standard structural arrangement. It was Lábos (1977a, 1977b) who could show in theoretical studies, using network logics, that individual triadic arrangements did not make much sense. However, in the lateral geniculate nucleus a series of triads lined up along a single Golgi II cell dendrite or over several mutually interconnected Golgi cell dendrites could be of great advantage in the neuron network in detection of object size, movement, speed, and even direction of movement. Essentially the same strategy was developed elegantly by Koch *et al.* (1982) for retinal ganglion cells. The difference in formalism is only that while they prefer to write down algorhythms of successive decisions, Lábos favours (as also done in Fig. 1) Boolean algebric expressions and threshold logic.

In Fig. 1 the basic information is assembled: part A shows an anatomically realistic diagram of the neuron network (in the cat); B shows one triad where the synapses of the three participating profiles fell sufficiently well into a single plane; C analyzes two cases of the recognition of moving signals, one (a) assumes independent triads leading towards the same decision making site (hatching and arrow); the projective neurons are represented in combination by their synaptic sites P (generally protrusions of their main dendrites) and the decision making site; the other elements of the triads R (for retina) and G (for Golgi II) are represented by simple circles, their synaptic actions heing symbolized by outline arrows if excitatory and full black hulbs if inhibitory. Network (a) signalises motion but not its direction. The other network (b) at right assumes that the G (Golgi) modules are coupled with one another, the shadowed represent a part of a Golgi cell dendrite with anisotropic conduction. See further explanation in the figure explanation. We know now that LGN cells may

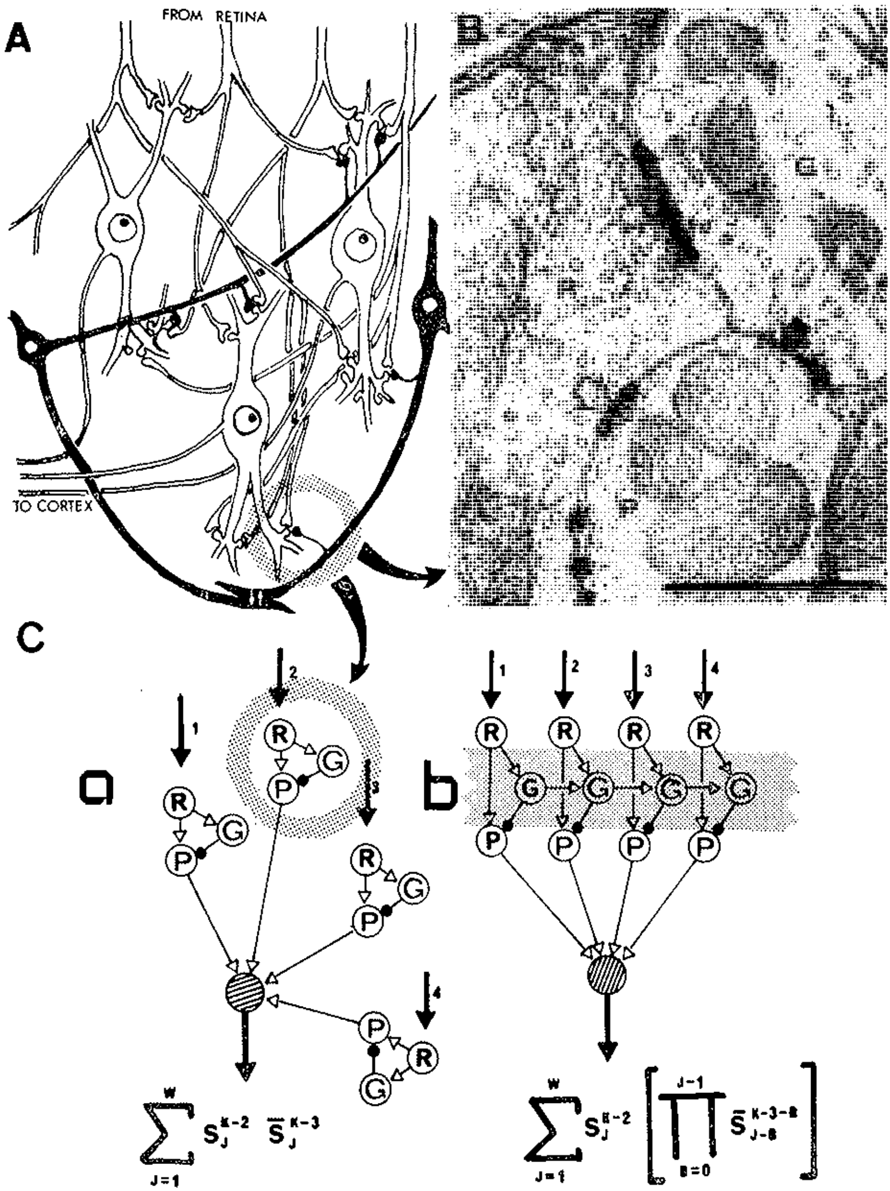

FIG. 1. Assembly for illustrating a theoretical model of synaptic triads in the lateral geniculate nucleus. A: overall neuronal arrangement in the LGN of the cat. Projective = geniculo-cortical relay cells are shown in outlines, Golgi type II inhibitory interneurons in full black. At bottom of this diagram dendro-dendritic contact between two Golgi cells is shown having synaptic attachments of reversed polarity (white arrows). One triadic element (stippled circle) is picked out for electron microscopy in part B. This shows an electron

be sensitive not only to direction of movement but also to orientation of the stimulus (Vidyasagar and Urbas, 1982). The same mental strategy as used in Fig. 1 could be applied also to models having some orientation sensitivity. However, explicit analysis in two dimensions would complicate the model considerably.

What was intended here, was to indicate that the anatomy of the neuron network in the subcortical relay nuclei would be well suited for a number of feature analysing processes that could be used in the recognition of patterns.

Sensory Cortex

Although the construction of neocortical neuron circuit models came increasingly under the influence of the concept of columnar organization suggested by physiological observations (Mountcastle, 1957; Hubel and Wiesel, 1959), the correspondence between anatomical and physiological data remained vague, if there was any correspondence at all. The ocular dominance stripe patterns (Hubel and Wiesel, 1974; Hubel *et al.*, 1978) did correspond in width of the monocular stripes with earlier Golgi observations and particularly with the arbor sizes of individually labeled specific sensory afferents (Gilbert and Wiesel, 1979). No correspondence

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micrograph (scale bar = 1 μm) of a retinal axon terminal (R) with a dendrite protrusion of a projective cell (P) and with presynaptic Golgi cell dendrite appendage (G). Synaptic contacts are indicated by arrows showing the structural polarity and whether excitatory (outline arrows) or of assumed inhibitory nature (black arrow). - C. Networks (a and b) capable recognizing moving input signals. Each network consists of 4 triadic subunits (R- for retinal, G- for Golgi type II interneuron, P- for projective neuron receiving site) converging upon decision making formal neurons (hatched circles). These symbolize the synaptic profiles coupled in the triads. Vertical arrows from above 1-4 symbolize signal flow from retina. - In network (a) the four triads receive independent input while in network (b) the b-subunits are coupled in chain-like fashion to represent anisotropic dendritic conduction. The shadowed zone corresponds to a segment of a Golgi interneuron dendrite. - The decision-making part (cell body and axon hillock of the projective cells) receives converging signals coming from the P-subunits and the decision-making part correspond together to the projective neurons). - Formulas at the bottom are written in Boolean terms and express the condition of activity of the output part as a function of previous states at the input units (i.e. the R-sites). - In CASE (a) movement is recognized without, while in CASE (b) with direction selectivity. Serial discharges are observable at the output, unit if the signal moves in contact direction, while if stationary or moving in the wrong direction only one impulse is produced. - Interconnections: arrows are + 1, edges with small dark circles are − 1 (i.e. inhibitory) matrix entries. Thresholds are adjusted uniformly at zero. -Subscripts denote loci, superscripts discrete instants in time.

does exist between the width of orientation selectivity columns and of arbor size specific afferents in view of the fact that a complete cycle of 180° orientation is usually completed by moving an electrode in the tangential (surface parallel) direction for 500-1000 μm (Hubel and Wiesel, 1968, 1974) in the monkey. This is experienced also in 2-deoxy-glucose experiments, when the width of the labeling corresponding to uptake in consequence of any orientation pattern does not exceed 200 μm in spite of the low resolution of the dioxy-glucose method (Hubel *et al.*, 1978; Le Vay *et al.*, 1980).

There is a great host of evidence about how far innate mechanisms are responsible for the columnar architectonics principle of the cortex and how far environmental factors play a role in its establishment. A coincise review of this question has been given recently by Swindale (1982b) for the visual system, and a large amout of new still largely unknown data have been analysed by Edelman and Finkel (1983) for the somatosensory cortex. All evidence so far available, points to the fact that a certain basic mechanism for producing columnar arrangement is innate but the final outcome of the arrangement depends on physiological functioning during later stages. Hence, any model aiming at describing elementary mechanisms of pattern discrimination has to account for some mechanisms of plasticity.

Anatomical neuron circuit models are static almost by definition, because the anatomical techniques can reveal, in most cases, only an instantaneous picture and there is little if any possibility to gain direct insight into dynamic changes of the structure. Only excessive circumstances, like total functional deprivation can usually induce recognisable anatomical changes. Plastic changes due to removal of one or the other presynaptic pathway do occur, mainly in young animals, but such models do not give any convincing basis of the plasticity that one might be looking for when trying to understand the mechanism of the final establishment of the columnar architecture. Even less so, of course, if one is thinking about dynamic changes that might still occur in adult life. Indirect anatomical evidence for the assumption that many of the existing connexions were not used, or at least not "designed for use" from the very beginning, was plentiful since long ago. The intracortical arborizations of many axons either of specific sensory afferents or the cortico-cortical afferents, but also many interneurons are filling in vast spaces containing thousands of cells. The arbors have synaptic enlargements widely scattered in many cases, so that it would seem preposterous to assume that such single contacts could have any significant influence on the receiving cell, apart from assuming some specific and selective mechanism for functional stabilization of such a synapse. I have been playing with such vague thoughts since many years, and even wrote a paper entitled "Specificity versus randomness in cortical connectivity" (Szentágothai, 1978b). I became soon aware that the term randomness was not correct for describing the nature of such of such non-specific connexions, therefore I often used the form "quasi-randomness", which is not much better either. It was not before Edelman's (1978) "group selection and phasic reentrant theory" became known, tha the concept of degeneracy was understood as a useful notion in this context. Yet in its original Edelman's theory was still too abstract for the accustomed reasoning of the neuroanatomist. Only its application to and elaboration into a coherent theory for the somatosensory cortex of the monkey by Edelman and Finkel (1983) made it clear immediately that we have to do here with a major breakthrough in the understanding how the group selection mechanism might work in neuron networks. It was gratifying to see that the theory incorporated many features of the cortical network that we could see earlier but were unable to interpret. A glimpse at two figures made entirely independently Fig. 6 of Edelman and Finkel on « group confinement » and Fig. 2 presented on the basis of new data on the interlaminar local connectivity by inhibitory interneurons (Somogyi *et al.*, 1983) may show the basic similarity in the assumed connectivity, although tbe approach was fundamentally different. Figure 2 is an attempt to illustrate the facts discussed in an earlier paper (Szentágothai, 1984) transformed for correspondence to the illustration of Edelman and Finkel (1983). The selection of a repertoire of connexions from a larger degenerate group of possible connexion seems to be a viable concept that might solve a number of difficult problems. It connects embryonic development during which similar selection mechanisms have to be assumed, with postnatal plastic changes and may eventually be a basic model for memory and learning mechanisms. The theory would show us also a solution of the very fundamental question how information may act operatively upon a dynamic function of the neuron networks.

There are other less radical and also less ambitious theoretical models of ocular dominance stripes (von der Malsburg, 1979; Swindale, 1980) and orientation columns pattern formation (von der Malsburg, 1973; Swindale, 1982a; von der Malsburg and Cowan, 1982). They share with the concept of Edelman and Finkel (1983) the assumption that innate

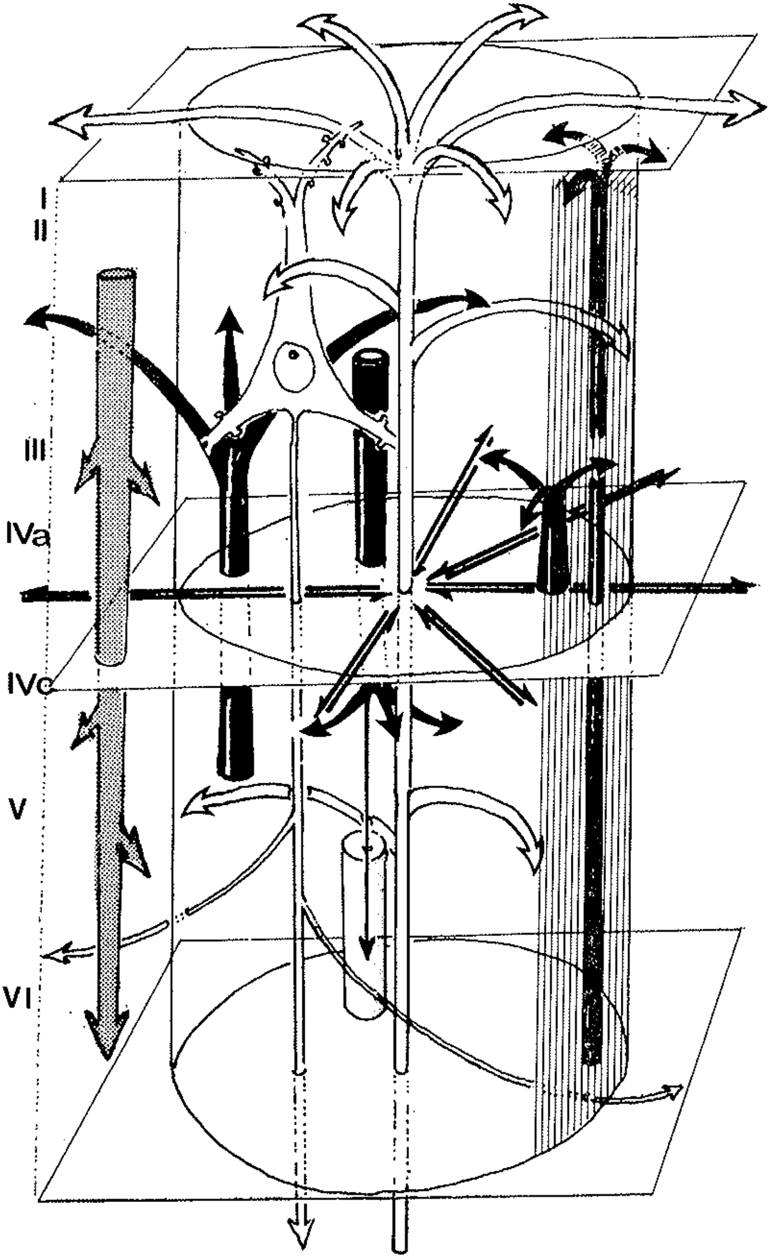

FIG. 2. Interlaminar connexions for excitation (very selectively) and for inhibition (dis-inhibition respectively) are shown by arrows connecting the different layers of the visual cortex. From the excitatory connections (drawn in outline) only one representative cortico-

connectivity although regular to certain degree, shows also a significant amount of randomness. Among the chief troubles with such models are radical species differences in 2-deoxy-glucose labeling of the orientation columns, which are stripe-shape in the cat (Singer, 1981) and in *Tupaia* (Humphrey *et al.*, 1980), but are lattice-like in the monkey (Hubel *et al.*, 1978). Recently I have proposed — with very great reservations (Szentágothai, 1983, Fig. 12) — a static model which might explain the lattice-like orientation columns in the monkey and new observations by Horton and Hubel (1981) on a grid of patterns with very high concentration of cytochrome oxydase, where columns for different orientations seem to coalesce. A somewhat similar model by Braitenberg and Braitenberg (1979) is more dynamic, but fails also to give any explanation of the orientation patterns in the cat and *Tupaia*. This is a clear indication that no model showing some apparent isomorphy with one type of observation or the other offers any hope to lead to really significant insights. For the time being neuroanatomy might fare better with continuing the inductive type of investigation into increasingly refined details of cortical neurons and their connectivities, preferably with quantitative data on the numerical relations on the synapses given and received, as well as some measure of divergence (how many synapses and to what sites of how many other neurons, with what distribution in space) and convergence (synapses of a certain type being derived from how many neurons, from what distance or what volume of space).

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cortical afferent is indicated ascending in the axis of a cylinder shape cortico-cortical column, and at upper left a pyramidal cell of lamina I. The cylinder is assumed to have a diameter of 300 μm, which may serve as a scale for the distances spanned by the several connexions. Specific sensory afferents and their excitatory interneurons for forward conduction are omitted, in order not to complicate the diagram. The inhibitory connexions are mapped out largely on the basis of new data (Somogyi *et al.*, 1983), with labeling of inhibitory interneurons by uptake of [^{3}H]GABA. Inhibitory connexions are most widely spread in lamina IVc and from lamina IVc to IVa. There is a major inhibitory input from lamina V cells into lamina III and a probably a narrowly spread input from lamina VI cells to lamina I and II (inhibitory Martinotti cells). There is a massive inhibitory input from lamina III to the bottom of lamina IV and into the upper layers of lamina V, narrow vertically descending inhibitory fibers reach lamina V (deeper) and lamina VI. - Descending stippled arrow at extreme left corresponds to vertically descending largely disinhibitory connexions by double bouquet cells.

CONCLUSION

From all this it might be concluded that no amount of refinement in hardware type neuronal wiring in the cortex will lead to even a modest breakthrough in understanding of pattern recognition. First of all because functional neuronal connexions are not predetermined but are selected by experience. The question of how much of this may appear in real changes in morphology is highly dubious. Modeling of the type practiced by Cowan, von der Malsburg, Swindale and others (references have been indicated above) may be helpful, although they have to restrict themselves to very elementary questions, like ocular dominance and orientation sensitivity. Since texture perception has been so successfully studied recently by Julesz (1981) and the concept of textons appears promising for further analysis, one might try to build such models for one or the other class of textons: the terminators may be one class that offers promises for both direct physiological study and for modeling.

My feeling is, though, that it is Edelman's concept that offers most potentialities for the future because it leaves the broadest space for self organization and certain continuity between prefunctional and functional stages. Additionally it holds the promise for the neuroanatomist, that his labourious studies on identified individual neurons are no "labour-lost".

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COMPARATIVE ASPECTS OF REPRESENTATION IN THE VISUAL SYSTEM

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Abstract — In the first part of this paper, the correspondences between visually excitable areas in cats, the new and old world primates are considered. Arguments are put forward which suggest a good correspondence between areas 17, 18, 19 and the infero-temporal cortex of the three species. In order to reach such a conclusion, however, the extent and borders of area 19 and of the infero-temporal cortex of cats and of area 18/19 of the old world monkey have to be reconsidered. Suggestions for such a reconsideration are made, taking into account the uncertainties of cytoarchitectonics in the exact delineation of these areas as well as the thalamic origin of afferents to the various visual areas. In the second part, the cooperative function of the visually excitable areas of the occipito-temporal cortex for guiding visual behavior is discussed. A model is proposed, in which not only the various representations of the visual afferents but also the various cortico-fugal outputs of the different visual areas are considered.

The concept of serial processing of information from sensory to motor systems in the cerebral cortex is an old concept in neurology. Meynert (1876) coined the term "association fibres" for intercortical connections, Wernicke (1874) proposed the conceptual serial scheme for language processing, Flechsig (1895) delineated the association areas as the final places of synthesis of the sensory inputs and as the "organs of mind", and Campbell (1905) saw, in the peristriate visual cortex, which he considered as one large area, a visuo-psychic field, a region responsible for higher cognitive tasks. Complementary to these ideas about the brain mechanisms and perception, which were strongly philosophically biassed in the sense of Hume's association philosophy, were ideas about the hierarchical organization of the motor system mainly formulated by Hughling Jackson at the end of the last century. But the "hierarchical" scheme of motor organization was the first to be challenged when it was realized that electrical stimulation of large parts of the cerebral cortex including sensory cortices produced motor effects in primates (O. and C. Vogt, 1919) and man (O. Foerster, 1936). Under the impression of these observations, Foerster imagined the functional organization of these various motor fields as a "working cooperative" (Arbeitsgemeinschaft) rather than a hierarchical command structure. Thus, parallel and serial representation of function are both familiar aspects of the functional organization of the cerebral cortex.

It is now a well established fact, that sensory organs are not represented only in one or two cortical fields, but several times (for review see, e.g., Merzenich and Kaas, 1980; Creutzfeldt, 1983). It is assumed that in some of these areas specific invariants of a sensory stimulus may be represented, such as colour, movement or certain Gestalt-aspects of a visual stimulus (Zeki, 1978; van Essen, 1979), modality of a somatic stimulus (Merzenich *et al.*, 1978) or location in space of an auditory stimulus (in bats) (Suga *et al.*, 1983). This has led to the model of parallel representation of various functional aspects of sensory inputs in contrast to the serial or hierarchical model. But considering the fact that there are 5-15 representations of each sensory organ found in the cortex, it is still a matter of debate as to what extent these various representations are specifically tuned to certain stimulus aspects and which is their specific function. A further controversy arises, if the problem is addressed as to whether the various functional areas receive their input from different thalamic structures or whether the primary sensory areas distribute specific outputs to the various functional subareas. In the latter case, which will be amply represented by several speakers at this conference, the parallel and serial model merge to some extent.

In my presentation, some of these aspects will be touched with special emphasis on the question of the correspondence of extrastriate visual areas in cat and monkey (I), and some functional aspects with special emphasis on the "cooperative" output from the sensory visual areas will be discussed (II).

I. COMPARATIVE ASPECTS OF THE EXTRASTRIATE VISUAL SYSTEM IN CAT AND MONKEY.

A different organization of the visual cortex in cat and primates?

It is often maintained that the cortical visual systems of cats and monkeys are not comparable in many aspects. But I shall try to show that this conclusion may not be justified and maybe largely due to a semantic confusion of the nomenclature of the cortical areas involved. A principal difference is, of course, that — at the more peripheral level — the primates lateral geniculate body is divided into the parvo- and magnocellular layers which correspond to a functional division into a system of chromatic filters and a panchromatic system, respectively, while such a functional division does not exist in the cat's lateral geniculate body between the A- and B-laminae.

This difference is obviously due to the difference of retinal organization of a cone and rod dominated retina, respectively, and need not represent a basic difference in the central representation. But it must play a role for the functional properties of some of the visual areas in cat and monkeys. Furthermore, the number of retinal ganglion cells increases 5-10 times from the carnivores to primates, so that additional cortical space must be available for retinal representations in primates.

This problem is, in area 17, partly solved by a higher neuron density in the primates striate cortex (Rockel *et al.*, 1980), but should have an important quantitative effect also on the further cortical visual representations.

At the cortical level, the area striata (area 17) is surrounded, in cats and primates, by area 18 (Fig. 1). But here, two differences of organization are claimed to exist: Area 18 of the cat only contains one representation of the visual field, V2 (Tusa *et al.*, 1979), while area 18 of the old world monkey contains several representations (V2, V3, V3A, V4 and STS) (Van Essen and Zeki, 1978). The other difference is that area 18 of the cat receives a strong thalamic input from the lateral geniculate body, while this was denied for area 18 of the rhesus monkey. The reason for this difference may not be so much one of principal but of nomenclature, which goes back to Brodmann (1909).

Area 18.

In his cytoarchitectonic map of Cercoleptes (Fig. 2A), which was then transferred to the cortex of the cat (Winkler and Potter, 1914) and also guided Gurewitsch and Chatschaturian (1928), Brodmann limited area 18 to a narrow belt around area 17, while in the old world monkey Cercopithecus, area 18 extends as a broad field through the lunate sulcus

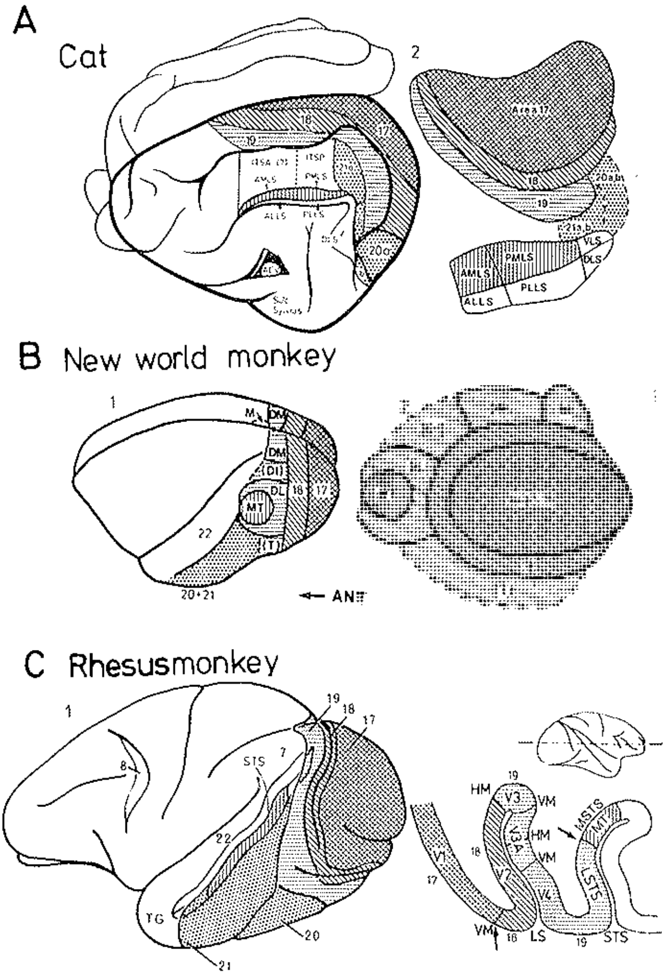

FIG. 1. *The occipito-temporal visual cortex of the cat, the new world and old world monkey.* A: Cat. After Palmer *et al.* (1978), with addition of AEV (anterior ectosylvian visual area). B: Aotus trivirgatus (after Allmann, 1977). C: Macaca mulatta. Left: compiled from several sources (Brodmann, 1909; Zeki, 1969, 1978). Right: A horizontal cut through the visual cortex at the level indicated on the figurine of the brain shown above (after Zeki, 1978). In the cytoarchitectonic map of Brodmann (1909), which is adopted by Zeki, area 18 extends, between the two arrows, as far rostrally as into the depth of the supratemporal sulcus (STS). In this sketch, the 18/19 border was located into the depth of the lunate sulcus (LS) (see text).

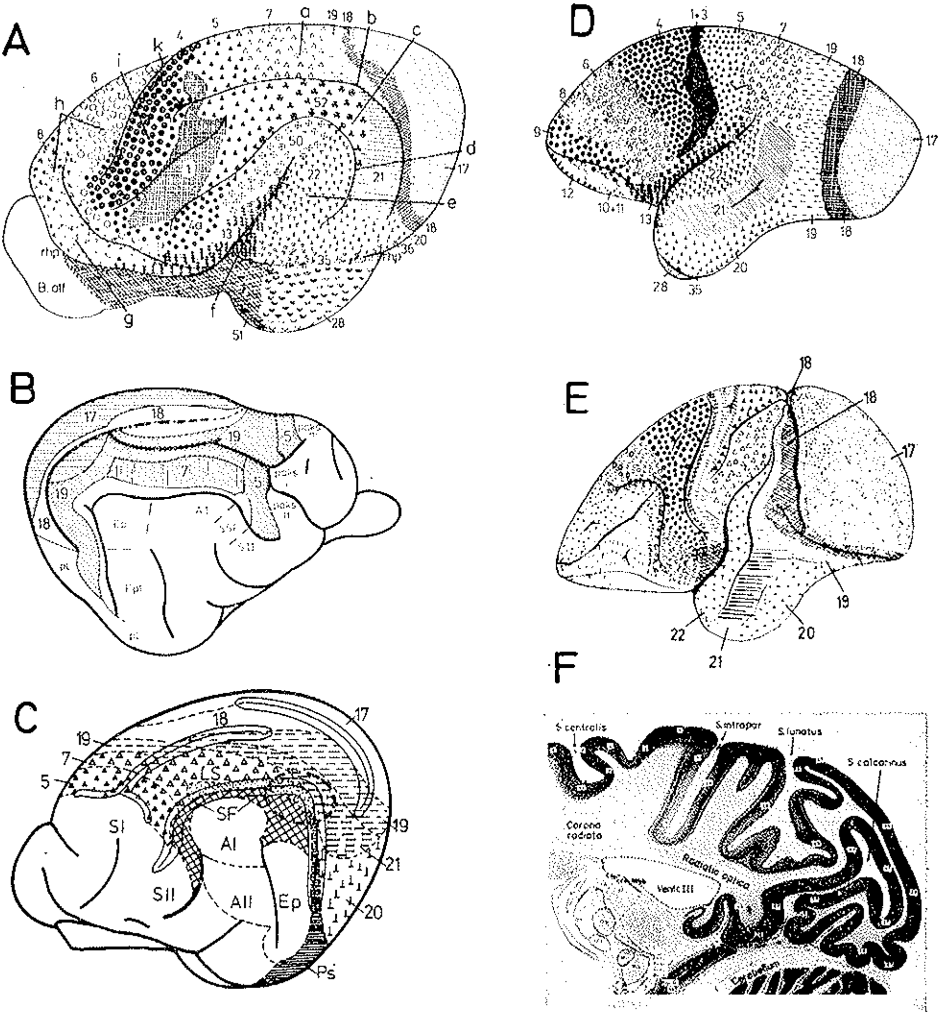

FIG. 2. The *cytoarchitectonic maps* of A: *Cercoleptes* after Brodmann (1909), B: the *cat* after Sanides and Hoffmann (1969), C: the *cat* after Heath and Jones (1971), D: *Callithrix* after Brodmann (1909) and E: *Cercopithecus* after Brodmann (1909). Note that in this map, area 18 (dark grey shading) only reaches, rostrally, to the top of Gyrus parietalis, while in the horizontal cut shown in Brodmann's original paper of 1905, the 18/19-border is located into the depth of S. supratemporalis. F: A saggital section about 10 mm lateral from the midline through the occipital lobe of the *rhesus monkey* (Krieg, 1975).

across the gyrus parietalis deep into the sulcus supratemporalis (arrows in fig. 1C). In the summary map, Brodmann puts the border between 18/19 across the convexity of the gyrus parietalis (fig. 2E). Vogt (1919) limits area 18 to the sulcus lunatus (its posterior bank?), while the whole Gyrus parietalis is, to him, area 19. Von Bonin and Bailey (1947) located the OB/OC-border (corresponding to the 17/18 border) in the rhesus monkey (Macaca mulatta) into the depth of S. lunatus, and they pointed out, specifically, that "the anterior margin (of OB, 18) goes over so gradually into OA (19) that the margin has apparently been variously located by different observers" (p. 73). Zeki (1969, 1978) was the first to propose that the circumstriate belt contained several representations of the visual field, but adopted the original Brodmann nomenclature of 1905 and thus put V2 as well as V3, V3A, V4 and later STS into Brodmann's large "Area 18".

Since the cytoarchitectonic borders between areas 18 and 19 are not very marked, as was actually also pointed out by Brodmann, and since in the depth of the lunate sulcus of the rhesus monkey one could quite easily define such a border if one looks at Nissl stained sections or at Krieg's sagittal sections through the occipital lobe (Krieg, 1975), the limitation of area 18 to V2 could be justified even on cytoarchitectonic grounds (see fig. 2F). In fact, Brodmann was not so generous with regard to area 18 in the new world monkey Callithrix, where the border between areas 18 and 19 are even more difficult to identify. As a consequence, in this species, the multiple representations of the visual field beyond V1 and V2 are all located in area 19 and beyond (Allmann, 1977). There is, therefore, no principal and only a historical difficulty to identify also in the old world monkey area 18 with V2 and to let it terminate in the depth of the lunate sulcus.

It may be mentioned, in parenthesis, that the nomenclature of the peristriate cortex in lagomorphs and rodents in terms of cytoarchitectonic numeration is even more confused. However, also in lower rodents a picture of multiple visual fields begins to emerge (see e.g. Olavarria and Montero, 1984). But as yet, no conclusions as to the similarity or dissimilarity of the peristriate visual areas of these species with those of monkeys or cats can be deduced. A difference in visual representation in these species to some extent should be expected, due to the fact that the visual field's of the laterally positioned eyes only have a small binocular segment and that most of the retinal afferents cross to the other hemisphere. Thus, the differences in cortical organization of the visual system of lower mammals are essentially due to differences of their peripheral visual apparatus.

As to the problem of projections from the lateral geniculate body to area 18, it is understandable that only few geniculate afferents are found to the rostral parts of "area 18", i.e. the cortex on the prelunate gyrus parietalis. On the other hand, injections of HRP or isolated lesions of the posterior bank of the lunate sulcus are difficult to perform without involvement of area 17. Here, neurophysiological methods would be necessary. Nevertheless, there is now anatomical evidence available that the prestriate cortex of the old world monkey also receives geniculate afferents (Fries, 1981; Iwai *et al.*, 1980).

If one restricts the area 18, the rostral border of which is so ill-defined, to that part of the peristriate belt which is next to area 17 and which contains, functionally, only V2, both, cat's and monkey's become comparable. Unfortunately, there do not yet exist sufficient neurophysiological data for a detailed functional comparison between V2 in cat and monkey. In area 18 of both, cat and monkey, a variety of functional cell classes are found, cells are more sensitive to moving stimuli in both species, the receptive fields of single neurons are larger and the magnification factor is smaller than in area 17. But, yet, the details are still too incomplete and, in the monkey, too anecdotal for making a decision as to whether the functional properties of the neurons in Area 18/V2 are the same in both species. In fact, this is a major difficulty in discussing the correspondence of cortical visual representation in various species, that data from different laboratories usually concentrate on different aspects and use different methods.

The problem of the cat's Area 19.

The next confusion comes with area 19. If the term area 18 is restricted to V2, then the further prestriate visual field representations in the old and new world monkey may all be summarized as "area 19" and, in addition, the occipito-temporal transition zone (see fig. 1; Allmann, 1977; Zeki, 1969; van Essen and Zeki, 1978). In the cat, however, area 19 is limited to the region delineated as "area 19" by Brodmann (1909), Winkler and Potter (1914), Otsuka and Hassler (1961), although it reaches somewhat more lateral in the map of Sanides and Hoffmann (1969) (see fig. 2B). But wherever one puts the exact cytoarchitectural border, it is functionally defined as one visual field though with a somewhat complicated and incomplete representation of the contralateral retina, essentially restricted to the lower visual field (Tusa *et al.*, 1979; Albus and Beckmann, 1980). The laterally adjacent areas are, traditionally, called area 20, 21 and — in Cercoleptus — even 52, i.e. homologues of the infero-temporal and insular cortex. The location of areas 20 and 21 in the cat on the posterior Gyrus suprasylvius and the posterior Gyrus lateralis, respectively, was restated by Heath and Jones (1971) and the borders of these areas redefined (see fig. 2C). Tusa and Palmer (1980) defined 4 separate, though incomplete and partially incoherent visual field representation in these areas and divided them, accordingly, into areas 20a,b and 21a,b. In a brief evaluation of the functional organization as well as the cortical afferents to these so-called areas 20 and 21, they came to the conclusion, that neither of these areas has a homologue in the monkey, and, more specifically, that none of them can be considered as a homologue of the infero-temporal or the medial temporal visual areas of the old and new world monkeys.

In fact, one may ask why the *cat's areas "20" and "21"* should be homologues to the infero-temporal cortex of primates. A homologuization on cytoarchitectonic grounds is weak, if there is any. One reason for the old anatomists to locate area 21 so far dorsally might have been an extrapolation of the evolutionary trend from the insectivores to the primates with a continuous expansion of the neocortex, a latero-ventral transposition of the neo-allocortical border and the identification of the primates sulcus lateralis (Sylvii) with what is wrongly called Sulcus Sylvii in the cat. But if one relates the positions of the somato-sensory and auditory cortex to the so-called Sulcus Sylvii of the cat and monkey, it becomes immediately evident, that the cat's Sulcus Sylvii is not at all the topographic homologue of the primates Sulcus lateralis. Once this is recognized, one may reconsider the topographical question whether the infero-temporal cortex of the cat, i.e. the real homologue of the primate's areas 20/21 may not be located far more laterally. Heath and Jones (1971) emphasize the pattern of association fibres to and from the cat's area 21 as being similar to that of the infero-temporal cortex. But these patterns are so general and could be applied to any other visual association area in the occipito-temporal cortex of the cat. Brodmann himself has pointed out (1909, p. 106), that "the same numbers and symbols in (the) brain maps often indicate only a relative, but not an absolute homology of the respective fields". Therefore, be would have been the last to object against questioning the justification of identifying the cat's areae "20" and "21" with those of the primate.

The infero-temporal cortex of the cat.

It appears therefore justified to propose that the homologue of the primates infero-temporal cortex is, in the cat, indeed much more laterally located than assumed hitherto, i.e. on the lateral part of Gyrus sylvius and possibly reaching, along the lateral part of the ectosylvian gyrus into the posterior end of the suprasylvian gyrus posterior. On the posterior bank of Sulcus ectosylvius anterior, a visual area has been described which is not clearly retinotopically organized, where the neurons have large visual receptive fields mostly including the central area and with sometimes quite peculiar trigger properties (Mucke *et al.*, 1982, and further yet unpublished experience) (see fig. 1A: AEV). Besides many neurons, which are sensitive to moving contrasts and to moving visual noise, often at high speed, and others which show short on- and off-responses to spots of light which may be much smaller than the receptive fields, we have observed some which are activated strongly by small dark and/or light spots moving quickly forth and back within their receptive field, especially in its central area part. This "*anterior ectosylvian visual area* (*AEV*)" receives its thalamic input from the anterior part of Nucleus lateralis posterior, pars medialis (Fig. 3A), sends efferents to the amygdala as well as to the frontal cortex, and receives a strong association fibre input from the Clare-Bishop area (Mucke *et al.*, 1982; Roda and Reinoso-Suarez, 1983; Norita, Mucke, Benedek, in preparation). Although we have not seen such specific trigger features as the shadow of a hand or certain aspects of faces, as found in one part of the monkeys infero-temporal cortex and as will be presented at this conference by Rolls and Gross, the functional properties as well as the anatomical connections of AEV leave no doubt that it belongs to the visually excitable cortex of the infero-temporal cortex.

Another experimental finding which supports the proposal to locate the infero-temporal cortex of the cat more laterally, is the demonstration that cells in Nucleus amygdalae can be excited by local electrical stimulation on the Gyrus sylvius and the lower part of Gyrus ectosylvius posterior, but not by stimulation in Gyrus ectosylvius medius and suprasylvius posterior, including the so-called areae "20" and "21" (Prelevic *et al.*, 1976). This pattern of neocortical-amygdalar efferents in the cat as determined with electrophysiological methods is similar to that of the afferent pattern from the temporal association cortex to the Nn. amygdalae in the rhesus monkey as described by Turner *et al.* (1980). None or at best very scarce amygdalar efferents (from one stimulation) were identified from area "21" or "20" of the cat with electrophysiological methods.

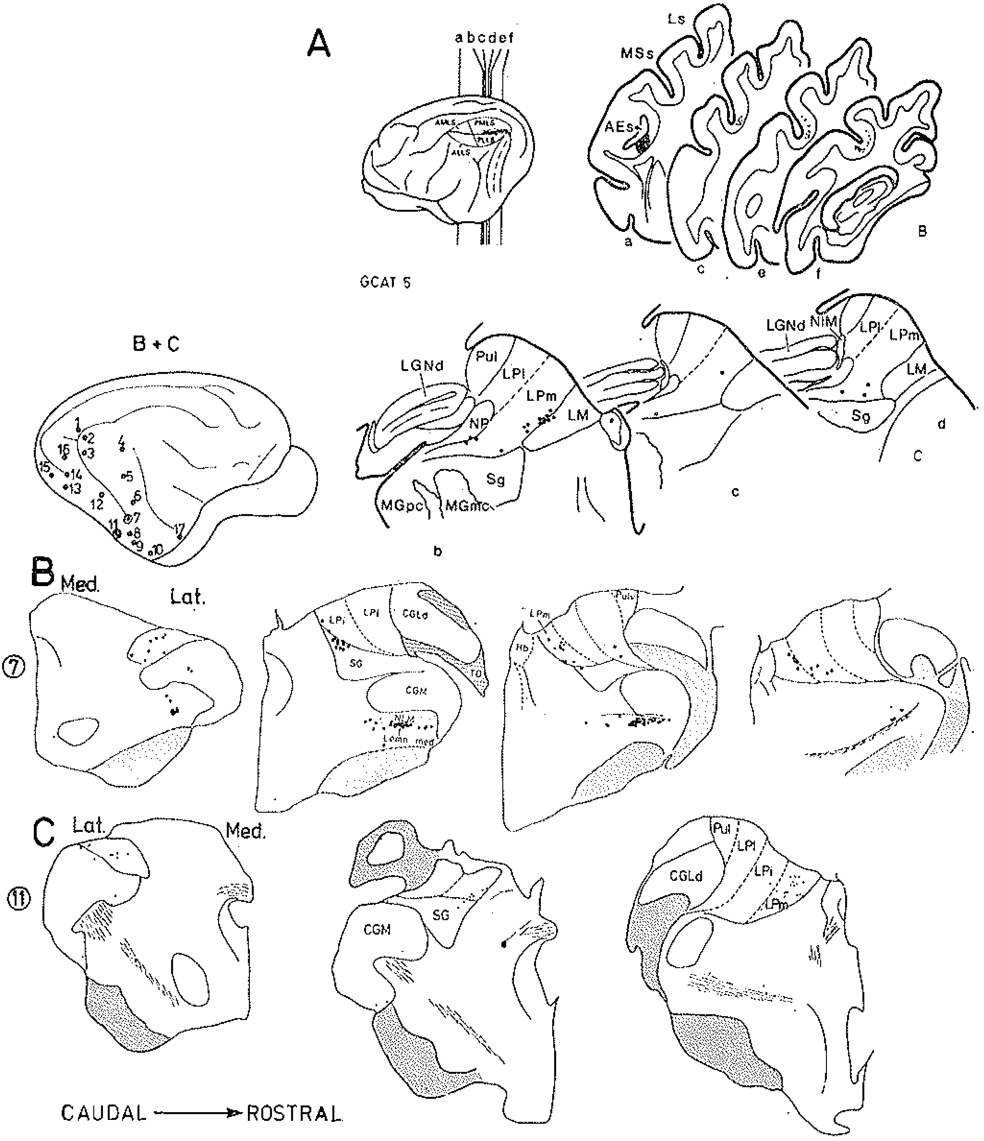

FIG. 3. *Localization of thalamic neurons projecting to the infero-temporal cortex of the cat.* Injection of horseradish-peroxidase into the indicated region and location of labelled cells. A: Injection into the anterior ectosylvian visual area (AEV) in the depth of the anterior ectosylvian sulcus (AES). Cells were labelled in the medial part of Nucl. lateralis posterior (in this nomenclature: medial border of lateralis posterior, pars medialis, LPm). Thalamic sections as indicated in inset (from Mucke *et al.*, 1982). B and C: Labelling of thalamic cells after injection at points 7 (B) and 11 (C) as encircled on the map (B+C). Thalamic neurons are labelled in a similar thalamic region, but more ventro-medially reaching from the ventro-medial segment of nucleus lateralis posterior (LP medialis) into N. suprageniculatus (SG). (From Escolar and Creutzfeldt, in preparation).

Area 19 of the cat reconsidered.

If the "infero-temporal cortex" of the cat is thus put further laterally into the lateral part of Gyrus sylvius, we may return to the visual fields located on the medio-posterior ecto- and the posterior suprasylvian gyri. The visual field on the posterior ectosylvian gyrus (Area 21a of Tusa and Palmer, 1980) horder medially on the incomplete representation of the visual field in area 19 and laterally onto the Clare-Bishop-area, i.e. the visually excitable cortex of the posterior suprasylvian sulcus.

The thalamic afferents to the posterior suprasylvian gyrus come from the lateral part of N. lateralis-posterior (LPl) and the pulvinar, rostro-dorsally from and partially overlapping with the location of neurons projecting into the medial bank of the posterior suprasylvian sulcus (PMLS) (Fig. 4). This thalamic region encompasses, in its latero-ventral part, neurons with large receptive fields in and around the central area of the visual field (Benedek *et al.*, 1983). Its thalamic projection neurones are situated in a region continuous and partially overlapping with the thalamic projection region to area 19 on the one hand, and the Clare-Bishop-area, on the other. If this thalamo-cortical projection pattern is compared with that to area 19 and MT in the new world monkey (Lin and Kaas, 1980), one recognizes the same type of continuity of thalamo-cortical relations (see fig. 5). There is, therefore, no reason which would prevent the inclusion of "area 21" of the cat in the old maps and as redefined by Heath and Jones (1971), at least its medial part, into the circumstriate belt or, more specifically, to consider it as a part of area 19 as defined by Brodmann (1909) and Allmann (1977) in the new world monkey and as defined here also for the old world monkey.

For area "20a" the same argument applies. The incomplete representation of the visual field with an underrepresentation of the lower quadrant is complementary to that in area 21a. Therefore, and due to its neighbourhood to area 18 (V2), one might include this medial part of area 20 (= 20a of Tusa and Palmer, 1980) also into the circumstriate belt.

This larger area 19 of the cat would then be part of the "circumstriate belt" and, like in the monkey, would contain several "visual areas" with more or less complete representations of the visual field, including area 20a on the posterior Gyrus lateralis. The argument of Tusa and Palmer (1980), that the visual fields on the posterior suprasylvian gyrus have no counter parts in the monkey, if the functional properties of the neurons and some details of the visual field representation are considered,

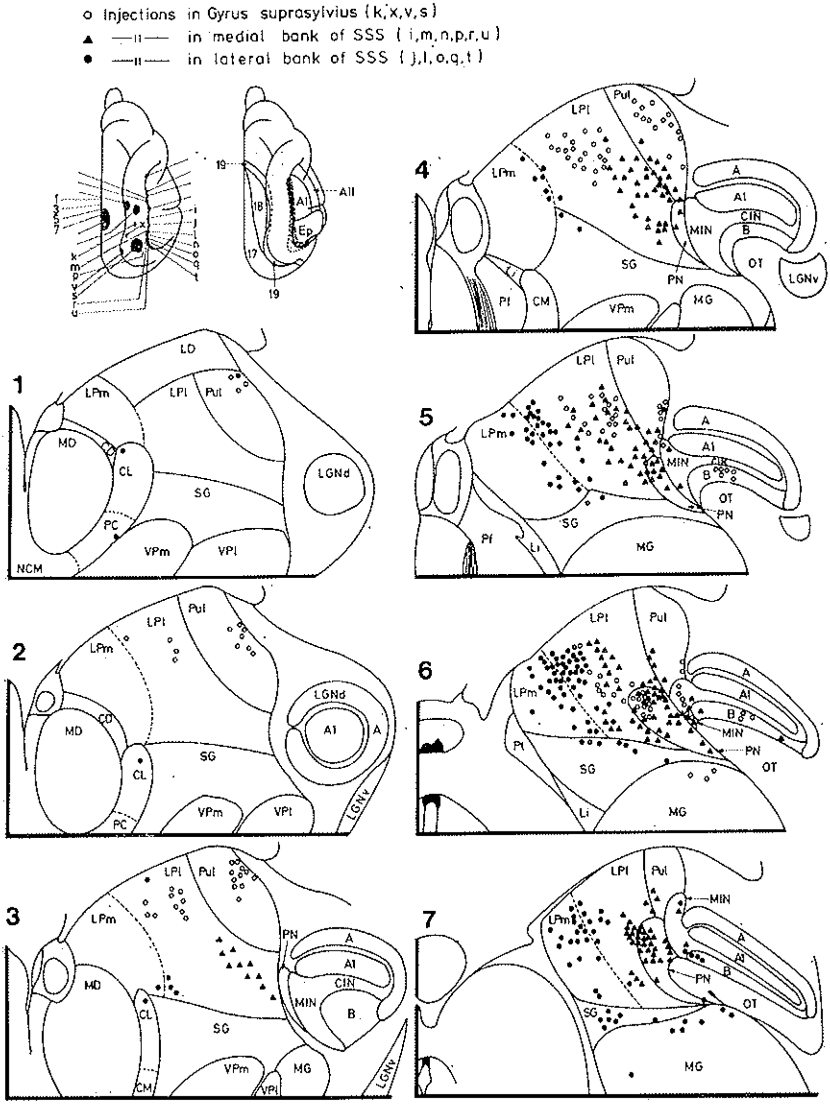

FIG. 4. *Thalamic neurons projecting to the extrastriate visual association cortex in the cat.* HRP-injection into the places indicated by letters in the map shown on the top left. Open circles: HRP-labelled cells after injections into the posterior part of G. suprasylvius medius. Closed triangles: cells after injections into the cortex on the posterior part of the medial bank of S. suprasylvius (PMLS). Closed circles: Labelled neurons after injection of the cortex on the lateral bank of S. suprasylvius (PLLS). Note, that the afferent neurons to the G. suprasylvius are located laterally in the N. posterior (LP)/Pulvinar (Pul) complex, while those projecting to the PLLS are located most medially. The projection neurones to the infero-temporal cortex (see fig. 3) are located further medio-ventrally (from Shoumura and Creutzfeldt, in preparation).

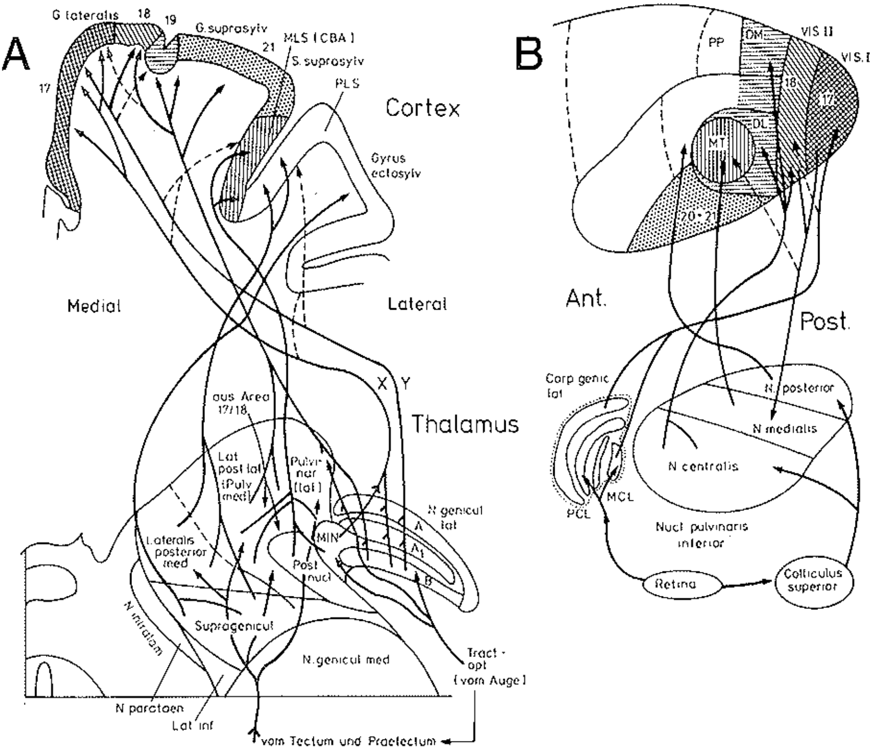

FIG. 5. *Semischematic representation of the thalamic afferents to striate and extrastriate visual cortex in cat (A) and new world monkey (B).* A: From data of Graybiel and Berson (1980) and own observations. B: After Lin and Kaas (1980). Note, that neighbouring cortical fields receive their thalamic input from adjacent thalamic volumes. (From Creutzfeldt 1983)

maybe well considered, but it meets with the principal difficulty of functional comparison as mentioned before. Its validity is furthermore restricted by the fact that functional differences between anatomically corresponding visual areas of the cat and monkey are to be expected due to the differences of their retinal organization. Furthermore, the exploration of the various visual areas in area 19 of the primate and the cat is far from being complete and we may yet miss the correct message with our means of physiological exploration (cf. Zeki, 1978). In addition, it should also be realized, that the exact representation of the visual field in the extrastriate visual areas may show considerable interindividual variations in one species (Albus and Beckmann, 1980; Albus, 1981). With respect to areas 21b and 20b of Tusa and Palmer (1980), the question is more difficult as to whether one might consider these areas as part of the circumstriate visual belt or of the infero-temporal cortex. But the transition between the posterior end of the infero-temporal and the lateral part of the occipital cortex is difficult to determine in either species, and one may even argue, with Campbell (1905), that there is no clear architectonic border.

The occipito-temporal transition zone.

Antero-laterally from this circumstriate belt of the cat, with the larger area 19 as defined here and with inclusion of the visually excitable area on the Gyrus suprasylvius posterior, follows the visual area of the medial bank of the middle and posterior Sulcus suprasylvius (Clare and Bishop, 1954; PMLS of Palmer *et al.*, 1978). This area contains caudally, in the posterior angle of the sulcus, a large representation of the central 10-15° of the visual field (Palmer *et al.*, 1978; Albus, 1981; Guedes *et al.*, 1982). On the lateral bank of Sulcus suprasylvius, another though incomplete representation of the visual field can be demonstrated (PLLS of Palmer *et al.*, 1978), including — in the posterior part of the sulcus — a relatively wide representation of the ipsilateral field with receptive fields of individual neurons extending 10-15° across the vertical meridian (fig. 6B) (Guedes *et al.*, 1983). This wide representation of the ipsilateral visual field reminds of the wide ipsilateral representation also in STS of the old world monkey (Zeki, 1983, and own observations in the awake monkey, to be published).

Palmer *et al.* (1978) assume that, altogether, the retina is represented 6 times on the medial and lateral cortex of Sulcus suprasylvius of the cat.

FIG. 6. *Receptive field positions in the cortex around the posterior ectosylvian sulcus (A, B) and in N. lateralis posterior of the cat* (C). A, B from Guedes *et al.* (1983), C from Benedek *et al.* (1983). Microelectrodes were moved down along the tracts as indicated in the diagrams. The recording points of single neurons are indicated as short lines and are numbered. The receptive fields determined for these neurons are marked with the appropriate numbers. Occasionally a somewhat systematic progression of receptive field positions is found (A), but over distances of several millimeters, the large receptive fields overlap. In the thalamus (C), similar receptive field sizes and a similarly loose retinotopy is found. Note, the wide ipsilateral overlap of receptive fields in the cortex and the thalamus. The penetration through the lateral bank of the suprasylvian sulcus (B, a) shows predominantly ipsilateral fields.

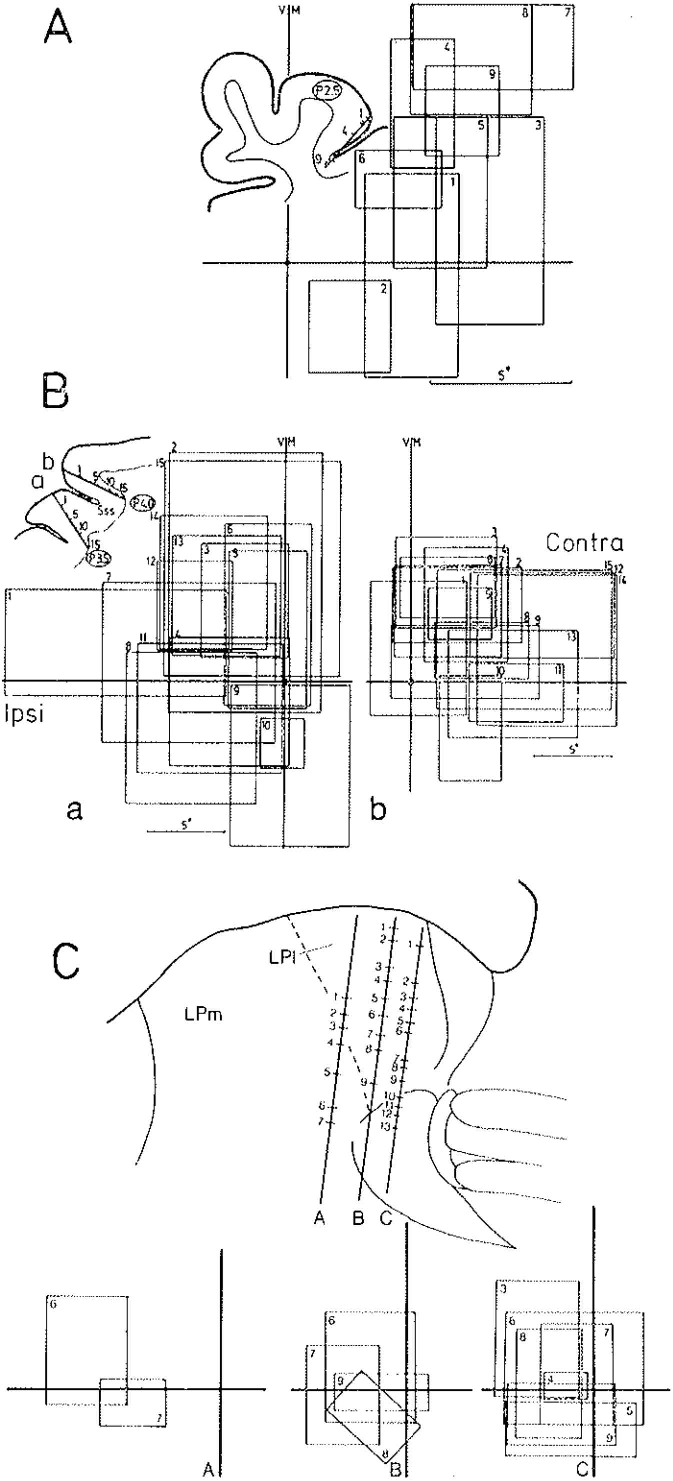
A
VM
P2.5
1
4
9
8
7
4
9
5
3
6
1
2
5°
B
VM
b
a
1
5
10
15
Sss
P4.0
P3.5
2
14
13
12
3
6
5
7
1
4
8
11
9
10
Ipsi
a
5°
VM
Contra
3
4
6
7
2
15
12
14
8
9
13
10
11
5°
b
C
LPl
LPm
A
B
C
10°

Fig. 6

Due to the large size of receptive fields of individual neurones in this area, the large scatter of field positions along single electrode tracts and the overrepresentation of the central 15-20° of the visual field in the depth of the sulcus, I find it difficult to draw exact maps of the visual field in this part of the visual cortex (Guedes *et al.*, 1983). Furthermore, a large interindividual variability is obvious to anybody recording from this area. It is, in my experience, not possible to exactly predict, in one experiment, the retino-topic progression from one single neuron to the next during one penetration along the medial or lateral wall of the Sulcus suprasylvius (Guedes *et al.*, 1983). Based on a study of intercortical connections, Albus (1981) also comes to the conclusion that only two representations of the visual field can be safely identified, one on the medial and one on the lateral bank of the suprasylvian sulcus.

The cortex around Sulcus suprasylvius posterior and medialis receives association fibres from area 17/18 (Shoumura, 1972; Heath and Jones, 1971). Its thalamic input comes from the Nucl. lateralis posterior and the Nucleus posterior Rioch, with the input to the lateral bank of the sulcus located more medio-ventrally than those projecting to the medial bank (Fig. 4 and 5) (Graybiel and Berson, 1980). Thalamic neurones in this part of the LP-complex have a loose retinotopic arrangement with the central visual field represented ventro-laterally near and around the Nucl. posterior Rioch, and single neurons have large receptive fields (fig. 6C) (Mason, 1978, 1981; Benedek *et al.*, 1983). Two adjacent representations of the visual field may be distinguished. Receptive fields often reach across the vertical meridian by 5-10° and the neurons have the same functional properties as those in the posterior suprasylvian sulcus in that they are sensitive to moving light or dark spots rather than to light flashes, with preference for a more or less narrow range of directions. Thalamo-cortical relay cells in the ventro-medial part of LP including the N. posterior are excitable by electrical stimulation of the superior colliculus, while those in the dorso-lateral part are excitable by cortical stimulation in area 17. Neurons in the contact region of the cortical and tectal recipient zones of the LP/Pulvinar-complex maybe excitable from both regions (Benedek *et al.*, 1983). The relation of the various input zones in the posterior thalamus from the retina, the visual cortex and the tectal/pretectal relay as derived from anatomical data (Graybiel and Berson, 1980) and from our own experience can be schematically represented as shown in fig. 7.

In the primate, the "middle temporal area" (MT) which was first described in new world monkeys (Woolsey *et al.*, 1955; Doty *et al.*, 1964),

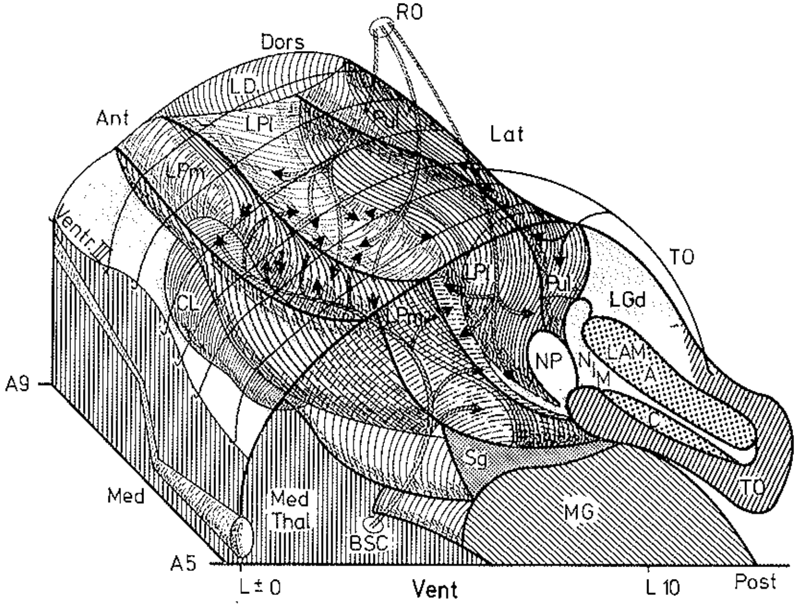

FIG. 7. *Schematic drawing of the retinal* (TO = tractus opticus), *the tectal/pretectal* (through the Bracchium colliculi superioris, BSC) *and the visual cortical input* (Via the Radiatio optica, RO) into the various zones of the posterior thalamus. Note, that the borders of these input zones are not sharp, and the inputs overlap. (From Benedek *et al.* 1983)

is also retinotopically organized with the vertical meridian running along its outer periphery (Allmann and Kaas, 1971). It is, in the new world monkey, surrounded by another visual field (the dorso-lateral area DL) with the representation of the vertical meridian touching that of MT (Allmann and Kaas, 1974). It receives its thalamic input from Nucl. medialis of the Pulvinar (Lin and Kaas, 1980), and this thalamic projection zone is continuous with the projection zone of the circumstriate belt (Areae 18/19) (Nucl. centralis) (s. Fig. 5B). MT receives, like the cat's MLS, association fibres from areae 17 and 18 (Spatz and Tigges, 1972) and sends association fibres, inter alias, to the inferotemporal cortex (Ungerleider and Mishkin, 1978). The anterior ectosylvian visual area (AEV) of the cat also receives a strong association fibre input from MLS (Norita, personal communication).

Considering the anatomical connections and physiological organization, it appears reasonable to consider the medial temporal area with its surrounding fields and including the visual area of the supra-temporal sulcus

(STS) as homologues to the medial and lateral visual areas of Sulcus suprasylvius (MLS and LLS) of the cat. A possible homology between the Clare-Bishop-area of the cat and MT of the new world monkey was, in fact, already suggested by Woolsey *et al.* (1955) and Doty *et al.* (1964). For the same reasons as mentioned earlier, i.e. functional differences of the retinal afferents in the monkey and the cat, the functional aspects of the two homologuous areas may show differences in detail. These differences should be considered as interspecies differences of a cone and a rod dominated visual system, respectively, but would not justify, in themselves, to assume a principal difference of the cortical representations of the retinae in the two species. On the other hand, one is well advised not to enter into arguments as to which subarea in the cat (LLS, MLS), the new world (MT, DL, DI) and the old world monkey (STS, MT) correspond exactly to each other, as long as the principal is accepted that these are corresponding representations of visual functions between the "circumstriate belt" and the infero-temporal cortex. Even an exact delineation of this occipito-temporal transition zone meets with difficulties in either species, so that even no serious argument could be brought up against inclusion of this region into area 19.

The infero-temporal cortex.

Let us now return to the question of the infero-temporal cortex itself, or more generally of the temporal association cortex, in the cat. We are left with the lower part of area 20 on the caudolateral end of Gyrus lateralis ("20b"), with the auditory association cortex Ep on Gyrus ectosylvius posterior, the anterior ectosylvian visual area (AEV, see above), and the cortex stretching along the lateral margin of the hemisphere from Gyrus lateralis posterior to the posterior wall of the ectosylvian cortex, including the cortex in the depth of the lateral part of S. suprasylvius posterior. The thalamic input to these areas comes from the ventrocaudal part of the posterior thalamus, i.e. a region stretching from the medio-ventral part of Nucleus lateralis posterior, pars medialis (LPm) through Nucl. suprageniculatus into the Corpus geniculatum mediale (Fig. 3). The auditory areas on Gyrus ectosylvius are clearly a homologue to the auditory areas of the Gyrus temporalis superior, i.e. the supratemporal association cortex (Area 22) and its continuation into the Planum supratemporale of the primates. Here, the classical cytoarchitectonic maps are, in their general outline, consistant with the functional properties of these areas, as Ep of the cat is largely though not completely coextensive with Area 22 of Brodmann's map of Cercoleptes. The stripe laterally surrounding Ep could then be considered with some confidence as the cat's equivalent of the infero-temporal cortex. Since the primates infero-temporal cortex appears to have more than one visually excitable region (Gross, 1973), it may be left open whether the visual areas "20b" and "21b" of Tusa and Palmer (1978) should he considered part of this "inferotemporal" visual cortex of the cat, or whether they are part of the occipito-temporal transition.

The visual cortices of cats and primates are comparable.

Not denying some difficulties in the elaboration of details, we arrive at a picture of principally homologuous organization of the extrastriate, temporo-occipital and infero-temporal visually excitable cortex in the cat, the new and old world monkey such as shown in fig. 8. Details may be subject to argument, but the principal homology of the circumstriate belt with area 18 as V2, several visual fields in area 19, a temporo-occipital transition zone and the infero-temporal cortex can be defended on grounds discussed so far. Without serious violation of cytoarchitectonic principles, the temporo-occipital transition zone may be included into area 19 because of its topographical continuity and the continuity of its thalamic afferent zone with that of area 19. This larger area 19, which due to its complex functional contribution to visual behavior and cognition would then well correspond to Campbell's (or Munk's) visuo-psychic area. It continues rostro-laterally into the infero- temporal cortex without a sharply definable border, and rostro-medially into the parietal association cortex (area 7). We thus end up in the cat as well as in the monkey with a large continuous occipito-temporo-parietal visual area with numerous subareas.

II. FUNCTIONAL CONSIDERATIONS

We may now ask the further question as to whether these various visual representations in area 17, 18, 19 and 21/22 represent a parallel representation of various outputs from area 17 or true parallel representation of retinal inputs transmitted to the cortex through the thalamus after relay in other retinal recipient zones (colliculus superior, pretectum, area 17). Since the times of Wernicke, Flechsig and Liepmann, it is assumed that the input to association areas comes essentially through association

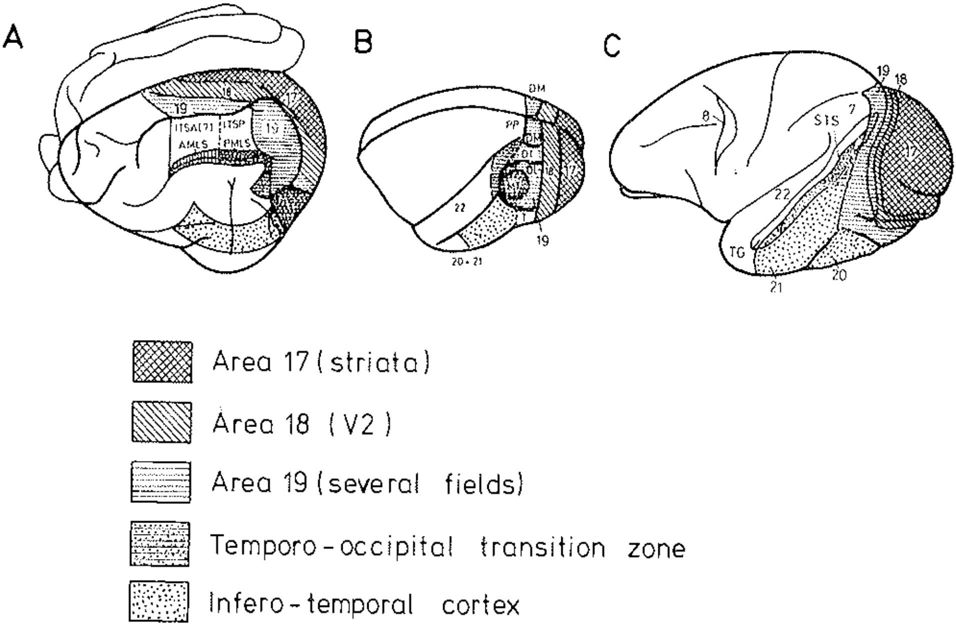

FIG. 8. *Corresponding arrangement of visual cortex in cat and monkey.* For further details see text.

fibres from the sensory fields. If we define — with Flechsig — as association areas those cortical fields, which do not receive a direct input from a sensory projection nucleus, then the visual fields in area 19, the occipito-temporal transition and the infero-temporal cortex are all "visual association areas". They receive their thalamic input from thalamic "association" nuclei in the Nucleus lateralis posterior/pulvinar-complex.

Functional significance of the thalamic input.

Here, by the way, comes up another terminological confusion. In the primate only a small, dorso-lateral segment of the thalamus is called Nucl. lateralis posterior, while in the cat the larger volume of the posterior thalamus is called Nucl. lateralis posterior with 3-4 subnuclei (lateral medial and internal part of Nucl. lateralis posterior as well as the Nucl. posterior Rioch). The name "Pulvinar" is restricted, in the cat, to its latero-dorsal segment. But due to their afferent and efferent connections as well as their topographic relation to the rest of the thalamus, the cat's Nucl. lateralis-posterior and pulvinar largely correspond to the pulvinar nuclei of the primate.

The LP/Pulvinar complex receives its visual input from the tectum and pretectum, from areae 17 and 18 and, in its lateral and possibly also in its superior part directly from the retina (Guillery *et al.*, 1980; Itoh *et al.*, 1983). In the cat as well as in the primates these inputs are topographically restricted to different zones of the LP/Pulvinar complex so that retinal, cortical, tectal and pretectal recipient zones may be distinguished (Graybiel and Berson, 1980; Lin and Kaas, 1978; Benevento *et al.*, 1975, 1977). But, at least the cortical and the tectal input overlap (Fig. 7) so that, in the overlap zone, thalamic neurons can be excited from area 17/18 as well as from the superior colliculus (Benedek *et al.*, 1983).

The more we learn about the functional properties of thalamic neurons, the more it becomes clear that many of the response and stimulus features in the various cortical areas are already present in the respective thalamic projection nuclei. These properties are, to some extent, enhanced and a selectivity for some stimulus features as e.g. directional sensitivity of visual cortical neurons may be added by intracortical mechanisms such as intracortical convergence and inhibition. But the principal properties of the functional organization of the cortical fields are already found in their thalamic projection neurons. In the striate cortex, this applies to the separation of inputs from the two eyes, orientation sensitivity and colour selectivity. However, the additional cortical features are, in the case of ocularity, the elaboration of binocular convergence with the appropriate functional specialization for stereoscopic binocular vision (see e.g. Poggio and Fischer, 1977), in the case of orientation sensitivity the sharpening of the geniculate orientation bias (see Vidyasagar and Urbas, 1982) to orientation selectivity, and in the case of colour sensitivity, only a minority of cortical cells retains colour selectivity comparable to parvocellular LGB-cells, while the majority shows a convergent input from various types of parvocellular cells and these cells become sensitive to luminance as well as to colour contrast contours (Gouras and Krüger, 1979; Tanaka *et al.*, 1984).

In extrastriate visual areas, the large receptive fields of cortical neurons, their preference for moving stimuli (including direction preferences) and the inaccuracy of the visual map are found already in the respective thalamic projection zones (Mason, 1978, 1981; Bender, 1982; Benedek *et al.*, 1983). These data are so compelling, that there is, at least in the cat, no need to assume that the extrastriate visual fields receive their major visual excitation and their response bias through association fibres from area 17 (Guedes *et al.*, 1983; Mucke *et al.*, 1982).

Association fibres.

The claim, that extrastriate visual association areas receive their visual drive predominantly or even exclusively through association fibres from area 17 are, in fact, only based on few experimental observations and were challenged by further experimental evidence. It is necessary, in my eyes, to redefine the function of association fibres and to compile more rigorous experimental evidence on their function, after we have learned so much about their anatomical organization in recent years (for further discussion see Creutzfeldt, 1983).

Specific representation of sensory features in the various visual fields?

Much has been said, in the literature, about the possible functional significance of the multiple representation of sensory surfaces in the brain and especially the visual systems (for reviews see Merzenich and Kaas, 1980; Creutzfeldt, 1979; van Essen, 1979). Some observations of Hubel and Wiesel (1965) suggested that features of increasing abstraction may be represented from areas 17 to 19, but these authors were also disappointed, not to find any hint of "higher order" representation in the Clare-Bishop area (Hubel and Wiesel, 1969). Zeki (1978) used the metapher of a division of labor and suggested, that different aspects of a visual stimulus are represented in the different extrastriate visual areas such as colour (V4) or movement (STS). However, he points out himself that the functional differences between these areas were not as marked as one might expect to see if different sensory features were in fact specifically represented in these various areas. These types of hierarchical models of feature abstraction of increasingly higher order certainly need rethinking, although they still dominate the thinking and search of many experimentalists as well as of theoreticians (e.g. Marr, 1981). Also the functional significance of weak retinotopy, of various topological transformations of visual space, and the lack of exact retinotopy in extrastriate visual areas still waits for a reasonable functional interpretation.

Erratum:

On page 75, the following line should be added between lines 3 and 4 of the first paragraph:

(with) "respect to their thalamic and cortical afferent input connections but also with"

Multiple sensory fields as multiple sensory-behavioral links.

I like to emphasize another important feature of the various representations of the visual (and other sensory) fields by turning the attention to the fact that the various visual fields do not only differ with respect to their efferents so that each visual area is a different link between the sensory organ and the motor or behavioral output (Creutzfeldt, 1981, 1983). The outputs from the striate and the extrastriate visual cortex into the motor control system differ in so far as cortico-collicular fibres predominate from the striate cortex and cortico-pontine efferents from the extrastriate cortex (Albus *et al.*, 1977; Brodal, 1978). Also in other aspects, the anatomical patterns of outputs from the various visual areas into subcortical structures of behavioral or, more strictly, of motor control differ significantly (Spatz *et al.*, 1970; Kawamura *et al.*, 1974; Diamond, 1979; Updyke, 1977; Graham *et al.*, 1979). The infero-temporal visually excitable cortex is characterized by its significant output into limbic structures (Ungerleider and Mishkin, 1980; Prelevic *et al.*, 1976) in addition to its collicular and caudate output (Whitlock and Nauta, 1956).

Neurophysiologically, a general property of neurons in extrastriate visual areas is their responsiveness to slowly or fast moving stimuli. This suggests some function in visuo-motor behavior. Indeed, many neurons may not only be characterized by their sensory trigger features, but also by their responses in relation to visuo-motor responses. Thus, in the awake monkey, neurons are found in the prelunate gyrus which are not only visually driven, but discharge also or even exclusively in relation to eye movements (Fischer and Bloch, 1981). These eye movement-related discharges appear before an eye movement is initiated and they begin when a visual stimulus becomes a target of a saccadic eye movement and usually last through the saccadic movement. The responses appear only if the target is located in a circumscribed area of the visual field (the so-called "goal field"). The authors of this report furthermore conclude, that the visual responses in this part of V4 in the prelunate gyrus must be derived from other than geniculo-striate inputs, probably from the retino-collicular-pulvinar projection. Also in area 17 (Wurtz and Mohler, 1976) and 18 (Robinson *et al.*, 1980) some neurons are found, whose responses to visual stimuli mayhe stronger before eye movements, but without directional preferences such as found in the prelunate cortex. In the infero-temporal cortex, some neurons are only activated when a stimulus has behavioral significance, i.e. whether it leads to a behavioral response or not (Ridly *et al.*, 1977, Rolls *et al.*, 1977).

These examples and my own experience in recording on prestriate neurons in the awake monkey during the last year demonstrate, that in the various visual areas not only different features of a stimulus are represented, but also different responses to stimuli. *The different visual fields could then also be understood as a co-operative of various sensori-motor links between the eye and visually guided behavior.* This idea is reminiscent of O. Foerster's (1936) metapher who compared the various motor fields to a working co-operative in the elaboration of motor acts. Of course, the emphasis on the behaviorally significant output of each visual area may appear to neglect the perceptual and cognitive significance of representation in these various areas. It should be realized, however, that both these aspects are complementary and maybe — to some extent — interchangeable (see Creutzfeldt, 1981, 1983).

The role of association fibres could be, in such a modell, to mutually reinforce the responsiveness of cortical neurons to their thalamic afferent inputs. They would also provide a mechanism for coordination of activities in the various sensory fields, so that the combined output from all the visual representations becomes functionally correlated with respect to the appropriate visuo-motor response. One might also consider a gating function for association fibres which allow certain afferent inputs to get through and others not, according to the state of activity in the connected field. All such suggestions must remain vague and can at best serve as models for further experimental testing. It could even be, that the functional role of association fibres may become more significant in primates than in lower mammals. But also this would need experimental proof.

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HOW MUCH OF THE INFORMATION FALLING ON THE RETINA REACHES THE VISUAL CORTEX AND HOW MUCH IS STORED IN THE VISUAL MEMORY?

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It is a strange coincidence that precisely 350 years ago the trial of Galileo was underway. After his abjuration he is purported to have mumbled "Eppur si muove". In Bertolt Brecht's play, Galileo Galilei (1564-1642) hears that Sunspots have been sighted and calls out "Take the cloth off the telescope and turn it to the sun." We do not now believe that the Sun goes round the Earth or that the Heavens are seven leagues away. Our knowledge of brain function is pre-Galilean. Have we even got a telescope? I think it might be the microelectrode! But Galileo and his successors did much more than map the Heavens — they thought carefully about what they saw and measured.

In 1977 Hubel and Wiesel wrote about Monkey visual cortex "This means that there is little or no opportunity for signals entering the cortex in one place to make themselves felt at points more than 1-2 mm away. As a corollary to this it may be added that the striate cortex must be analysing the visual world in piecemeal fashion: information about some region in the visual field is brought to the cortex, digested, and the result transmitted on with no regard to what is going on elsewhere. Visual perception, then, can in no sense be said to be enshrined in area 17 — the apparatus is simply not made to analyse a percept that occupies more than a small region of visual field. All of the single cell physiology in fact suggests that area 17 is concerned simply with what may be thought of as building blocks for perception . . . We end up, then, with a view of the cortex as containing a thousand small machines of more or less identical structure."

I much prefer the word machine to hypercolumn for it raises the issue of why do we need these 1,000 machines and what are they doing? (Sakitt and Barlow (1982) estimate that in the human the number is nearer 5,000). Of course, this speculation is a dangerous, although essential, activity. The famous Italian anatomist, Gabriele Falloppio (1523-1562) thought that the uterine tubes were to "permit noxious vapours to leave the uterus"!

In Galilean tradition let us imagine that we are lying on our backs viewing a clear night sky. Let us compute how much visual information could be placed there. A hemisphere has an area of 21,000 square degrees. Therefore, 80,000 Moons could be packed into the sky. On each Moon could be printed 17-19 alphanumeric characters of 5′ subtense separated by a space of 5′. If the Moon is flashed up at a random position there would only be a 1 in 80,000 chance of its image falling on the fovea; even then one would not be able to read all 19 characters. A total of 1.5×10^6 letters could be displayed in the sky. If we read at the rate of 1 per second for 16 hours per day it would take 21 days to count them all! Clearly we are able to process a very small fraction (1 in 100,000) of the potential visual input per perception time.

Most visual scenes contain much less information than the one described. If a given point in the scene has a certain contrast level, there is a high probability that points immediately adjacent will have the same or similar contrast values. If the amplitude spectrum of an average scene is computed most of the energy is at zero frequency (f) and the amplitude falls at a rate of between $1/f$ to $1/f^2$. Does the visual system take advantage of this statistic about our visual environment? If it did it would want to get rid of the unnecessary low frequency scene detail as early as possible to prevent overloading the later memory and analytical mechanisms leading to image recognition. Fig. 1 shows the well known contrast sensitivity function. Below 3 cycles/deg there is a low spatial-frequency attenuation at threshold with a slope of + 1. Mark McCourt and I have recently checked that it continues down linearly to 1 cycle/360° — the lowest frequency that a sine wave grating can be detected even when it is of high contrast. Thus, the visual system does correct approximately for the contrast redundancy in visual scenes. The visual system puts the low frequencies back again so that we are normally not aware that they are missing (Campbell, Howell and Johnstone, 1978).

Let us now consider the properties of a single "machine" which we will assume transmits only essential information. We shall concentrate

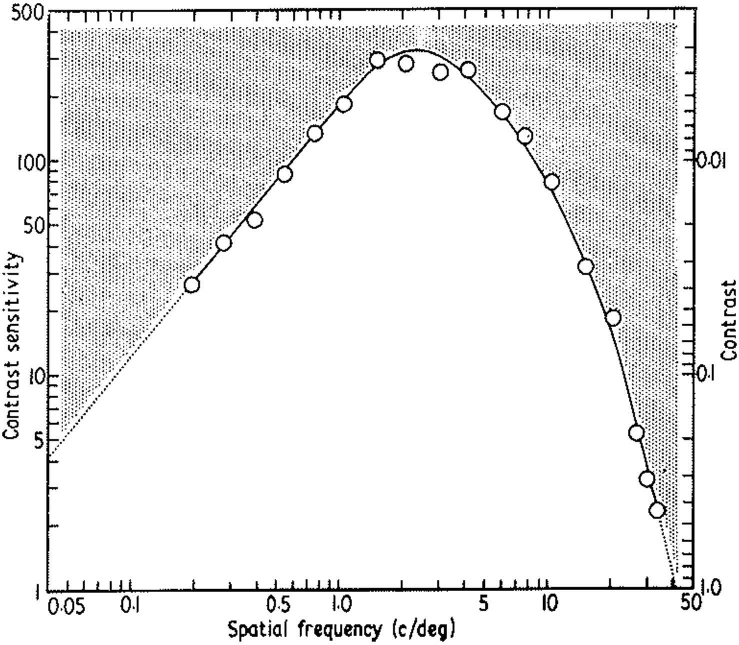


FIG. 1. The shape of human contrast sensitivity function, at threshold, for sinusoidal gratings. Our visual world is restricted to the clear region under the curve.

on the "machines" subserving foveal vision. As Stuart Anstis (Braddick and Sleigh, 1983) puts it "A retina with a fovea surrounded by a lower-acuity periphery can be compared to a low-magnification finder telescope with a large field of view, which would find any interesting target and then steer on to it a high-powered main telescope with a very small field which could examine the target in more detail."

Let us study initially a single object which the visual system is good at naming — a human face. Computer engineers know from experience that we need 64 contrast levels to display a halftone picture without contrast artifacts (usually 128 are used). What is the smallest number required for face recognition? Look at the faces in Fig. 2. Clearly they belong to the same person, so that only two levels are required (1 bit). Now view from a distance of many meters so that only the smallest machine is operating. The faces are identical.

The famous picture of Leon Harman's Lincoln face, shown in Fig. 3, has more contrast levels but it would also work with less (Harmon, 1973).

FIG. 2. (*Left*) continuous tone print. (*Right*) two-tone print.

When you blur the face, or view it from a great distance, it is easily recognised. The high spatial frequencies induced by the pixels masks the low frequencies containing the face information. The face is contained in about 14 high by 11 across = 151 pixels.

Woodhouse (1975) and I did the following experiment. A group of students (17), who worked together, slowly approached the 17 photographs of each other until they could name each face (the hair, neck, etc., was masked out). The average distance was found to be equivalent to viewing a normal size face from a distance of 47 m. It is a simple calculation to show that this would involve, in the fovea, a cone matrix of 19 × 19 = 361 cones. Note that the Lincoln picture (including the beard) is 151 pixels.

There is a great commercial and military interest in developing machines which can undertake image detection and recognition as efficiently as the human visual system; for example, Marr (1982). One can reverse the logic of most pattern recognition research by asking the question "Can we define mathematically an object which is recognised by us?". Then we might be able to design a machine to detect and recognise it.

Recall the statistical argument that if you allow a monkey to strike typewriter keys at random he will finally produce all the plays of Shakespeare. If we display a picture of black and white pixels selected at

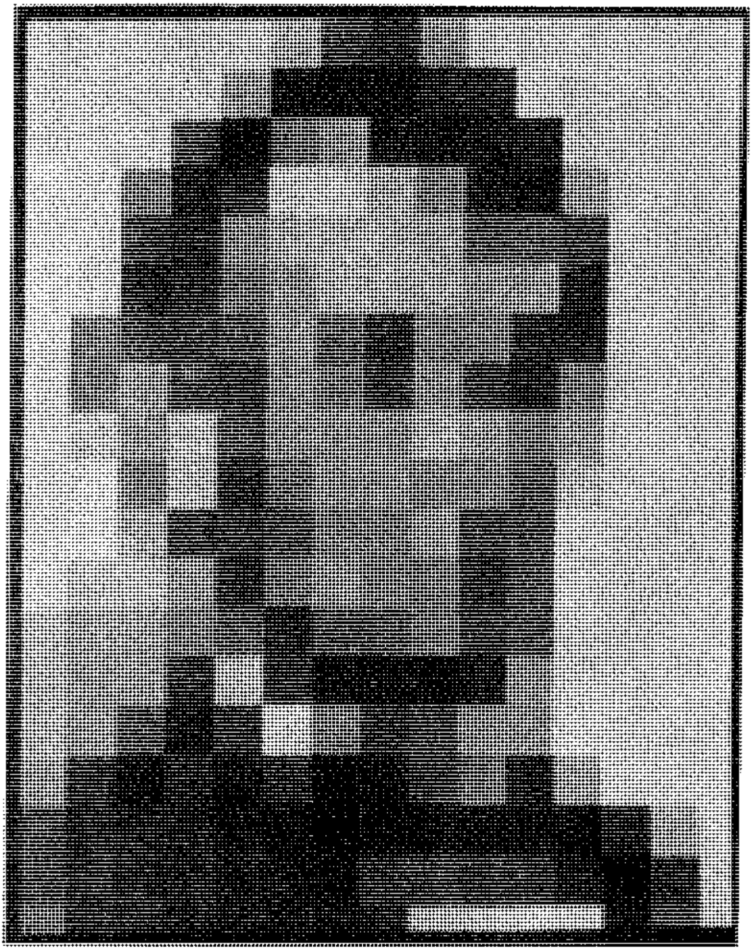


FIG. 3. Block portrait of Abraham Lincoln (Harmon, 1973).

random and blur the display, so that the pixels cannot be resolved, recognisable objects must appear, all-be-it rarely. How frequently and how big a matrix size will be required?

To give you hands on experience I want each of you to take a random pixel sheet (Fig. 4) and place on top of it the diffuser supplied which masks a matrix of 12 × 12 = 144. The mask is simply 3 to 4 sheets of artists tracing paper mounted in a 2.7 × 2.7 cm projection slide. Slide it slowly over the random pixel sheet, you will be surprised at the number of human and animal faces that you will perceive.

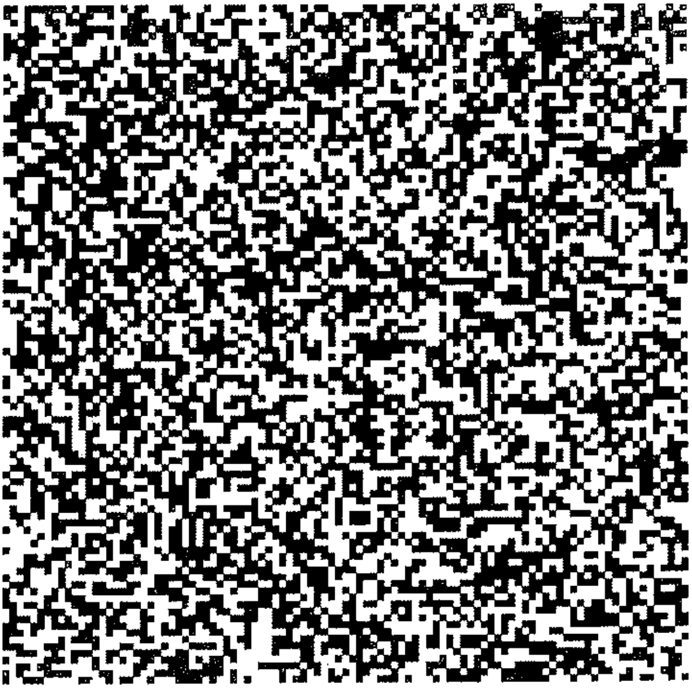


FIG. 4. Random Pixels.

You can mark with a pencil the position of a vivid face. Now increase your viewing distance and you will note that the face gets sharper and sharper. Also, try and describe each human face in terms of sex, age and expression. Now show the face to a colleague and get his description. It usually agrees very accurately. Occasionally, two objects occur which can lead to different descriptions. The two differing descriptions can be married by drawing their appearance and then both observers see both. A face is never seen upside down or tilted through 90°. By turning the pixel display through 90° you can increase by 3 × the number of potential pictures.

The algorithm for generating the random pixels turns on a pixel and also turns it off at random, so that on average 50% are off. If a window of 10 × 10 is used the total number of different objects which could be generated by chance would be $2^{100} = 10^{30}$. Eddington's estimate of the number of atoms in the visible universe is 10^{79}. If one lives to the age of Sir John Eccles and one's visual memory retains one object per second

18 hours per day, the total store required is only 2×10^9. This is the maximum number of different visual objects we need to store assuming we had a perfect visual memory covering our entire life.

A matrix domain has been chosen here to enumerate the minimal requirements for face recognition as the theory is better known and applies directly at receptor level in the central fovea. However, the Fourier Theorem can be used which is more insightful at higher levels where the orientational and spatial frequency properties of simple and complex neurones have been established (Piotrowski and Camphell, 1982).

Of course, there are special cases in face recognition. As a casualty surgeon I once treated a pair of identical twins. One of them required a suture across the left eyebrow. Forever after I could only tell them apart by looking carefully to detect the few missing hair follicles in the eyebrow. As they were girls they shared the same wardrobe! (Just as well I gave up surgery). In this case at least two memory modules are required to differentiate the two faces, one of them requiring high spatial resolution.

So far, we have considered images that arise from a small number of randomly placed pixels. If we were to mark the resulting objects with a separate description such as "cat's face, baby's face, elderly male, young female, etc." and each matrix pattern was stored and the statistics of the position of each element was collected, it should be possible to generate objects at will. This could be done by placing a boundary on the random selection of pixel position. Conversely, these statistics could be used to make a face recognition machine which would also give a description of a particular face presented. It may turn out that faces are unique objects but hopefully a similar analysis could be extended to any class of object, such as teapots and automobiles. The work of Dr. Edwin T. Rolls (see p.) does suggest that face recognition is neurologically rather special in monkeys. It would be interesting to present them with a dynamically changing random and diffused pixels. It may turn out that when the neurones "see" a face so do we.

Kenneth J.W. Craik (1914-1945), while discussing how the human visual system recognised objects, wrote:

> Now in mathematics it is legitimate to seek transformations through which certain quantities (such as the physical laws of nature and the velocity of light in relativity theory) remain invariant. In fact, the action of various physical devices which "recognise" or respond identically to certain simple objects can be treated in terms of such transformations. Thus the essential part

> of physical "recognising" instruments is usually a filter — whether it be a mechanical sieve, an optical filter, or a tuned electrical circuit which "passes" only quantities of the kind it is required to identify and rejects all others. Mathematically, the situation here is that, in a perfect filter, the transformation leaves the desired quantity unaltered, but reduces all others to zero.

So, Craik saw clearly that to separate anything from a population of similar or different things one needs a filter. To separate say, eggs into small and large we need only one sieve; but to separate them into small, medium, and large we require two filters, that is, a low-pass plus a high-pass filter. These can be physically separate, as in the case of the egg filters, or combined into one as in the case of many electronic filters or all mechanical resonators, like a tuning fork.

It is conceivable that Hubel and Wiesel's machines are filters breaking down each object to a very simple code and thence each code is compared in the visual memory for purposes of recognition. If this is the case, then there must be certain more complex tasks that cannot be performed as the necessary information required for identification has been rejected at an early stage of visual processing. There is one task which the visual system does badly. If one presents a human observer with a row of say, dots equally spaced, as in the inset of Fig. 5, and such a target of dots is presented briefly, so that there is no opportunity of eye movements, subjects can count with complete accuracy up to four dots. Thereafter, the accuracy drops rapidly (Atkinson, Campbell and Francis, 1976). The right hand ordinate in Figure 5 shows the percentage of errors against a number of dots on the abscissa. The hatched area gives the results. It is important to note that when an error is made for five dots, it is always because the subject confuses five with six. He never calls five dots four dots.

The response time for the subject to call out the number is at the left ordinate. Note that the response time is almost constant up to four. Thereafter, it increases rapidly. Clearly, he is using some different strategy to judge the number and is doing so most inaccurately.

If the subject is asked to respond with the words, "1, 2, 3, 4 and 4 +" his response time is again almost constant (lower data in the figure). Thus one can very quickly and accurately put any number of regularly spaced items into five categories. On a binary count, the counting performance might be 1 = 00, 2 = 01, 3 = 10, 4 = 11 (2 bits) and 4 + could be coded as more than one 2-bit machine is active. The output

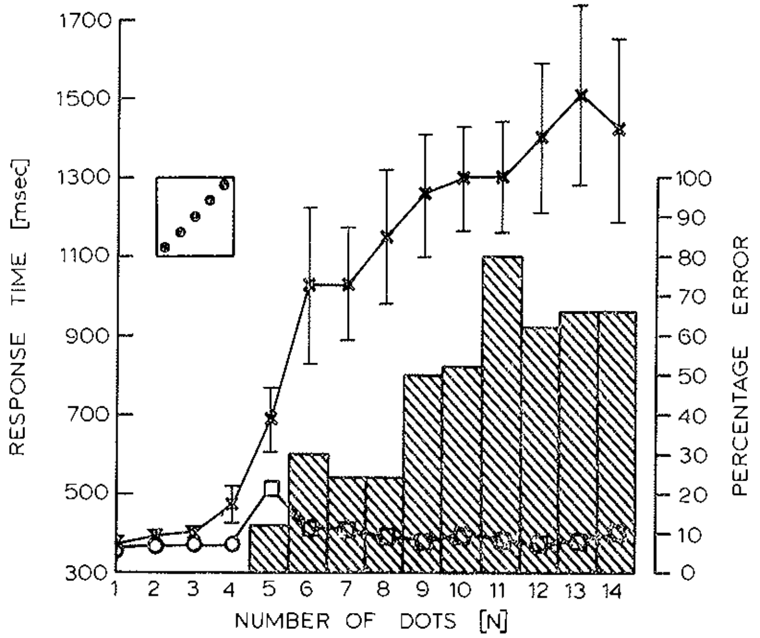


FIG. 5. Mean response times (*left*) and per cent errors (*right*) as a function of the number of dots, N.

of two or more machines cannot be added accurately if the items are in the same orientation. If the items are in a matrix at right angles the numbers can be multiplied; for example, if 4 by 4 dots are present, 16 is accurately reported, but only after a long reaction time as the subject has to recall "four fours is sixteen" (Atkinson, Francis and Campbell, 1976). Maybe each orientational neurone is a 2-bit machine. Sakitt and Barlow (1982) contains a recent summary of similar ideas including a more detailed mathematical approach modelled on receptive field profiles and spatial frequency channels.

It could be argued that the numerosity limit is due to the brief viewing period and the limited "short term memory".

The following experiment showed that even if the stimulus can be observed for 10 s, there is still a limit of 4 for arrays of low spatial frequency (Fig. 6). Six observers looked at a bright after image of an array of dots (2.5 cycles/deg, obliquely oriented, see inset figure 6). The after image, produced by exposing the array in front of an electronic flash, was clearly seen for at least the first 10 s. Observers were asked

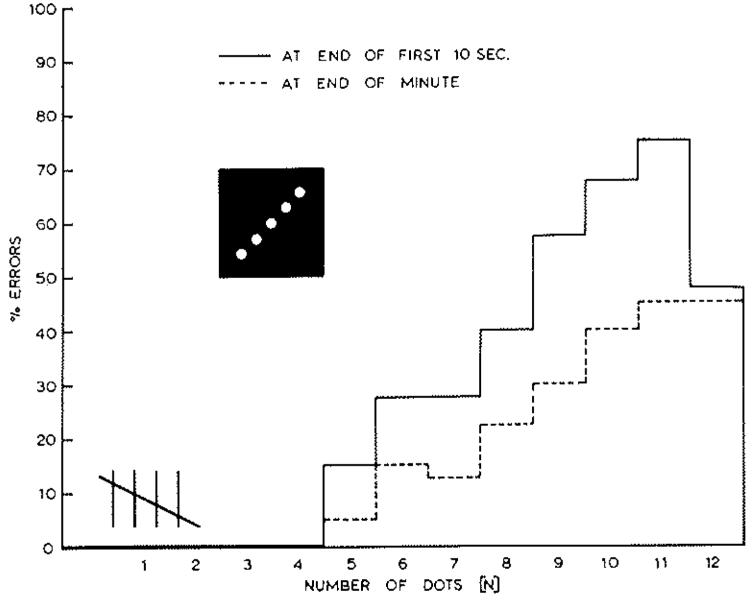
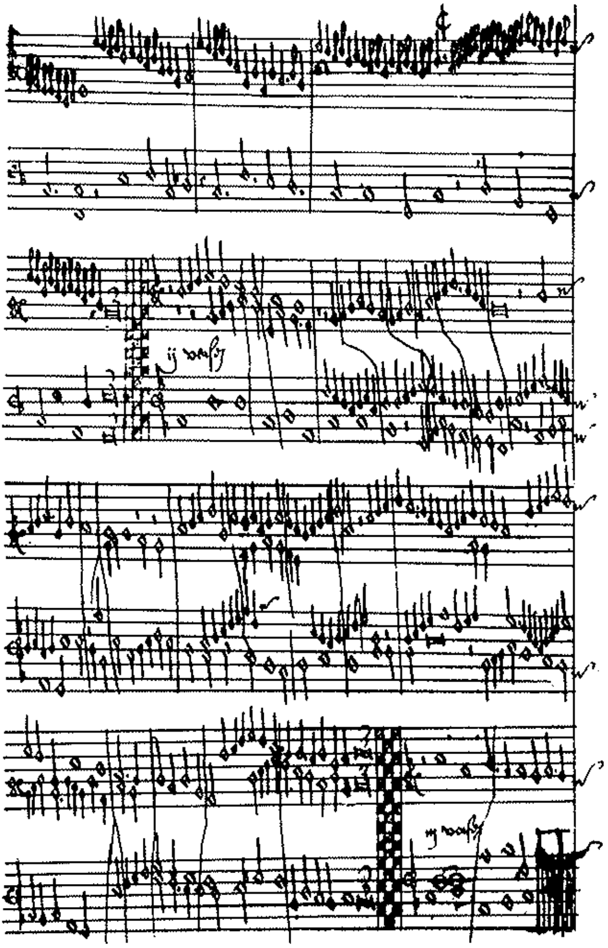


FIG. 6. Mean per cent errors for six subjects as a function of the numbers of dots in an after image (stabilised).

to give a first estimate of the number of dots at the end of 10 s and a second estimate at 60 s after exposure. Mean accuracy on ten trials for each array is shown in figure 6. Again errors were made on arrays of 5 or more dots, the second estimates being slightly more accurate than the first. As the after image tends to partially fade and reappear during the course of 60 s after exposure, sometimes certain dots disappear while others remain visible. The observer used these extra cues from disappearances to improve his second estimate compared to his first estimate. However, errors on arrays of 5 dots are still sometimes made at the end of 60 s. The result suggests that it is not a short-term memory buffer that sets the numerosity limit (Atkinson, Campbell and Francis, 1976).

There are many examples of our limited capacity to count. Figure 7 shows an early example of a music manuscript using six and seven lines. The modern staff was introduced in 1662 and consists of only five lines with a separation between the treble and the bass clef. Many centuries ago there was an efficient method of transmitting news in the Mediterranean countries. On top of suitable hills was erected two walls widely separated. Five firebrands could be inserted in each wall for signalling



MS London, British Museum *Add. 29996* (*ca.* 1540)

FIG. 7. An early example of a music manuscript. The modern staff was introduced in 1662.

purposes. The light from the brands was visible at night and during the day their smoke could be used. The lower inset in Figure 6 shows a common form of keeping a tally — four vertical strokes were grouped into five with an oblique stroke. There are, of course, the dots on the face of a dice.

The recent work of De Valois, Yund and Hepler (1982) and De Valois, Albrecht and Thorell (1982) shows that their is a range of orientational and spatial frequency tuning even in the fovea. This range maybe required to normalise for different object sizes and therefore distance.

Today there is just a hint that an explosion of insight into the workings of the cortex is ahead. What will be achieved in the next 350 years? Let us leave the last words to Galileo who obviously enjoyed the science of ideas and the rejection of fallacies.

> So we shall start our observations of the sun with the inexorable determination to prove that the earth *stands still.* Only when we are defeated, utterly and hopelessly defeated, and are licking our wounds in the most miserable dejection, shall we begin to ask ourselves whether we may be right after all and perhaps the earth does move! *With a wink.* And if every conception but this one goes up in smoke, then there can be no more mercy for those who have not searched and yet speak.

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ENCODING AND PROCESSING OF VISUAL INFORMATION IN CORTICAL NEURONES

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A first analysis of spatial information takes place in the retina, and particularly at the level of the ganglion cells which show the well known subdivision of their receptive fields into a centre and antagonistic surroundings.

Mach had already envisaged excitatory and inhibitory interactions in the retina and the possible role of retinal ganglion cells in vision. In one of his articles (Mach, 1868) on the effect of distributed light stimuli, he wrote: "We cannot understand the state before we understand the man. Likewise we will not understand the psychology of man before we understand the much simpler psychology of the ganglion cells".

One interpretation of retinal ganglion cell function is that these cells subserve the task of enhancing contrast and therefore the appearance of borders and contours.

The abstract painter Paul Klee in 1924 in the notes for his lectures at the Bauhaus described a way for emphasizing contrast effects in drawings or in paintings, which in practice reproduces the organization of a ganglion cell receptive field. The similarity is very striking as is shown by the lecturing sketch by Paul Klee himself (Fig. 1).

A more modern and probably more correct way of looking at the function of the ganglion cells is that of interpreting them as filters in the time and space domains. Their job would be that of reducing redundant information falling onto the retina to allow the cortical processing of the essential features required for the recognition of objects. One advantage of this process is that it corrects for the gain changes required to permit vision in a wide range of ambient illuminations.

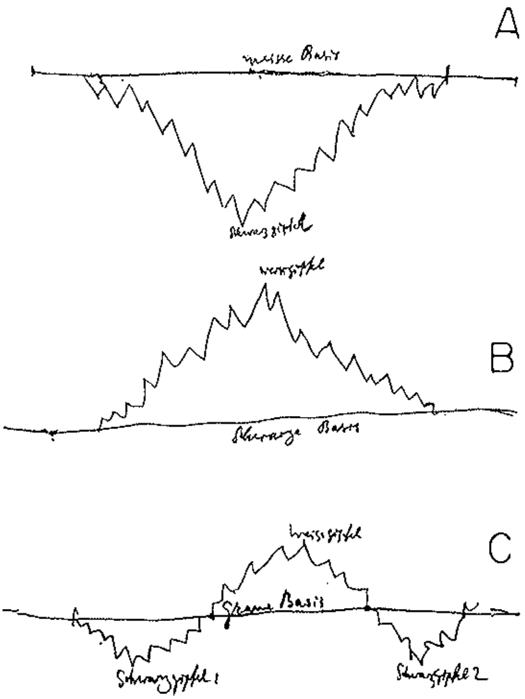

FIG. 1. Sketch by Paul Klee. Reproduced from "*Teorie della Forma e della Figurazione*", Vol. II, *Storia Naturale Infinita*, Edizioni Feltrinelli, Milano, 1970. Weisse = white; schwarz = dark; Gipfel = peak. In *C* is indicated the spatial distribution of dark (*A*) and white (*B*) to achieve contrast effects.

The filtering process of spatial information begins in the retina and is progressively sharpened in the lateral geniculate body, and particularly in the simple and complex cells of the cortex. Indeed cortical neurones, both in the cat and in the monkey, are very selective for the spatial frequency of the stimulus (for reference, see Maffei, 1978).

Responses of simple and complex cells to sinusoidal gratings

The response of simple and complex cells to sinusoidal gratings is very different, which suggests that these two cortical cell types may serve a completely different function in the analysis of visual information. In

1973, Maffei and Fiorentini pointed out that simple cells respond to the single bars of a drifting grating with a modulation of their discharge, whereas complex cells do not. The complex cells simply change their average rate of discharge as a function of the spatial frequency or contrast of the grating. This characteristic of simple and complex cells is illustrated in Fig. 2 (*A* and *C*). The response of simple and complex cells to phase reversed sinusoidal gratings is also different. Simple cells modulate to the first, and complex cells to the second harmonic of the stimulus (Fig. 2 *B* and *D*).

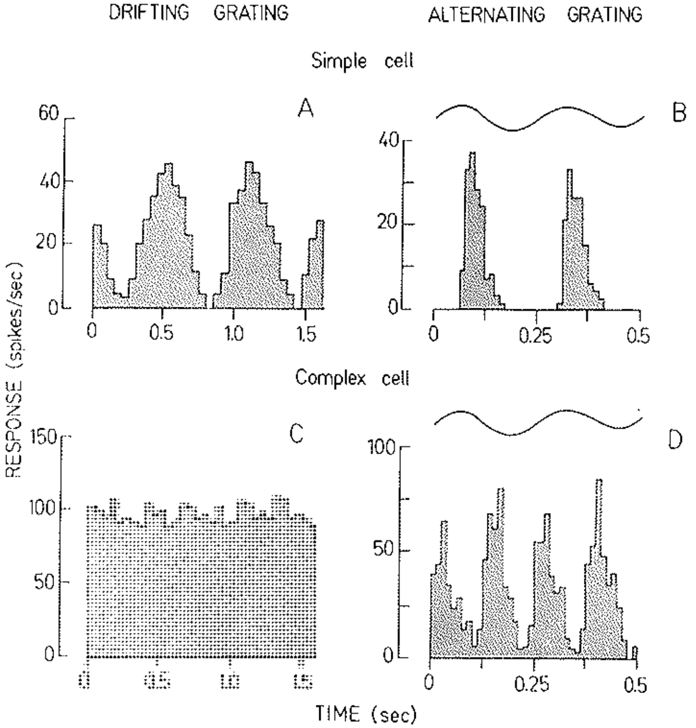

FIG. 2. *A* and *C*: response of a simple (*A*) and a complex (*C*) cell to a drifting sinusoidal grating. Spatial frequency 0.5 cycle/deg. Velocity 3.5 deg/sec. Contrast 20%. *B* and *D*: response of a simple (*B*) and a complex (*D*) cell to phase reversed sinusoidal gratings. The sinusoids above the histograms indicate the temporal modulation of contrast of the grating. Spatial frequency 0.75 cycle/deg, contrast 20%. Note that the discharge modulation in *B* is about 180° out of phase with the discharge of the complex cell in *D* (redrawn from Maffei, 1981 and Morrone *et al.*, 1982).

Different patterns of discharge in simple and complex cells

Complex cells have a maintained discharge even in the absence of visual stimuli while most simple cells do not. When complex cells are stimulated with drifting gratings two different firing patterns in their average discharge become apparent. Numerous clusters of spikes, which are rare or absent in the spontaneous discharge, appear in their firing pattern in addition to spikes which are not organized in clusters and that we will call isolated spikes. Similar observations have been made when the stimulus was a drifting bar (Pollen and Ronner, 1975; Bodis-Wollner *et al.*, 1976). The intervals between the spikes are rather constant for the same cell and range from 2 to 4 ms in different cells. The internal structure of the cluster does not change with stimulus conditions, although the frequency of clustered spikes may vary considerably.

The presence of clusters is not related to the level of anaesthesia or to the physiological conditions of the animal. Indeed clusters of spikes are still present in the discharge of complex cells of alert animals. Figure 3 illustrates an example of these findings. Figure 3*A* illustrates the spontaneous activity of a complex cell recorded in an alert animal and Fig. 3*B* its response to a drifting grating. It may be noted that the typical clusters of spikes are rare in (*A*) but rather numerous in (*B*).

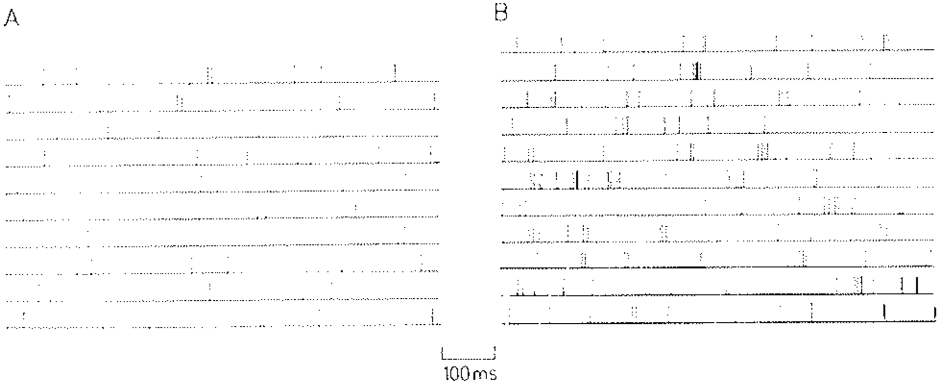

FIG. 3. Activity of a complex cell recorded from area 17 of an alert cat. (*A*) Specimen of the spontaneous discharge. (*B*) Specimen of the cell response to a sinusoidal drifting grating (spatial frequency 0.4 cycle/deg; contrast 8%, drifting velocity 3 deg/s). Note that clusters of spikes, absent in the spontaneous discharge (*A*), are present in (*B*).

Cattaneo, Morrone and I (1981a; 1981b) have investigated whether the two components of complex cell discharges, clusters and the so-called isolated spikes, are significant for the coding of visual information or whether they are an epiphenomenon of the discharge. The frequencies of clustered spikes, as well as of isolated spikes, were measured separately for each cell as a function of various stimulus parameters.

1. *Spatial frequency.* The results show that only clustered spikes are tuned for spatial frequency. Figure 4*A* illustrates these findings. The curves for isolated spikes show a non-specific increase within the band of spatial frequency to which the cell is sensitive. Clustered spikes, however, show a sharp selectivity for spatial frequency: their frequency varies by over an order of magnitude in the range where the responses for isolated spikes remain constant.

2. *Orientation.* The clustered component of the discharge of complex cells is the only component that is tuned for the orientation of the stimulus. Figure 4*B* illustrates typical results for a complex cell. It shows the response of the cell as a function of the orientation of the grating. As was the case for spatial frequency, isolated spikes show a non-specific increase in the range of orientation to which the cell is sensitive, and only clustered spikes show selectivity for orientation. It should be also noted that the tuning curve for orientation obtained by measuring the clustered component of the discharge has a narrower band width than the corresponding curve obtained by measuring the overall discharge (compare in Fig. 4*B* the continuous with the dotted curve).

3. *Velocity.* Figure 4*C* is an example showing how the various components of the discharge of a complex cell change as a function of the velocity of the stimulus. Only clustered spikes are tuned for the velocity of the stimulus (or for its temporal frequency) while the isolated spikes show a non-specific increase in firing rate at all velocities.

4. *Contrast.* The contrast of the stimulus is the only variable, that we have tested, which is capable of influencing the activity of isolated spikes. Figure 5 illustrates the results. The isolated spikes and the clustered component are equally sensitive to contrast variations: both increase monotonically when the contrast increases.

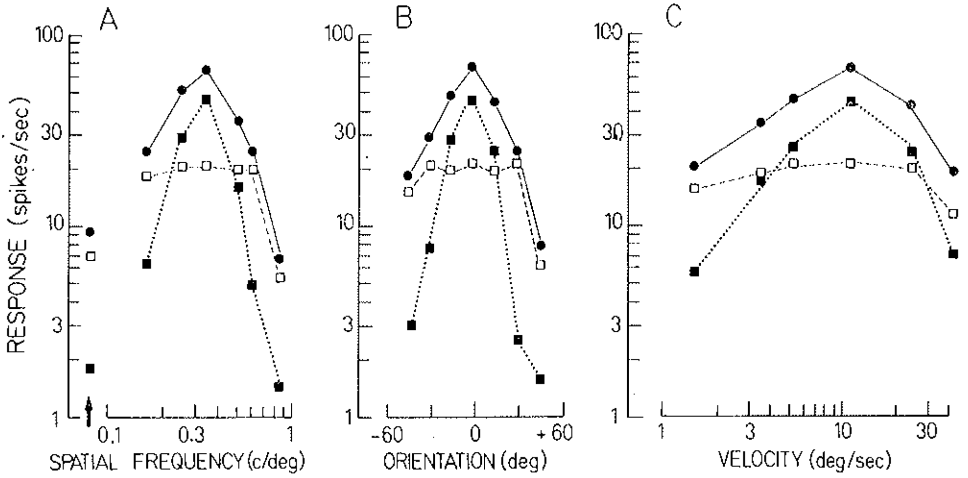

FIG. 4. Complex cell responses to sinusoidal drifting gratings of various spatial frequencies (*A*), of various orientations (*B*) or of various drift velocities (*C*). Filled circles and continuous line: frequency of overall discharge. Filled squares and dotted line: frequency of spikes grouped in clusters (two consecutive spikes separated by less than 8 msec were considered to be organized in clusters). Open squares and broken line: frequency of isolated spikes. The symbols indicated by the arrow report data for the spontaneous activity of the cell. Stimulus parameters: (*A*) contrast 15%, velocity 11 deg/sec, vertical orientation, (*B*) contrast 15%, spatial frequency 0.8 cycle/deg; 0° indicates the vertical orientation, (*C*) contrast 15%, spatial frequency 0.35 cycle/deg. (Redrawn from Cattaneo *et al.*, 1981 and Maffei, 1981).

Intracortical inhibitory mechanisms

Many models of the processing of visual information take into account only nervous excitatory connections. It is generally assumed, for instance, that the orientation selectivity of cortical units derives from the spatial organization of the receptive fields of the lateral geniculate body input. It becomes increasingly clear, on the contrary, that many emerging properties at the cortical level are due to intracortical inhibitory mechanisms (Benevento *et al.*, 1972; Blakemore and Tobin, 1972; Bishop *et al.*, 1973; Creutzfeldt *et al.*, 1974a, 1974b; Watkins and Berkley, 1974; Sillito, 1975; Tsumoto *et al.*, 1979; Sillito *et al.*, 1980; Burr *et al.*, 1981). Sillito and collaborators have shown, for instance, that orientation selectivity of cortical cells (at least of simple cells) is caused by intracortical inhibitory processes. They have demonstrated that iontophoretic injection of bicuculline, an antagonist of GABA, which is thought to be an inhibitory

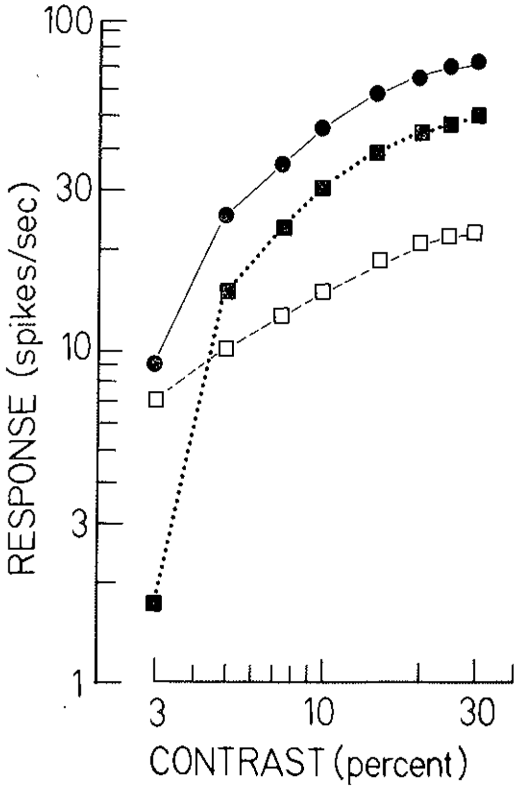

FIG. 5. Response of a complex cell to a drifting sinusoidal grating as a function of contrast. Filled circles: overall average discharge; filled squares: frequency of clustered spikes; open squares: frequency of isolated spikes. (Reproduced from Cattaneo *et al.*, 1981).

transmitter in the visual cortex, abolishes orientation selectivity of simple cells. Preliminary experiments performed in my laboratory by Sillito and Berardi indicate that injection of bicuculline also abolishes the spatial frequency selectivity of simple cells.

The excitatory pathways convey the visual information, but inhibitory mechanisms seem to provide a major contribution to the elaboration of this information.

Morrone, Burr and I (1982) have recently done a series of experiments which offer additional evidence for the essential role of intracortical inhibition in the visual cortex. We have measured the selectivity of these cortical inhibitory processes, both for spatial frequency and orientation, not very selective for orientation suggests that it originates from a pool of cells, with combined responses encompassing all orientations to which the cell does not respond. In the Discussion a possible origin from a particular component of complex cell discharge will be considered. In complex cells the inhibitory effects were much smaller and more variable, so that a reliable tuning curve for inhibition could not be obtained.

3. *Spatial frequency tuning of inhibitory effects.* In this case, one-dimensional visual noise at the cell's preferred orientation was drifted at the optimal velocity, providing the conditioning stimulus, and an orthogonally oriented sinusoidal grating of variable spatial frequency was the inhibitory stimulus. Figure 8 shows the results for two simple cells. Their

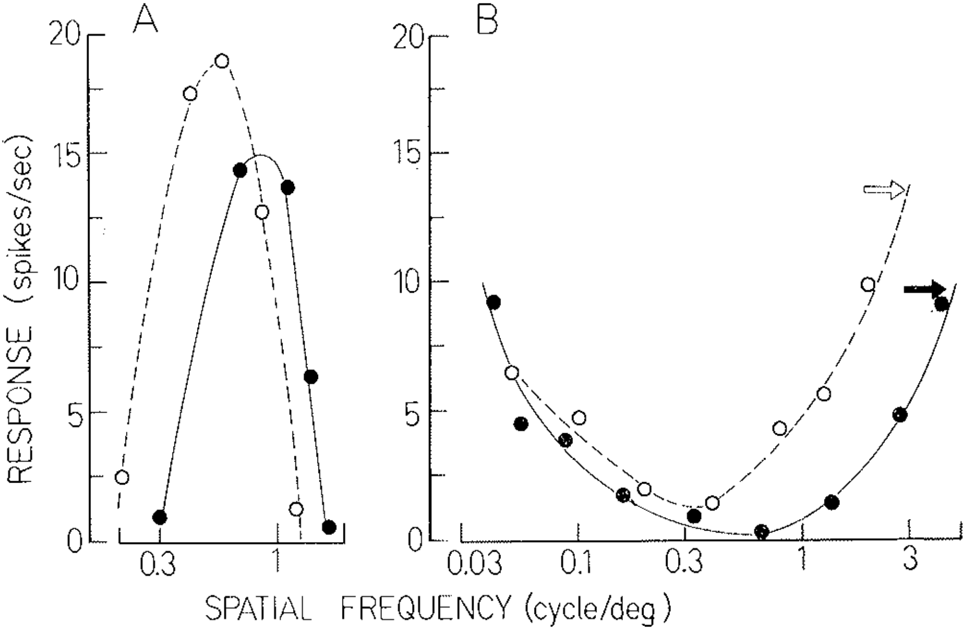

Fig. 8. Spatial frequency tuning of the inhibition for two simple cells. *A*: the spatial frequency tuning curve of the two cells (mean discharge), obtained by stimulating with a sinusoidal grating (temporal frequency 2 Hz; contrast 30%) of varying spatial frequency. *B*: the spatial tuning of the *inhibition*, obtained with a noise conditioning stimulus of 37% contrast, together with an orthogonally oriented grating (temporal frequency 4 Hz; contrast 30%) of variable spatial frequency. The arrows indicate the response to the conditioning noise alone. The inhibitory "tuning curves" have nothing like the sharp bandpass characteristics of the excitation curves, suggesting that the inhibition arises from a wide range of spatial frequencies. (Reproduced from Morrone *et al.*, 1982).

spatial frequency tuning is shown on the left, and is quite selective as is usually observed in simple cells (Maffei and Fiorentini, 1973). The inhibitory tuning curves, however, are very broad and similar to the spatial frequency transfer function of the entire visual cortex as determined by recording evoked potentials (Campbell *et al.*, 1973) or by using behavioural techniques (Bisti and Maffei, 1974).

If 1-D noise is used as inhibitory stimulus the inhibitory effect is more powerful than that elicited by a sinusoidal grating of the same orientation and comparable contrast. This effect can be interpreted as due to the fact that noise contains energy over a wide range of spatial frequencies (see power spectrum in Fig. 6), and therefore, presumably stimulates a larger pool of cells than the grating which has energy at only one spatial frequency. This result, taken together with the lack of true spatial frequency selectivity for inhibition, suggests that each simple cell is inhibited by a pool of cortical cells tuned to a wide range of spatial frequencies.

Response of cortical cells to 2-D visual noise

As we have seen, simple cells are selectively tuned both for orientation (Watkins and Berkley, 1974) and for spatial frequency (Maffei and Fiorentini, 1973), and receive a strong inhibitory influence from a broad range of orientations and spatial frequencies. For these reasons simple cells should respond poorly if at all to 2-D visual noise. Complex cells which are more broadly tuned for orientation and spatial frequency and receive only weaker intracortical inhibition should respond more vigorously. Indeed, it is well known that complex cells respond well to 2-D visual noise while simple cells do not (Hammond and MacKay, 1977). Simple cells, however, do respond to 1-D visual noise with a power spectrum identical to the 2-D noise in that orientation (Burr *et al.*, 1981). Simple cell responses to 1-D and 2-D noise are reported in Fig. 9 as a function of contrast. The 1-D noise we used (Burr *et al.*, 1981) was a mathematical subset of the 2-D noise (see Fig. 6), and therefore, the silence of simple cells does not result from a paucity of energy in the pattern, but rather from an inhibitory process.

Inhibition of simple by complex cells

The next question we investigated was: which type of cells provides these inhibitory influences. Our evidence suggests that complex cells

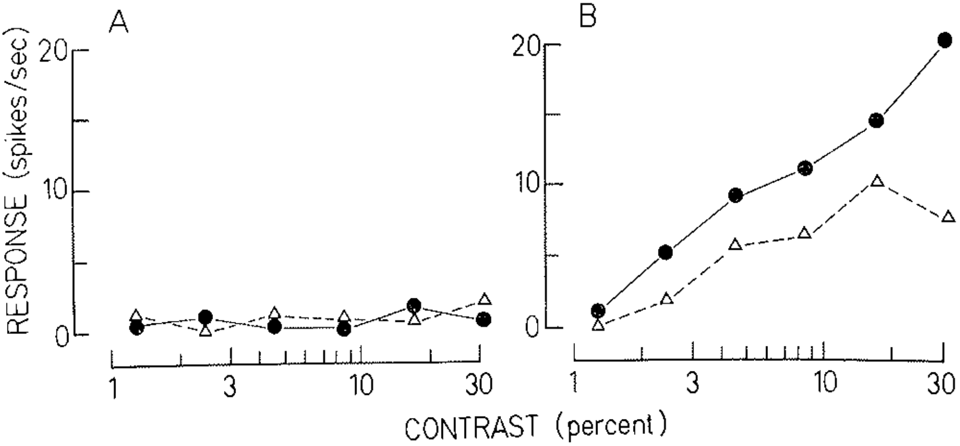

FIG. 9. Responses of two simple cells (circles and triangles) to 2-D (left) and 1-D (right) random noise visual patterns as a function of contrast. (Reproduced from Burr *et al.*, 1981).

might be responsible for the inhibition of simple cells. The hypothesis that complex cells might influence simple cells is based on the following observations:

1. Gratings alternated in phase outside the cell orientation tuning curve decrease the response of simple cells to other stimuli. Figure 10 illustrates an example of such findings. Figure 10*A* shows the response of a simple cell to a drifting 1-D noise. Figure 10*B* shows the response to the combination of 1-D noise and an alternating grating oriented orthogonally with respect to the cell's preferred orientation (and 1-D noise). The orthogonally oriented alternating grating depresses not only the mean firing rate of the cell but also causes the response to modulate at twice the temporal frequency of the stimulus. This inhibitory modulation of simple cell activity has characteristics indicating that the modulating influences might come from complex cells. Indeed, complex cells are known to respond in this fashion to an alternating grating. Moreover, Morrone *et al.*, (1982) have demonstrated that the modulation of simple cells (Fig. 2) is 180° out of phase with respect to the characteristic response of a complex cell to an alternating grating.

2. Gratings driftings in orientation outside the cell's orientation tuning curve decrease uniformly the response of simple cells to other

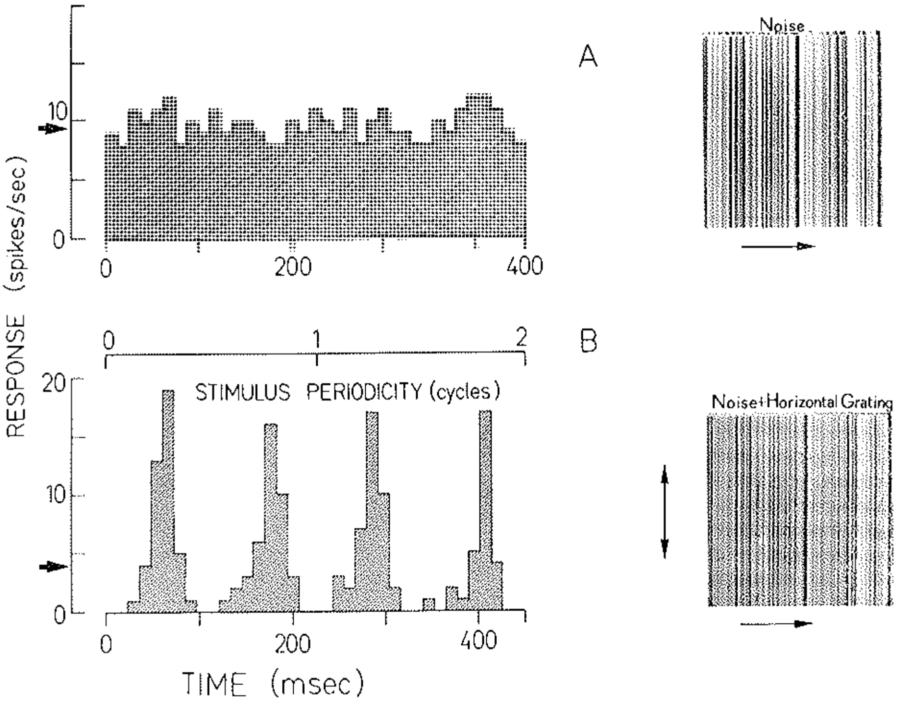

FIG. 10. Responses of a simple cell to a vertical one-dimensional drifting noise superimposed either to a homogeneous background (*A*) or to a horizontal sinusoidal grating alternated in phase (*B*). The stimuli are illustrated on the right part of the picture. The average of the responses have been computed on a time double that of the frequency of grating alternation. Average on 100 runs. Bin width 12.5 msec; arrows indicate the mean firing rate of the responses. Luminance 10 cd/m². Drifting velocity of the visual noise 4 deg/sec. Spatial frequency of the grating 1.0 cycle/deg. Contrast of the grating 20%. Frequency of alternation of the grating 4 Hz. (From Burr, Morrone and Maffei, 1982).

stimuli. Figure 11 shows an example of the results of this experiment. The experiment was similar to that reported in the previous Figure, but the grating, orthogonally oriented with respect to the cell preferred orientation, was drifting. The decrease of the response (Fig. 11*B*) is uniformly depressed and does not show any correlation with the passage of the single bars of the grating. These results are quite consistent with the idea that complex cells are involved in intracortical inhibition. However, the unlikely possibility that the inhibition arises from a battery of simple cells with receptive field positioned to cover 360° of phase cannot be excluded at present.

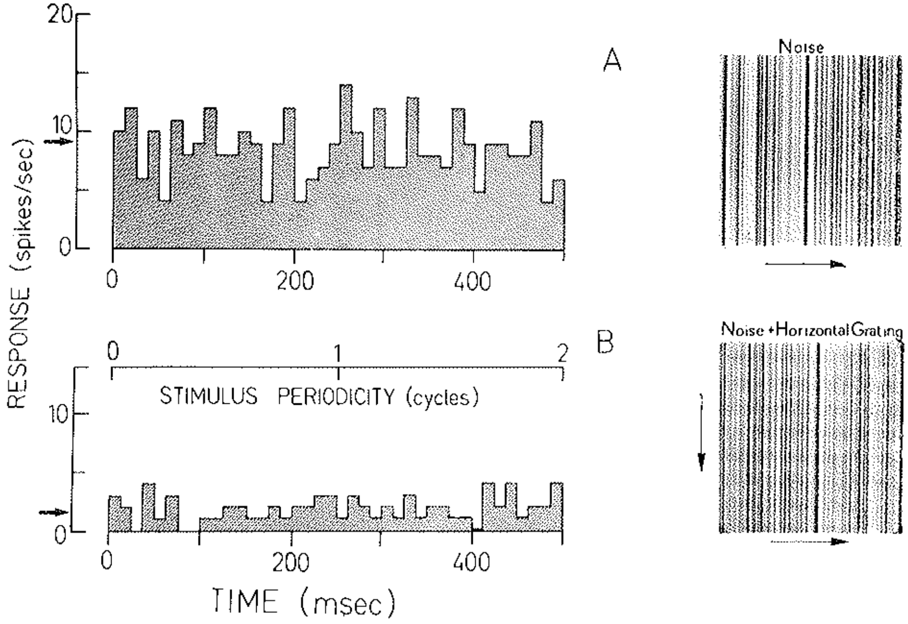

FIG. 11. *A*: Response of a simple cell to a one-dimensional drifting noise. Sums 100. Bin width 2.5 msec. Drifting velocity 5.5 deg/sec. Stimulus periodicity 3 sec. Luminance 10 cd/m^2. The arrow indicates the mean firing rate of the response. *B*: Response of the same cell to the two-dimensional pattern reported on the right. The stimulus is the superposition of the vertical one-dimensional noise in *A* and a horizontal sinusoidal grating. The directions of movement of the two patterns are indicated by the arrows. Spatial frequency of the grating 1 cycle/deg. Contrast of the grating 20%. Drifting velocity of the two patterns 4 deg/sec. Luminance 10 cd/m^2. The post-stimulus time histogram has been computed on a time which is the double of the periodicity of the drifting grating. Average on 100 runs. Bin width 12.5 msec. The black arrow indicates the mean firing rate of the response. (From Burr, Morrone and Maffei, 1982).

DISCUSSION

The results we have reported indicate that cortical cells in area 17 share a set of similar properties as well as some relevant differences. Indeed, simple and complex cells respond to drifting or alternating gratings in a completely different manner (Maffei, 1981). Furthermore complex cells encode spatial frequency, orientation and contrast into two different firing patterns, clusters and isolated spikes. In sensory physiology, the mean firing rate of single neurones is usually assumed to be the parameter which encodes information about the sensory input. Our results show there may be other ways of encoding nervous messages. Clustered spikes.

seem to play a very important role in carrying visual information. Indeed, only the clustered spikes are tuned for spatial frequency, orientation and velocity of the grating, while both the isolated and the clustered spikes vary as a function of contrast. The selectivity of complex cells for spatial frequency, orientation and velocity is much greater if the cluster component of the discharge is considered in isolation from the overall discharge (Fig. 4).

Two carriers for the transmission of visual information may be advantageous for the cell. The cells receiving the messages from the complex cells can distinguish when the sender of information is spontaneously active (only isolated spikes) from when it is visually stimulated (clusters), and can recognize a variation in the contrast of the visual stimulus.

The different way of coding information in simple and complex cells is compatible with the hypothesis proposed by Hubel and Wiesel that simple cells relay information onto complex cells for further elaboration. However our results, reported in the second part of this paper, show that for at least a class of complex cells this cannot be the case. On the contrary, complex cells which receive a substantial Y input through fast conducting axons could be the controllers of the activity and function of simple cells through inhibitory circuits (Creutzfeldt *et al.*, 1974a, 1974b; Singer *et al.*, 1975; Hammond and MacKay, 1978) as our results suggest. The elaboration performed by complex cells could even precede that of simple cells, despite the presence of an additional synapse. Indeed, Singer *et al.* (1975) found that in response to electrical stimulation of the lateral geniculate body, the inhibitory postsynaptic potentials preceded the excitatory postsynaptic potentials, which frequently remained subthreshold.

Complex cells exhibit a resting discharge which is rather high in the type described by Palmer and Rosenquist (1974) and Gilbert (1977). This spontaneous discharge could generate, as our results suggest, a spontaneous inhibition of simple cells and probably of other complex cells showing low spontaneous activity. The spontaneous inhibition is most probably the cause of the fact that simple cells do not show any spontaneous discharge.

In conclusion, the cortical scheme suggested by our results is one in which information is processed not by a hierarchical sequence (Hubel and Wiesel, 1962) but rather by a cooperative inhibitory network (Creutzfeldt, 1977) in which the complex subserve the simple cells, shaping their selectivity and suppressing background noise.

In the first part of this paper, we have seen that the complex cell discharge pattern consists of isolated spikes and of spikes organized in clusters. Isolated spikes show, contrary to clusters, very poor selectivity for both orientation and spatial frequency. We have also seen that cross-orientation inhibition of (supposed) complex cells onto simple cells shows similar properties. The hypothesis can be formulated therefore that the isolated spikes of complex cells are responsible for the cross-orientation inhibition. This hypothesis is also in agreement with the observation that clusters are very rare in the spontaneous activity of complex cells and with the further observation that simple cells do not show any spontaneous discharge as if isolated spikes were sufficient to keep them inhibited.

Simple cells as spatial frequency analysers of borders and edges

Complex cells respond to two-dimensional visual noise while simple cells do not. The latter class of cells therefore cannot perform the type of two-dimensional spatial frequency analysis of a retinal image proposed for example, by De Valois and De Valois (1980). Consequently, the concept that simple cells can integrate spatial information of a complex stimulus along the cell's preferred orientation is no longer valid. This concept must be restricted to a particular class of stimuli as bars and edges but cannot be extrapolated to visual texture in general. The fact that simple cells are unable to extract information from a 2-D noise pattern restricts their function to the detection of edges or borders of the visual stimulus. A system selective to visual contours could form an important part of a visual pre-analysis, delineating visual scenes into discrete features, which could then receive more extensive analysis or even processing aiming at the reconstruction of the object in the complex cells or in neurones of other visual areas. Marr and Hildreth (1980) have recently proposed that simple cells detect contours of objects by extracting the zero-crossing of an image prefiltered at the geniculate level. Their model, although mathematically ingenious and elegant, particularly in the exploitation of the Logan theorem (this theorem states the conditions for a function to be described by its zero-crossings) is not in good harmony with what cortical cells actually seem to do. We propose that simple cells act as visual contour detectors by performing a spatial frequency analysis along gradients of luminance of a given orientation. We have reported elsewhere that simple cells can detect the harmonics of a luminance gradient better than the luminance difference in the gradient. An example of such behaviour is illustrated in Fig. 12. It may be noted that the response of

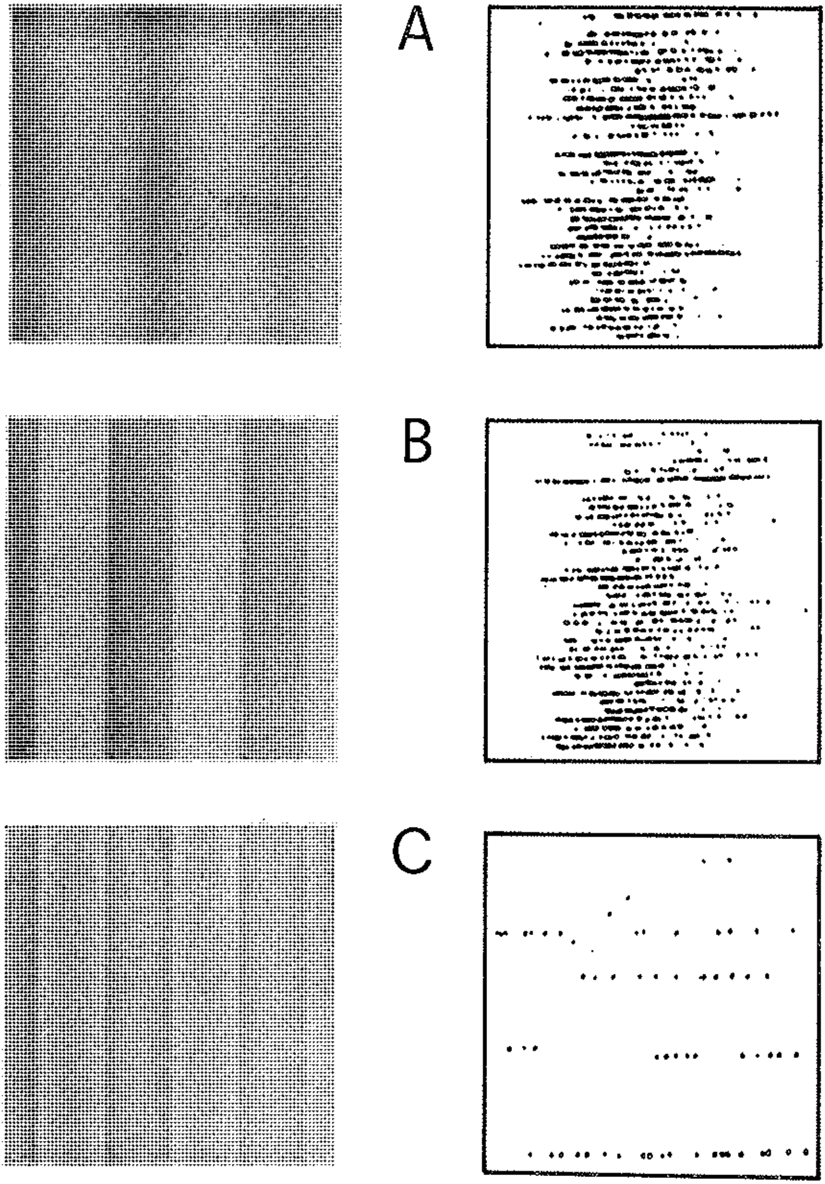

Fig. 12. Responses of a simple cell to drifting gratings of different profile but of the same periodicity. The periodicity of the grating was that for which the cell gave maximal responses: 0.5 cycle/deg with a velocity of 2.7 deg/sec, contrast 15% for the sinusoidal grating and 11.8% for the square-wave grating and average luminance 5 cd/m^2 On the left, visual stimuli are illustrated: sinusoidal, square-wave and missing-fundamental gratings. The missing-fundamental grating (*C*) is obtained by subtraction of the fundamental harmonic (in *A*) from the square-wave grating (in *B*). Each dot in the responses reported on the right is a nervous impulse. Each row of dots is the response to a period of the grating. (Reproduced from Maffei *et al.*, 1979).

the simple cell is very similar when the stimulus is a sinusoidal or a square wave grating of the same contrast. The square-wave has indeed the sharpest contours while the sinusoidal wave has the most blurred ones. In addition the cell does not show any response to the missing fundamental grating (square wave grating minus the fundamental) which still has contours, but which does not contain the fundamental harmonic component to which the cell is tuned.

The grammar of vision. Most data on the electrophysiology of vision refer to the functional specialization of single units although not to the rules of visual information processing. If we want to follow Mach's suggestion and go, as he says, from the single cell to the psychology of man a form of unification of neurophysiological data becomes necessary. In this regard, the concept of visual competence may turn out to be useful (Maffei and Mecacci, 1983).

Visual competence is understood here in a manner similar to that used in linguistics (Chomsky, 1967), namely a finite system of rules by means of which the functional units of the visual system, the neurones, generate the probably infinite system of perceptual phenomena. This search for a grammar of vision, to use Gregory's expression (1974) aims at the description of rules governing interactions among the nervous elements: just as linguistics has illustrated the rules for generating sentences from their components, nouns, verbs, etc.

My work of the last 15 years has been devoted to investigating neurophysiological and psychophysical problems using the tools of Fourier analysis. My work and that of many others, first in the line being Campbell and his collaborators, may indeed be considered as an attempt to develop a neurophysiology of visual competence. The outside world spatial information is considered in terms of its harmonic spatial components and the visual system as an analyser of these spatial components. The evidence that the visual system may work in this way is now rather substantial (for references, see Campbell and Robson, 1968; Maffei, 1978; De Valois and De Valois, 1980; Pollen and Ronner, 1981).

The common language or, one could dare say, the common grammar of Fourier analysis and synthesis, has made comparison between psychophysical and neurophysiological results much more attractive and often very compelling. Psychophysical and neurophysiological experiments seem to complete one another.

These correlations which attempt to bridge the gap between the single cell and the "Psychology of man" are not casual findings but the results of hypotheses concerning the rules governing the processing of visual information.

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THE ANALYSIS OF MOVING VISUAL PATTERNS

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and WILLIAM T. NEWSOME ***

INTRODUCTION

There is abundant evidence that the orientation of contours is a feature of considerable importance to the visual system. Both psychophysical and electrophysiological studies suggest that the retinal image is treated relatively early in the visual process by orientationally-tuned spatial filters (see Hubel and Wiesel, 1962; Campbell and Kulikowski, 1966, among many others). Orientational filtering undoubtedly plays a role in the analysis of the structure of a visual *pattern*, but the visual system has other tasks, most obviously that of extracting information about the *motion* of objects. A simple analysis reveals that separating a two-dimensional image into its one-dimensional (that is, oriented) components presents problems for a system concerned with extracting object motion. Here we outline the problem, propose a novel formal solution to it, and consider the applications of this solution to a variety of perceptual and electrophysiological phenomena.

The ambiguity of motion of one-dimensional patterns. The motion of a single extended contour does not by itself allow one to determine the motion of the surface containing that contour. The problem is illustrated in Fig. 1. The three sections of the figure each show a surface containing an oblique grating in motion behind a circular aperture. In Fig. 1A the surface moves up and to the left; in Fig. 1B it moves up; in Fig. 1C,

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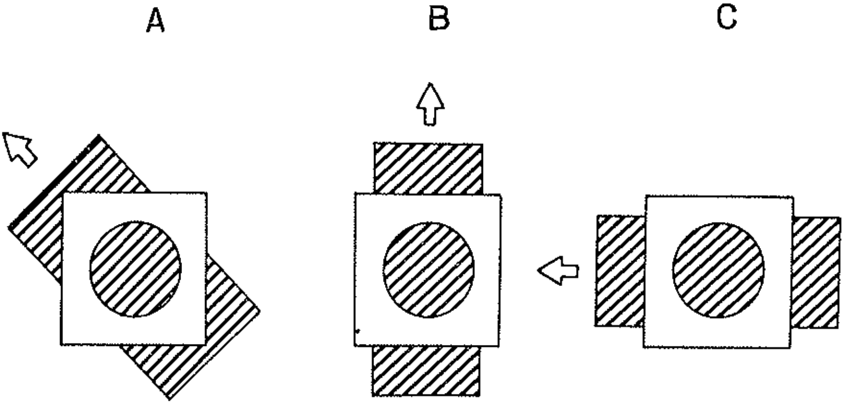

Fig. 1. Three different motions that produce the same physical stimulus.

it moves to the left. Note that in all three cases the appearance of the moving grating, as seen through the window, is identical: the bars appear to move up and to the left, normal to their own orientation, as if produced by the arrangement shown in Fig. 1A. The fact that a single stimulus can have many interpretations derives from the structure of the stimulus rather than from any quirk of the visual system. Any motion parallel to a grating's bars is invisible, and only motion normal to the bars can be detected. Thus, there will always be a family of real motions in two dimensions that can give rise to the same motion of an isolated contour or grating (Wohlgemuth, 1911, Wallach, 1935; Fennema and Thompson, 1979; Marr and Ullman, 1981).

We must distinguish at the outset between what we term *one-dimensional* (1-D) and *two-dimensional* (2-D) patterns. A 1-D pattern is one like an extended grating, edge, or bar: it is uniform along one axis. In general, such a pattern would have to extend infinitely along its axis to be truly 1-D but for the present purposes it is sufficient that the pattern extend beyond the borders of the receptive field of a neuron being studied, or beyond the edge of a viewing aperture. The essential property is that, when a 1-D pattern is moved parallel to its own orientation, its appearance does not change. By convention (and in agreement with its appearance), we will represent the "primary" motion of a 1-D pattern as having the velocity normal to its orientation. 2-D patterns are not invariant with translation along any single axis; they include random dot fields, plaids, and natural scenes. Such patterns change no matter how they are moved, and their motion is not ambiguous in the same way as the motion of a 1-D pattern is.

In this paper we are concerned only with uniform linear motion. For certain other kinds of motion (e.g. rotation or curvilinear motion, or motion in depth), analogous ambiguities exist and can be described and solved in a manner similar to the one we present here (but see also Hildreth, 1983).

The disambiguation of motion. If the motion of a 1-D pattern such as an edge is ambiguous, how is it possible to determine the motion of an object at all? It turns out that, although a single moving contour cannot offer a unique solution, two moving contours (which belong to the same object) can, as long as they are not parallel. As Fig. 1 shows, there is a family of motions consistent with a given 1-D stimulus. Naturally, this is also true of the 1-D elements of a 2-D stimulus. Consider the diamonds shown in Fig. 2A. The left-hand diamond moves to the right; the right-hand diamond moves down. Note that in both cases, in the local region indicated on each diamond by the small circle, the border moves downward and to the right. The moving edge in Fig. 2B, which could represent a magnified view of the circled regions of the diamonds' borders in Fig. 2A, can be generated by any of the motions shown by the arrows. Motion parallel to the edge is not visible, so all motions that have the same component of motion normal to the edge are possible candidates for the "true" motion giving rise to the observed motion of the edge. We may map this set of possible motions as a locus in "velocity space", as shown in Fig. 2B. Velocities are plotted as vectors in polar coordinates, starting at the origin. The length of the vector corresponds to the speed of the motion, and the

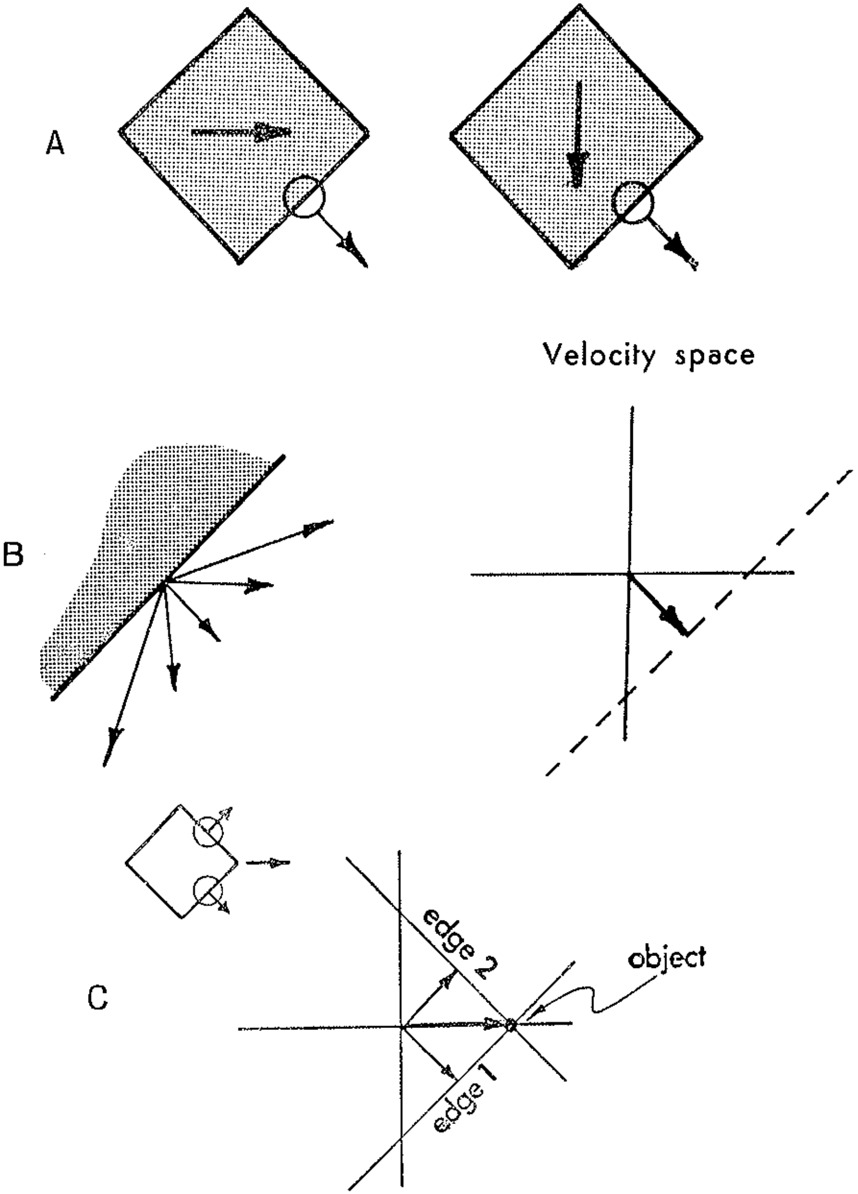

FIG. 2. A. Two moving diamonds. The local regions circled on each diamond's border have identical motions. B. A single moving contour, with the representation of its possible motions in a polar "velocity space", in which each vector represents a possible direction and speed. C. The solution to the ambiguity of one-dimensional motion based on an intersection of constraints. Each border's motion establishes a family of possible motions; the single intersection of these two families represents the only possible motion for a single object containing both contours.

angle corresponds to the direction. As shown in Fig. 2B, the locus of motions consistent with a given 1-D stimulus maps to a line in velocity space. The line is perpendicular to the primary vector representing the motion normal to the 1-D pattern.

It now becomes clear how one may unambiguously assign a velocity to a 2-D pattern, given knowledge only of the motion of its 1-D components. Consider, for example, the diamond moving rightward in Fig. 2C. One edge (viewed in isolation) moves up and to the right; the other moves down and to the right. In velocity space the two edges set up two lines of possible motions. Only a single point in velocity space is consistent with both — namely, the point of their intersection, which corresponds to a pure rightward motion (Fennema and Thompson, 1979; Horn and Schunck, 1981; Adelson and Movshon, 1982).

There are, of course, other ways of combining vectors. For example, one might argue that a simple vector sum would do just as well as the more complex "intersection of constraints" just described. Indeed a vector sum happens to give the correct answer for the diamond of Fig. 2C, but this is only by chance. Consider, for example, the triangle of Fig. 3, which moves straight to the right. The velocities normal to the edges all have a downward component. Thus, when they are summed, the resultant itself goes down and to the right, instead of straight to the right. On the other hand, applying the intersecting constraints principle leads to the correct solution of a pure rightward motion, as shown in the lower part of Fig. 3.

The solution to motion ambiguity just described is purely formal, and does not imply a particular model of how the visual system actually establishes the motion of objects. In the case of the triangle, there are a number of strategies, such as tracking the motion of the corners, which would not give ambiguous results. But while alternate solutions exist in particular cases, the ambiguity inherent in 1-D motion remains a constant problem when we try to understand how the visual system analyzes motion. 1-D stimuli such as bars and gratings are among the most important stimuli used in studying motion mechanisms. Moreover, the visual system itself seems to analyze the world via orientation selective neurons or channels, which necessarily discard information along one axis in favor of another. In this chapter, we consider some issues this analysis raises in the perception of motion, and describe a series of psychophysical and physiological experiments that address these questions.

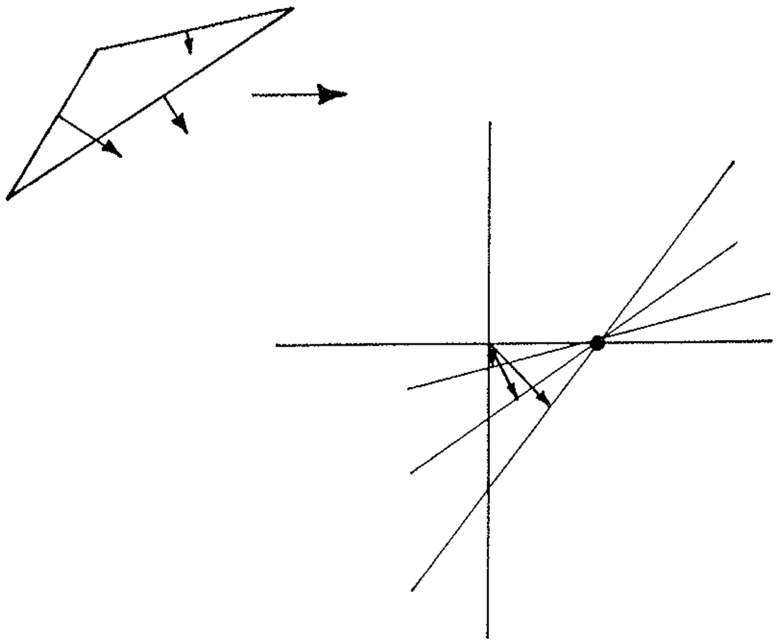

Fig. 3. An illustration of the inadequacy of vector summation as a solution to motion ambiguity. All three primary motion of the triangle's borders have a downward component, but the true motion is directly to the right, as given by the intersection of constraints.

Stimuli

We used two kinds of stimuli in our experiments: sine wave gratings and sine wave plaids. The sine wave grating is our 1-D stimulus, and is therefore mathematically ambiguous in its motion. A moving grating can be diagrammed as occupying a line in velocity space, as shown in Fig. 4A. A pair of sine wave gratings, when crossed, produce the "plaid" pattern of Fig. 4B. In this case, there is no ambiguity about the motion of the whole pattern, since the two families of possible velocities (shown by the dotted lines) intersect at a single point. These stimuli have some advantages for experimentation over more conventional patterns like single contours and geometric figures. For one thing, all of our stimuli were identical

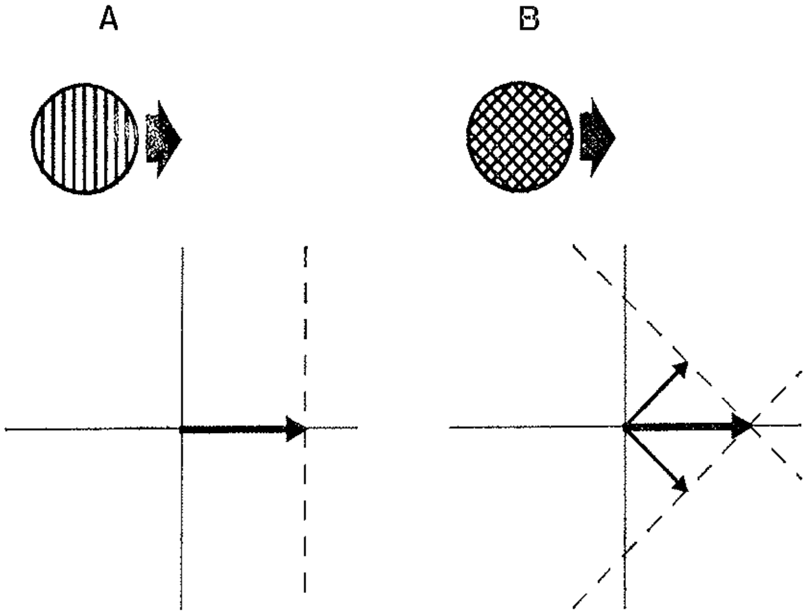

FIG. 4. A single grating (A) and a 90 deg plaid (B), and the representation of their motions in velocity space. Both patterns move directly to the right, but have different orientations and 1-D motions. The dashed lines indicate the families of possible motions for each component.

in spatial extent, and uniformly stimulated the entire retinal region they covered. This sidesteps the issue which arises in considering stimuli like the diamond of Fig. 2, of how the identification of spatially separate moving borders with a common object takes place. Moreover, the plaid patterns were the literal physical sum of the grating patterns, which makes superposition models particularly simple to evaluate.

These stimuli were generated by a PDP11 computer on the face of a display oscilloscope, using modifications of methods that are well established (Movshon *et al.*, 1978). Gratings were generated by modulating the luminance of a uniform raster (125 frames/sec, 550 lines/frame) with appropriately timed and shaped signals. The orientation of the raster could be changed between frames, permitting the presentation of superimposed moving gratings on alternate frames. Plaid patterns were generated by this interleaving method at the cost of reducing the effective frame rate of each component of the display. The spatial frequency, drift rate, contrast and spatial extent of the test patterns were determined by the computer.

The same computer was responsible for organizing the series of experimental presentations and collecting the data, using methods detailed elsewhere (Movshon *et al.*, 1978; Arditi *et al.*, 1981). In psychophysical studies, subjects' responses were normally yes-no decisions concerning some aspects of the immediately preceding display; in electrophysiological experiments, the computer collected standard pulses triggered by each action potential and assembled them into conventional averaged response histograms. In both kinds of experiment, all of the stimuli in an experimental series were presented in a randomly shuffled sequence to reduce the effects of response variability.

PSYCHOPHYSICAL STUDIES

When presented with a pair of crossed gratings in motion, the visual system usually chooses the percept of a plaid in coherent motion, rather than the equally consistent percept of two gratings sliding over one another. Informal preliminary observations suggested to us that the likelihood that two gratings would phenomenally cohere was determined by various features of the gratings. We decided to examine the mechanisms that underly this percept of coherent motion. We first established the conditions that produce or prohibit coherence, and then used masking and adaptation techniques to test the hypothesis that the mechanisms responsible for coherence represent a later and different stage of motion processing than the mechanisms responsible for the detection of simple moving patterns.

The conditions for coherence

We quickly found that the likelihood that a pair of gratings would cohere depended critically on the similarity between them. The first and most obvious dimension we examined was contrast, and the results of these experiments led to the methodology that we used for subsequent studies

(Adelson and Movshon, 1982). Figure 5A shows the results of an experiment on the effect of contrast.

The two gratings were of 1.5 and 2.0 c/deg, and they moved at an angle of 120 deg to one another with a speed of 3 deg/sec. The contrast of the lower-frequency grating was fixed at 0.3, and that of the other was varied from trial to trial. The absolute orientations and directions of the two gratings were varied randomly from trial to trial. We performed two experiments in this situation. In the first (results given by open symbols), we asked the subject to indicate whether the second grating was detectable in the display. For this sequence, 14% of the tirals were blank containing only one grating, and the probability that the observer signalled the presence of the second grating in this case was about 0.05 (half-symbol on the ordinate). As the contrast was increased, the probability that the observer detected the grating increased rapidly and monotonically, so that his performance was perfect by a contrast of about 0.008. In the second experimental series (results given by filled symbols), we showed the same family of 120 deg plaids, but now asked the subject to indicate whether the two gratings moved coherently, as a single plaid, or slid incoherently across one another. This judgement is, of course, criterion-dependent, and naive subjects often required several practice sessions before they gave stable data. It was also especially important to maintain stable fixation on the mark at the center of the display, since coherence seems to depend strongly on retinal speed. The data show that as the contrast increased, the likelihood of a coherence judgement also increased. It is clear, however, that there was a considerable range of contrasts (between about 0.01 and 0.07) over which the two gratings were clearly visible, but failed to cohere. As the contrast of the weaker grating was increased (i.e. made closer in contrast to the "standard" grating), the probability of coherence increased. Because of the monotonicity of this kind of data, it is possible to define a "coherence threshold", as the contrast of the weaker grating that produces a 50% probability of coherence. In subsequent experiments, we measured this coherence threshold for various combinations of gratings using a staircase technique.

Figure 5B shows the results of two experiments that tested the dependence of coherence on the relative spatial frequency of the test gratings (Adelson and Movshon, 1982). In these, the spatial frequency of the "standard" grating was set at 1.2 (open arrow and symbols) or 2.2 c/deg (filled arrow and symbols), and the coherence threshold measured for a variety of test spatial frequencies. The two gratings were separated in

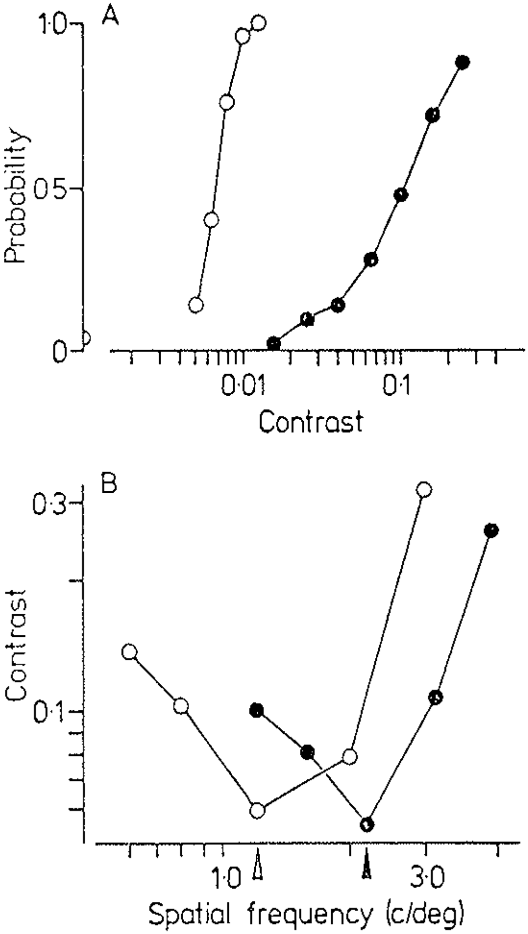

FIG. 5. Two experiments on perceptual coherence. A. The effect of contrast on coherence. The two curves show the subject's probability of detecting the second grating (open symbols), and of seeing coherent motion (filled symbols). See text for details. B. The effect of spatial frequency on coherence. The standard grating was of 1.2 (open symbols and arrow) or 2.2 c/deg (filled symbols and arrow), and the data represent the coherence thresholds for a number of gratings of different spatial frequencies. See text for details. From Adelson and Movshon (1982).

direction by 120 deg, and their absolute orientation and direction were again varied randomly from trial to trial. The speed of all test gratings was fixed at 3 deg/sec. It is clear that the relative spatial frequency of the gratings importantly influenced coherence: when the test and standard gratings were of similar spatial frequency, the coherence threshold was low, but when they were made more than about a factor of two different, threshold rose sharply. The coherence threshold when the two gratings were of the same spatial frequency was about 0.7 log units higher than the detection threshold.

We performed a variety of experiments conceptually similar to these, investigating the effects of the angle between the gratings, their relative speeds, and also the effects of the absolute speeds and spatial frequencies of the gratings. In general, coherence threshold rises as the angle between the gratings is made larger, as their speeds increase, and as the spatial frequency increases, although this latter effect is rather weaker than the others. Under ideal conditions (identical spatial frequencies, low speeds, and a modest angle), the coherence threshold approaches detection threshold so closely as to make the measurements problematic, since coherence is difficult to judge when the observer is not even certain that the second grating is visible.

Models for the perception of coherent pattern motion

The experiments just described gave us a base from which to construct models for various aspects of motion perception. One of the striking features of coherent motion perception is its spatial frequency tuning: two gratings cohere into a moving pattern only if they are of similar spatial frequencies (Fig. 5B). This suggests that the visual system imposes a bandpass spatial filtering on the stimulus before extracting the coherent percept. The filtering could be isotropic — such as the filtering imposed by mechanisms with circularly symmetric receptive fields (e.g. retinal ganglion cells). It could also be oriented — such as the filtering imposed by mechanisms with elongated receptive fields (e.g. cortical simple cells). We consider two models, schematically outlined in Fig. 6.

Model 1: analyzing motion without orientational filtering. The first scheme (Fig. 6A) passes the image through a set of non-oriented bandpass channels. The outputs of these stages are sent to a motion analysis system, which might track salient features such as local peaks, or might perform a cross-correlation between successive views (e.g. Reichardt, 1957; van Santen and Sperling, 1983). This analysis must proceed in parallel in several spatial frequency bands, schematically indicated by the small and large symbols in Fig. 6A. After the determination of motion direction has proceeded within each spatial frequency band, the results are combined (in an unspecified way) to give the final motion percept. The results

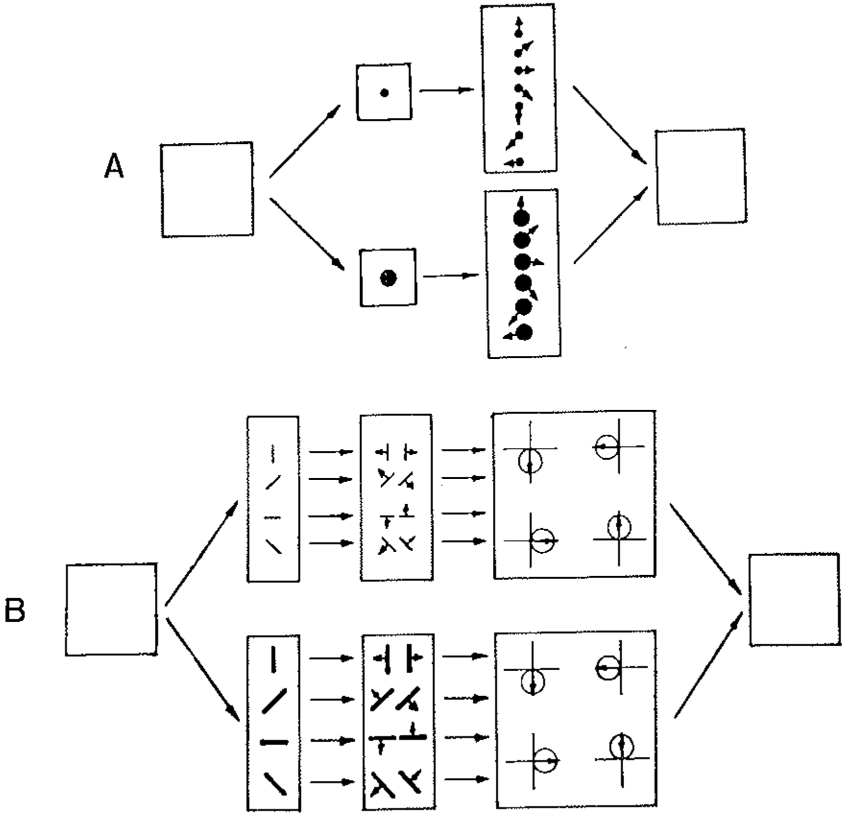

FIG. 6. Two models of the mechanisms underlying perceptual coherence. See text for discussion.

shown in Fig. 5B would come about in the following way: when two gratings are of similar spatial frequency, they would both pass the same spatial filter, and so would produce strong local peaks and troughs where their bars crossed. Thus, a feature tracker or a cross-correlator would be able unambiguously to assign a single motion to the whole pattern. If, on the other hand, the two gratings were of different spatial frequencies, they would not pass the same filter, and so would not produce, in the output of any filter, local peaks and troughs that could be tracked. Indeed, within each frequency band, it would be as though there were only a single grating present, and the familiar problem of motion ambiguity would cause this grating to appear to move normal to its own orientation — the motion extraction stages would operate in their default mode, with only

1-D patterns to process. Thus, two separate motions would be seen, rather than a single coherent one. This model, incidentally, bears a close resemblance to one put forward by Marr and Poggio (1979) for stereopsis.

Model 2: analyzing motion after orientational filtering. An alternate scheme (Fig. 6B) would begin by filtering the image with orientation-selective mechanisms (shown as bars), similar to those commonly associated with cortical neurons or psychophysical channels. The outputs of these mechanisms would then pass to motion analyzers, which would not need to track localizable features, because they only provide information about the motion normal to their own orientation (bars with arrows). As we will see below, motion-sensitive cells in striate cortex behave in this way. But here, of course, arises the problem of motion ambiguity — how does one determine the motion of the pattern as a whole, given the velocities of its oriented components? There are several ways in which this problem can be solved, but they are all formally equivalent to the "intersection of constraints" scheme we outlined at the start of this chapter. This might be implemented in neural terms by combining the signals from several appropriately distributed 1-D motion detectors by circuitry similar to a logical "and" or a conjunction detector, requiring the simultaneous activation of several 1-D analyzers before the second-stage 2-D analyzers would respond. The combination rule here corresponds to a cosinusoidal relationship between component velocity and direction; since this relationship maps to a circle in the polar velocity space, we symbolize the second-stage analyzers by these circles. As in model 1, this analysis must take place in parallel in several frequency bands, two of which are symbolized by the small and large symbols in Fig. 6B.

The question of empirical interest is whether the visual system begins with oriented motion channels, and deals with the ambiguity problem later, or begins analyzing motion before orientation in order to avoid the ambiguity problem. Almost all of the psychophysics and physiology available points to the prevalence of oriented filtering at early stages in the visual system, and it would be surprising to find that the task of extracting pattern motion used mechanisms very different from those inferred in other experiments. Yet, on the other hand, it appears that early oriented filtering makes the task needlessly difficult. If the first stage were non-oriented, there should be no problem in finding the local features and using them to infer the pattern's motion.

Affecting coherence with one-dimensional noise. To study the role of orientation selectivity in coherent motion perception, we combined sine wave plaid stimuli with one-dimensional dynamic random noise, which appears as a rapidly and randomly moving pattern of parallel stripes of various widths. This noise pattern masks the gratings that compose the moving plaid (e.g. Stromeyer and Julesz, 1972). If coherence depends on the outputs of oriented analyzers, then noise masking should elevate coherence threshold more strongly when the mask is oriented parallel to one of the gratings than when it is oriented differently from either. If, on the other hand, the process involves non-oriented filtering, then the orientation of the noise mask should not matter. Only the noise energy within the frequency band of interest, and not its orientation, should have effects on coherence. Our observations of the effects of one-dimensional noise on the threshold for coherence unambiguously demonstrate an orientation dependence in the masking. If the orientation of the noise pattern is within about 20 deg of the orientation of either component of the plaid, the pattern's coherence is reduced in a manner that seems consistent with the reduction in the apparent contrast of the component masked by the noise. If, on the other hand, the noise orientation is different from that of the components, even if it is normal to the direction of pattern motion, little or no effect on coherence is observed. We conclude from these observations that the mechanisms responsible for the phenomenal coherence of moving plaids belong to a pathway which, at some point, passes through a stage of orientation selective spatial analysis.

The effects of adaptation on coherence

As we have seen, the apparent direction of a pattern's motion can be quite different from the motions of the components that comprise it. We suggested earlier that pattern motion might be extracted in two distinct stages. The first stage is presumably revealed by the many orientationally-selective effects seen in experiments on the detection of moving gratings (e.g. Sekuler *et al.*, 1968; Sharpe and Tolhurst, 1973). The second stage, involving further analysis of complex 2-D motions, reveals itself in our experiments on the coherence of plaids. If these stages are really distinct, it might be possible to affect them differentially in adaptation experiments. That is to say, it should be component motion, rather than pattern motion, that elevates detection threshold, whereas it should be pattern motion, rather than component motion, that affects coherence phenomena. We have presented some preliminary data suggesting that this is the case (Adelson and Movshon, 1981).

It is well established that adapting to a moving grating elevates threshold for the detection of a similar grating moving in the same direction (Sekuler and Ganz, 1963). This adaptation is both direction and orientation selective: an oblique drifting grating has little or no effect on the threshold of a vertical grating (Sharpe and Tolhurst, 1973). Suppose now that we combine two oblique gratings into a plaid, so that the plaid appears to move directly to the right. Suppose further that the oblique gratings have been chosen so that they cause no threshold elevation of a vertical grating (moving rightward), when presented alone. If adaptation is caused by the motion of the components, then threshold for the vertical grating should remain unchanged. If adaptation is caused by the coherent motion of the pattern as a whole, then threshold should be elevated, since the plaid adapting pattern, like the test grating, moves directly rightward. Similarly, the effect on the detection of a rightward moving plaid of adaptation to a vertical, rightward moving grating may be assessed.

Figure 7 shows threshold elevation data for four different test-adapt combinations of this sort. All the stimuli in the experiment moved directly to the right at a constant speed of 1.5 deg/sec. Two kinds of stimuli were employed: single vertical gratings (spatial frequency 3 c/deg), and 120 deg plaids whose component gratings (oriented plus and minus 60 deg from vertical) had a spatial frequency of 3 c/deg. Thus all stimuli were identical in direction and speed of movement, but the orientational components of the plaids and gratings differed by 60 deg. We examined the elevation of contrast threshold for each kind of test stimulus following adaptation by each kind of adapting stimulus; the adapting stimuli were all of high contrast (0.5), and thresholds were measured by the method of adjustment. We tested for threshold elevation both in the adapted and unadapted directions. Inspection of Fig. 7 reveals that the results of these experiments conformed closely to the expectations of a model involving orientation selectivity. The detection threshold for a plaid or grating pattern could be strongly elevated in a directionally-selective manner following adaptation to a similar pattern, but was only slightly changed after adaptation to a different pattern. This result is in line with the ample evidence in the literature concerning the orientation and direction selectivity of the threshold elevation aftereffect (Blakemore and Campbell, 1969; Blakemore and Nachmias, 1971; Sharpe and Tolhurst, 1973), and suggests that the 2-D motion of patterns is not encoded at the level of visual processing where these effects are expressed. There is some reason to suppose that threshold elevation effects of this kind are mediated by

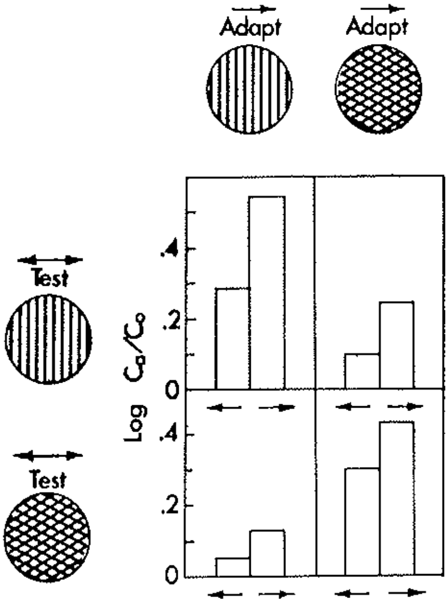

FIG.7. The effects of adaptation to moving gratings and plaids on the detectability of gratings and plaids. Contrast threshold elevation is the ratio of adapted to unadapted contrast threshold, expressed in log units. The two bars of each histogram represent the effects on test stimuli moving in the adapted and unadapted direction, as indicated by the arrows. The data shown are the means of values obtained for three observers; the standard error of the mean was about 0.025 log units.

neurons in the primary visual cortex (e.g. Maffei *et al.*, 1973; Vautin and Berkley, 1977; Movshon and Lennie, 1979).

Adaptation also alters the perception of coherent motion (Wallach, 1976; Adelson and Movshon, 1981). The most interesting case here is one of those used in the threshold elevation experiments described above, in which the adapting stimulus is a rightward moving grating, and the test stimulus a rightward moving plaid. The data in Fig. 7 show that this condition produces no important change in the detectability of the plaid, yet our results show profound effects upon its coherence. We measured this effect by determining coherence thresholds in the manner described earlier above, following adaptation to a high-contrast vertical grating moving to the right. The test plaids had a 120 deg angle, and we varied the spatial frequency of the plaid's component gratings so that either the spatial frequency of the components or the spatial period of the plaid matched the adapting grating. As may be seen from Fig. 8, this paradigm

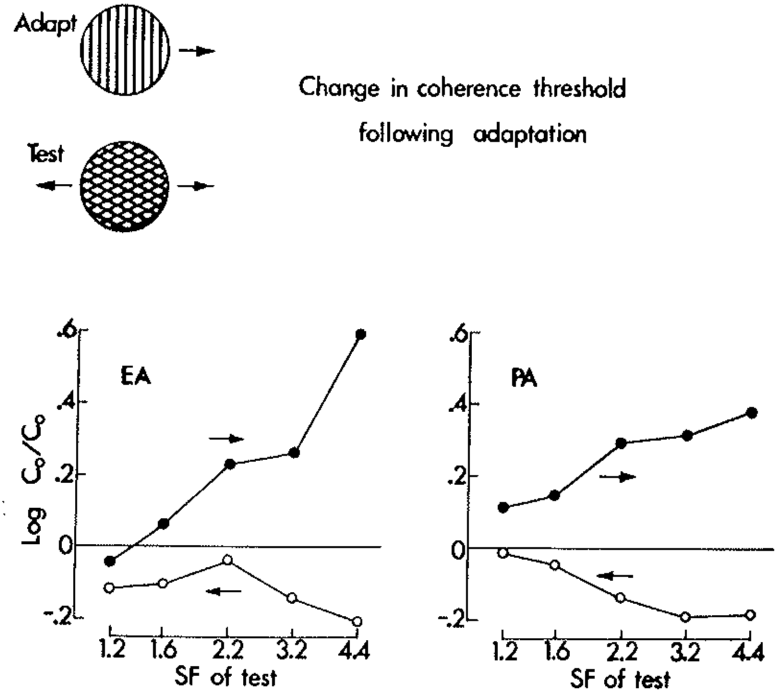

FIG. 8. The effect of grating adaptation on the coherence threshold for plaids. The adapting grating was constant, and coherence was tested for plaids of several spatial frequencies moving in the adapted (filled symbols) and unadapted directions (open symbols). Threshold elevation is the ratio of adapted and unadapted coherence thresholds, expressed in log units. The standard error of the mean was about 0.05 log units.

produced very large elevation of coherence thresholds for patterns that moved in the adapted direction; this effect was most marked for test plaids of relatively high spatial frequency. Conversely, the threshold for coherence of plaids moving in the opposite direction was, if anything, reduced following adaptation.

Evaluation of psychophysical models

The results of these two adaptation experiments suggest the existence of two different sites at which the adapting effect of a moving pattern may be expressed. At the first level, presumed to mediate the detection of moving patterns in our conditions, it is the similarity of 1-D motions that determines the effectiveness of adaptation. At the second level, responsible for the coherence of moving plaids, it is the similarity of 2-D motions that is critical. Combined with the evidence from masking experiments, this suggests that our psychophysical model 2, with an initial oriented stage followed by an analysis of 2-D motion, is an appropriate framework within which our data on the perception of moving patterns may be understood. Some issues concerning this model do, however, deserve some further consideration.

The first issue concerns the sequential link between stages 1 and 2 of the model. While our results demonstrate with reasonable clarity that there are two separate systems involved in motion analysis, they do not demonstrate a serial link between the two processes. Some aspects of the results do, however, suggest such a link. For one thing, the effects of one-dimensional noise masks on coherence appear to be related to the effect of the noise on the perceived contrast of the component gratings. That is, the change in coherence seen under masked conditions appears similar to that which would be produced by simply reducing the contrast of the masked grating by a modest amount. If we suppose that the effects of noise on perceived contrast represent a stage 1 effect, this result tends to suggest that the contrast signals from stage 1 feed into stage 2. Similar evidence can be obtained in adaptation experiments, by examining the effect on coherence threshold of adapting to one or another component of the test plaid. Such adaptation reduces the apparent contrast of a single test grating (Blakemore *et al.*, 1973), and causes a small change in coherence threshold that is of roughly the expected magnitude for one due to a change in the effective contrast of one of the plaid components. Thus while we cannot rule out the possibility that we may be studying the effects of two parallel stages, we continue to favor a serial scheme like that of model 2.

Implicit in this serial scheme is that the signals determining the percepts we have studied arise wholly from elements in the model's second stage. The percepts of coherent and incoherent motion are mutually exclusive — when one grating is "captured" by another, it becomes impossible to see the separate motions of the component gratings. In this, the coherence phenomenon resembles such other multistable visual stimuli as the Necker cube and Attneave's triangles (see Kaufman, 1975). It therefore follows that signals related to the "component" stage of processing do not influence the perception of motion when coherence is seen.

Even if the second stage is the only level at which perceptual information is available, our model must explain how it is that signals related to the component motions are ignored when coherence is seen. After all, a single grating is an effective stimulus for both component- and pattern-level analyzers. It seems that we must postulate that the responses of analyzers at the second level to component motion are actively suppressed when coherent motion is seen. Interestingly, we will show electrophysiological data in a later section that reveals precisely this sort of behavior. We may then outline the events that occur in each stage of the model as we alter a parameter (contrast, for example) that influences coherence. When the contrast of one of the two gratings of a plaid is low, signals in the second-stage analyzer sensitive to the pattern direction are weak, while those in an analyzer sensitive to the direction of the components are more prominent. As the weaker component increases in contrast, we suppose that the second-stage analyzers sensitive to the component motions are suppressed, while those sensitive to the pattern motion are activated. Mutual inhibition among these detectors could achieve this result, and assure the mutual exclusivity of the two percepts; this is, of course, only one of several ways in which this might be achieved, so we do not make it a specific feature of our model.

In summary, we believe that our psychophysical studies reveal the existence of two motion-analyzing processes, probably serially linked, having "component-analyzing" and "pattern-analyzing" properties. We now proceed to examine some electrophysiological evidence that suggests the existence of two analogous stages of processing of motion information in the visual cortex.

ELECTROPHYSIOLOGICAL STUDIES

Our electrophysiological studies concerned the motion-analyzing properties of single neurons in the visual cortex of cats and macaque monkeys. It is well-known that neurons both in and outside the primary cortex (V1, area 17) are selective for the direction and speed of motion of visual stimuli (e.g. Hubel and Wiesel, 1962, 1965, 1968; Pettigrew, Nikara and Bishop, 1968; Zeki, 1974; Movshon, 1975; Spear and Baumann, 1975; Hammond, 1978). A distinction emerges from our analysis that had not been carefully studied between what we term "component" and "pattern" direction selectivity. As we have discussed, one may consider the motion of an object in two ways: as the motion of the various 1-D components of the object, or as the motion of the object as a whole. Now, cortical orientation selectivity is typically conceived as part of a process by which cortical neurons break up an image into 1-D constituents. It is natural to ask whether motion signals are similarly parsed, especially since it is from the ambiguities inherent in the motion of isolated 1-D features that our ideas arise . Our results suggest that striate cortical neurons in cats and monkeys are selective only for 1-D motion, and cannot distinguish 2-D motion. We have, however, encountered neurons that appear to be sensitive to 2-D motion in MT, an extrastriate area of the monkey's visual cortex.

Pattern and component directional selectivity

In the course of our experiments on directional processing we have developed definitions and a simple test that allows us to distinguish two types of direction selectivity. We have applied this to the responses of neurons in V1 of both cat and macaque (Movshon, Davis and Adelson, 1980), to neurons in the lateral suprasylvian visual cortex (LS) and superior colliculus of the cat (Gizzi *et al.*, 1981; Gizzi, 1983), and to neurons in MT of the macaque (Gizzi *et al.*, 1983). *Component directional selectivity* corresponds to what previous workers would have termed orientation selectivity with directional selectivity. Neurons showing component direction selectivity respond to the direction of motion of single oriented (1-D) contours presented in isolation, and to the direction of motion of those contours when they form part of a more complex 2-D pattern. *Pattern direction selectivity* corresponds to what previous workers have termed "pure" direction selectivity. Neurons showing pattern direction selectivity, like component neurons, respond to the direction of motion of isolated 1-D contours. When those contours are embedded in a more complex 2-D pattern, however, these neurons respond not to the motion of the contours, but to the motion of the pattern as a whole.

These two kinds of direction selectivity have been of concern for some time in visual electrophysiology, but no satisfactory test has been devised to distinguish them. Previous approaches have relied on two tests designed to establish orientation selectivity; if these tests fail, the neuron is — by default — considered to be "pure" or (in our terms) pattern direction selective (Barlow and Pettigrew, 1971; Zeki, 1974; Spear and Baumann, 1975). First, neurons have been considered orientation selective when they respond to stationary flashed line or grating stimuli in an orientation selective manner. Second, they have been considered orientation selective if their specificity for the direction of motion of a line is more refined than their selectivity for the direction of motion of a spot (Henry *et al.*, 1974). The first of these tests seems to us unimpeachable; its problem lies in the fact that many of the neurons of interest respond poorly to any stationary stimuli. It can also give misleading results if the stimulus is improperly placed in the receptive field. The second test is unreliable for two reasons. Since small spots and random textures contain energy at all orientations, the presence of strong inhibition in the orientation domain (e.g. Blakemore and Tobin, 1972; Nelson and Frost, 1978) can have the effect of making direction selectivity for spots or texture fields as tight as, or tighter than for bars, even in an orientation selective neuron. Moreover, the test specifies no reasonable decision rule — how much difference between the two curves is tolerable before the test fails? And both tests suffer from the problem that they are negative tests when applied to pattern direction selectivity: when a neuron *fails* to show some property it is pattern direction selective, and no positive attribute is associated with this classification.

Our test to distinguish between the two types of direction selectivity relies on the difference in response between moving grating and plaid stimuli. It does not require that the neuron respond to stationary patterns, and it has the further advantage that the stimuli to be compared are identical in spatial extent and physical contrast. It is not applicable to neurons that fail to respond to gratings, but we have found very few neurons in cat or monkey V1, in the cat's lateral suprasylvian visual cortex, or in macaque MT, which will not respond reliably to gratings confined to the central activating region of the receptive field.

Response predictions. Figure 9 illustrates the response of a hypothetical direction selective neuron. In each plot the direction of motion of the stimulus is given by the angle, and the response of the cell to that direction is given by the distance of the point from the origin. The left-hand plot reveals that this "neuron" responded best to gratings moving directly rightward and did not respond to leftward motion. The direction tuning curve for a single grating therefore has a single peak corresponding to the best direction of motion. When one component of a 90 degree plaid (one whose components are oriented at 90 degrees to one another) is within the direction bandwidth of the neuron, the other component will be outside the acceptable range. If the neuron is component direction selective, the predicted direction tuning curve to a plaid then, is the sum of the responses to the two components presented separately. Before the

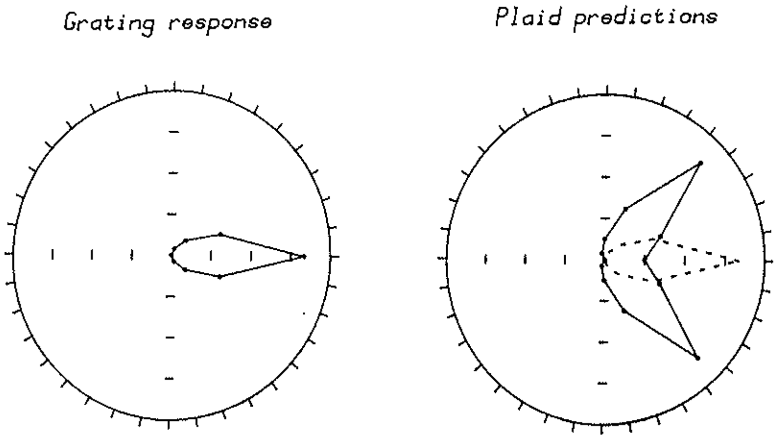

FIG. 9. Hypothetical data illustrating component and pattern directional selectivity. See text for details.

responses are added, however, any spontaneous firing rate (here zero) is subtracted from each. After the two responses are added, the spontaneous rate is added back in. In the right-hand plot, responses are plotted as a function of the direction of motion of a plaid. When the plaid is moving in the optimal direction (as determined with a single grating), the components will be oriented 45 degrees to either side of the optimum (see Fig. 4). Thus the response peaks are also shifted to either side by 45 degrees, and the predicted tuning curve for the plaid is a bi-lobed curve whose peaks straddle the single peak derived from the single grating experiment. This prediction is shown by solid lines in the right-hand plot. The prediction for pattern direction selectivity is even simpler: the neuron's tuning curves for the two stimuli should be similar since their directions of motion are the same. The predicted tuning curve is thus simply the curve derived from the single grating experiment, and is shown by dashed lines in the right-hand plot.

The basis of this test is to dissociate the oriented components of a pattern from the direction in which they move: a single grating always moves at right angles to its orientation, but the plaids move at a different angle to their oriented components (45 deg in the case shown in Fig. 9). The two predictions for the different types of direction selectivity are radically different and one may simply see whether the neuron's response depends on the overall direction of motion, or on the orientation of the moving components. To compare the goodness of fit of the component and pattern predictions, the actual response was correlated with each of the predictions. Since the two predictions are not necessarily uncorrelated themselves, a comparison of the simple correlations might be misleading. In order to make the two predictions independent, we used a partial correlation of the form:

$$R_p = (r_p - r_c\, r_{pc}) \;/\; [(1 - r_p)\;(1 - r_c)]^{1/2}$$

where R_p is the partial correlation for the pattern prediction, r_c is the correlation of the data with the component prediction, r_p is the correlation of the data with the pattern prediction, and r_{pc} is the correlation of the two predictions. A similar partial correlation for the component prediction was calculated by exchanging r_c and r_p. These two correlation values may be used to assign each neuron to a "pattern" or "component" class, or to some intermediate grouping.

At this point the close similarity between linearity of spatial filtering and component direction selectivity should be evident. A neuron that behaves as a linear spatial filter and that possesses orientation selectivity must, in our terms, be component direction selective; our analysis of component direction selectivity here is thus similar to that used by De Valois *et al.* (1979) in their studies of the responses of striate neurons to gratings and checkerboards. Pattern directional selectivity would, however, involve important nonlinearities.

Directional selectivity in visual cortical neurons

Figure 10 shows typical responses of a component direction selective neuron, in this case a neuron of the "special complex" type (Gilbert, 1977) recorded from area 17 of a cat. The left-hand polar diagram shows the neuron's response to single grating stimuli as a function of direction of motion; the inner circle represents the spontaneous firing level in the absence of a stimulus. The neuron had a marked preference for gratings moving downward and slightly to the right. On the right, the filled symbols show the neuron's response to 90 deg plaids. Two preferred directions are evident, symmetrically displaced by 45 deg from the directional optimal for single gratings. Note that the neuron did not give any response to a plaid that moved downward and to the right, in the direction optimal for single gratings. The dashed lines in the right-hand plot show the component direction selective prediction for the neuron's response, and it is

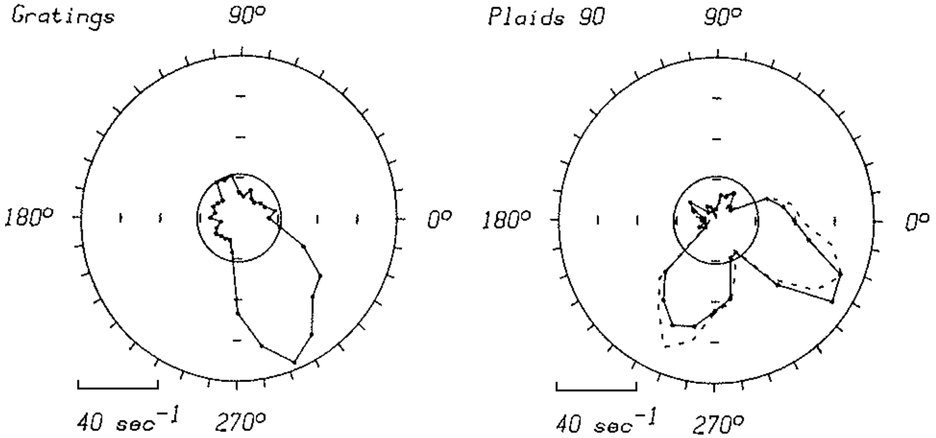

FIG. 10. Directional selectivity of a special complex cell recorded in area 17 of a cat. The spatial frequency was 1.2 c/deg, and the drift rate was 4 Hz. On the left is shown the neuron's tuning for the direction of motion of single gratings, and on the right is shown the neuron's response to moving 90 deg plaids. The dashed curve on the right shows the expected response of a component direction selective neuron. The inner circles in each plot show the neuron's maintained discharge level. For this cell the component correlation was 0.976, and the pattern correlation was − 0.076 (n = 32).

evident that this describes the data very well. In this case, the component correlation value was 0.976 (n = 32), and the pattern correlation value was − 0.076. Behavior of this sort was typical of all neurons we studied in area 17 of the cat and in the primary visual cortex of the monkey; this behavior is similar to that observed by De Valois *et al.* (1979) in macaque striate neurons. Cells of the simple type were often sensitive to the relative phase of the two gratings, and variations in phase tended to make one or the other peak enlarge or disappear. No manipulation of phase, however, ever produced pattern direction selective behavior in these neurons.

It is well known that contours of non-optimal orientation may have an inhibitory influence on cortical neurons (Blakemore and Tobin, 1972; Nelson and Frost, 1978). An inhibitory influence of this sort is evident in the single-grating tuning data on the left in Fig. 10, but is visible only because of the relatively high maintained discharge shown by this cell (about 21 impulses/sec). Most cortical neurons have much less spontaneous discharge, and consequently reveal inhibitory influences incompletely; it is therefore not surprising that the magnitude of the responses we observed to plaids tended to be somewhat less than those predicted from simple superposition. The magnitude of the inhibitory effect varied widely, but on average the response to plaids was between 25% and 40% less than predicted. This inhibition was what originally motivated us to use the correlation measure described earlier, since this is insensitive to deviations in response magnitude from the predictions.

We have also studied the behavior of a number of neurons in the lateral suprasylvian cortex of the cat, an area thought to be involved in processing motion information in that species (Spear and Baumann, 1975; Gizzi *et al.*, 1981). Almost all neurons in LS, like those in V1, showed clear component direction selectivity, and none gave a convincingly pattern direction selective response.

In order to examine the distribution of behavior of neurons in different areas, we prepared scatter diagrams in which the values of the pattern and component correlation coefficients were plotted against one another. Figure 11A illustrates the significance of various regions of these plots. The region marked "component" is a zone in which the component correlation coefficient significantly exceeds either zero or the pattern correlation coefficient, whichever is larger. The region marked "pattern" similarly marks neurons that were unambiguously pattern direction selective. The region marked "unclassed" represents cases in which both the pattern and component correlations significantly exceeded zero, but did not differ significantly from one another, or cases in which neither correlation coefficient differed significantly from zero.

Figure 11B shows a scatter plot of data in this space for 69 neurons recorded from cat and monkey V1. It is clear that these cluster around a component correlation value of 1 and a pattern correlation value of zero. While a few neurons lie in the two indeterminate regions of the plot, no clearly pattern direction selective cases exist. Figure 11C shows a similar plot for data from 61 cells recorded in the cat's LS cortex. Here the data are slightly more scattered, but the result is again unambiguous: most neurons lie in the component zone, and only one is (barely) within the pattern zone. It thus appears that neurons in these areas are capable of signalling only the motion of 1-D components, and cannot unambiguously define the motion of whole patterns. Our search for pattern direction selective neurons then turned to MT, an extrastriate area in the macaque's cortex thought to be involved in analyzing motion information.

MT is the natural place to study motion sensitivity in primates. In macaque, MT is a heavily myelinated area on the posterior bank of the superior temporal sulcus. It is one of three cortical areas to receive a

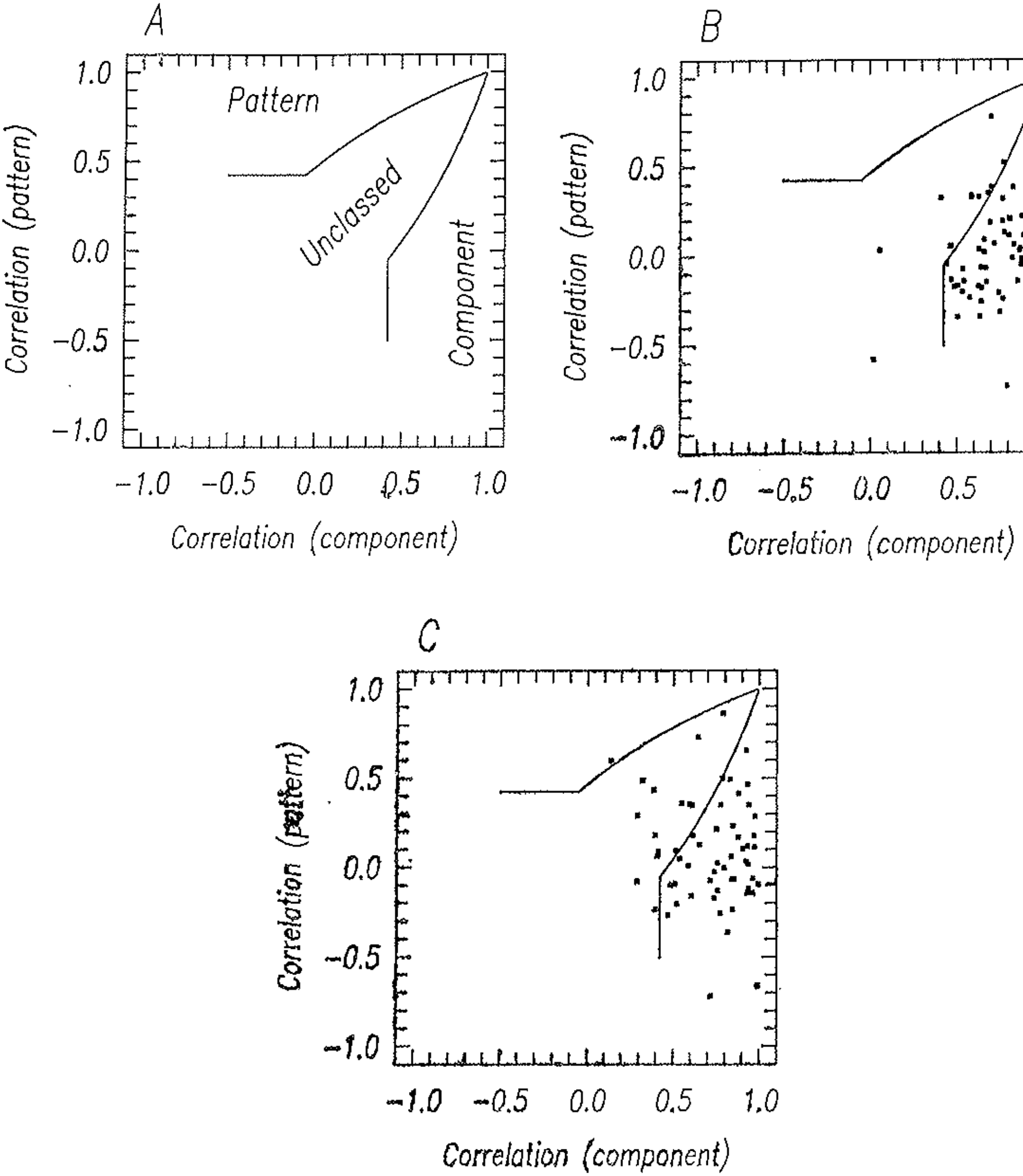

FIG. 11. Scatter diagrams of the directional selectivity of neurons in the visual cortex. A. The space within which the data lie (see text for details). B. Diagram of the behavior of 69 cells from area 17 of cats and monkeys. C. Diagram of the behavior of 61 cells from the lateral suprasylvian visual cortex of cats (Gizzi *et al.* 1981).

major projection from striate cortex, the others being V2 and V3 (Zeki, 1978a; Maunsell and Van Essen, 1983). The physiological properties of neurons in macaque MT were first described by Duhner and Zeki (1971; Zeki, 1974), who reported that the area contained a high proportion of directionally selective neurons. This observation is in marked contrast to the very low frequency of directional selectivity in V2 and V3 (Zeki, 1978b). This area was renamed MT by Van Essen (1979) because of its clear homology with the middle temporal area in the owl monkey (Allman and Kaas, 1971; Zeki, 1980; Baker *et al.*, 1981). The areas receive similar projections and contain neurons with similar receptive field properties. Van Essen *et al.* (1981) reported that some cells in macaque MT showed orientation selectivity when tested with stationary stimuli, as has been reported for the majority of cells in owl monkey MT (Baker *et al.*, 1981). Nevertheless, as orientation selectivity distinguishes V1, so direction selectivity distinguishes MT. It is not certain whether this reflects the selectivity of that afferent input or whether direction selectivity is a result of the processing within MT. Only about a quarter of the neurons in macaque V1 are directionally selective (Hubel and Wiesel, 1968; De Valois *et al.*, 1982); in V2, the proportion may be even lower (Baizer *et al.*, 1977; Zeki, 1978b). These areas provide the major intracortical input to MT. On the other hand Dow (1974) reported that many neurons in layer IVb of V1 are directionally selective — the projection from striate cortex to MT arises from this layer and layer VI (Lund *et al.*, 1976; Maunsell and Van Essen, 1983). There is also input (which may be directionally selective) to MT from the inferior pulvinar (Trojanowski and Jacobsen, 1976; Benevento and Rezak, 1976).

Figure 12 shows data, in a format similar to that used in Fig. 10, for two neurons recorded from MT. The neuron in Fig. 12A preferred upward movement of single gratings; like its component direction selective counterpart in V1 (Fig. 10), this preference was translated into a dual preference for two directions 45 deg apart when it was tested with 90 deg plaids. As comparison of the data with the dashed lines in the right-hand plot of Fig. 12A reveals, the component direction selective prediction provided a very good description of this behavior. About 40% of the cells we studied in MT were clearly component direction selective. Figure 12B shows data from a neuron in MT whose behavior was rather different. This neuron preferred downward and rightward movement of grating stimuli, and maintained this preference when tested with 135 deg plaids. The actual response to plaids differed very dramatically from the com-

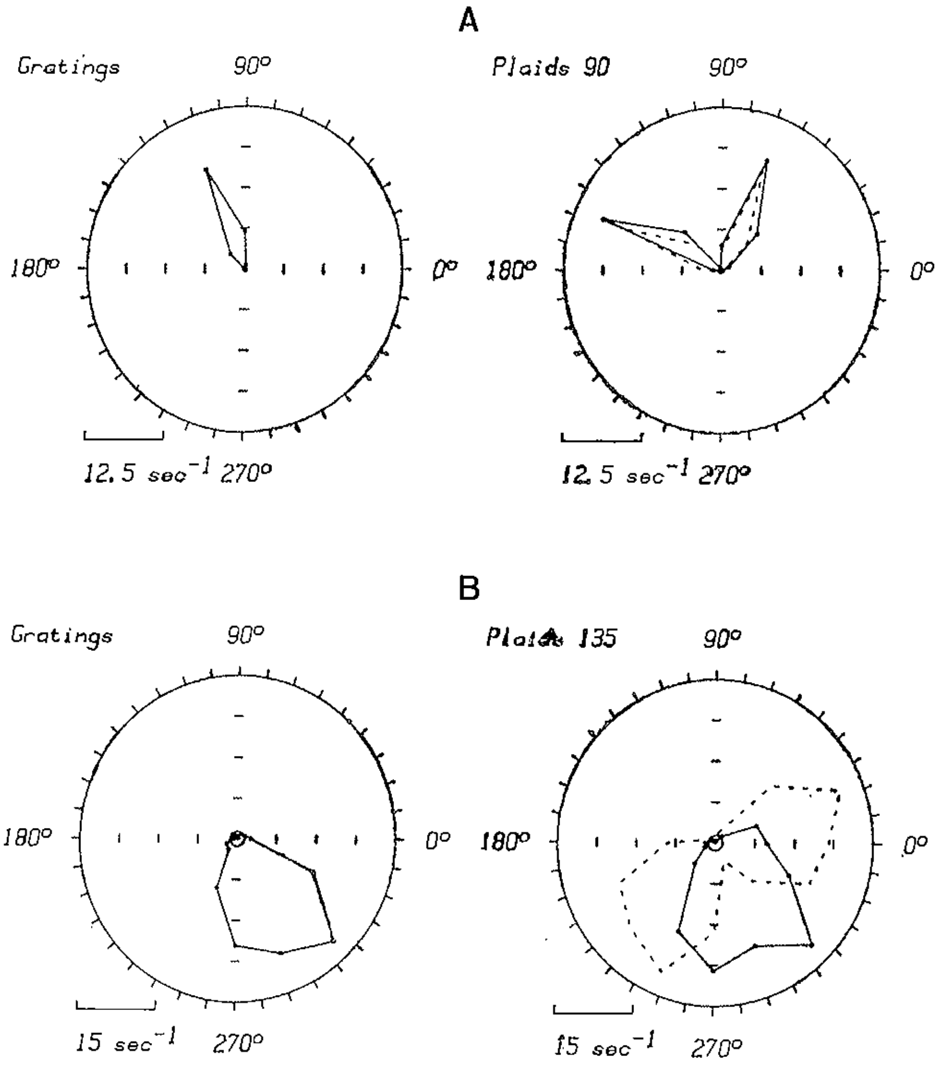

FIG. 12. Directional selectivity of two neurons from MT. The format for each figure is the same as in Fig. 10. A. Spatial frequency 3.6 c/deg, drift rate 4 Hz, component correlation 0.991, pattern correlation − 0.092 (n = 16). B. Spatial frequency 2.7 c/deg, drift rate 4 Hz, component correlation 0.349, pattern correlation 0.940 (n = 16).

ponent direction selective prediction. About 25% of the neurons we studied in MT behaved in this way. This apparently simple behavior must involve some remarkable neural circuitry. Consider that the most effective plaid stimulus was composed of two gratings which, in isolation, had directions 67.5 deg different from the optimum; neither direction alone elicited a significant response. Thus the most effective plaid pattern was composed of two gratings which were by themselves ineffective; conversely, when the most effective grating stimulus was combined with another to form a plaid, the response was poor. These features of the tuning characteristics suggest that a combination of suppressive and facilitatory processes must be involved in the generation of pattern direction selectivity. We have some evidence from further experiments that this is the case, and that some neural operation similar to the "intersection of constraints" that we described in the introduction is in fact performed by pattern direction selective neurons in MT.

Figure 13 shows a scatter diagram of the directional behavior of 108 neurons from MT, in the format laid out in Fig. 11A. The data here were derived from experiments using 135 deg plaids. Most neurons in MT are rather more broadly tuned for direction than their counterparts in

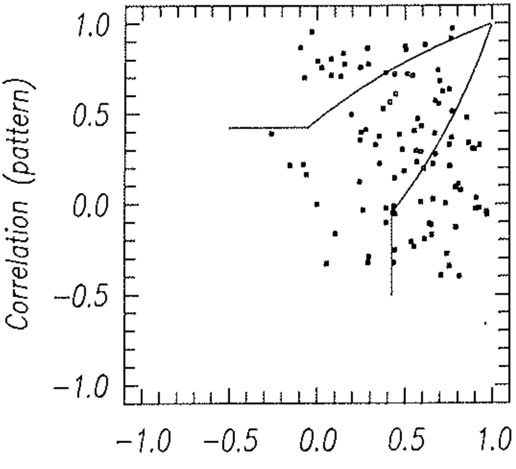

FIG. 13. A scatter diagram of the directional selectivity of 108 neurons in MT, tested with 135 deg plaids. The format is the same as in Fig. 11.

V1, and in consequence the distinction between the component and pattern predictions cannot often be made very clearly with 90 deg plaids. In contrast to the data from V1 and from cat LS shown in Fig. 11, the distribution of values for MT cells shown here is very broad. About 25% of the cells fall into the pattern category, and 40% into the component category. The significant population of cells that falls in the "unclassed" region deserves comment. Most of these (about 30% of the total) are in the upper right corner of the plot, where both correlation coefficients are different from zero, but do not differ from each other. These cells generally had very broad tuning curves, so that even using 135 deg plaids the variability of the response made statistical distinction between the accuracy of the two predictions difficult. It would thus be a mistake to conclude that these cells were of some "intermediate" type. Rather, the particular standard test conditions and statistics used were insufficiently sensitive to classify them. The remainder of the unclassed cells (about 10% of the total) gave plaid responses that did not correlate well with either prediction. In most of these cases, the response to single gratings was rather weak and variable, resulting in an unsatisfactory pair of predicted tuning curves; in a number of these cases, the response to plaids was brisk and reliable.

The continuity of the distribution in Fig. 13 does not immediately suggest the existence of two discrete cell classes in MT. We do, however, have some evidence that the laminar distribution of the component and pattern cells may differ, with the pattern cells primarily encountered in layers II, III and V, and the component cells more often being in layers IV and VI; thus two genuine classes of cell may exist in MT. Regardless of the resolution of this issue, it is clear that information about both types of motion is available in the signals relayed by neurons in MT, including the pattern direction selective type that we have not encountered elsewhere.

DISCUSSION

Our psychophysical studies revealed the existence of two stages in the processing of motion information in the human visual system. The first stage appears to analyze the motion of 1-D patterns, and to be responsible for the detection of simple moving patterns. The second stage seems to be concerned with establishing the motion of complex patterns on the basis of information relayed from the first stage. In our experiments, the action of this stage is most clearly seen in the various coherence phenomena that we have described. These two stages of analysis appear to have natural analogs in our electrophysiological results. The properties of component direction selective neurons in V1 and MT seem to correspond to the first stage, while the pattern direction selective neurons in MT seem to correspond to the second stage.

This parallel between psychophysical and electrophysiological data is gratifying, but it is important to examine in a little more detail the basis for the parallels we draw. Our arguments in both the psychophysical and electrophysiological domain rest on evidence concerning the way in which neural mechanisms represent information. Our knowledge of this representation derives from an examination of tuning characteristics, established with stimuli designed to reveal particular properties of the system we studied. One may ask whether it is legitimate to conclude that the two putative stages genuinely differ simply because their tuning characteristics differ. This issue has been a disputatious one in electrophysiology in recent years, largely as a result of a debate concerning the kinds of signals relayed by striate cortical neurons. On the one hand, traditional descriptions of striate neurons (e.g. Hubel and Wiesel, 1962) have emphasized their sensitivity to contours such as lines and edges, and given rise to the idea that these neurons function as edge-detectors. More recent studies (e.g. Maffei and Fiorentini, 1973; De Valois *et al.*, 1979) have characterized striate neuron responses using sinusoidal gratings, and emphasized their sensitivity to the spatial frequency of these patterns. With the exception of some specific nonlinear models (e.g. Marr, 1982), this debate has centered around matters of interpretation rather than of testable fact. Most available data suggests that striate cortical neurons function as approximately linear spatial filters, and that their responses to aperiodic patterns and to sinusoidal gratings can be simply related to one another (e.g. Movshon *et al.*, 1978). Thus the various ways in which striate neurons have been described are probably formally identical, producing an argument about semantics rather than substance.

Our results and claims differ from these in an important respect. Our notion of pattern direction selectivity involves specific nonlinear properties in computing the "intersection of constraints"; the results we have obtained from pattern direction selective neurons in MT are incompatible with a linear model. Now, given the specific nonlinearity present in these neurons, it is natural to argue that they are different in an important way from neurons in the other cortical areas we have studied, whose directional selectivity may be more simply understood. There is also the matter of motion ambiguity with which we began this paper. Our results on striate neurons demonstrate that they provide ambiguous signals about the motion of complex objects. This ambiguity may be resolved by a specific kind of neural computation, and our results from MT show that this computation may be performed there. Thus the signals from pattern direction selective neurons contain an important kind of information not available from the output of any single striate neuron. It is this particular synthesis of information relayed from V1 to MT to which we attribute the greatest significance.

Thus we may plausibly argue from the way in which information is represented in V1 and MT neurons that the two stages of motion processing are present. We cannot, of course, prove that assertion merely with psychophysical or electrophysiological data, for these only allow the development of reasonable hypotheses. Proof of these must await combined psychophysical and electrophysiological study of the consequences of inactivating MT for the perception of moving visual patterns.

ACKNOWLEDGEMENTS

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CORTICAL SYSTEMS FOR VISUAL PATTERN DISCRIMINATION IN THE CAT AS ANALYZED WITH THE LESION METHOD

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In this paper we shall concern ourselves with some aspects of the problem of the identification of the brain structures necessary for the recognition of visual patterns and forms in the cat. Most of the data we will discuss come from ablation studies, i.e. from studies in which performance is tested before and after selective cortical or subcortical lesions. Inferences about the biological significance of cortical areas or subcortical centers based exclusively on the effects of the removal of such areas or centers are open to several methodological criticisms (see e.g. Dean, 1982). It is often suggested that the continuous improvement of neuroanatomical, neurophysiological and neurochemical techniques, allowing a direct analysis of structures and mechanisms of the working brain, will eventually lead to the abandonment of the lesion method. We have argued elsewhere (see Berlucchi and Sprague, 1981) that direct anatomo-functional investigations of the nervous system and lesion studies are complementary rather than alternative, and that, when planned and interpreted in accordance with anatomical and physiological knowledge, behavioral analyses of the effects of cortical or subcortical lesions still provide the tool of choice for constructing biologically plausible and meaningful theories of cortical and cerebral organization.

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Assumptions about the role of given brain areas in the control of behavior derived from anatomical and/or physiological information, however appealing and stimulating, are often vague and indirect, and must be substantiated by different kinds of evidence, such as, for example, the effects of the selective ablation of the areas in question. While it is reasonable to expect that a part of the brain containing neurons uniquely responsive to a certain stimulus is indispensable for the behavioral response of the entire organism to such stimulus, it is not unusual that this behavioral response survives the removal of that part of the brain. Similarly, a behavioral ability which on anatomical grounds alone appears to require a flow of information along a unique route in the brain may not be lost after surgical interruption of this route. In these instances the lack of the expected effects after the lesion forces one to consider remaining parts of the brain as possible substrates for the spared behavior, thus redirecting the anatomical, physiological and behavioral localization of the function under examination. This consideration has consistently guided our ablation studies on the cat visual system, where we have systematically assessed the effects of selective lesions against the available anatomical and physiological evidence on the centers and pathways affected by such lesions.

The primary visual cortex and pattern vision in the cat. The primary visual cortex (also known as area 17 or striate cortex) is traditionally regarded as the brain region where visual information transmitted from the retinae through the lateral geniculate nuclei is first submitted to cortical processing. Anatomical, physiological and behavioral work in the monkey has led to the concept that the striate cortex is by far the most important source of visual information to the many other areas of the cortex which have been shown to subserve vision. A pathway interconnecting the striate, prestriate and inferior temporal areas is thought to be involved in the visual identification of objects and, more generally, in form and color analysis. Another pathway running from striate cortex to prestriate, middle temporal and inferior parietal cortex is thought to mediate visual location of objects and motion analysis (Van Essen and Maunsell, 1983; Mishkin, Ungerleider and Macko, 1983).

The hierarchical and serial organization of these areas is still incompletely understood, but it seems clear that in all cases the initial step in the analysis of visual information in the cortex is assumed to take place in area 17. A similar serial and hierarchical model for cortical analysis of visual information, beginning in area 17, has been repeatedly suggested for the cat, first and foremost by the work of Hubel and Wiesel on the functional architecture of visual cortex (1962, 1965), and second by a host of investigations aimed at establishing correlations between the physiological properties of neurons in area 17 and various aspects of visual perception under normal and abnormal conditions of visual experience (for reviews see, e.g., Barlow, 1972; Movshon and Van Sluyters, 1981; Sherman and Spear, 1982).

This serial model has been questioned on several grounds. Firstly, it has been shown that the retinal outputs are organized in at least three different channels, corresponding to the so-called X, Y and W ganglion cell types. These cell types differ in size (and consequently in conduction velocity) as well as in response properties. Among the large-sized Y cells and the medium-sized X cells the former show a better temporal resolution of the visual stimulus while the latter show a better spatial resolution. The small-sized W cells form an heterogeneous population with poor contrast sensitivity, poor spatial and temporal resolution, and, in some cases, motion sensitivity (see Stone, Dreher and Leventhal, 1979; Sherman, 1984). Secondly, anatomical investigations on the cat (as well as on a variety of other species) have demonstrated a number of pathways which run in parallel to the pathway projecting from lateral geniculate nucleus to striate cortex, thus providing alternate avenues by which visual information can reach the cerebral cortex. These parallel paths are directed both to the striate cortex and to several extrastriate cortical areas, with a considerable overlap at their cortical targets, via relays in the superior colliculus, pretectum and parts of the pulvinar complex, as well as from the ventral laminae and medial interlaminar nucleus of the lateral geniculate (see review in Sprague, Hughes and Berlucchi, 1981).

An important property of these parallel pathways is that geniculate cells receiving an X input from the retina project exclusively to area 17, whereas geniculate and extrageniculate projections conveying Y and W inputs to the cortex terminate in virtually all visual cortical areas. Thus, area 17 is presumably indispensable for passing information transmitted along the X channel from the retina on to other cortical areas, but otherwise the "parallel" arrangement of the visual thalamocortical projections in several paths terminating in extrastriate as well as striate cortex allows a considerable expanse of the cerebral cortex beyond area 17 to receive visual information independent of the latter area.

Effects of removing area 17 on visual discrimination in cats. Confirming and extending previous work by Spear and Braun (1969), Doty (1971) and Winans (1971), we (Sprague, Levy, DiBerardino and Berlucchi, 1977) found that after extensive lesions of areas 17 and 18 cats showed normal learning curves on various visual pattern discriminations, thus suggesting that these tasks could be mediated by spared visual systems. This suggestion was confirmed by the presence of conspicuous learning deficits in cats with large lesions placed in cortical areas outside areas 17 and 18 (areas 19, 20, 21, LSA and 7).

In cats with these lesions the ability to discriminate forms on the basis of orientation or shape was degraded, similar to cats with an intact cortex but with extensive lesions of the pretectum and superior colliculus (Berlucchi, Sprague, Levy and DiBerardino, 1972; Tunkl and Berkley, 1977). On these grounds we concluded that the cortical substrates for perceiving and discriminating simple, large planimetric patterns and forms lie outside areas 17 and 18, presumably in those parts of the suprasylvian gyri and sulci which are the principal targets of the extrageniculate tecto-thalamo-cortical visual pathways. This conclusion was hard to accept from the physiological viewpoint, given that area 17 is the sole recipient of the information transmitted by the X ganglion cell system of the retina, possessing the highest spatial resolution. Further, receptive fields of neurons in areas 17 and 18 are tightly tuned for orientation (Hubel and Wiesel, 1962; Watkins and Berkley, 1974), and the visuotopic map in area 17 is the most detailed and precise of all visual areas so far studied (Tusa, Palmer and Rosenquist, 1978).

All these physiological characteristics point to area 17 alone or in conjunction with area 18 as the most likely substrate for the neural encoding of visual forms, and the finding of a virtually normal capacity for form discriminations of cats deprived of these areas is obviously counter-intuitive. This finding, however, may still be compatible with the hypothesis that area 17 plays a primary role in pattern vision in the intact brain if one postulates that following ablation of the striate cortex there occurs a reorganization of the remaining visual systems, so that receptive field properties of neurons and visuotopic maps in these systems acquire properties similar to those normally found in the ablated area. Yet the available evidence not only indicates that after cortical removals or inactivations including or extending beyond area 17 there is no reorganization of receptive field properties in other visual cortical areas, but also shows that some of the normal properties of neurons in these extrastriate areas, such as directional selectivity or even responsiveness to visual stimuli, may be lost as a result of the removal of area 17 (Donaldson and Nash, 1975; Spear and Baumann, 1979b).

These pejorative changes, however, obviously do not interfere with the capacity of destriated cats to learn visual pattern discrimination, and even more strikingly, to retain pattern discriminations learned before the cortical ablation. This was shown in a study aimed at testing postoperative retention of a flux and various pattern discriminations in 4 groups of cats with different cortical lesions (Sprague, Antonini and Berlucchi, in preparation; see also Berlucchi and Sprague, 1981). There were a) four cats with a bilateral 17-18 lesion; b) four cats with a bilateral 17, 18, 19 lesion; c) five cats with a bilateral suprasylvian lesion (including areas 7, 21a and b and AMLS and PMLS of Palmer, Rosenquist and Tusa, 1978), uncomplicated by involvement of the geniculate projections to areas 17 and 18; d) three cats with a similar bilateral suprasylvian lesion complicated by various degrees of undercutting of areas 17 and 18. Preoperatively all cats learned a flux discrimination and seven form discriminations on food reinforcement. They were retested as normals for retention on all problems, and then were submitted to cortical ablation.

Two weeks after the operation, with no intervening experience with the discrimination apparatus and stimuli, a postoperative retention test using a different order of presentation of the stimuli was run again on all problems and the performance compared with that on the preoperative retention test. In brief, we found that a) cats with 17-18 lesions behaved as though in spite of their cortical lesion they could recognize the discriminative stimuli as efficiently as before the lesion, with no need for retraining; b) cats with 17-18-19 lesions showed a substantial postoperative loss of all discriminations, and relearning of the most complex discrimination was strongly impaired or impossible within the allotted number of 200 trials (which corresponded to the maximum number of trials required during original learning for reaching a level of performance corresponding to the retention criterion); c) the group with uncomplicated suprasylvian lesions showed a substantial impairment of retention on all problems, but relearning was more efficient than in the previous group; d) the group with complicated suprasylvian lesions suffered from a severe disruption of discriminative capacities both in retention and in relearning, thus exhibiting the most severe deficits of all groups.

The fact that cats with 17-18 lesions could immediately recognize the discriminative stimuli without any postoperative retraining rules out the possibility that their successful performance was caused by reorganization and readaptation processes, given the brevity of the time interval between the operation and the retention test, and the absence of any practice with the discriminanda during such postoperative period. The absence of area 17 and of the X input to the cortex was obviously not incompatible with a good capacity for form vision, a fact which leads one to attribute this capacity to the remaining visual systems receiving Y and W inputs from the retinae. That these extrastriate systems were indeed responsible for the good retention of destriated cats is shown by the presence of conspicuous retention deficits after lesions involving area 19 in addition to areas 17 and 18 (group b), or the suprasylvian visual areas (group c).

The inability of cats with lesions disturbing both striate and extrastriate cortical areas to perform visual discriminations proves that visual discrimination tasks such as those used in our experiments do require the presence of cortical substrates, although the demonstration of "subcortical vision" might have become possible after a more prolonged retraining (see e.g. Spear and Baumann, 1979a). It is worth emphasizing that the high-level retention of form discrimination in our cats with 17-18 lesions was not due to the employment of discriminative strategies based on the utilization of partial flux cues (see e.g. Winans, 1971) rather than total stimulus configuration, since these cats performed successfully on generalization and figure-ground reversal problems which can only be solved by overall shape recognition. In addition, Hughes (1982) and Hughes and Sprague (unpublished) have convincingly demonstrated that cats with 17-18 lesions are capable of figural synthesis, i.e. of the ability to organize various features within a simple pattern into a unified percept, thus reinforcing the hypothesis that complex form vision can occur in cats deprived of the striate cortex and of the X input to other cortical areas.

Visual deficits following removal of area 17 in the cat. The above description should not misguide the reader into the belief that destriate cats can see normally. Berkley and Sprague (1979) found that grating and orientation acuity is impaired in cats with 17-18 lesions, although to a moderate degree, while the ability to make judgments based on contour alignment (vernier offset) is severely degraded or lost. Coupled with the observation that no such acuity deficits follow extrastriate damage, this finding suggests the concept that area 17, and by inference the X input from retina to cortex, contribute to shape recognition chiefly by increasing the resolution capability of the system, rather than by providing the essential machinery for the encoding of form. Berkley and Bush (1983) have described additional evidence showing that vernier and orientation acuity rely on separate intracortical processes in areas 17 and 18. The findings of Berkley and Sprague (1979) have been confirmed and extended by Lehmkuhle, Kratz and Sherman (1982), who measured spatial contrast sensitivity to sine-wave gratings in cats with bilateral 17-18 lesions. The cortical lesion had virtually no qualitative effect on the visual capacities, except for a moderate reduction of contrast sensitivity at middle and higher spatial frequencies. The ability to resolve the low-frequency gratings was apparently normal on the first postoperative test (2-4 weeks after the lesion), thus demonstrating a perfect retention of pattern vision (except for stimuli requiring the highest acuity) in spite of the 17-18 lesion, as shown by Berlucchi and Sprague (1981) and by Hughes (1982).

Striking visual discrimination deficits have been observed in cats with bilateral 17-18 lesions by H. Heitländer and K. Krüger (unpublished). The experiments were performed at the Institut für Biologie of the University of Mainz, West-Germany, on cats operated by one of us (G.B.). These cats showed, as expected, a normal capacity for discriminating geometric figures presented against a clear background, provided the size of the figures did not require high-acuity abilities. However, if the same patterns were partially "masked" by imposing a random visual noise upon the background, the pattern-discrimination ability of destriated cats was drastically impaired compared to that of normal cats. More specifically, although normal and destriated cats were equally capable of discriminating such patterns when presented against a noiseless background, the addition of a random visual noise of varying intensity to the background allowed a clear differentiation between the two groups. Destriated cats were incapable of discriminating the same patterns at signal-to-noise ratios that in normal cats were still compatible with a perfect discriminative performance.

Such deficits, which were not seen after a bilateral lesion of the superior colliculus, or after a bilateral removal of area 19, may be taken to imply that areas 17 and 18 are important for "extracting" a visual figure or object from a complex textured background, in agreement with previous work on "hidden figures" and visual cortex lesions (see Cornwell, Overman and Ross, 1980). Hughes and Sprague (unpublished) have reexamined this conclusion using simple global patterns composed of oriented rows of dots. The discrimination of these dot patterns is not based on analysis of the local elements in the pattern but rather on their spatial distribution, a function called "figural synthesis". Once a set of such patterns was mastered, these rectilinear dot patterns were embedded in visual noise consisting of additional dots positioned randomly throughout the screen. Under these conditions, removal of areas 17-18 resulted in only a modest impairment of the cat's ability to perceive a global pattern structure in the presence of large amounts of random noise.

Future avenues for research. The above evidence poses a number of problems which provide stimuli for further investigations. The *first* problem is that of the specification of the various residual pathways which mediate visual performance after removal of areas 17 and 18. Although it is clear that in these conditions vision must depend exclusively on the Y and W inputs from the retina, until recently the respective functional roles of these two input channels for form perception have been ignored. In addition, although we are obviously wary of underestimating the role of the pretectum and superior colliculus in higher visual functions (Berlucchi *et al.*, 1972), we feel that such higher functions can hardly occur without a cortical substrate. The analysis of the division of labor between striate and extrastriate cortices is just beginning, and important issues, such as the relative function of the geniculo-cortical and tecto-pulvinar-cortical pathways to extrastriate cortex, remain to be clarified. Electrophysiological work indicating a near-to-normal organization of receptive fields of neurons in area 19 of cats submitted to a cooling inactivation of areas 17 and 18 (Kimura, Shiaa, Tanaka and Toyama, 1980) must be related to behavioral work on the importance of this area for visually guided behavior after removal of areas 17 and 18. It will be recalled that in our study perfect retention of preoperatively learned discrimination was seen in cats with 17-18 lesions, but no retention was present in cats with an additional 19 lesion. On the other hand, we have not found specific deficits after a bilateral removal of area 19 alone, either in retention experiments or in the studies on the ability to extract figures from noise (Krüger, unpublished).

The *second* problem is that of the correlations between the physiological properties of single neurons in various parts of the visual system and experimentally induced alterations of visual perception. In a previous paper (Berlucchi and Sprague, 1981) we pointed out several inconsistencies in studies trying to establish parallels between physiological changes in area 17 and visual deficits in strabismic and visually deprived cats. Although the conclusion of many of these papers was that the physiological alterations in area 17 were parallel to, and could account for, the visual deficits, particularly those in pattern vision, we felt that on the contrary the evidence from these studies was congruent with that from our ablation experiments which indicated that visual pattern discrimination in the cat is mainly performed in extrastriate systems. Our conviction is now shared by Lehmkuhle *et al.* (1982), who found that the amblyopia produced by early visual deprivation is much more severe than that of cats with striate cortex lesions. On these grounds they concluded that "attempts to relate deprivation amblyopia to striate cortex abnormalities should be reconsidered". A similar conclusion was reached by Holopigian and Blake (1983) who found that the behavioral deficits caused by an experimental strabismus induced by cutting a single eye muscle can be more severe than those produced by wholesale removal of area 17, suggesting that strabismus can affect neural centers other than striate cortex. This hardly surprising suggestion must be qualified by the statement that strabismus and other distortions or abnormalities of the visual input probably induce differential effects on different cortical areas and subcortical centers. For example, binocular interaction can be disrupted more in areas 17 and 18 than in the superior colliculus (Gordon and Gummow, 1975; Gordon and Presson, 1977; Antonini, Berlucchi, Di Stefano and Marzi, 1981) and in lateral suprasylvian areas (Marzi, Antonini, Di Stefano and Legg, 1982).

The *third* problem is that of the comparison between the results in the cat and those in other species. In general, it can be said with some certainty that extrastriate vision has been shown in most mammalian species, in that considerable visual capabilities remain after removal of the striate cortex (for reviews see Diamond and Hall, 1969; Berlucchi and Sprague, 1981; Sprague *et al.*, 1981; Keating and Dineen, 1982). However, much work remains to be done in order to compare and contrast exstrastriate visual mechanisms in different species, and particularly the problem of vision in destriated primates, including man, must be submitted to a more stringent scrutiny (Weiskrantz, 1980; Campion, Latto and Smith, 1983). It is our conviction that significant achievements in this area will come from experiments combining the analysis of the effects of lesions with that of single-neuron or integrated neural activity in anatomically specified cortical regions and subcortical structures.

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FORM, COLOR, AND MOTION ANALYSIS IN PRESTRIATE CORTEX OF THE MACAQUE

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Areas V4 and MT in macaque extrastriate visual cortex appear to have different functions in visual processing. Anatomical and behavioral experiments indicate that V4 forms part of an object recognition system that extends from striate cortex into the temporal lobe, while MT seems to be more closely allied with a spatial perception system that extends from striate cortex into the parietal lobe (see reviews by Ungerleider and Mishkin, 1982; Ungerleider, 1984). In the first part of this chapter we will describe some possible neural mechanisms for form and color analysis in area V4; in the second part we will describe the representation of direction of stimulus motion in area MT.

Zeki originally reported that neurons in V4 were highly selective for wavelength (1973, 1978, 1980). Later, several groups reported that V4 neurons were not more narrowly selective for wavelength than were neurons in other visual areas (Kruger and Gouras, 1980; Fischer *et al.*, 1981; de Monasterio and Schein, 1982; Schein *et al.*, 1982). If V4 was not necessarily unique as a "color area", we wondered what role V4 did play in visual processing. To help answer this question, we studied both the spatial and spectral properties of V4 neurons. Using quantitative methods, we found that V4 neurons are selective for both the spatial and spectral properties of stimuli. Although the properties of excitatory receptive fields in V4 are similar in some respects to those found in striate cortex, we propose that a special contribution of V4 neurons to visual

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processing lies in specific spatial and spectral interactions between their excitatory receptive fields and large suppressive surrounds.

Spatial Organization of V4 Receptive Fields

Although receptive fields in V4 are several times larger than those in striate cortex, we found that they are not less spatially selective (Desimone and Schein, 1983; and in preparation). Over half the cells in V4 are sensitive to the length and width of a bar within the receptive field, and they appear to be at least as selective for the dimensions of bars as has been reported for cells in striate cortex (Schiller *et al.*, 1976a; De Valois *et al.*, 1982). The distribution of orientation tuning bandwidths is also overlapping in the two areas, although there may to be a somewhat greater proportion of unoriented cells in V4. Likewise, the distribution of peak spatial frequencies in V4, which ranges from less than .12 cycles/deg to 8 cycles/deg, almost completely overlaps that reported in striate cortex (De Valois *et al.*, 1982), although there is a greater proportion of cells in V4 tuned to low spatial frequencies. Thus, while there are quantitative differences between the spatial properties of cells in V4 and striate cortex, there appears to be a comparable degree of spatial selectivity in both areas.

The structure of excitatory receptive fields in V4 can also be compared with those in striate cortex. We found that almost all receptive fields in V4 have overlapping dark and light excitatory zones. The dark and light excitatory zones are not always equivalent: some cells have a preference for either light or dark, and in some cells the peaks of the dark and light zones may even be displaced. Yet, the zones are almost always at least partially overlapping, so in this respect V4 receptive fields resemble those of complex cells in striate cortex.

In other respects, the responses of neurons in V4 can span the full range of characteristics reported for both simple and complex cells in striate cortex. For example, both simple cells (Hubel and Wiesel, 1962, 1968; Maffei and Fiorentini, 1973; Schiller *et al.*, 1976a, 1976b; Movshon *et al.*, 1978a; De Valois *et al.*, 1982) and many cells in V4 respond best to a grating of bar that fills the response zone (one-half cycle or less within the field), distinguish between light and dark phase, and give a modulated response to an optimal drifting grating. Other cells in V4, like complex cells in striate cortex (Hubel and Wiesel, 1962, 1968; Maffei and Fiorentini, 1973; Schiller *et al.*, 1976a, 1976b; Movshon *et al.*, 1978b; De Valois *et al.*, 1982), respond best to a grating with many cycles within the receptive field, fail to distinguish between dark and light phase, and give sustained, unmodulated responses to a drifting grating. While we are not able to classify cells as purely simple or purely complex in V4, many V4 neurons could be placed along a continuum from simple-like to complex-like based on the degree of summation, modulation, or phase sensitivity they exhibit.

What is the significance of differences along a simple to complex response dimension? We can speculate that high-frequency, phase insensitive cells with relatively large receptive fields might be particularly useful for the analysis of texture, while low-frequency cells with greater phase sensitivity might be more useful for the analysis of borders and contours. A similar suggestion has been made for cells in striate cortex (Hammond and Mackay, 1977; see Maffei, this volume), and our results suggest that such a separation of function may be carried into V4.

Spectral Properties of V4 Receptive Fields

Many of the same V4 neurons that are selective for length, width, orientation and spatial frequency are also selective for wavelength. In neither the spatial nor the spectral domain, however, do the cells respond to only one particular stimulus, such as a bar of particular length or color. Rather, cells are broadly tuned along these dimensions. When we measured the response of V4 cells to white stimuli and to blue, green, yellow, and red broad-band colored stimuli, we found that most cells had a peak response to one color stimulus but gave at least a small response to all stimuli. Across cells, the average response to the least effective color stimulus tested was 20% of the response to the best stimulus, and the average response to white was 60% of the response to the best color stimulus. Thus, we have found, as have other studies, that V4 cells are not narrowly tuned color "detectors" (Van Essen and Zeki, 1978; Fischer *et al.*, 1981; Kruger and Gouras, 1980; Schein *et al.*, 1982).

Nonetheless, the vast majority of V4 cells show evidence of spectral selectivity. When tested with narrow-band stimuli equated for either photopic luminosity or number of quanta, most V4 cells have a response that peaks at some wavelength and falls to zero at others. The spectral bandwidths of the majority of cells are narrower than the cones and are comparable to those of the color-opponent cells in the retina and lateral geniculate body (de Monasterio and Schein, 1982). Indeed, though most V4 cells give a moderate response to white, so do broadly tuned color-opponent cells in the lateral geniculate (Creutzfeldt *et al.*, 1979; see review by Creutzfeldt, this volume). Thus, consistent with previous studies (Zeki, 1973, 1978, 1980, 1983), we found that the majority of V4 cells carry some information about wavelength.

The results from the cell illustrated in Figure 1 are representative of most V4 cells. The stimuli were narrow-band spectral lights, ranging in wavelength from 460 nm (blue) to 660 nm (red). The cell was wavelength sensitive, with a peak response to the 500 nm stimulus, in the blue-green part of the spectrum. The color information provided by the cell, however, was not highly specific. It gave an excitatory response over most of the spectrum, and also responded well to white light. In addition, there were no explicitly color-opponent responses, such as inhibition or off-responses in the red part of the spectrum.

The broad spectral response curve, the absence of color opponent responses and the good response to white seem in many ways analogous to properties of a broad-band color filter, such as a piece of colored glass. Such a filter simply lets energy at some wavelengths pass more efficiently than at others and always lets some energy through from a white light, as white contains all wavelengths. If a V4 cell acted like a photocell covered with a broad-band filter, we would expect it to respond not only to white light but also to other broad-band lights that contain energy at many wavelengths. Thus, to a first approximation it appears that the nature of the representation of colored stimuli in V4 may be a color filtered one.

Receptive Field and Surround Interactions

One clue to the special contributions of V4 neurons to visual processing may come from the study of the large silent suppressive surrounds which we found lie beyond the excitatory receptive fields of most V4 cells. A stimulus placed outside the excitatory receptive field elicits no response, yet such a stimulus can completely suppress the response to a stimulus within the excitatory receptive field. These suppressive surrounds can be 30° or more in diameter and can even extend up to 16° or more into the ipsilateral visual field (Moran *et al.*, 1983). The extension of the suppressive surrounds into the ipsilateral visual field is particularly intriguing, as V4 receives a widespread projection via the corpus callosum that is not limited to the representation of the vertical meridian (Van Essen and Zeki, 1978).

Our experiments with white light revealed that stimuli placed out-

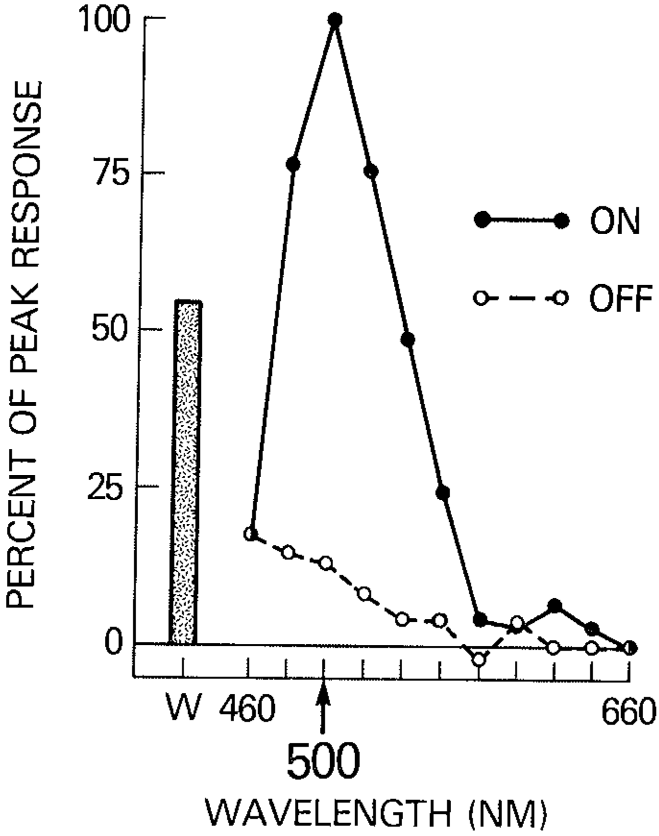

FIG. 1. Responses of a representative V4 neuron to a white stimulus (W) and to narrow-band spectral stimuli. All stimuli were .75° × .75° slits flashed within a 1° × 1° excitatory receptive field. Spectral stimuli were produced by narrow-band interference filters (10 nm full-width at half-amplitude). All stimuli were equated for photopic luminosity (CIE) and had a luminance of 1.5 ft-L on a neutral background of 0.5 ft-L. Stimuli were randomly interleaved by computer and were presented for five trials each, with a 1.28 sec presentation each trial. The intertrial was 5 sec. "On" responses were calculated from the average firing rate during the stimulus presentation minus the baseline firing rate. "Off" responses were calculated from the average firing rate during a 0.64 sec period following the stimulus presentation, minus the baseline firing rate. All responses are shown as percentage of the peak response, which was to the 500 nm stimulus.

side the excitatory receptive fields of V4 cells could have a powerful effect on the response to a receptive field stimulus. Might this stimulus interaction be color specific? To answer this, we examined the effect of colored surround stimuli on the response to an optimal color receptive field stimulus.

We first determined the optimal wavelength for the receptive field stimulus of a given cell. This optimal color stimulus was then flashed within the excitatory field, and large colored annuli were simultaneously flashed a small distance beyond the receptive field. The responses of most V4 cells were almost totally suppressed when the surround stimulus was the same wavelength as the receptive field stimulus. As we increased the spectral difference between the receptive field surround stimulus, however, the suppression declined and occasionally there was evidence of enhancement. The surround stimulus itself elicited no response. Thus, most V4 cells respond best to a receptive field stimulus if there is a spectral difference between the receptive field stimulus and its surround.

Other results suggest that form differences are important as well, as most V4 cells respond better to a grating that is restricted to the receptive field than to a grating that covers both the receptive field and the surround. Preliminary results indicate that this suppression of V4 cells by gratings in the surround is spatial frequency specific, i.e. cells may respond best if there is a spatial frequency difference between the receptive field grating and a surround grating.

What is the significance of the large suppressive surrounds in V4? Certainly center/surround type receptive fields have been described at all levels of the visual pathways, and these presumably serve to enhance contrast. Given the much larger receptive field size in V4, we wonder if this organization might serve more global perceptual mechanisms. One possibility is that the spectral interactions reflect a mechanism for color-constancy, which is crucial for accurate color-identification (Land and McCann, 1971; Land, 1977). Color-constancy depends on spectral interactions over a wide portion of the retina, and we have found that V4 cells are influenced by spectral lights throughout a large retinal area. Indeed, Zeki (1980, 1983) has recently suggested that some V4 neurons demonstrate color-constancy. In addition, the sensitivity of V4 cells to both form and color differences might be useful for figure/ground separation, or "breaking camouflage", an essential element of both form and color vision.

Miezen *et al.* (1982; and Allman, personal communication) have speculated that some type of figure/ground mechanism may operate in other prestriate areas as well. They have found that for neurons in areas MT and V2 that respond to one direction of stimulus motion within their excitatory receptive field, the response is suppressed by the same motion in the surround. Thus, these areas may participate in figure/ground separation based on differences in motion. Similar results have recently been reported for neurons in the lateral suprasylvian area of the cat (von Grunau and Frost, 1983).

The spatial and spectral properties of V4 cells would seem to be useful for extracting local object contours and describing local object surfaces. Because V4 cells have restricted receptive fields, however, an individual V4 cell can provide little information about overall surface shape. By contrast, neurons in inferior temporal cortex, which receives a converging input from V4 (Desimone *et al.*, 1980), have large receptive fields that cover the central visual field (Desimone and Gross, 1979). Thus, inferior temporal cortex might process the locally filtered representation conveyed by V4 and provide a more global representation of surface contours, or shape. Evidence has recently been reported for such a global shape-encoding mechanism in inferior temporal cortex, a mechanism that is relatively independent of the size and position of the stimulus on the retina (Schwartz *et al.*, 1983; see chapter by Gross *et al.*, this volume).

Representation of direction of motion in area MT

The properties of neurons in area MT stand in sharp contrast to those of area V4. Compared to neurons in V4, neurons in MT are reported to be less sensitive to form and color but more sensitive to direction of stimulus motion (Zeki, 1974). To gain insight into the mechanisms for motion analysis in MT, we have examined the functional architecture for direction-of-motion (Albright *et al.*, 1984).

On a large number of penetrations into MT we sampled the preferred direction-of-motion of cells at 50-um intervals. On most penetrations we found that preferred direction-of-motion shifted gradually, in a clockwise or counterclockwise fashion, from cell to cell. Thus, most penetrations indicated a systematic representation of direction-of-motion in the cortex (see Fig. 2). On other penetrations, however, we occasionally found sharp discontinuities in the representation of direction-of-motion.

The penetration yielding the most chaotic data is illustrated in Figure 3. On this penetration, there were often large differences in the preferred direction of motion of adjacent cells and apparently no orderly sequence of changes in preferred direction along the penetration. On this and other penetrations with such discontinuities, however, we observed that the discontinuities were usually due not to random changes in preferred direction between cells but rather to shifts of approximately 180°. It

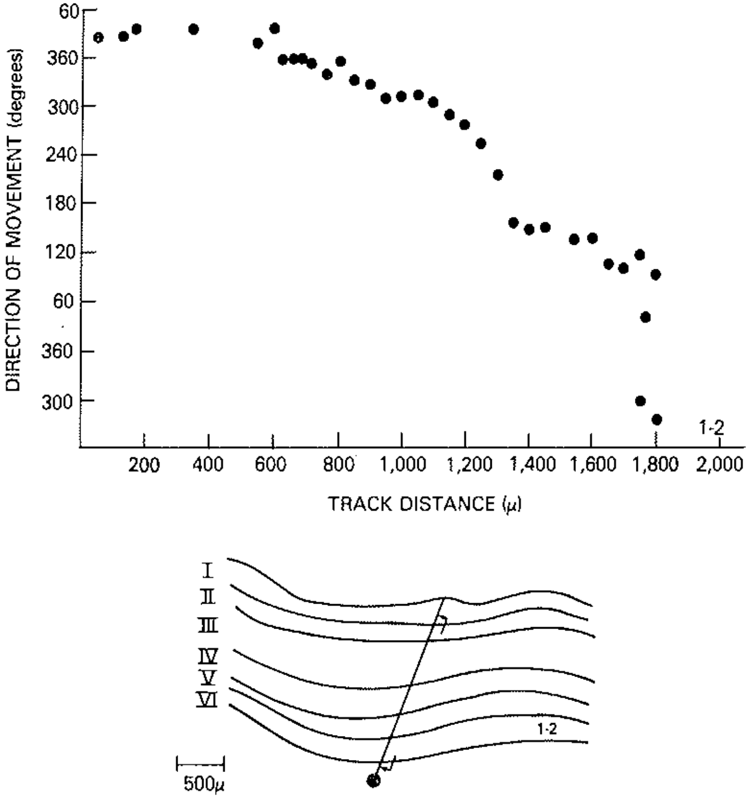

Fig. 2. Direction selectivity of cells recorded on a penetration within area MT. *Top*: Optimal direction of stimulus motion as a function of electrode track distance. Each point represents the optimal direction-of-motion for a single cell. Direction-of-motion changes systematically from cell to cell. *Bottom*: Reconstruction of the electrode penetration in area MT. Recording sites are bounded by the two arrows.

appeared that cells selective for opposite directions of motion could exist side by side in the cortex. Similar results have been found in area MT of the owl monkey (Baker *et al.*, 1981).

To take the shifts of 180 degrees into account, we determined the optimal axis-of-motion for each cell. Axis-of-motion is defined as the orientation of the path along which a stimulus moves, independent of its direction along that path. Stimuli moving in opposite directions have a common axis-of-motion. When optimal axis-of-motion rather than direction-of-motion is plotted as a function of track distance, most of the dis-

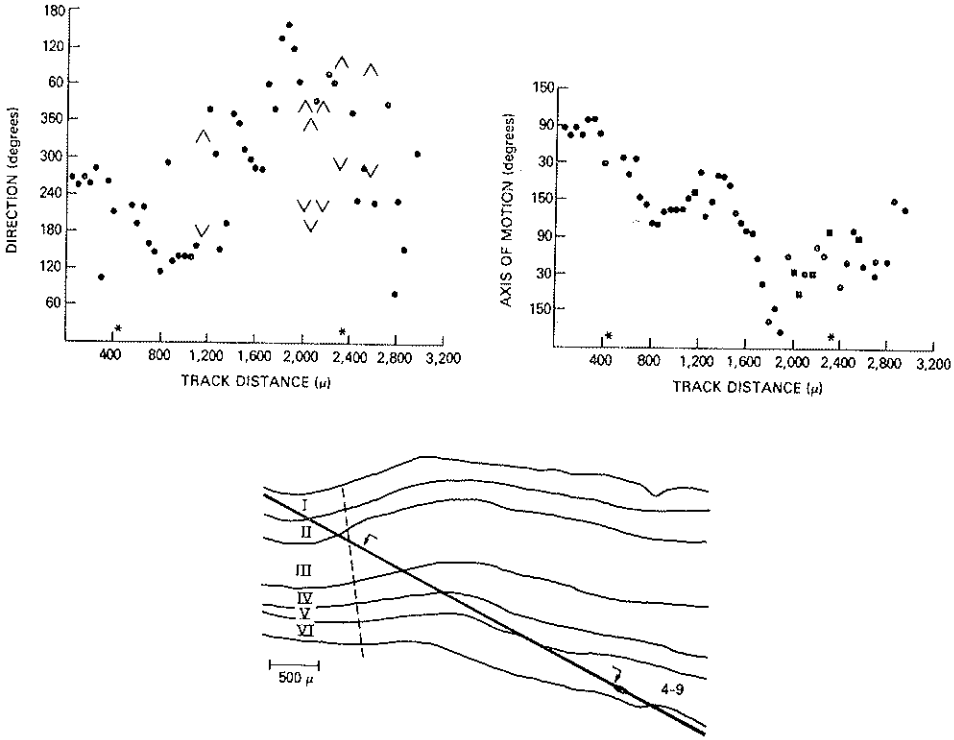

FIG. 3. Example of a penetration with a highly discontinuous progression of preferred directions of motion. *Top left*: Optimal direction of stimulus motion as a function of track distance. Each dot represents the optimal direction-of-motion for a single unidirectional cell. An asterisk along the abscissa represents a pandirectional cell. This progression appears disorderly because of the large number of 180° reversals in preferred direction. *Top right*: Optimal axis of stimulus motion as a function of track distance. Axis-of-motion is defined as the orientation of the path along which the stimulus moves, independent of its direction along that path. Cells with 180° opposite direction-of-motion preferences have the same axis-of-motion preference. Squares represent the optimal axis-of-motion of bidirectional cells. The representation of axis-of-motion is more continuous than that of direction-of-motion on this and many of penetrations. *Bottom*: Reconstruction of the electrode penetration in area MT. The dorsal myeloarchitectonic border of MT is indicated by the broken line across the cortex.

continuities in the penetrations are eliminated. In the penetration illustrated in Figure 3, the sequence of preferred axis-of-motion is orderly for at least two-thirds of the penetration, and for other penetrations there were virtually no discontinuities in the sequence of preferred axis-of-motion.

In summary, both preferred axis-of-motion and preferred direction-of-motion are represented in a regular, systematic fashion within MT. The representation of direction-of-motion is sometimes discontinuous, while the representation of axis-of-motion is nearly always continuous.

Although the representation of axis-of-motion appeared to be continuous across the cortex, we were also interested in whether cells with the same axis-of-motion preference were located in the same vertical column of cells, similar to the columnar organization of orientation-selective cells in striate cortex (Hubel and Wiesel, 1974). Since we could not make precisely vertical penetrations into MT, we compared the rate of change of axis-of-motion on vertical and tangential penetrations. If cells with the same preferred axis-of-motion in MT were located in vertical columns, the preferred direction-of-motion of cells should shift slowly on the more vertical penetrations and rapidly on the more tangential.

When we compared the rate of change of axis-of-motion to the angle of the penetration in the cortex, we found that the rate of change was directly proportional to the sine of the angle of the penetration. The more vertical the penetration, the smaller the rate of change. Thus, there appears to be a vertical columnar organization for axis-of-motion.

Across all penetrations, the maximum rate of change of axis-of-motion is 420° per millimeter of cortex parallel to the cortical surface. This means that 180° of axis of motion, a full representation, is represented in 400 to 500 microns in MT. This is very similar to the size of the representation of 180° of orientation in striate cortex (Hubel and Wiesel, 1974; Hubel *et al.*, 1978).

How are the cells with opposite preferred directions-of-motion arranged within the axis-of-motion columns? To determine whether cells with opposite preferred directions were located in the same vertical column of cells, we compared the frequency of 180° reversal on vertical and tangential penetrations. The more vertical the penetration, the fewer the number of reversals, indicating that cells with opposite preferred directions are located not in the same vertical column, but in adjacent direction-of-motion columns. A hypothetical model of the columnar system consistent with these data is illustrated in Figure 4.

The columnar organization of direction and axis of stimulus motion suggest that MT plays a fundamental role in the analysis of stimulus motion. In macaque striate cortex, approximately 500 um of cortex includes cells with receptive fields representing the same portion of the visual field, and these cells include a full complement of preferred orientation (Hubel and Wiesel, 1974; Hubel *et al.*, 1978). Although MT is much smaller

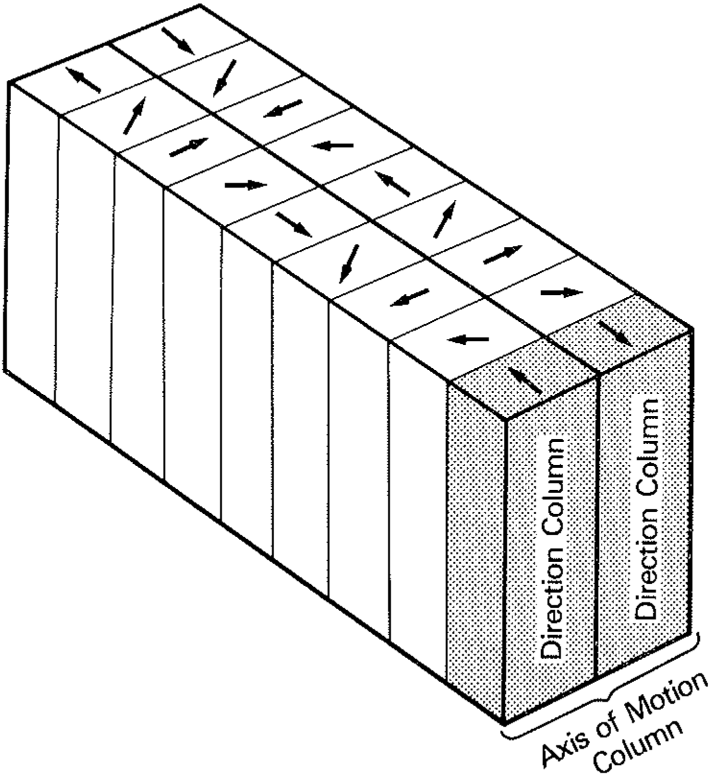

FIG. 4. Three-dimensional depiction of a block of cortical tissue containing one configuration of axis and direction-of-motion columns that is consistent with our data. The vertical dimension represents cortical depth. The long axis of the figure may be viewed as two complete revolutions of axis-of-motion columns. Moving in this dimension, one would encounter gradual changes in preferred direction. Within each axis-of-motion column (along the short axis of the figure) the two opposite directions-of-motion along that axis-of-motion are represented as adjacent columns. Moving in this dimension, one would encounter frequent 180° reversals in preferred direction-of-motion with no change in preferred axis-of-motion.

than striate cortex, because of its larger receptive fields approximately 500 um of MT also includes cells with receptive fields that overlap in the visual field. This area includes cells representing a full complement of preferred directions. Thus, in both MT and striate cortex a roughly 500-um-wide region of cortex contains the neural machinery sufficient to process information about a specific stimulus parameter in one portion of the visual field.

How do other parts of the visual system make use of the local direction-of-motion information provided by MT? MT supplies a variety of additional visual areas in the superior temporal sulcus and the parietal cortex with direction-of-motion information, and at least some of these areas also contain directionally selective cells (Ungerleider *et al.*, 1982; Maunsell and Van Essen, 1982; Ungerleider and Desimone, unpublished data). One of the areas to which MT projects in the superior temporal sulcus contains neurons whose activity is related to tracking eye movements, suggesting that direction-of-motion information may be used by the oculomotor system (Newsome and Wurtz, 1982). Another area in the superior temporal sulcus that probably receives information indirectly from MT is the superior temporal polysensory area (Desimone and Gross, 1979; Bruce *et al.*, 1981; Bruce, Ingalls, Desimone, and Gross, unpublished data). Cells in the superior temporal polysensory area are sensitive to direction-of-motion throughout the entire visual field of the monkey. Many cells are sensitive to motion in depth or motion directed towards or away from the center of gaze, which are precisely the motions generated in the visual array by movement of the animal through space. Thus, the local direction-of-motion information provided by MT may ultimately be used by more global direction-of-motion mechanisms in subsequent visual areas.

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INFERIOR TEMPORAL CORTEX AND PATTERN RECOGNITION

C.G. GROSS *, R. DESIMONE **, T.D. ALBRIGHT * and E.L. SCHWARTZ ***

Background

Although the study of the visual properties of single neurons in inferior temporal (IT) cortex is less than 20 years old (Gross *et al.*, 1967), it has been clear for a much longer time that IT cortex is involved in visual recognition. The prehistory of IT cortex began in the late 19th century when Brown and Schaefer (1888) reported that after temporal lobectomy, monkeys became tame and no longer appeared to recognize the meaning of the sights and sounds that reached them. Yet these monkeys appeared to have normal sensory capacities. This was a period before the cortical areas for seeing or hearing were established and these rather strange symptoms were lost in the welter of controversies over the location or even the existence of a cortical visual area or "cortical retina" as it was often then called (Polyak, 1957).

Fifty years later, similar observations were made by Kluver and Bucy (1938) and the unusual pattern of behavioral changes following temporal lobectomies became known as the Kluver-Bucy syndrome. These investigators stressed the inability of animals with temporal lobe damage to recognize or learn about visual stimuli, and called this aspect of the syndrome "psychic blindness". Later, Chow (1951) and Mishkin and Pribram (1954), working in Lashley's laboratory, showed that portions of

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the Kluver-Bucy syndrome could be produced independently by partial temporal lobe damage. Specifically, the so-called "psychic blindness" followed removal of the cortex of the inferior convexity of the temporal lobe, IT cortex, shown in Fig. 1.

From many subsequent studies it became clear that IT cortex is necessary for normal visual pattern recognition (see reviews by Gross, 1973 a,b; Mishkin, 1966, 1972; Dean, 1976). Monkeys without their IT cortex have a severe and permanent impairment in learning to discriminate visual stimuli. Yet their visuo-sensory capacities are intact. That is, they have normal visual acuity, intact visual fields and normal thresholds for a variety of psychophysical functions. Furthermore, after IT lesions, learning ability in modalities other than the visual remains intact. In man, removal of the corresponding cortex in the right hemisphere has similar effects on visual learning and memory (e.g. Milner, 1968).

In summary, the effects of damage to IT cortex in both macaque and man indicate that it is involved in high-order visual mechanisms underlying

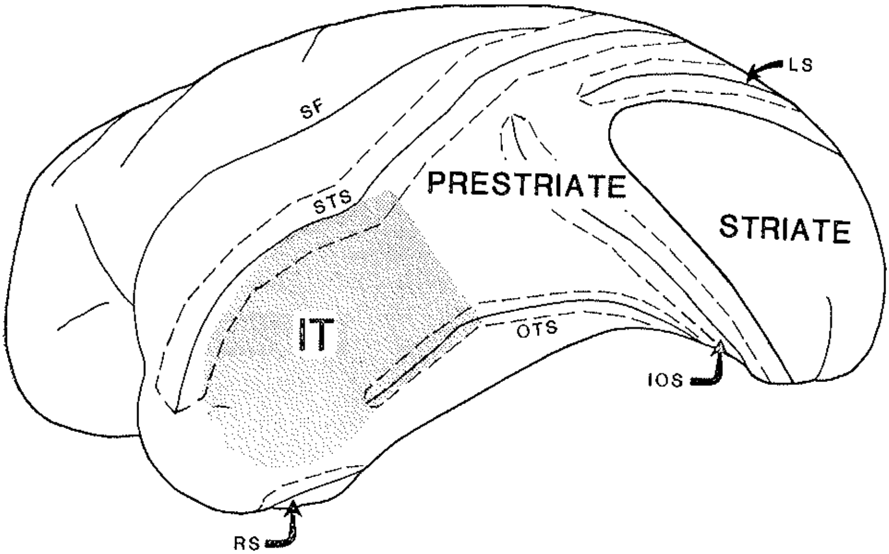

Fig. 1. Ventrolateral view of macaque brain showing inferior temporal (IT) cortex shaded. Sulci in the occipital and temporal lobes have been opened up and their banks shown with dashed lines. IOS, inferior occipital sulcus; LS, lunate sulcus; OTS, occipitotemporal sulcus; RS, rhinal sulcus; SF, Sylvian fissure; STS, superior temporal sulcus.

visual pattern recognition. Indeed, IT cortex would appear to contain the final stages in the process of visual pattern recognition.

VISUAL PROPERTIES OF IT NEURONS

Receptive Fields

Consistent with the findings that IT lesions impair visual and only visual discrimination, IT neurons respond to visual and only to visual stimuli. Like neurons in most other visual areas, IT neurons have discrete receptive fields. Their receptive fields, however, have four characteristics which, taken together, make them unique (Gross *et al.*, 1972; Desimone and Gross, 1979).

First, there is no map of the visual field (or retina) in IT cortex. That is, unlike most other visual structures, IT cortex is not visuotopically organized. Rather, virtually every receptive field includes the center of gaze. Second, IT receptive fields are very large. The median size is about 25×25 deg. In the most anterior portions of IT cortex, receptive fields are even larger. Third, more than half the receptive fields extend well into both visual half-fields, unlike those in striate and prestriate cortex. Thus, in IT cortex visual space is unified at the neuronal level for the first time. Fourth, although the strongest response is usually elicited at the center of gaze, the stimulus selectivities of an IT cell remain similar throughout the receptive field. That is, the neurons show stimulus equivalence across retinal translation. This stimulus equivalence within the receptive field may underlie the perceptual equivalence across retinal translation (Gross and Mishkin, 1977).

These four unique receptive field properties of IT cells are found in both immobilized animals anesthetized with nitrous oxide and in awake, behaving animals (Gross *et al.*, 1979; Richmond *et al.*, 1983). They are restricted to and characteristic of neurons throughout Von Bonin and Bailey's (1947) cytoarchitectonic area TE. Thus, inferior temporal cortex, as defined by these receptive field properties, is identical with cytoarchitectonic area TE. As one moves out from IT cortex in any direction, the response properties change (Desimone and Gross, 1979). In the cortex dorsal, rostral and ventral to IT, many of the neurons are polysensory, responding to auditory or somesthetic stimuli as well as visual. Caudal to IT in prestriate cortex, the neurons are exclusively visual, but unlike IT neurons, they are visuotopically organized and their receptive fields are confined to the contralateral visual field.

Stimulus Selectivities

The response properties of IT neurons are very heterogeneous. Some IT neurons fire equally well to a number of different stimuli while others are highly selective for one or more stimulus parameters. Furthermore, it is often difficult to ascertain which aspects of a complex stimulus are responsible for a unit's response (Gross *et al.*, 1972, 1977; Desimone *et al.*, 1984).

In a recent experiment we attempted to estimate the incidence of IT units with particular types of stimulus sensitivities (Desimone *et al.*, 1984). In addition to using projected white and colored slits and edges, we tested the response of each cell with a set of 14 three-dimensional colored objects. They included models of a head, a hand, an apple, a banana, a flower, a snake, an insect and a brush. If a unit showed selective responses to members of this set, we then attempted to determine the critical features underlying this selectivity. To do so we used colored and black and white photographs of the objects, scrambled photographs and variations and portions of the objects and their photographs as well as simpler projected lines, edges and gratings. The stimuli were presented mechanically under computer control in an interleaved fashion and histograms of the units' responses were computed.

We were unable to drive 13% of our sample with visual stimuli and the visual responses of another 14% were too weak to study adequately. (These percentages are very similar to those in our previous studies in both unanesthetized and anesthetized animals). Another 30% of the units appeared nonselective. Specifically, they fired about equally well to all the 14 test objects as well as to white and colored slits and edges. Within this group, however, there was a tendency for the complex objects to elicit somewhat stronger responses than the simpler slits or edges.

The remaining 43% of the cells responded differentially to the set of objects and projected slits and therefore were classified as selective. Further analyses revealed that for 28% of these units stimulus shape was a critical determinant of the response. Some fired optimally to a slit of a specific width or length but most were selective for a more complex boundary. A few of these shape selective neurons were also selective for color or texture or both. Sixteen percent of the selective cells were classified as selective for color, that is, they responded more strongly to a particular colored stimulus than to a white stimulus of any luminance. Seven percent of the selective cells responded best to patches of artificial hair or fur, which we interpreted as selectivity for texture. Defocusing these stimuli reduced their textured appearance and eliminated the neuron's selectivity. None of these texture selective units showed any selectivity for high spatial frequency gratings, although we have seen units selective for spatial frequency in IT cortex (Desimone, unpub. obs.). Another 7% were selective for either faces or hands. This type of unit is discussed further in the next section.

The remaining selective neurons responded differentially to a subset of the complex objects but we were unable to determine what specific features underlay this specificity. That is, we could not find common properties among the adequate stimuli that proved critical for eliciting a response.

Face and Hand Selective Cells

Although cells selective for hands or faces are rare, we have repeatedly seen them since we first reported a hand selective cell in IT cortex in 1969 (Gross *et al.*, 1969). Some data from a recently studied hand selective cell (Desimone *et al.*, 1984) are shown in Fig. 2. This unit responded best to hands and models of hands and not to other complex objects or projected slits, edges, or gratings. The unit responded to the hand stimuli throughout at least a 20 deg. wide receptive field, with the best response to the hand positioned over the fovea. Furthermore, the unit responded to photographs of human and monkey hands of any orientation and over sizes from 2.5 deg. to 10 deg. wide. White cutouts in the shape of a hand also elicited strong responses, but not quite as strong as the colored, three-dimensional model. Thus, the response to the model of the hand was probably based primarily on its shape but the color or internal detail of the model probably also contributed to the unit's response. Consistent with this interpretation, there was a small response to a scrambled photograph of the hand which preserved the overall color and many of the internal details of the hand but not its shape. The unit's response to the shape of the hand was apparently very specific as "grating-like" cutouts elicited no response even though they mimicked the periodicity of the fingers and the general shape of "spokes" emanating from one end of a central "core". By contrast, a cutout of a monkey hand, which was much

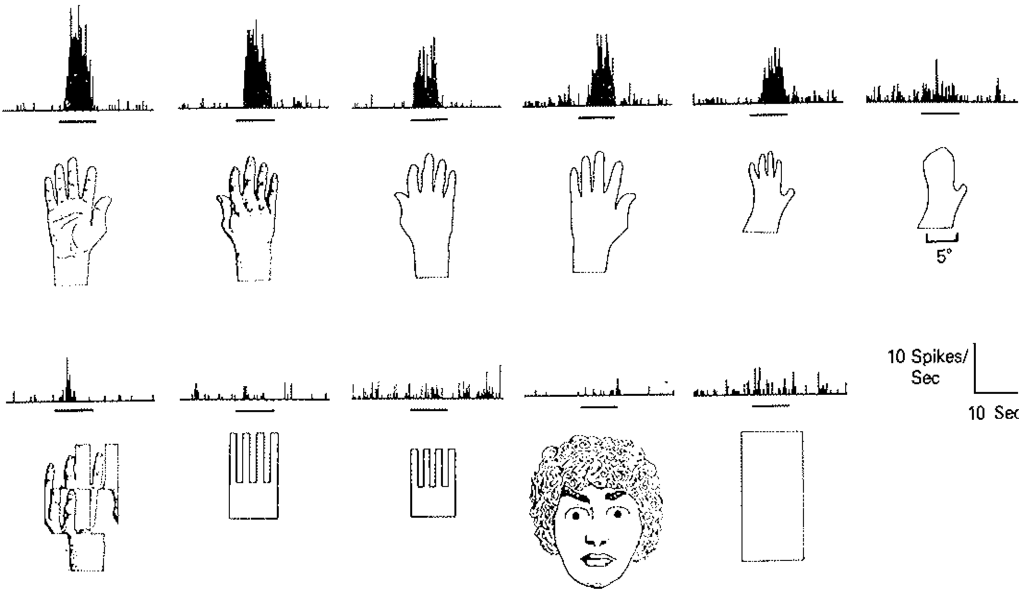

FIG. 2. Responses of an IT neuron that fired more strongly to hands than any other stimulus tested. The stimuli are drawn to scale and were moved under computer control at 1.2 deg./sec. from the contralateral to the ipsilateral visual field. They were visible within a 15 deg. wide window centered at the fovea during the period indicated by the horizontal line under each histogram. The histograms were based on five trials and the presentation of the different stimuli was interleaved. Starting at the upper left, the stimuli were the front and back of a model of a human hand, white cutouts with the same shape as the human hand model, a cutout with the shape of a monkey hand, a cutout of a monkey's hand with the space between the fingers eliminated, a scrambled photograph of the model of the human hand (ten rearranged pieces), two "grating-like" hands, a model of a human face, and a plain rectangle (Desimone *et al.*, 1984).

smaller than the cutout of the human hand and with less prominent fingers, elicited a good response. Fingers proved to be a critical feature of the hand cutout, since filling in the spaces between them significantly reduced the response.

Cells selective for faces appear to be somewhat more common than ones selective for hands. Furthermore, there appear to be a greater variety of face selective cells (Desimone *et al.*, 1984). Results from one such cell, tested with projected photographic slides, are shown in Fig. 3. This cell fired strongly to the photograph of a frontal view of a face and its response fell off as the photographs showed the head rotated into a profile view. This cell also responded well to different monkey faces but its response was reduced about 40% by removing either the eyes, the snout or color

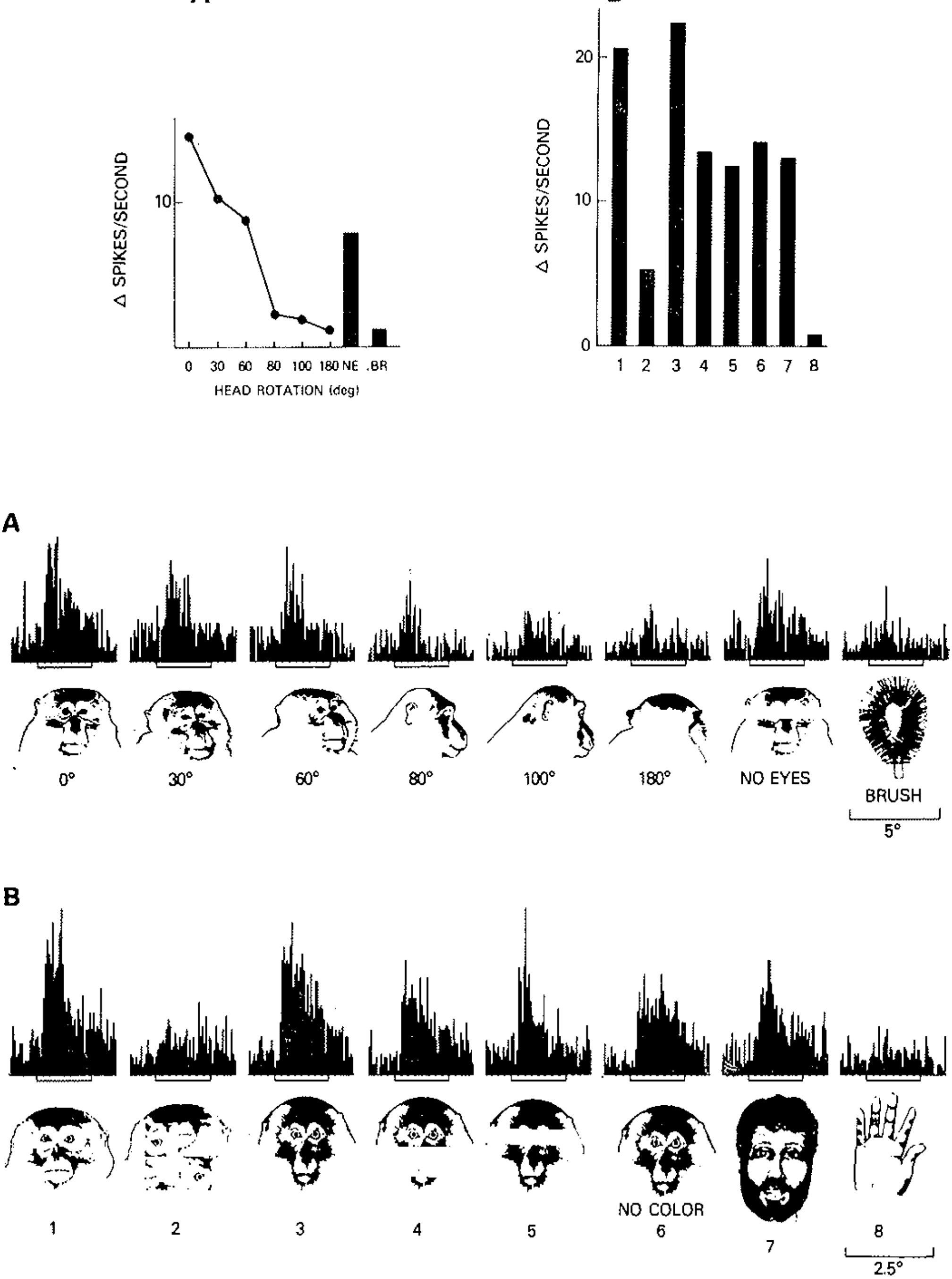

Fig. 3. Responses of an IT neuron that fired more strongly to faces than any other stimulus tested. The stimuli, which are drawn to scale, were colored slides projected at the center of gaze for 2.5 seconds indicated by the horizontal line under each histogram. The histograms are based on ten trials and the presentation of the different stimuli was interleaved. The bar graphs indicate the firing rate during stimulus presentation minus the firing rate in the prestimulus period. Note that the frontal view was most effective. Removing the mouth, eyes, color or substituting a human face reduced the response. The scrambled face elicited a very small response as did a hand or brush (Desimone *et al.*, 1984).

from the photograph. Thus, the eyes, snout and color each contributed to the response, but any of these components alone were not sufficient to explain the response to the complete face. Scrambling the internal features of the face, however, virtually eliminated the response, indicating that the configuration of the internal features played an essential role in the unit's response to the unaltered face. Stimuli other than faces were ineffective. The response to a photograph of a human face was less than to the frontal monkey photographs but greater than to other stimuli. For other face selective units, however, human faces elicited as strong a response as monkey faces.

Fig. 4 shows data from another type of IT face selective cell. This one responded only to faces in profile. It did not respond to either front or rear views of a head. Furthermore, it did not respond to the anterior or posterior portions of the profile presented alone, to the silhouette of a profile or to the other face variations shown in Fig. 4. Unlike the previous unit, portions of the face were insufficient to elicit any response, i.e. the full profile was necessary. Yet this unit did respond to a variety of different face profiles.

Are there more parsimonious explanations of these neurons' properties than labeling them "hand" or "face selective"? For two reasons, the responses of these and similar hand and face cells were unlikely to have been due to "arousal". First, none of these units responded to intense somesthetic or auditory stimuli or to the models of the snake or spider which elicited strong emotional reactions from monkeys tested in their home cage. Second, general arousal, or even arousal confined to visual stimuli, could not explain why some units were selective for hands and other units for faces, nor why some face selective units responded preferentially to the front of the face and others to the profile.

It is also unlikely that the face and hand selective units were actually selective for some simple, local stimulus feature such as a line of a particular length, a specific patch of color or a certain texture in a particular retinal location. Each of these units responded to a wide variety of hands or faces, including real ones, plastic models and photographs or slides. Furthermore, each responded selectively to both monkey and human faces or hands over a wide range of sizes and orientations throughout a large receptive field. It is hard to imagine a specific "simple" stimulus feature that would remain invariant over such transformations. Conversely, none of the units responded well to hands or faces which had been scrambled even though many component lines and edges remained intact.

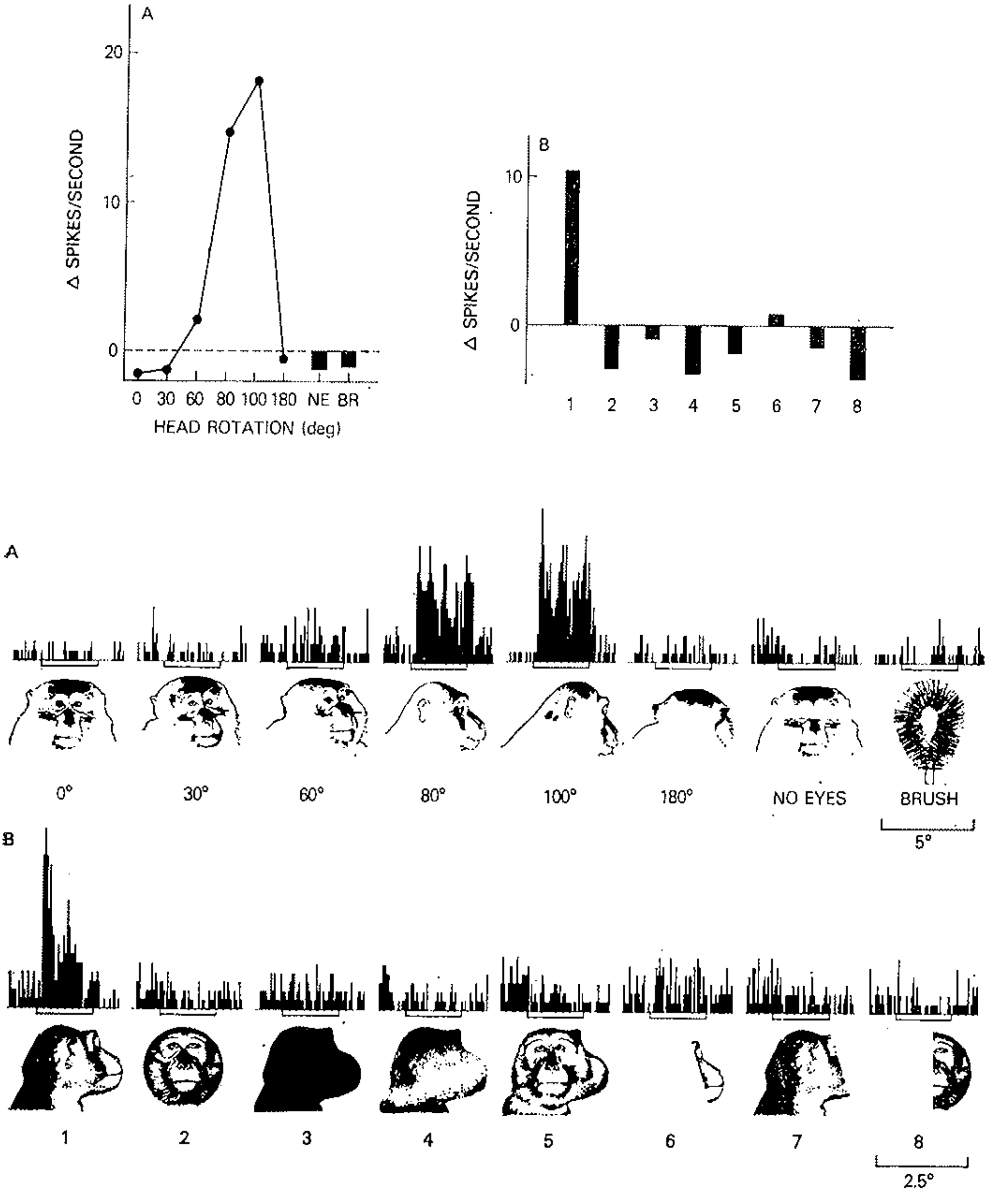

FIG. 4. Responses of an IT neuron that fired more strongly to profiles of faces than to any other stimulus tested. See also legend to Fig. 3. Note that the profiles of different monkeys elicited strong responses whereas the other stimuli elicited no responses. The ineffectual stimuli included the silhouette of the profile (No. 3), the profile filled with fur (No. 4), and anterior and posterior portions of the profile (Nos. 6 and 7) (Desimone *et al.*, 1984).

To what extent might it be more appropriate to describe hand selective cells as selective for a specific shape rather than for a "hand"? The hand selective units responded best to the outline or shadow of a variety of monkey and human hands but not to many other shapes. As the shape of the hand was altered so that it looked less to us like a hand, the responses of the units declined or disappeared. For example, a grating-like hand, which mimicked the periodicity of the fingers and the general property of spokes radiating from one side of a central core, elicited a much smaller response than more hand-like shapes. Still, one might argue that it was the curvature of the fingers in combination with their periodicity that was the crucial feature for the neuron's response and not "handness" per se. Similarly, although the responses of these units were enhanced when the hand had a skin color and appropriate internal details, this might have reflected a specific color or texture specificity of the cells. At this point the list of the stimulus conditions that elicit the maximum response begins to approach a description of the essential features of a hand, i.e. "four long and one short curved spokes, emanating from one end of a central core, flesh colored and covered with fine texture". While a simpler sensory feature may eventually be found that will explain the properties of such cells, at present, the most appropriate description of their properties may indeed be that they respond best to hands.

Analogous arguments apply to the cells apparently selective for faces. Faces contain numerous shapes, contours, colors, and textures, and all of these components must be arranged in a limited set of configurations in order to look like a face. Every face selective unit we studied was sensitive to the many features of a face. Removing the eyes, snout, outline of the head, or color always reduced the response. Furthermore, the overall configuration was crucial. Scrambling the components of the face always markedly reduced the unit's response. Thus, many of the components of the face appeared to contribute to the selectivity of these neurons and the list of stimulus requirements approaches a general description of a face.

Although the proportion of cells selective for hands or faces was very small in this and our previous studies, from one point of view the number might be viewed as surprisingly large. If many IT cells were each selective for a highly specific stimulus, one might expect never to find more than one or two cells to be selective for the same specific stimulus. The fact that across this and previous studies we have found dozens of face selective units and the fact that they have also been found in other laboratories (Perrett *et al.*, 1982; Rolls, 1983) suggests that faces may be a special class of visual patterns. This possibility is consistent with both the importance of facial expression for primates and the reports of specific deficits in face recognition (prosopagnosia) after occipito-temporal lesions in man (e.g., De Renzi and Spinnler, 1966; Hecaen, 1981; Whiteley and Warrington, 1977).

We have no good evidence for the existence of IT cells selective for specific objects other than hands and, especially, faces. The fact that many IT units will respond to a particular shape independent of its color or a particular color independent of its shape make them unlikely candidates for detectors of specific objects. On the other hand, for other cells whose properties we never understood, it is conceivable that we did not try enough stimuli that are particularly important for macaques. We may have stumbled across the hand and face units only because a) these stimuli are ubiquitous in the experimental room and b) they are among the few stimuli particularly important for both humans and monkeys. Perhaps if we had tried many more monkey rumps or tropical fruits or tree branches we might have found units selective for such stimuli. Alternatively, faces may be so special for primates that it is possible that evolution has provided special purpose devices only for them or only for a small class of critical stimuli.

Coding of Shape by Fourier Descriptors

In the experiments described in the previous sections, the overwhelming majority of IT cells did not show selectivity for a specific object but, rather, were selective for aspects of shape, color or texture. Might these cells form part of an ensemble of cells whose pattern of firing could, collectively, code specific objects? In this section, we consider a possible way in which shape might be coded by an ensemble of IT cells.

One problem in our previous experiments was that we had no way of varying shape in a systematic and parametric way such as one can do for orientation or color. So we turned to a method for describing and representing shapes that is used in computer pattern recognition. There are a variety of such methods and we chose one, the method of Fourier Descriptors (Zahn and Roskies, 1972; Persoon and Fu, 1977), because it seemed capable of a physiological embodiment (Schwartz, 1980).

A common feature of neurons on the main pathway to IT cortex, namely V1, V2 and V4, is sensitivity to orientation of local contours or boundaries (Hubel and Wiesel, 1962, 1965; Zeki, 1978; Desimone, Schein and Albright, 1984). Furthermore, many years ago Hubel and

Wiesel (1962) suggested that the sensitivity of striate units to local orientation might be subsequently built up at later stages to provide a description of more complex forms. The method of Fourier Descriptors is a formalism for carrying out such a synthesis of local boundary orientation into a global shape descriptor.

The method depends first on determining the boundary orientation function for the shape, that is, the orientation or tangent angle of the shape's boundary measured at regular intervals around the perimeter (Fig. 5). Then, the boundary orientation function is expanded in a Fourier series. Each term in the Fourier expansion is associated with a particular frequency, amplitude and phase and is known as a Fourier Descriptor or FD. Any shape is fully described by its constituent set of FDs, and a set of only the low-frequency terms can often provide the "gestalt" of a shape. Furthermore, this method of describing shape is independent of both the position and size of the stimulus. Thus, the FDs are a powerful and efficient alphabet for representing and classifying shapes. The inverse transform of a single FD uniquely determines a plane closed boundary with a specific number of lobes (frequency), lobe indentation (amplitude) and orientation (phase) (Fig. 6). We refer to these shapes as "FD stimuli".

There is both a practical and a theoretical use of Fourier Descriptors in the study of IT cortex. The practical use is simply that by systematically varying the frequency or amplitude of FD stimuli, we have a way of testing IT units with parametrically varying shapes and thereby characterizing their shape selectivity. The theoretical relevance rests on the possibility that ensembles of IT neurons code shape on the basis of global features like Fourier Descriptors. If this were the case then different IT neurons should be selective for different FD stimuli. Furthermore, selectivity should be independent of the size, contrast, and position of the stimulus on the retina. The activity of a specific ensemble of such neurons could specify or code any complex shape.

To explore this possibility, we tested the responses of IT units to a series of FD stimuli (Schwartz *et al.*, 1983). Fig. 6 shows the standard set of FD stimuli that was initially used on all cells. Their frequency varied from 2 to 64 cycles/perimeter. Their amplitude and phase were the same, all had an area of 28 deg.^{2} and were white on a dark background. They were projected onto a tangent screen at the center of gaze. The stimuli were always oscillated 1 deg. peak to peak, 1 cycle/sec. for 2.5 seconds and were presented in a randomly interleaved fashion for ten trials each.

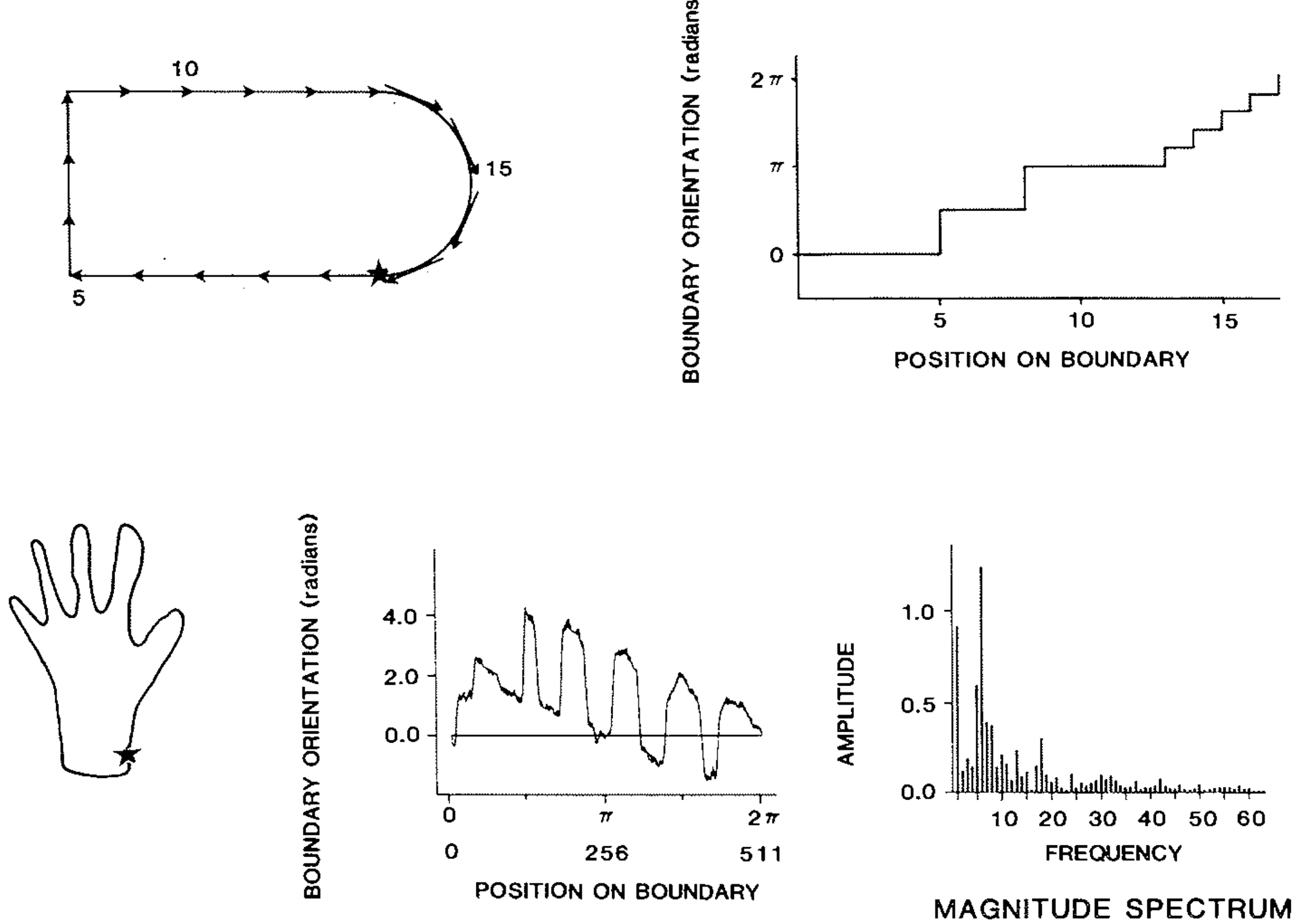

FIG. 5. Top. Derivation of boundary orientation function (right) for simple closed curve (left). The boundary orientation is the angular deviation of the tangent from every point around the perimeter starting at the point indicated by the star. The tangent angle is plotted for very large intervals for purposes of illustration. Bottom. Boundary orientation function (middle) for the shape shown on the left. In this case the boundary orientation function has been normalized to the interval $[0,2\pi]$. On the right, the amplitude of each term of the Fourier expansion in the boundary orientation function is plotted as a function of frequency. For further details

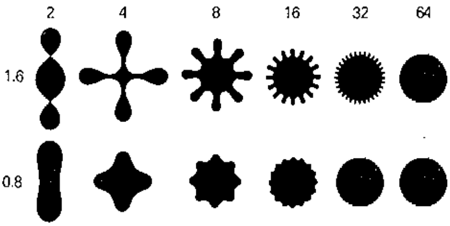

FIG. 6. Examples of FD stimuli varying in frequency (2-64 cycles/perimeter) and amplitude (0.8 and 1.6). The upper row is the "standard" set of stimuli. Unless indicated otherwise, white stimuli were presented on a dark background.

We found that about half the neurons responded selectively to the frequency of the standard set of FD stimuli, i.e., they were "tuned" to the FD stimuli. The remaining cells either did not respond to any of the FD stimuli or responded about equally to all members of the set. Of the selective cells, some fired best to the lower frequencies and others to the higher frequencies as shown in Fig. 7.

To test whether IT neurons are selective for a particular shape regardless of its size, a sample of the tuned cells was retested with FD stimuli of the same frequency, amplitude and phase as the standard ones but either larger (50 deg.^{2}) or smaller (13 deg.^{2}) in size. For two-thirds of these cells, the optimum frequency and the shape of the tuning curve remained similar over changes in stimulus size, although the absolute level of the response varied (Fig. 8). Thus, the selectivity of these neurons for shape remained invariant over changes in stimulus size.

To test whether IT neurons were selective for a particular shape independent of its position on the central retina, some of the frequency tuned cells were retested with the FD stimuli repositioned within their receptive field 3-5 deg. from the center of gaze. For about three-quarters of these cells, the optimal frequency of the FD stimuli and the shape of the tuning curve remained similar at the more peripheral retinal site, although, as with size retesting, the absolute level of the response varied. Responses generally decreased with eccentricity. See Fig. 9. Thus, the selectivity of these neurons for shape remained invariant over retinal translation.

Reversing the contrast of the stimuli did not alter the shape of the tuning curves for several neurons (Fig. 10); they showed shape constancy over contrast reversal.

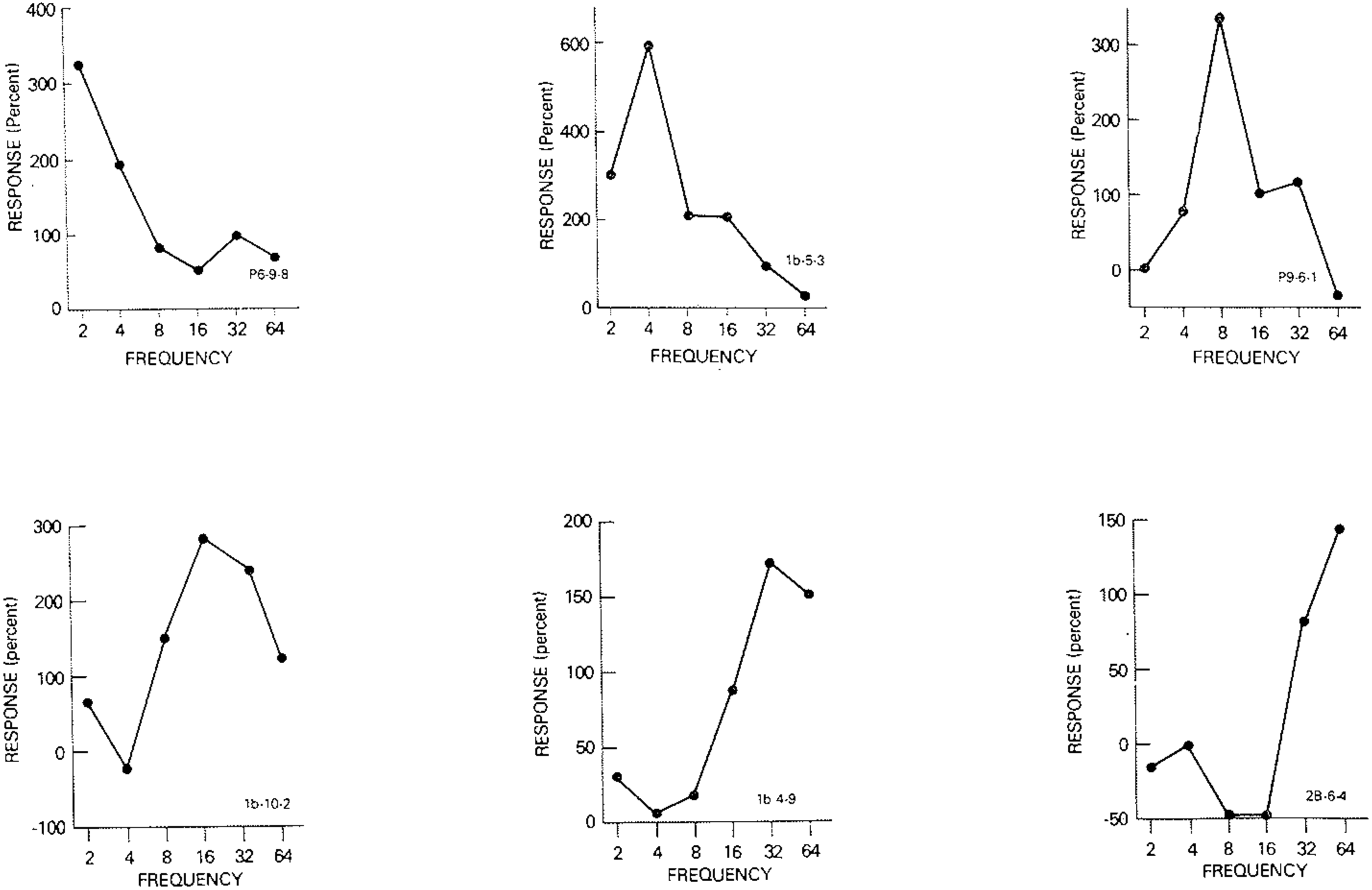

FIG. 7. Responses of six IT units to the standard set of FD stimuli. The graphs show the percent change from base line firing rate during the presentation of the stimuli. Note that different IT cells are tuned to different frequencies.

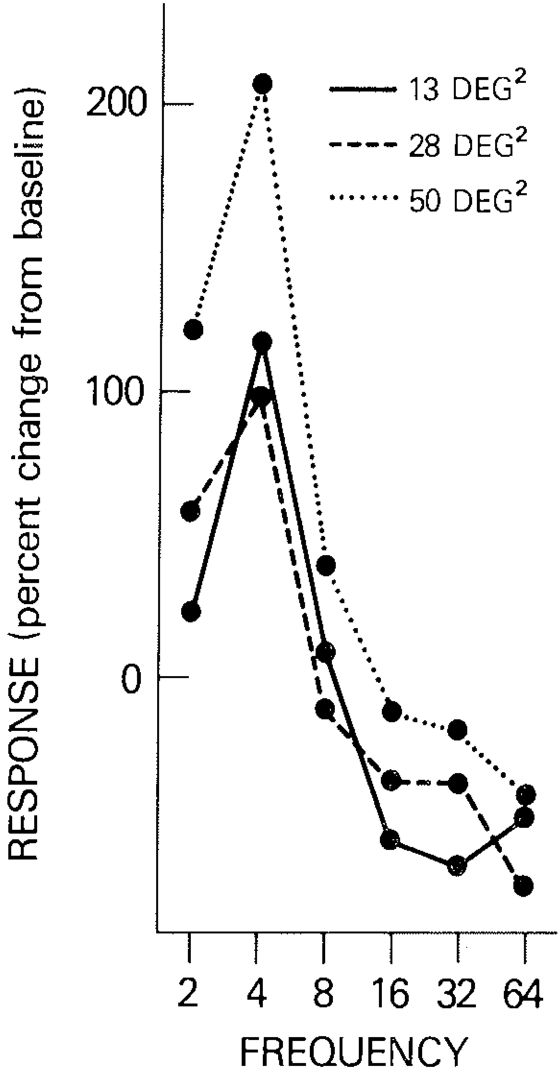

FIG. 8. Effects of FD stimulus size. Responses of an IT unit to the standard set of FD stimuli at three sizes. Note that the best frequency and the shape of the curves are similar at different sizes (Schwartz *et al.*, 1983).

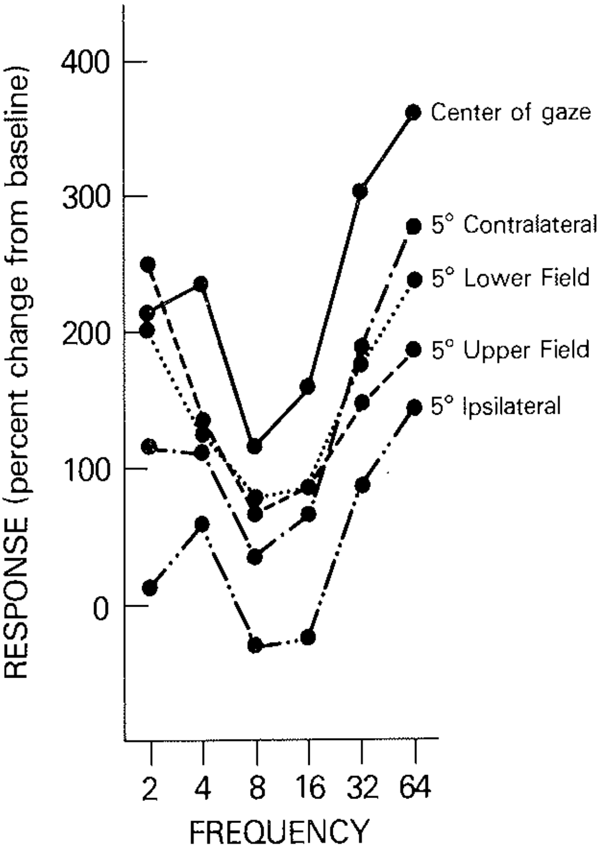

Fig. 9. Effects of FD stimulus position. Responses of an IT unit to the standard set of FD stimuli centered at the center of gaze or 5 deg. into the upper, lower, contralateral, or ipsilateral visual field. Note that the frequencies eliciting the maximum and minimum responses at each location remain the same but the magnitude of the responses is greatest at the fovea and least in the ipsilateral field (Schwartz *et al.*, 1983).

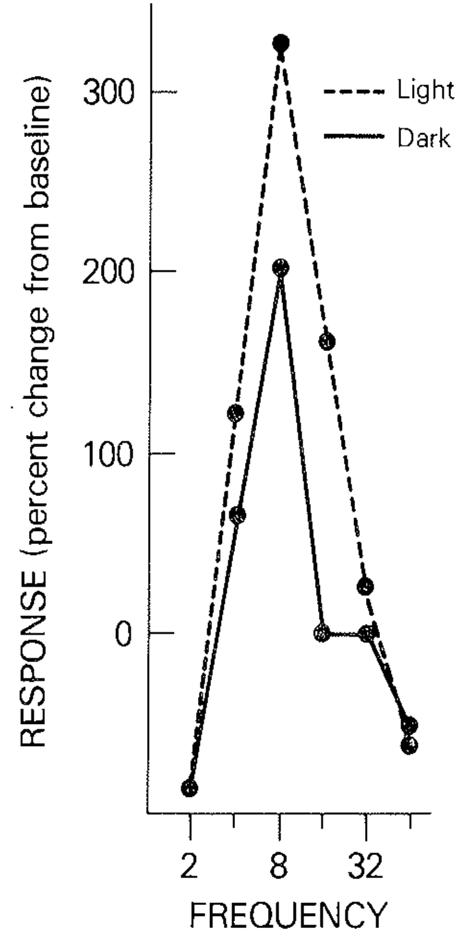

FIG. 10. Effects of FD stimulus contrast. Responses of an IT unit to the standard set of FD stimuli which are light on a dark background and to the same stimuli with the contrast reversed. Note that the tuning is independent of contrast (Schwartz *et al.*, 1983).

The finding that some IT cells maintain their selectivity for FD stimuli of a particular frequency over changes in size, position and contrast cannot be easily explained in terms of selectivity for local features such as the position or orientation of an edge. These cells must have been sensitive, in some fashion, to the overall shape of the stimulus.

Turning to our theoretical question, if IT cortex is coding shape using a mechanism similar to that of Fourier Descriptors, at least some cells should be sensitive to the amplitude of the FD stimuli. We studied the effect of amplitude by holding frequency constant and varying amplitude over five octaves. For more than half of these cells, the magnitude of response was a monotonic function of amplitude. An example of amplitude tuning in one such cell is shown in Fig. 11.

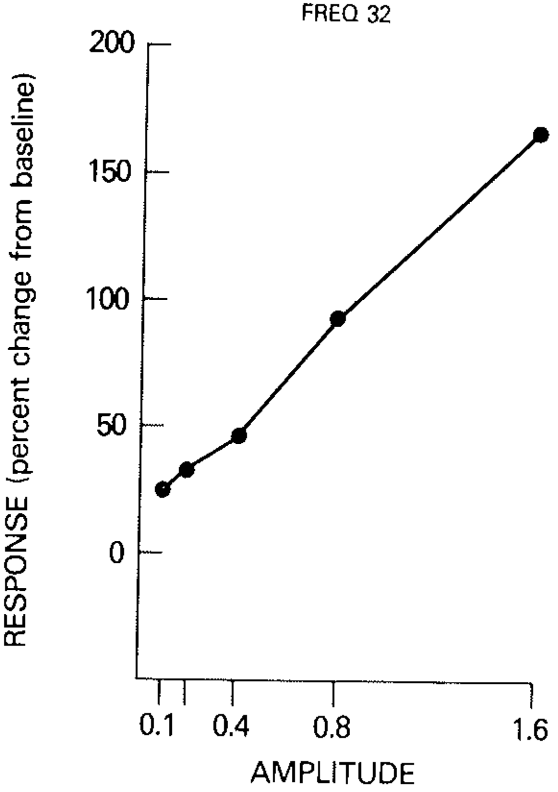

FIG. 11. Effects of FD stimulus amplitude. Responses of an IT unit to FD stimuli with frequency of 32 cycles/perimeter as a function of amplitude. When tested with the standard set, this unit was tuned to a frequency of 32 cycles/perimeter. Note that the response increases linearly with amplitude (Schwartz *et al.*, 1983).

Whether or not IT is actually representing shape by a process similar to Fourier Descriptors is, of course, still an open question. The first requirement, selectivity for individual FD stimuli, has been met by some units. The second and more stringent test will be to determine if IT responses to complex shapes can be predicted by their responses to individual FD stimuli.

In any case, the present results support the hypothesis that shape is an important stimulus dimension processed by IT cortex. Just as striate cortex analyzes local boundary orientation, IT cortex may be involved in the analysis of global boundary orientation. However, it should be stressed that even if some IT neurons represent or code boundary curvature, this cannot be the exclusive function of IT cortex. Some IT cells are selective for color, for texture, for spatial frequency, for three-dimensionality and for such complex stimuli such as faces. These stimulus dimensions are not readily described only in terms of boundary curvature. Selectivity for boundary curvature appears to be neither a characteristic of all IT cells nor the exclusive response property of many.

CONCLUDING DISCUSSION

Several of the characteristics of IT neurons are precisely what we would expect of an area involved in the final stages of pattern recognition. These include absence of visuotopic organization, large receptive fields that always include the center of gaze, and invariance of stimulus selectivity over changes in exact retinal location, size and contrast.

There are at least two types of ways that IT cells might code the visual world. One way, originally proposed by Kornorski (1967) in his "gnostic cell" hypothesis and later, by Barlow (1972), in his "cardinal cell" hypotheses, suggests that the firing of individual IT cells might code or represent complex stimuli or percepts. The second way is through some type of ensemble code, that is, through the pattern of firing across a population of cells. Our results do not enable either of these types of hypotheses to be rejected. Indeed, they suggest that at least some IT units may be involved in each type of mechanism.

The finding that the majority of IT cells gave at least a small response to virtually every stimulus tested is supportive of the ensemble idea, the view that the neural representation of objects in IT is the pattern of activity across a population of neurons. We found some IT cells selective for a particular color, independent of the shape of stimulus, others selective for some aspect of shape, independent of color, and a few selective for texture, independent of either color or shape. Such cells, which made up a large proportion of our sample, are likely candidates for members of an ensemble mechanism for representing visual stimuli. They are certainly very unlikely to be detectors for specific percepts. More specific support for ensemble coding of shape comes from our finding that many IT cells were tuned to a specific boundary curvature. On the other hand, the existence of a few IT neurons selective for faces and for hands demonstrate that there may indeed be IT units that serve as detectors or narrow filters for highly specific and complex stimuli. However, such detectors may be restricted to a very small class of particularly important stimuli such as faces.

ACKNOWLEDGEMENTS

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NEURONAL ACTIVITY IN RELATION TO THE RECOGNITION OF STIMULI IN THE PRIMATE

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INTRODUCTION

In this article three aspects of the neural basis of pattern recognition are discussed. First, investigations of how neuronal activity in different brain regions implicated in memory is related to the recognition of visual stimuli in tests of relatively long as well as short term memory are described. Second, the way in which the activity of certain populations of neurons in regions of association cortex in the primate temporal lobe, and in certain connected subcortical regions, is specialized for the analysis of a particular class of stimuli, faces, is discussed. Third, neural systems which receive inputs from the temporal lobe visual areas but specialize in different ways in how they use this pattern-specific visual information are discussed.

Neuronal Responses Related to Recognition Memory.

The inferior temporal visual cortex receives visual information via a number of different prestriate visual areas, and has outputs directed to a wide variety of limbic as well as cortical regions (see Fig. 1). One output pathway from the inferior temporal cortex projects via the parahippocampal gyrus to the entorhinal cortex, which in turn has connections to the hippocampus (Van Hoesen and Pandya, 1975 a, b; Van Hoesen, 1982 (see Fig. 1). On anatomical evidence there is thus a potentially important sequence for visual information as follows: inferior temporal cortex, entorhinal cortex, hippocampus, fornix, mammillary bodies, and

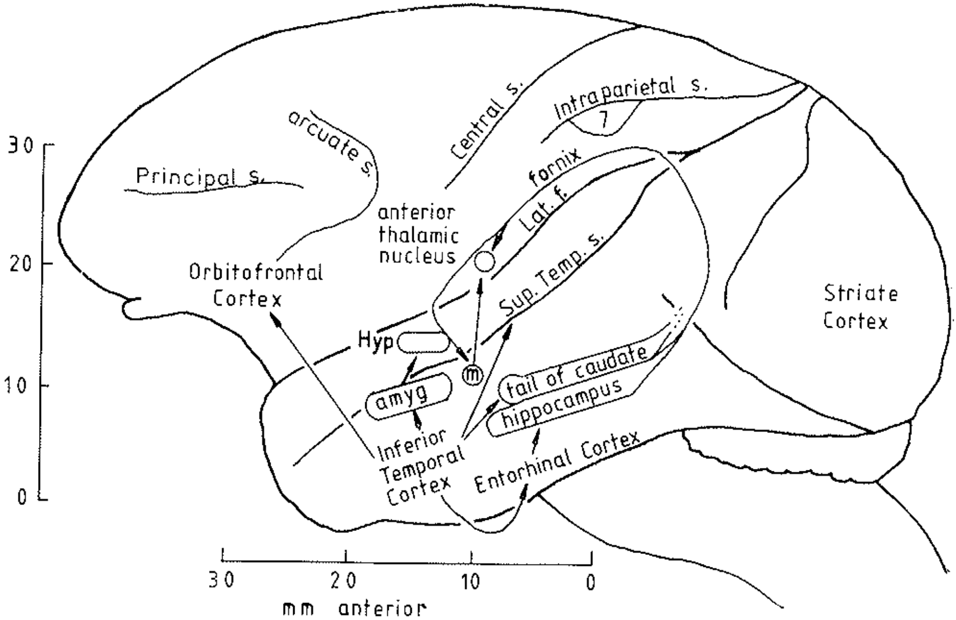

FIG. 1. Some of the pathways described in the text are shown on this lateral view of the rhesus monkey brain. amyg = amygdala; central s = central sulcus; Hyp = hypothalamus / substantia innominata / basal forebrain; Lat f = lateral (or Sylvian) fissure; m = mammillary body; Sup Temp s = superior temporal sulcus; 7 = posterior parietal cortex, area 7.

anterior thalamus. There is evidence relating damage to different parts of this sequence to anterograde amnesia in man, evident as a major deficit in learning to recognize new stimuli (Scoville and Milner, 1957; Milner, 1972; Mair, Warrington and Weiskrantz, 1979; Kesner, 1982). Clinically, this type of amnesia can be so severe that the patient does not learn to recognise the physician who sees him every day. Recently, the evidence relating hippocampal damage to the amnesia has been questioned, and instead it has been suggested that damage to cortical association fibers in the temporal stem (Horel, 1978) or combined damage to the hippocampus and amygdala (Mishkin, 1978) is important in producing the amnesia. Also, there is evidence for (O'Keefe and Nadel, 1979) and against (see Olton, 1982) the hypothesis that the hippocampus is involved in spatial or cognitive mapping. To determine in which of the postulated neural systems neuronal activity is related to visual recognition, and to investigate how neuronal processing in the identified system is related to visual recognition memory, recordings are now being made in the monkey from the different systems implicated in amnesia.

The recordings are being made from single neurons while the monkeys are performing a visual recognition task of the type impaired in anterograde amnesia in man. Each visual stimulus is shown twice per day, once as novel, and after 0-17 other intervening items in the recognition task, on a second trial, as familiar, when the monkey can lick to obtain fruit juice if he recognizes the stimulus correctly. In recordings made during the performance of this task, a population of neurons was found at the anterior border of the thalamus which responded to the stimuli only when they were familiar (see Rolls, Perrett, Caan and Wilson, 1982). The activity of these neurons was not related to lick responses. Further, in the different, visual discrimination, task a number of these neurons were found to respond both to the familiar reward-associated stimulus to which the monkey always licked, and to the familiar aversive stimulus to which he did not lick. This shows that in a reward association task these neurons respond on the basis of familiarity, providing evidence for a dissociation of recognition and stimulus-reinforcement association memories.

Analysis of the responses of these neurons in the serial visual recognition task showed that the responses to familiar stimuli were time-locked to the onset and duration of the visual stimulation (brief exposures producing brief responses). The response latencies were in the range 100-200 ms. A 100 ms exposure of the stimulus was sufficient for the stimulus to be encoded, and a 100 ms exposure was also sufficient for a recognition-related response. The magnitude of the neuronal response on trials with familiar stimuli decreased as the number of trials between the first (novel) and second (familiar) presentation of the same stimulus increased. The rate of this decay or "forgetting" varied from cell to cell and was best described by an exponential function. Repeated exposure tended to slow the rate of forgetting, and two or three repeated presentations prolonged some cell "memories" for more than 100 intervening trials. The neurons showed some ability to respond to stimuli as familiar despite changes in viewing conditions and transformations such as 90 degree rotation.

These neurons are in an anterior midline thalamic region in or close to which there is often damage in humans with memory disorder of the Korsakoff type (Victor, Adams and Collins, 1977; Mair, Warrington and Weiskrantz, 1979). This region is close to and probably connected with the thalamic region in which lesions produce memory impairments in monkeys (Mishkin and Aggleton, 1981). Also, this region is closely connected with temporal lobe regions which have been implicated in amnesia (see Rolls, Perrett, Caan and Wilson, 1982).

This type of experiment thus indicates that neuronal activity related to recognition can be found in one of the systems implicated in amnesia, and suggests fascinating possibilities for tracing the processing related to recognition memory through the system, and quantifying to what extent neuronal activity in different regions is related to the formation of memories which can persist over long time intervals which include interfering stimuli. This type of experiment also allows parameters affecting such memory mechanisms to be investigated, and has in addition provided evidence on the separate nature of stimulus-reinforcement association memory and recognition memory (see Rolls *et al.*, 1982).

There is some evidence that earlier in these pathways, in the inferior temporal visual cortex, neuronal activity is related in some way to memory (Mikami and Kubota, 1980; Fuster, 1977). This evidence has heen obtained in a delayed matching to sample task, in which a sample stimulus is shown, and after a delay of a number of seconds, a second stimulus is shown again. If the second stimulus matches the first, the monkey can make one response, and if the stimulus does not match, a different response must be made. Usually a limited number of visual stimuli are used in this task (non trial-unique stimuli), so that the task specifically requires use of a relatively short term of memory, for whether a particular stimulus has been seen in the last few seconds; it will have been seen in any case many times in the last few minutes. In this type of task, some neurons respond more to the sample stimulus, and some to the match stimulus, and some are stimulus selective, responding more for example to a red than to a green stimulus (Mikami and Kubota, 1980; Fuster, 1977). To determine whether these neurons in the inferior tempral visual cortex were particularly specialized for this relatively short term type of memory, or whether these or other inferior temporal neurons might be involved in the longer term recognition of visual stimuli, we (Baylis and Rolls, 1983) are comparing the activity of inferior temporal cortex neurons in a delayed matching to sample task with their responses in the test of longer term recognition memory described above. In the present sample of approximately 300 neurons, the majority have had visual responses which were not related to memory in either the delayed matching to sample or the longer term serial recognition task. The only aspect of their responses which bore any relation to memory was that for some neurons if a stimulus was shown repeatedly for trial after trial with no other intervening stimuli, then the response might habituate a little. (Of course, if the monkey stopped performing the task, and was no longer paying any attention to the stimuli, then the responses declined more rapidly.) Of the inferior temporal neurons which did have activity related to memory aspects of the delayed matching to sample task, some responded less to the match stimulus if it was the same as the sample stimulus, and others responded more if it was the same. When these neurons were tested in the recognition task, it was found that their "memory spans" were quite short, as shown by the small number (usually 0-2) of intervening stimuli over which a neuron could still respond differently to a stimulus which had been seen before on a previous trial. Thus these inferior temporal neurons have responses which would be useful for a relatively short term memory of visual stimuli lasting a number of seconds without intervening visual stimuli, but do not appear to be adequate for longer term recognition of visual stimuli. Indeed, no inferior temporal neurons were found in this sample with activity related to longer term recognition memory. This evidence suggests that the inferior temporal cortex may be involved in relatively short term memory for visual stimuli, but not in longer term recognition memory. Structures which receive from the inferior temporal cortex could be involved in this. One possible system is the entorhinal cortex (which receives from the inferior temporal visual cortex via parahippocampal areas - Van Hoesen, 1982) / hippocampus / mammillary bodies system, and this has connections to the rostral midline thalamic region in which we have found neurons with activity related to recognition memory (Rolls *et al.*, 1982). We are recording in different parts of this hippocampal system now to determine whether neuronal activity in it becomes related to recognition.

The evidence just described indicating that inferior temporal cortex neurons do not have activity related to the long term recognition of visual stimuli is of interest in relation to the pathways which return to the neocortex from limbic structures (see Mishkin and Aggleton, 1981), for it suggests that limbic structures do not through these pathways influence inferior temporal cortex neurons in such a way as to make these neurons respond in relation to the relatively long term recognition or recency memory tested-here.

One system other than this hippocampal system described above which does receive from the inferior temporal visual cortex, is the amygdala, and as damage to this combined with damage to the hippocampus produces a severe deficit in memory (Mishkin, 1978), we (E.T. Rolls and

F.A.W. Wilson) have investigated whether neurons in the amygdala have activity related to memory. It has been found so far, using the recognition task, that some neurons in the amygdala respond more to novel than to familiar stimuli, but that the responses of these neurons do not reflect such prior experience for more than a few intervening trials. This preliminary evidence thus indicates that such neurons could make a contribution to memory lasting for up to perhaps one minute with a few intervening stimuli, and may thus play some role in what is still relatively short term pattern recognition.

Neurons in visual association cortex and connected regions with responses selective for faces.

The visual responses of the majority of neurons which we have recorded in the inferior temporal visual cortex did not occur uniquely to particular objects, but instead occurred to a number of objects. In some cases it was possible to show that the selectivity of the responses was due to physical features of the stimuli such as texture, color or shape (Rolls, Judge and Sanghera, 1977). However, in one part of visual association cortex we have found that neurons respond particularly well to one class of biologically important stimuli, faces. These neurons were recorded in the cortex in the depths of the anterior part of the superior temporal sulcus in the rhesus monkey, Macaca mulatta (Perrett, Rolls and Caan, 1982), which is a part of association cortex which receives from the inferior temporal visual cortex (Jones and Powell, 1970; Seltzer and Pandya, 1978) (see Fig. 1). In a sample of 497 single neurons recorded in the depths of the superior temporal sulcus, analysis of the responses of 48 neurons with responses selective for faces showed the following (Perrett, Rolls and Caan, 1982). All 48 neurons responded to faces (which were human or rhesus monkey, 3-D or projected images, and shown to the monkey through a large-aperture shutter with visual fixation monitored), and were almost unresponsive or much less responsive to gratings, simple geometrical, and other complex 3-D visual stimuli. The neuronal responses to the sight of a face were sustained and had latencies of 80-160 ms. The neurons were in general unresponsive to auditory or tactile stimulation which was aversive or arousing as shown by the GSR, or to stimuli such as a hand which signified a human or a monkey. Masking out, or presenting isolated parts of, faces showed that some cells responded on the basis of different features. Some required eyes, some hair, some the mouth, and others showed parallel responses to each of a number of features. Some cells responded more strongly when such component features of faces were combined. Presenting the face in profile failed to elicit a response for some cells. Transformations of the face such as isomorphic rotation, or alterations of color, size or distance, did not greatly affect the magnitude of the neuronal responses. These results provide evidence that in the primate there are neurons specialised to respond to the component visual features present in faces (Perrett, Rolls and Caan, 1982).

In further experiments of E.T. Rolls, G. Baylis, F.A.W. Wilson and C. Leonard, the response properties of these neurons are being analysed further, and the distribution of neurons with responses which occur primarily to faces in different brain regions is being investigated. First, it has been found that although many of these neurons respond to most faces, some of these neurons can respond only to some individuals. In some cases it has been possible to demonstrate the basis on which the neuron responded selectively only to one individual. One such individuating feature for a neuron was a high and straight hairline, and if this was disturbed, then the neuron no longer responded even to that individual. Second, it has been found that some of these neurons can respond differently to different facial expressions. For example one neuron responded to an open mouth but not to a closed mouth, and this neuron responded phasically to lip-smacking (a social greeting) by the stimulus monkey or human. Third, it has been found that these neurons can be found over a large anterior-posterior extent of the cortex in the superior temporal sulcus (from 5 to 16 mm anterior to the interaural plane), and are found not only in the fundus of the superior temporal sulcus (Perrett, Rolls and Caan, 1982), but also extend out in the banks of the sulcus. We have also found a small number of similar neurons in the inferior temporal cortex itself (see also Desimone *et al.*, 1980).

A small number of neurons which responded primarily to faces has also been found in the amygdala (Sanghera, Rolls and Roper-Hall, 1979; Rolls, 1981 b), which receives a projection from the cortex in the superior temporal sulcus (Aggleton, Burton and Passingham, 1980). It is suggested that a system specialised for the perception of faces might have evolved because of the importance of rapid and reliable identification of individuals by their face and of face expression in the social behavior of primates, useful for example in the maintenance of dominance hierarchies in monkeys; and that damage to this system may contribute to some of the symptoms, such as tameness, which are part of the Kluver-Bucy syndrome, and are produced by temporal lobe lesions in monkeys (Kluver and Bucy, 1939; Jones and Mishkin, 1972; Kling and Steklis, 1976).

A hypothesis consistent with current evidence is that the neurons in the superior temporal sulcus with responses selective for faces provide in their overall pattern of activity information useful (by virtue of their responses to parts of faces, or to combinations of parts of faces, which in some cases have been shown to provide differential information between individuals, or to reflect facial expression), to connected brain areas for face identification and for emotional and social responses. The amygdala may be particularly involved in the utilization of this information for emotional and social responses, as shown by the evidence that it is such behavioral responses to faces which are disrupted by amygdala damage (Weiskrantz, 1956; Kling and Steklis, 1980; Aggleton and Passingham, 1981). The neurons in the superior temporal sulcus do not themselves appear to be involved in the emotional aspects of this processing (but rather to be afferent to it), in that their responses are tightly time locked to the offset as well as the onset of the visual stimuli (Perrett, Rolls and Caan, 1982), and in that their responses do not depend on whether the face stimulus is rewarded, is punished, or is neutral, that is on the emotional response produced to the face (experiments in progress). The output from the superior temporal sulcus to the parahippocampal gyrus (Amaral, Insausti, and Cowan, 1983) may be particularly involved in recognition of particular faces, and dysfunction along this pathway may be involved in prosopagnosia, in which individuals cannot be recognized from the sight of their face (Damasio, Damasio and Van Hoesen, 1982). Again, the neurons in the superior temporal sulcus may not themselves be involved in the decision as to whether a particular face has been seen before (but rather may be afferent to it), in that these neurons do not respond differently to novel and familiar faces (experiments in progress). Thus these neurons in the superior temporal sulcus may provide an analyzed representation of faces, and the overall pattern of their activity may be used for different functions by different systems connected to them. They may be part of a system which has evolved specially for faces because of their biological significance, and it may not be expected that most environmental stimuli will be represented in such a naturalistic way (Rolls, 1984).

Outputs from the inferior temporal visual cortex to other brain regions.

The inferior temporal visual cortex has outputs to a number of different brain regions (some indicated on Fig. 1), each one of which appears to specialize in the use to which it puts the pattern-specific visual information it receives (Rolls, 1981 a), as follows. The outputs to the amygdala appear to be to a system involved in determining whether the visual stimulus has previously been associated with reward or punishment, as shown by lesion evidence and the responses of neurons in the amygdala (see Rolls, 1981 a, b; 1984 a, b). Further connections of this system to the basal forebrain and hypothalamus appear to be involved in refining this further, and in relating the stimulus to the motivational state of the animal, so that in the basal forebrain there are for example neurons which respond to visual stimuli only if the monkey has learned that they mean food, and if he is hungry (see Rolls, 1981 a,c, 1983, 1984). The outputs of the inferior temporal cortex to the orbitofrontal cortex may be involved in the determination of whether a particular visual stimulus is no longer associated with reward or punishment, a function in which the orbitofrontal cortex is implicated by lesion evidence and by responses of single neurons in the orbitofrontal cortex (Thorpe, Rolls and Maddison, 1983). The outputs to the tail of the caudate nucleus may be involved in short term pattern-specific behavioral habituation to visual stimuli, a process to which the responses of neurons in this region are related (Caan, Thorpe and Rolls, 1983). Finally, the outputs of the inferior temporal cortex to the hippocampal system described above may be involved in the evaluation of whether a particular stimulus has been seen before. It is of interest that each of these outputs of the inferior temporal visual cortex is being used for a different function, each requiring a pattern-specific representation of the visual stimulus, so that there may be no unique "recognition" of a stimulus, but rather use of a representation of a stimulus by a number of different, subsequent, probably partly parallel and independent processing systems.

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CORTICAL ACTIVITY IN MAN DURING DISCRIMINATION OF EXTRINSIC PATTERNS AND RETRIEVAL OF INTRINSIC PATTERNS

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Somatosensory detection of unknown objects. An introductory example

Imagine that a subject, with his eyes closed, tactually has to detect an unknown object (Fig. 1). He takes the object in his hand. The tips of the thumb, indexfinger and long finger slide independently across the surface. At times, the object is transferred to the palm, and totally encompassed by the mechanoreceptive fields of the glabrous skin. Next, the fingertips are again sliding across the surface in space curves that continuously change directions in a three dimensional coordinate system. The axes of the fingers turn continuously, occasionally, the skin of the middle and proximal phalanges comes into contact with the object surface. Only after a few thousand milliseconds of palpation the object seems sufficiently examined so that the subject has a clear image of the size, shape, surface-properties and thermal qualities of the object.

This sequence of events was taken from a videofilm of naive subjects who for the first time, blindfolded, were asked to examine the object in Fig. 1. It was apparent that the sampling of information about the object was sequential. Different manipulation and sampling strategies were used in succession. Sixty-three normal subjects were studied while they discriminated the shape of ellipsoids. From these, fourteen had videofilms taken of their manipulation of the ellipsoids. More than 1000 discriminations were studied in each individual (Roland and Mortensen, 1984).

The only way the subjects could get information about the ellipsoids was through palpating the surface. Ellipsoids are non redundant objects.

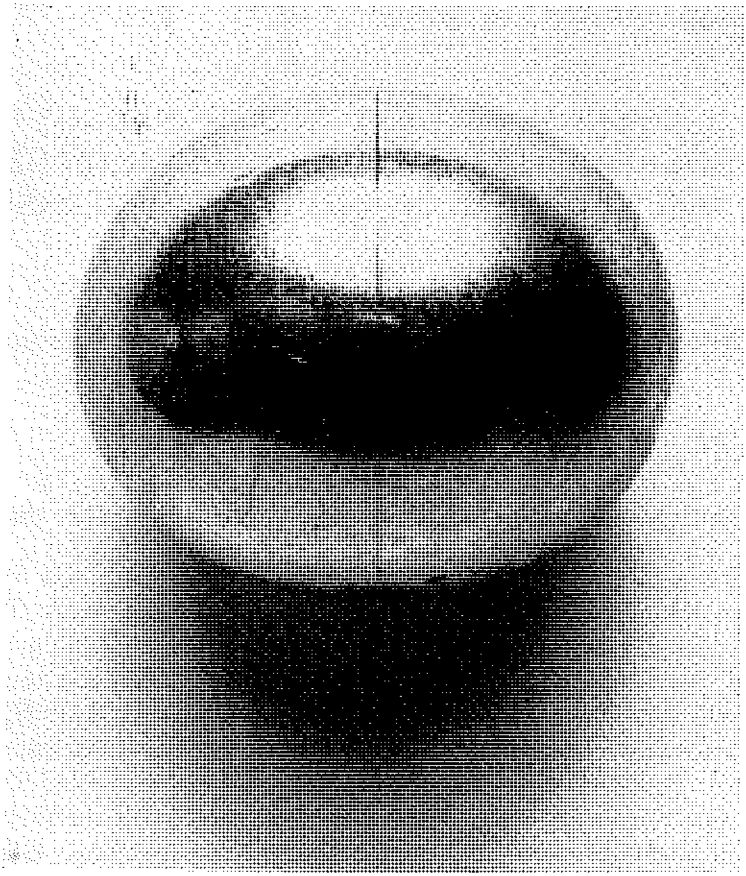

FIG. 1. An ellipsoid, an example of an object which information theoretically is compact (non-redundant). The object can be described entirely by the equation:

$$\left(\frac{x}{a}\right)^2 + \left(\frac{y}{b}\right)^2 + \left(\frac{z}{c}\right)^2 = 1$$

The object can be fully recognized when the parameters *a*, *b*, and *c* are known or when all possible sets of (x, y, z) are known. By tactile examination a subject can only get information about the object through palpation of the surface. Since the curvature is identical in only four symmetrical points on the surface, full recognition (identification) will in practice be impossible. Such computergenerated ellipsoids have been used in the somatosensory discriminations described in the text. The two halves of the object were glued together, but the line of transition could not be felt.

Their shape is determined by the curvature in each point of the surface. Since the curvature is identical only in four symmetrical points of the whole surface, ellipsoids are very compact (non redundant) signals. From the study of the many discriminations, it was apparent that normal subjects, even those who were naive, used a uniform way of sampling the information from the ellipsoids: the palpation mode described in the introduction.

It could be shown that this mode of somatosensory information sampling was *optimal* in several respects. First, the path that each finger described across the surface was so that the maximum possible number of points with different curvatures were touched. Second, the error that arises in any tactile determination of objects due to the distance between the mechanoreceptors in the skin was minimized. This error is an error of spatial resolution. It appears in directions orthogonal to the direction of movement for the receptive surface, the fingertip. In the direction of movement there is another error that also limits a complete tactile perception. This is the quantification error that arises because the mechanoreceptors of the skin, although they continuously receive information about the surface, convert this information to discrete nerve impulses. Since the quantification error is smaller than the error of resolution the turning of the axes of the fingers during the palpation minimizes the error of resolution of the examined surface.

Somatosensory perception is subjugated to a principle of complementarity. It is impossible at a first grasp to recognize the object in Fig. 1 as an ellipsoid. The reason is that the central nervous system is a priori unaware of the parameters that define the object as an ellipsoids. Furthermore, even if it, after a relatively short manual examination, is apparent that the object with great likelihood is a round object that may be an ellipsoid or an object composed of two paraboloids — it will take a tedious examination to find out whether the object, as in this case, is rotational symmetrical or not, (i.e. $b = c$ in the equation, Fig. 1). Such accuracy may not be feasible. The somatosensory system recognizes objects *iteratively*. The sequentially sampled information is used to detect the palpated object with successively declining uncertainty.

If the somatosensory detector is an optimal detector it must recognize objects on the basis of the total sum of information that was sampled about the object. Likewise, if two objects have to be descriminated, the discrimination must be based on the total sum of information sampled from both the first and the second object. Most likely the central nervous system reconstructs an internal image of the palpated object. It follows, that if the nervous system lacks a priori knowledge about the object or the object is compact — the reconstruction is iterative.

The optimal sampling of somatosensory information requires a minute collaboration between the control of the voluntary movements and the areas that integrate the sampled information. If two compact objects have to be discriminated, the central nervous system must in addition judge whether the reconstructs are sufficiently different, or whether resampling or new sampling strategies are necessary.

In Fig. 2 is an example of a regional cerebral blood flow (rCBF) measurement in 254 cortical regions of a neurologically normal subject that discriminates the shapes of ellipsoids under a two alternative forced-choice paradigm (2 AFC). In accordance with the informational constituants of the task, the rCBF increased in the somatosensory hand area, the motor hand area, the superior prefrontal cortex, the midfrontal cortex and the somatosensory association cortices in the anterior part of the superior parietal lobe and the supplementary sensory area. In addition there were rCBF increases in the motor areas that plan the path of palpation, the sequence of palpation paths, object rotations and encompassings of the object: the supplementary motor area and the premotor cortex. Roland and Larsen (1976) studied the rCBF as an indicator of neuronal activity while subjects were discriminating the shape of rectangular parallelepipeda. We used the same 2 AFC paradigm and found rCBF increases in the same cortical areas with the exception of the supplementary sensory area. The reason why this area was missed was that we at that point did not take vertex projections of the patients that were studied.

That the three motor areas really were responsible for the motor control of the sampling paths and the sequences of object rotations and encompassings is apparent in Fig. 4. Here the subjects are passively stimulated with rectangular parallelepideda pressed in different configurations against their palms. No movements occurred. Accordingly there are no measurable rCBF change in the primary motor area, the supplementary motor area or the posterior part of the premotor cortex. There was, however, a slight increase of rCBF on the border between premotor cortex and posterior prefrontal cortex (7 per cent and 11 per cent, Fig. 4, top). This region may be an obligate station for the outward progression of somatosensory information from the postcentral cortex. Otherwise the same cortical areas were activated as in Fig. 2.

Not all somatosensory association areas may be seen with the two dimensional rCBF technique used for the production of the results in Fig. 2.

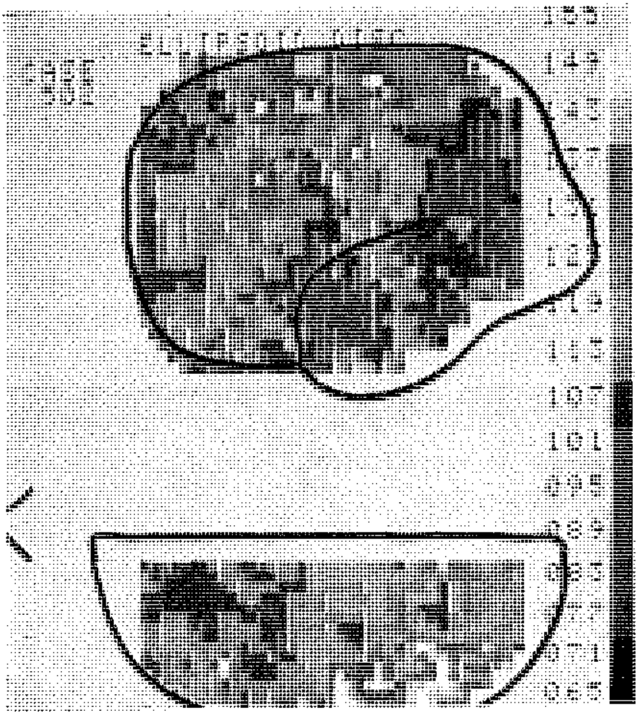

FIG. 2. The regional cerebral blood flow (rCBF) changes in the left hemisphere of a subject discriminating the shapes of ellipsoids with the right hand. The paradigm was a temporal two-alternative forced choice discrimination, in which the subject was only allowed to palpate the ellipsoids in succession. The scale shows the increase of rCBF in percent + 100. *Top*, lateral view: increases in sensory and motor hand area, anterior superior parietal cortex, the premotor area, the supplementary motor area, the posterior superior frontal region (mesial and lateral), the anterior midfrontal region, and the superior anterior prefrontal region. *Lower*: vertex view, same subject, note the increases in the supplementary motor area and the supplementary sensory area (close to midline). The activation of the sensory and motor hand area is also seen together with the superior prefrontal increases. The increases in the motor mouth area and the slight increase in Broca's area was due to the verbal responses from the subject. The rest of the increases were not statistically significant in the small group investigated. Nose marked on Fig. Subject has closed eyes and plugged ears, and he was manipulating the objects optimally as described in text. (from Roland and Friberg, unpublished observations).

Recent experiments on somatosensory shape discrimination in patients with focal cerebral lesions show that damage not only to the postcentral gyrus, but also to the anterior superior parietal lobule the supplementary sensory area, the parietal operculum, and retroinsular cortex in the contralateral hemisphere impair shape discrimination. It was demonstrated that these effects were sensory (Roland, 1984). The second somatosensory area may also be included in the somatosensory association areas (Roland *et al.*, 1982a), although damage to this area did not impair shape discrimination. The primary somatosensory cortex, the anterior superior parietal cortex, the supplementary sensory area and the retroinsular cortex are thus assumed to participate in the reconstruction of the palpated objects.

The internal reconstruction of objects may be under the control of prefrontal cortical areas. For reasons that will be apparent a little later, the anterior midfrontal cortex is the most likely candidate to exert this control (for nomenclature of cortical regions see Fig. 6). Damage to this region caused no sensory defects in discrimination, but the variance in signal to noise ratios of shape discriminations was abnormally large (Roland, 1984). The activity in the superior prefrontal cortex is not limited to somatosensory discriminations. As discussed later, it is assumed to reflect the maintenance of the intention. In an experimental situation, for example 2 AFC discrimination, the intention of the subject is a result of what we asked him to do with the sensory stimuli.

The organization of the cortical activations during somatosensory discrimination is not produced by the stimulation with somatosensory stimuli. The brain organizes its own activity. If a subject is expecting a very weak threshold touch on the tip of the indexfinger, the rCBF increases in the contralateral somatosensory hand-finger area, the immediate somatosensory association cortex in the anterior superior parietal lobe, the superior prefrontal cortex and the anterior midfrontal cortex (Roland, 1981). That is, despite the total absence of somatosensory stimulation (or other stimulation) the rCBF increased in the same cortical regions as during passive stimulation (compare Fig. 3 with Fig. 4). The increase of rCBF in the primary sensory hand-finger area was interpreted as a metabolic increase in this region due to preparatory tuning. By tuning was meant a facillitatory preparation of the receptive area such that it became an optimal receiver for the expected signal. The metabolic increase in the somatosensory hand-finger area was assumed to be due to a local increase in the number of excitatory postsynaptic potentials (EPSP's) (Roland, 1981). One might ask how it is possible to distinguish rCBF increases due to the effects of attention from rCBF increases due to information processing. The answer is that it is a destinction that has to be made on behavioral grounds. In Fig. 2 the subject demonstrably discriminated the ellipsoids, the subjects depicted in Fig. 3 demonstrably received no stimuli.

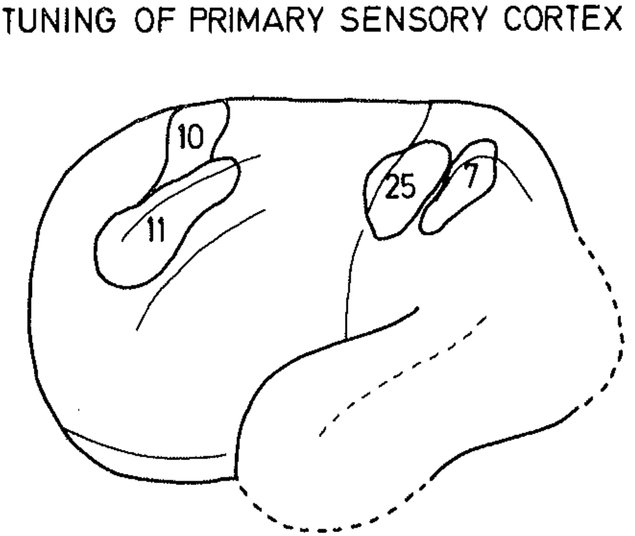

FIG. 3. Mean percent increase in rCBF during somatosensory attention directed towards the tip of the contralateral indexfinger. Eight subjects, expecting a threshold touch with a von Frey hair, but who were not stimulated at all prior to or during the rCBF measurement. Eyes were closed and the ears were plugged. Each individual focus of rCBF change was after proportional reduction/magnification, transferred to this chart of the brain in standard dimensions. The chart shows the projection of the cortical surface achieved from the hemisphericly arranged collimator tubes (Fig. 5). Every increase in rCBF is shown by its average extension. All increases shown were statistically significant beyond 0.05 level. (Redrawn after Roland, 1981).

The preparatory tuning was seemingly controlled partly by the anterior midfrontal cortex.

The rCBF method

The use of rCBF as an indicator of local cortical metabolism is based on the linear relationship between the local cortical oxygen consumption and the rCBF and between the local cerebral glucose consumption and the rCBF (Raichle *et al.*, 1976; Reivich *et al.*, 1975). Lassen and Munck (1955) developed the inert gas method for cerebral blood flow measurements in humans after the original measurements with N_2O by Kety and Schmidt (1945). In the experiments described in this chapter, the blood flow was measured with ^{133}Xe or ^{77}Kr. In both cases the washout of the isotope from the brain is exponentially declining. If the arterial concentration of isotope is known as a function of time, the rCBF can be calculated (Roland *et al.*, 1982a). With intracarotid injection of the isotope (^{133}Xe) the time resolution is 30 sec. The spatial resolution in cortex is 1.0-1.2 cm. However, it is not possible to monitor the order in which the different cortical areas are activated. The figures show the average increase of rCBF in a cortical region during 30 sec of brain work. Another drawback of the ^{133}Xe-intracarotid injection method is that only the cortex supplied by the branches of the carotid artery can be monitored. For example, the primary visual cortex is not visible in general with this method.

Due to absorption of the isotope in the brain tissue, it is not possible to see cortical areas buried in the lateral sulcus, i.e. the primary auditory cortex. These limitations can be overcome by positron emission tomography with ^{77}Kr, where rCBF in the whole brain can be measured with a time resolution of 200 sec (Roland *et al.*, 1982a).

Changes in blood flow due to brain work are measured in relation to a control state called rest (Fig. 7). Rest is an ill defined state in which the subjects are relaxed, awake, with closed eyes and plugged ears. The galvanic skin response is stable, the blood pressure and pulse rate are as seen in physical rest (Roland and Larsen, 1976). Nevertheless, although the subjects are carefully instructed and adapted to all procedures, we cannot prevent them from thinking. Until a stable awake state of the mind has been found, one has to accept that the baseline for behavioral studies of the brain is no better than "rest".

Increases of rCBF in a cortical area is most likely due to a local net increase in excitation (action potentials and EPSP's). Postsynaptic inhibitory neurotransmittors (GABA-antagonist's) decrease the cortical blood flow powerfully (Roland and Friberg, 1983). The rCBF level, thus, reflects to the local balance between excitation and inhibition in the cortex. It must be stressed, however, that this conclusion holds only for the cerebral cortex.

An rCBF increase can be due to increased activity in the afferents to the cortical area or to increased intrinsic activity in the aera or due to increased activity in efferent neurons. On the basis of the observation of an rCBF increase, in an intact human being, there is no way of distinguishing which of these mechanisms are responsible.

Cortical areas participating in discrimination of auditory extrinsic patterns

Auditory signals are seldom repeated. If it was not for a very efficient immediate memory, auditory pattern recognition would be impossible. Auditory signals are sequential. Consequently, their initial sampling must be sequential. In this respect sampling of auditory information resembles sampling of somatosensory information. But in contrast to somatosensory information sampling, resampling of auditory information is often impossible. In man, the motor apparatus attached to the auditory sense organ is outmost rudimentary, presumably as an expression of the poor possibilities of reexamining the signal.

The term recognition covers a diversity of brain processes. The demodulated signal can be compared to a multitude of patterns from memory in a multitude of ways. The number of degrees in freedom of signal processing becomes immeasurable if language is used as input. The result is, in our experience, a great individual variance in the intensities and the cortical areas activated in such circumstances. Discrimination of non verbal signals at a certain pace in contrast, gives a sharp behavioral and information theoretically definition of what is required by the cortical nervous system. In a study some years ago we let subjects discriminate tone sequence patterns that only differed in the pauselength between the single tone bursts (Roland *et al.*, 1981). Each signal consisted of six tone bursts of 500 Hz delivered to one ear at 64 db. The test paradigm was again a temporal 2 AFC, the two signals were presented in succession. Only two pause lengths differed in each signal pair to be discriminated. The signals were compact.

All subjects reported that they were unable to determine which of the tonal intervals that differed, although they successfully discriminated the pairs correctly in 75-80 per cent of the presentations. Pollack (1968) tried to let subjects discriminate auditory pulsed Doppler sequences, and found that the subjects could not identify the ascending-descending sequences, although they could discriminate pairs of such sequences. It is likely, thus, that subjects reconstruct the whole signal in the brain before they compare the two signals in the pair. Such a procedure would be an optimal detection procedure.

The cortical areas that are activated during tone sequence discrimination are shown in Fig. 4. Apart from the differences between the activations of the dominant (left) and the non-dominant (right) hemisphere which were highly statistically significant ($p < 0.005$), the pattern of activations was

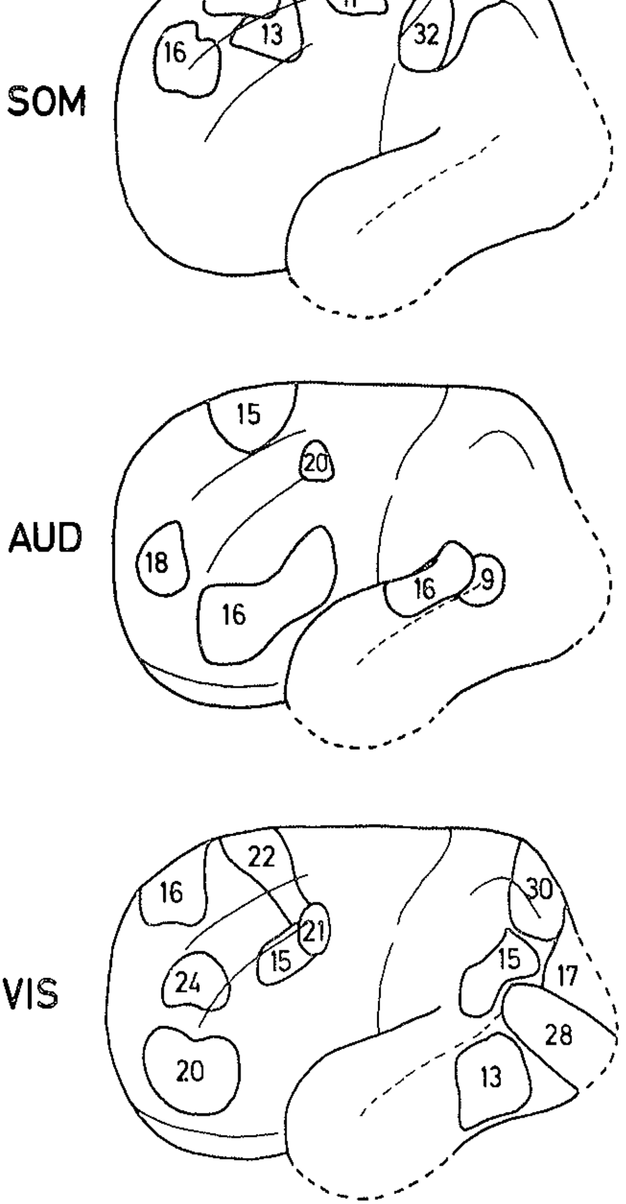

Fig. 4. Mean increases of rCBF in % and their average distribution in subjects discriminating somatosensory auditory and visual patterns. Right side of Fig. shows right hemispheres, left side shows left hemispheres. *SOM*: somatosensory discrimination, without manipulation, of rectangular parallelepipeda. The parallelepipeda were pressed in different configuration against the palm. Note only a slight increase in the premotor cortex, otherwise no motor area rCBF increases. Increases in the anterior and posterior superior prefrontal cortex and the midfrontal areas in addition to the increase in the somatosensory hand area and the somatosensory association cortex. The incraese in the right auditory cortex appeared, although no auditory stimulation was given. Apparently the subjects were listening for auditory cues. (cf. Fig. 3). (Data from Roland and Larsen, 1976). AUD: Auditory discrimination of tone sequences, temporal 2AFC-paradigm. (Redrawn from Roland *et al.*, 1981). VIS: Visual discrimination of computergenerated ellipses. 2AFC paradigm with simultaneous presentation of stimuli. (Redrawn from Roland and Skinhøj, 1981).

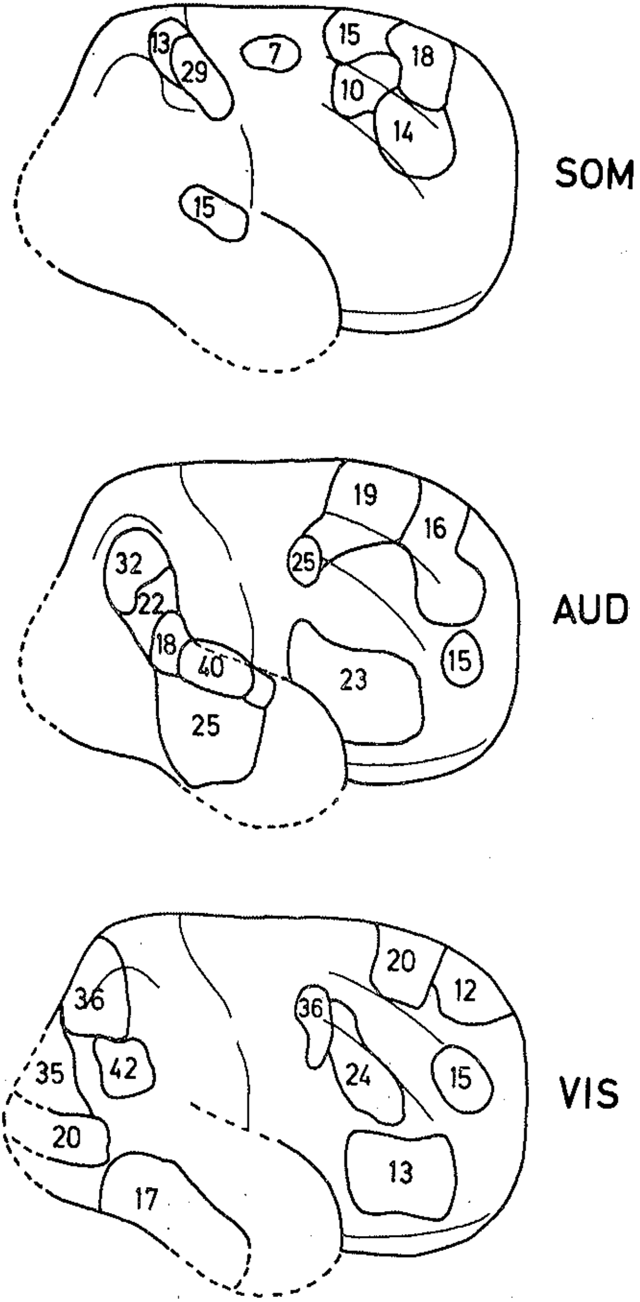
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Fig. 4

a parallel to the somatosensory activation pattern. The auditory association cortex and the superior prefrontal cortex were activated. But in addition many other prefrontal areas and parietal areas increased their rCBF. The latter cortical areas also participated in many other non-auditory tests (see later).

The three cortical areas: in the middle of the superior temporal region, the area that surrounds it, and the midtemporal area below all participate specifically in auditory pattern analysis and retrieval. They constitute the auditory association cortex. Increases of rCBF or glucose consumption in these three areas have also been found while subjects were listening to onomatopoeia; or when subjects discriminated tone patterns of different frequencies (Nishizawa *et al.*, 1982; Mazziotta *et al.*, 1982). The auditory association cortex probably participates in the reconstruction of the auditory signal in the tone discrimination tests.

The Broca area and its right sided homologue were also activated in tone discrimination tests, without any verbal elements (Roland *et al.*, 1981; Mazziotta *et al.*, 1982). The Broca area and its right sided homologue has also been activated while subjects were listening to a story. Damage to Broca area causes defects in analysis of verbal material (L. Taylor, Montreal, personal communication). Clearly the Broca area and its right sided homologue participate in the analysis of auditory patterns. Electrical stimulation of Broca's area causes arrest of sequential vocal output or verbal output (Penfield and Roberts, 1959). The area is of course also active when people talk (this article). It was suggested that the cortex in the posterior inferior frontal region can make copies or images of sound patterns, which can be used for internal language or for expressive language (Roland *et al.*, 1981). To this should be added that the Broca area, or in the tone discrimination tests the right homologue, probably play back the auditory signal and that this may be their general function. This play back is a part of the internal reconstruction of the auditory signal. Since resampling of auditory signals is often impossible, the brain may compensate with a play back function in which different stages of the reconstructed auditory pattern can be distrihuted to other brain regions for analysis for distinctive features. The Broca area is often activated together with the superior temporal cortex and the intermediate auditory association area (see the examples in this article). The area on Fig. 4 which has an increase of 23 per cent of the rCBF, is clearly larger than the Brodmann area 44. In the tone discrimination tests this middle inferior frontal region on the right side was always activated (Roland *et al.*, 1981; Mazziotta *et al.*, 1982). The middle inferior frontal region is often activated together with the remote auditory association cortex in the midtemporal region.

The posterior superior mesial prefrontal cortex in front of the supplementory motor area was also activated in auditory discrimination (Fig. 4). The per cent increase in the posterior mesial frontal cortex was similar to the rCBF increase in the same cortex during somatosensory discrimination (Fig. 4). Since the same temporal 2 AFC-paradigm was used in both cases the activity here could be due to metabolic increases of neurons participating in the formal aspects of discrimination; to compare two reconstructs and decide whether further resampling play back was necessary or whether the reconstructs could be separated. One might question the regions might have something to do with reactivation of immediate memory, since the first signal reconstruct has to be compared with the very recent reconstruct of the second signal and the first reconstruct, thus must be recalled again from memory when the time for discrimination comes. To test these hypotheses we changed the modality and the paradigm into a 2-AFC with simultaneous presentation of the signals.

Cortical areas participating in discrimination of visual extrinsic patterns

At a first glance immediate recognition of visual patterns should be possible. That is, visual signals might not need to be sequentially processed by the brain as somatosensory and auditory signals do. Resampling should not be necessary. However, resampling probably occurs always anyway due to the 100 Hz microtremor of the eyes which is present even during periods of fixation (Campbell *et al.*, 1959). Microtremor of the eyes is an example of resampling that increases the spatial resolution of the visual system. Pattern recognition at a frequency above 100 Hz is presumably impossible. Recognition of compact patterns require several hundred milliseconds of exposition (Bela Julesz, this volume).

Ellipses are compact signals. In the study referred to above, to evaluate the significance of the posterior superior mesial frontal rCBF increase during 2 AFC discriminations, subjects were simultaneously presented with two ellipses of the same area but slightly different shape (Fig. 5). The subjects had to, as in the 2 AFC discriminations of the other modalities, discriminate the shape of the ellipsoids within four seconds (Roland and Skinhøj, 1981). The subjects had to saccade between the ellipses to sample the information. All subjects used the whole exposure time to make between three and nine saccades between the ellipses, before

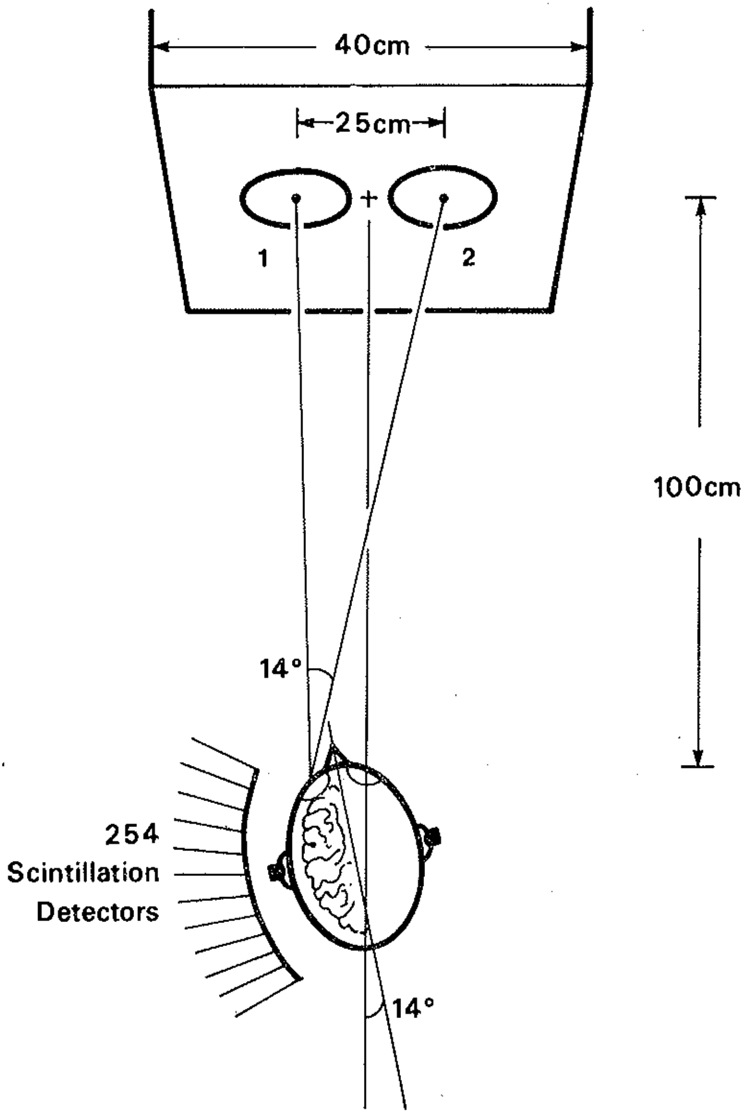

Fig. 5. Visual discrimination. The computer drawn ellipses are projected on a screen with a cobalt blue background. They have the same area but slightly different shapes. In half of the exposures the long axes of the ellipsoids were parallel to the body axis, in the rest the axes were orthogonal to the body axis. Exposure time 3.5 sec., 89.3 lumen • m^{-2}. The subjects had to saccade between the ellipses to sample information from both. The only verbal answers allowed were "one" or "two" as in the other two-alternative forced choice (2AFC) discriminations.

they decided. Either the subjects compared the ellipses during several successive independent samplings, and when a difference appeared the first time, they made their choice. This would be a suboptimal procedure. Or, each of the two ellipses were iteratively reconstructed by successive integrations of the sampled information and the reconstructs thereafter compared. This would be an optimal procedure. It was not possible in the given setting to prove which of the alternatives the subjects actually used, but the subjects clearly, demonstrated resampling.

The rCBF increased in visual association cortex which comprises the lateral occipital cortex, the superior occipital cortex and the posterior inferior temporal cortex (Fig. 4). The remote visual association area in the posterior inferior temporal cortex was situated behind the auditory association cortex in the midtemporal region and in front of the lateral occipital area (Roland and Skinhøj, 1981).

Other investigators have found rCBF increases in these three areas when subjects were requested to name familiar objects shown to them on photographs (Larsen *et al.*, 1979). Increases of the glucose consumption in the superior and lateral occipital cortex, as well as in the primary visual cortex, have been observed by Reivich *et al.* (1978), when subjects in a vigilance task were requested to count the number of occasional dimmings of a white light. The effect of opening the eyes and watching a plain white light on the glucose consumption in the primary visual cortex and lateral and superior occipital cortex was only half as big as the 35-40 per cent increase in these areas when subjects were watching the university campus (Phelps *et al.*, 1981). Similarly, the effect on the rCBF in the superior and lateral occipital cortex of opening and moving the eyes in a homogenously white visual field was only 50-65 per cent of the effect measured during discrimination of ellipses (Fig. 4). One must therefore assume that the rest of the metabolic activity in the immediate and intermediate visual association areas was due to reconstruction of the visual signals. The rCBF increase in the posterior inferior temporal cortex seem related to the reconstruction or analysis of compact or complex visual signals (see also Gross, this volume).

The posterior superior parietal cortex had a very marked increase in rCBF. This cortical area is particularly active when subjects analyse or require information about directions in extrapersonal space (see later). The reason why this area was activated in ellipse discrimination, was assumed to be due to the fact that all our subjects had their heads tilted (Fig. 5). This may apparently cause difficulties in visual shape discrimination related to the slight distortion of the perception of extrapersonal space (Roland and Skinhøj, 1981). It is seen from Fig. 4 that activation of the frontal eye fields does not depend on visual stimulation. Neither has the rCBF increase in the frontal eye fields been correlated with the number of saccades during the discrimination tests (Roland, 1982). On the other hand, the frontal eye fields have been clearly activated in pursuit eye movements as well as during saccades (Melmed and Larsen, 1979). The area of a 2-3 cm^3 that we recognize as the frontal eye field in man, covers both motor functions and functions in the treatment of information that comes from extrapersonal space. The frontal eye fields are active when either the auditory or the visual immediate or intermediate association areas are activated (Melmed and Larsen, 1979; Roland *et al.*, 1980b; Roland *et al.*, 1981; Roland and Skinhøj, 1981; Roland, 1982). They obviously have a function in the control of resampling of visual information, and in addition a function that has something to do with tuning or preparation of the associative areas with which the frontal eye fields are coactivated.

Despite the simultaneous presentation of the signals the posterior superior mesial prefrontal cortex was activated. This activation, thus, could not be due to any recent memory factor in 2 AFC discrimination. Moreover, the activation of this area is not related to any particular modality. The participation of this area in 2 AFC discrimination could therefore be in the formal aspects of discrimination: decisions about whether resampling/playback would be necessary or whether the reconstructs of the signals differed sufficiently. However, since this area, as well as many other prefrontal areas, has many jobs that are at present impossible to characterize and categorize firmly on the basis of the relation between metabolic activity and behaviorally defined experimental situations, one should abstain from behaviorally labelling of cortical areas. At most, we can, with a maximum of information available, try to suggest what the participation in the informational treatment in a *concrete* task may consist of.

The middle inferior frontal region was activated both in visual and auditory discrimination (Fig. 4). This region (see later) is usually activated together with activations of the remote association cortex in the midtemporal region or together with activation of the remote visual association area in the posterior inferior temporal cortex. Like the other anterior prefrontal areas its activation is not limited to sensory discrimination. In addition, visual discrimination of these compact signals were associated with increases of rCBF in hypercomplex processing regions in the parieto-temporo-occipital region, and in the anterior prefrontal cortex. However, in the pattern in Fig. 4 lower, only the activity in the visual association cortex tells that visual information is being processed.

The effects of attention upon the cortical activation patterns during sensory discrimination

In a recent study (Roland, 1982) subjects were stimulated simultaneously with the exact same stimuli used in the three previous studies. The task of the subjects was to ignore the stimulation in two of the modalities and discriminate the stimuli presented in the third. Each subject went through the three different combinations of focusing attention on one modality and ignoring the signals from the two irrelevant modalities.

No matter on what modality the subjects focused their attention the rCBF increased in the somatosensory association cortex, the immediate visual association cortex, and the auditory association cortex. The rCBF increases in the immediate visual association cortex, in the superior temporal region (immediate and intermediate), and in the somatosensory association cortex in the anterior part of the superior parietal cortex, were not statistically different from the rCBF increases when the signals from each modality were discriminated exclusively (Fig. 4). However, when the visual modality was irrelevant the rCBF increases during tri-modal stimulation in the superior occipital cortex and the posterior inferior temporal cortex, were less than during visual discrimination in the single modality paradigm (Fig. 4). Similarly the rCBF increase in the midtemporal region when the auditory modality was the irrelevant, was less than the rCBF increase during auditory discrimination in the single modality paradigm (Fig. 4).

The simultaneously presentation of stimuli in all three modalities also induced changes compared to the single modality stimulation situation (Fig. 4), in the prefrontal cortex. In the left prefrontal cortex the rCBF in the frontal eye field was reduced when the subjects discriminated somatosensory signals, i.e. when the information came from intrapersonal space. However, when the attention again was turned towards either the auditory or the visual modality the rCBF increase here was of the same size as during single modality stimulation. The rCBF increase in the whole left midfrontal cortex and the anterior and middle inferior frontal cortex was reduced during tri-modal stimulation. The rCBF increase in the Broca area during somatosensory discrimination was less than during single modality auditory discrimination. However, when the attention was turned towards the auditory modality the rCBF increase in Broca's area was of the same size as during single modality auditory discrimination. Apparently, most of the information processing in tri-modal stimulation was transferred to the right prefrontal cortex. The low activity in the frontal eye field and the Broca area when signals belonging to other modalities were discriminated, might be due to limitations in resampling/playback under these conditions. The reduced rCBF increase in the left midfrontal cortex and the left middle inferior frontal cortex corresponded to a reduced rCBF in the left superior occipital cortex, the left posterior superior parietal cortex and the midtemporal cortex on the right side. On the other hand when the attention was turned towards the auditory signals the rCBF in the right middle inferior frontal cortex was enhanced above the values seen during single modality auditory discrimination. The operations that the midfrontal cortex and the middle inferior frontal cortex exerted upon the remote association cortices were apparently restricted to the right hemisphere.

In the right superior lateral frontal posterior region the rCBF was modulated in extent and intensity according to which modality that was discriminated.

The most marked modulations of rCBF appeared in the intermediate and remote auditory and visual association cortices. When attention was turned towards the auditory signals the rCBF was enhanced above the values of single modality discrimination in the superior temporal cortex and the midtemporal cortex on both sides. When attention was turned towards the visual signals the rCBF was enhanced in the right superior occipital cortex and the right posterior superior parietal cortex. This was taken to indicate that these areas could be selectively or differentially tuned depending on whether the signal reconstructions that they participated in were relevant or irrelevant.

Since the rCBF increase in the right posterior superior mesial frontal cortex was twice as high as the rCBF increase during single modality discrimination, this area was supposed to maintain some control over this mechanism of differential tuning or recruitment of cortical areas relevant to the task (Roland, 1982b).

General cortical organization of extrinsic pattern discrimination

The brain has two problems in 2 AFC discrimination. How to get sufficient information about the extrinsic patterns and how the collected information can be reduced to one bit of information.

The information about stable extrinsic patterns is retrieved by sampling and resampling. This part of the task is solved by superpositioned sensory motor loops. Correspondingly, the rCBF increases in primary somatosensory cortex and the primary motor cortex, and in the supplementory motor area and the premotor cortex which plan the single course of palpation and the modification of palpation (Roland *et al.*, 1980a, 1980b). The planning of new sequences of palpation can be influenced by other cortical areas especially the posterior superior lateral frontal cortex which is active in addition to the premotor cortex when the manipulation is modified under guidance of sensory information from presumably the intermediate somatosensory association cortex (Roland and Larsen, 1976; Roland *et al.*, 1980a, 1980b). Eventually the second somatosensory cortex also participates in these loops (Roland *et al.*, 1982).

The sensory primary receptive cortical areas together with the sensory association areas reconstruct the objects or signals internally. The visual organization of pattern discrimination is similar to the somatosensory. The frontal eye fields control both the motor functions for resampling as well as presumably the preparation of visual association areas for further signal reconstruction.

In the same cortical belt, presumably corresponding to the dysgranular zone of von Bonin and Bailey (1951), there is activation of the Broca area which probably plays a generated copy of the auditory signal back to the intermediate and remote auditory associative areas during auditory discrimination. The superior mesial frontal posterior cortex is always activated during pattern discrimination. Beyond this, the posterior superior mesial frontal cortex is generally activated when two different sets of cortical areas have to be activated sequentially and the recruitment of the second set is contingent on the result of the work done by the first set (Roland, 1982, this chapter, Fig. 7, 8 and 9). The contribution of this area in pattern discrimination could be participation in decisions of whether further resampling/playback of the reconstructs is necessary or a final answer can be delivered.

Overriding this control of resampling and modifications of sampling are a set of anterior prefrontal areas. The superior anterior prefrontal area is always activated when subjects have to perform a task after a prior given instruction (Roland and Larsen, 1976; Larsen *et al.*, 1979; Roland *et al.*, 1980a, 1980b, 1981; Roland and Skinhøj, 1981; Roland, 1982). The instruction imposes a set of constraints on the way the sensory information has to be treated. In 2 AFC discrimination the requirements are that a binary output has to be delivered concerning a specific physical attribute of a pair of signals to be presented shortly. That is, a definite set of information processing modes has to be established in the brain. This internal organization presumably also requires energy and can provoke rCBF increases. In other words, the plan that defines when in the course of information processing a certain set of cortical areas have to be recruited is the intention of the subject, and tbe anterior superior prefrontal cortex is assumed to participate in this function.

The anterior midfrontal cortex has been activated in concert with the somatosensory association cortex in the anterior superior parietal lobule or the superior posterior parietal cortex or the midtemporal cortex. The middle inferior frontal cortex has been activated in concert with the posterior inferior temporal cortex or the middle temporal cortex, that is the remote visual and auditory association cortices. In addition these two areas are also activated during retrieval of information from the above mentioned areas for internal use (see next section). A working hypothesis is that these two areas search for sensory information both past and present.

In addition other areas in the anterior prefrontal cortex and the posterior inferior parietal cortex have been activated during discrimination of patterns, without it being possible at present to characterize their function.

In Fig. 6 the results of external pattern discrimination are summarized.

Retrieval of intrinsic patterns

The brain can decide to operate on the external world through motor activity, actions or language. But, brain activity of action can also be directed internally towards specific cortical areas without there being any transfer of information between the brain and the outer world or between the brain and the body or without there being any motor activity. Sometimes motor activity is dependent on retrieval of information which is necessary for its execution. This internal retrieval of information preceedes the execution (Roland *et al.*, 1980a).

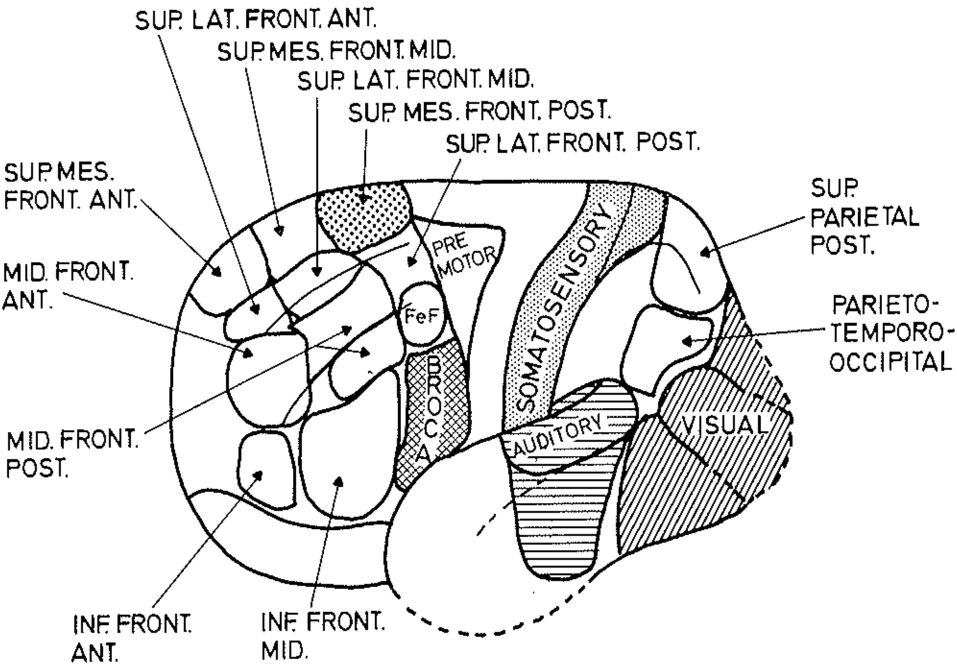

FIG. 6. Summary of cortical areas participating in discrimination of extrinsic patterns. All areas with hatching or provided with a name participated in discrimination of patterns from one or more modalities. Each primary receptive area is surrounded by immediate, intermediate and remote associative areas reconstructing the external patterns. The somatosensory associative area in the parietal operculum and retroinsular cortex is hidden from view. The premotor area together with the supplementary motor area and the primary motor area participates in resampling if the motor system is recruited. In the dysgranular belt are the superior lateral frontal posterior cortex, the frontal eye fields and the Broca area or its right homologue participating in control of resampling and playback. The superior mesial frontal posterior cortex participates in decisions about resampling or strategy alteration or final response, it also participates in the direction of attention. When attention is directed towards one modality the intermediate and remote cortical area show enhanced activation. The anterior midfrontal cortex and the inferior frontal middle cortex presumably participates in search for sensory cues in the reconstructed patterns made by the remote associative areas and other posterior areas in close relation to these e.g. the posterior superior parietal cortex.

The body is a natural and mobile reference system for voluntary movements. This system is self up-dating and no additional information is required to move one body part in relation to other body parts. The extrapersonal space is a three dimensional reference system fired by points in the surroundings. Voluntary movements can also be executed with reference to extrapersonal space. Reaching for a tea cup on a table is an example of a movement in extrapersonal space. The number of extrapersonal space reference systems is infinite. Every time a movement has to be coducted in extrapersonal space, the transformative relation between the bodily field reference system and the extrapersonal space reference system has to be worked out (Roland, 1979).

To study from where in the cerebral cortex the information about extrapersonal space coordinates and the transformation relation to intrapersonal space was retrieved (Roland *et al.*, 1980b) trained subjects to perform a quick series of movements within a frame that had 49 fields of equal size. The subjects had their eyes closed. The frame was placed on the couch besides the supine subjects. The subjects were trained to do quick movements with the index finger from field to field on verbal commands from the experimentator. Each field was bounded by steel sticks. In the beginning of the training the subjects frequently hit these sticks, but after a while they were quickly able to move their arm and pointing index finger from field to field without hitting the sticks. The directions of movement were for example "two left — three backwards — one right —" and so on.

In Fig. 7 one of the subjects' cortical rCBF is shown while he was performing this "maze test". The following regions show rCBF increases in all subjects (Roland *et al.*, 1980b).

The sensory hand-arm area, the motor hand-arm area, the premotor area, the supplementary motor area, the superior anterior and superior posterior prefrontal cortex. Further more, as a sign of the auditory information inflow from extrapersonal space: the frontal eye fields, the auditory immediate and intermediate associative cortex and the Broca area were activated. Finally, there were marked increases in the somatosensory association cortex in the anterior superior parietal region and an increase in the posterior superior parietal region and the posterior inferior parietal region.

Since movements executed in intrapersonal space activate the supplementary motor area, the sensory and motor hand-arm area, and the anterior superior parietal cortex including the supplementary sensory area (Roland *et al.*, 1980a, 1982); these regions cannot be responsible for the retrieval of the learned information from extrapersonal space. The premotor cortex has been active where subjects were performing movements in intrapersonal space guided by sensory information (Fig. 2). The auditory association cortex the Broca area and the frontal eye are activated

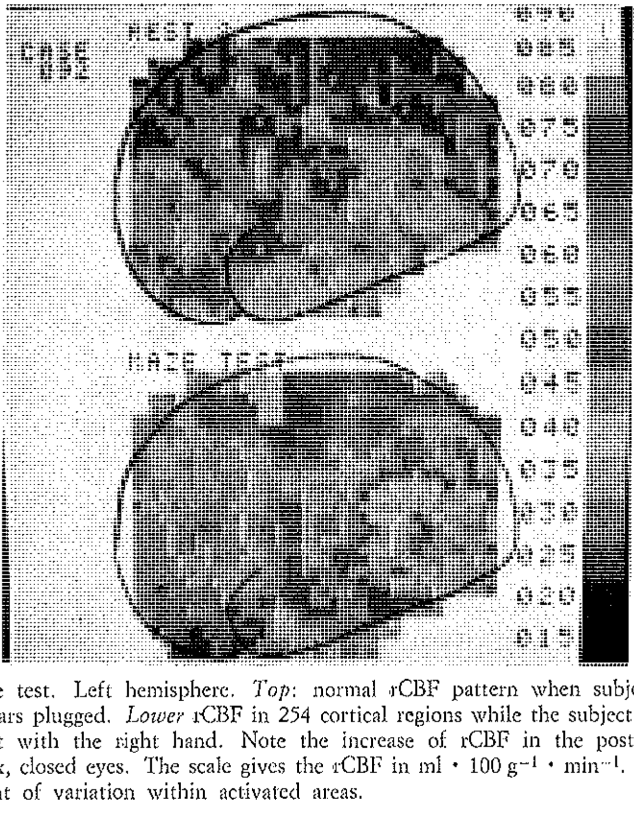

FIG. 7. Maze test. Left hemisphere. *Top*: normal rCBF pattern when subject is at rest, closed eyes, ears plugged. *Lower* rCBF in 254 cortical regions while the subject is performing the maze test with the right hand. Note the increase of rCBF in the posterior superior parietal cortex, closed eyes. The scale gives the rCBF in ml · 100 g^{-1} · min^{-1}. Note also the low coefficient of variation within activated areas.

because the subjects receive auditory information, and the posterior inferior parietal cortex might have participated in the analysis of the verbal commands as well (Fig. 4, Nishizawa *et al.*, 1982). By exclusion therefore, the region most likely to participate in the generation of information about the directions for the movements in extra personal space is the posterior superior parietal cortex. This was supported by the observation that other movements in extrapersonal space, without verbal commands strongly excitated the posterior superior parietal cortex (Roland *et al.*, 1980b).

Although the posterior superior parietal cortex was activated during visual discrimination (Fig. 4) this area is not a visual association cortex since it was also activated during a motor task. The subjects performing the maze test did not at any point have any visual information about the surroundings in which the frame was placed nor any visual information of the frame itself. The activation of this area in the maze test was ascribed to the retrieval of the necessary information about the direction of the movement in extrapersonal space coordinates. This information was apparently stored in the brain during the training period and the activation of the posterior superior parietal cortex was essential for its retrieval. The intense concomitant activation of the anterior superior parietal cortex was assumed to reflect the transformation relation between the extrapersonal and intrapersonal reference system.

Information about extrapersonal space can he recruited for other reasons. Recently we (Roland and Friberg, 1984) did an experiment in which subjects had, with their eyes closed, to verbally describe every piece of furniture in their living room. The description should be as accurate as possible. The subjects were thus required to describe the appearance of a spatially arranged, finite number of well known objects. The test consisted of a retrieval of visual memory and contingent on this retrieval the verbal memory had to be retrieved for the proper verbal expression. Finally the verbal expression had to be translated into a motor code for voluntary motor output. Apart from these components, the test, like all other tests, had the component of the maintenance of the intention — the internal organization of the cortical and subcortical structures to satisfy the requirements in the instruction.

Like all other tests referred to in this chapter this test was performed by 10-12 subjects. In this case, the subjects, in addition, had their hemispheric dominance determined by an injection of a GABA-agonist in the internal carotid artery (Roland and Friberg, 1983). The regions that showed statistically significant changes from rest to test are illustrated by the typical examples of Fig. 8. There were increases of rCBF in both the dominant and non dominant hemisphere. As expected we found bilateral increases in the superior anterior prefrontal cortex. In accordance with the sequential and contingent activation of three different sets' of cortical areas: those for visual retrieval, those for verbal retrieval and those for the motor areas, there was a bilateral increase in the posterior superior mesial prefrontal cortex.

The supplementary motor areas were activated, the left more than the right (non dominant), and the motor mouth areas were activated as signs of the transformation of the Broca generated pattern into sequential motor code and the execution of the motor act. It was also seen that the Broca area was more intensely activated than its rightsided counterpart. In addition there was an increase in the auditory association cortex in the

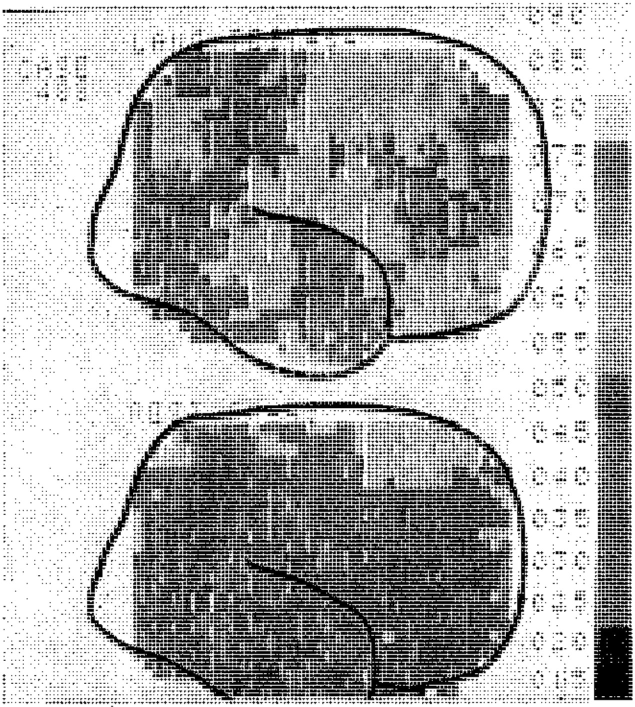

FIG. 8. rCBF in subject who reports from visual memory. Right hemisphere. The subject described with his eyes closed as detailed as possibly every piece of furniture in his living room. This subject had 30% of his language representation in the right hemisphere. The increase in the midtemporal cortex was not statistically significant in the whole group of right hemisphere subjects. The retrieval of visual memory caused an rCBF increase in the posterior superior parietal cortex. The anterior midfrontal cortex participated in the search of the retrieved pattern. Increases found also in the same prefrontal areas that were activated during discrimination of extrinsic visual patterns. Increases found also in the Broca homologue, the supplementary motor area and primary motor mouth area due to the generation of the language pattern and the motor coding of this pattern. (Roland and Friberg, 1984).

mid-temporal region probably reflecting the retrieval of the verbal memory.

In the right hemisphere there was a clear activation of the posterior superior parietal cortex (Fig. 8). This increase could not be due to the analysis of external visual patterns since the eyes were closed. Neither could it be due to motor activities or command functions for motor activities in extra personal space, since only the mouth was working Movements of the mouth are voluntary movements in intrapersonal space par excellence. Neither could the increase be due to attention turned towards something external visual since the eyes were closed. We therefore assumed that the activation of the posterior superior parietal cortex was due to the directional search in a memorized visual reconstruction of the living room.

The right posterior superior parietal cortex was again coactivated with the anterior midfrontal region. The left inferior middle frontal cortex was again coactivated with the middle temporal cortex. These two areas might therefore have participated in the search of the directional visual memory and the verbal memory for which the posterior superior parietal lobule and the midtemporal cortex was necessary. The same prefrontal regions which are capable of participating in a visual pattern discrimination task were activated when the brain itself was retrieving memory that has visual character.

Further support to the hypothesis that the activation of the posterior superior parietal cortex was due to the directional search in visual memory, came from a series of experiments on pure thinking done in collaboration with Dr. Lars Friberg (see Roland, 1983 for abstract). In these experiments the subjects received no information from the outer world while the rCBF was measured. Neither was there any motor activity. Prior to the rCBF measurements the subjects were requested to imagine that they were standing at their front door and then had to walk to the left. Then when they reached the first street on their right side they had to walk down that street in their imagination — and then alternatively walk to the left, right until they were asked by the experimentator "where they were". This control question was always postponed to several seconds after the rCBF measurement was finished.

A typical result from the right hemisphere (non dominant) is shown in Fig. 9. There was an rCBF increase bilaterally in the superior anterior prefrontal region, most likely reflecting the intention of the subject. Likewise as expected, an increase in the right posterior superior prefrontal cortex, most likely due to the contingency of the task. The Broca area, but not its right sided homologue, was activated. The left frontal eye field was activated perhaps due to internal resampling of information from visual memory. The anterior and middle inferior frontal cortex were activated again bilaterally. Correspondingly there was a marked increase bilaterally in the posterior inferior temporal cortex (the remote visual association area). Also, the anterior midfrontal cortex was activated bilaterally. Concomitant with these areas was the posterior superior parietal cortex bilaterally activated. In some subjects

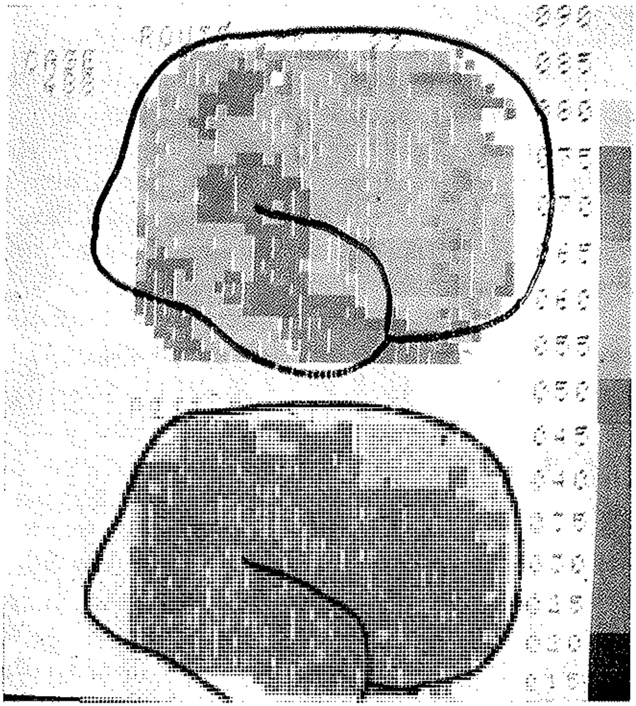

FIG. 9. rCBF increases in the right hemisphere provoked by thinking. The subject *imagined* that he was walking in familiar surroundings alternally to the right and left. Eyes closed, ears plugged. No transfer of information between the outer world and the brain. No motor activity. The retrieval of the memorized intrinsic pattern, the internal reconstruct of the familiar surroundings caused activation of the whole intermediate and remote visual association cortex (superior occipital cortex and posterior inferior temporal cortex) and the posterior superior parietal cortex (directions in extrapersonal space). Marked increases in the anterior midfrontal cortex and the middle inferior frontal cortex. In addition increases were found in the superior prefrontal cortex (all subdivisions) and the frontal polar cortex. Posteriorly there were increases in the parieto temporooccipital region. Note the homogeneity of the rCBF within activated regions. (Roland and Friberg, 1984).

rCBF increases also showed up in the intermediate visual association area in the superior occipital cortex (Fig. 9). Finally the left supramarginal cortex was activated in all subjects.

All these increases occurred with the intensities shown in Fig. 9, despite the fact that the subjects did not receive any visual or other external information. None of the increases can be explained as retrieval of information for motor purposes either.

The task consisted of a recall of a sequence of visual images of the surroundings where the subject lived for some years. In this sequence of visual images a few simple directional operations had to be made. Each directional operation should elicit a new sequence from visual memory, and contingent on how the internal image looked the subject had to perform another directional operation (i.e. "go to the left"). This obviously required that the subject examined the image retrieved from memory. It is possible that the middle inferior frontal cortex could have participated in such an examination. The anterior midfrontal cortex, in turn, could have participated in the directional operations on the recalled image, since this area has been co-activated with the posterior superior parietal cortex in previous directional operations in extrapersonal space.

The intermediate and remote visual association areas that have been participating in the reconstruction of external visual patterns are also activated when internal patterns representing extrinsic visual patterns have to be recalled. The posterior superior parietal cortex which has been shown to participate in visual extrinsic pattern discrimination, and recall of extrapersonal space representations, is in the present task most likely participating in the directional operations on the representation of the recalled visual image of the surroundings. This area, might simply be the cortical locus of spatial memory. Like the posterior inferior temporal cortex, it has a dual function to process and probably reconstruct incoming signals and to display the reconstructs when the memory for such signals are retrieved.

Cortical Fields

The examples of cortical activations in individuals shown in this chapter (Fig. 2, 7, 8, and 9) demonstrate that the rCBF change usually comprises at least three to four detectors. Often an area of five to seven detectors show a rCBF increases of nearly the same size. A closer analysis of the variation coefficient of single subject rCBF values (in ml $\cdot$ 100 g^{-1} $\cdot$ min^{-1}) within a cortical area, showed that this was very often less than 10% if the area investigated was an area that in the whole group of subjects showed a statistically significant increase. Such areas usually comprised 4-6 channels (Roland and Larsen, 1976; Roland *et al.*, 1980a, 1980b, 1981; Roland and Skinhøj, 1981; Roland, 1981, 1982; Roland and Friberg, 1984).

This homogeneity in rCBF values over a few cm^2 of cortex indicates that such an area function as a unit in brain work. The homogeneity was not due to correlation between adjacent detectors, since this was less than

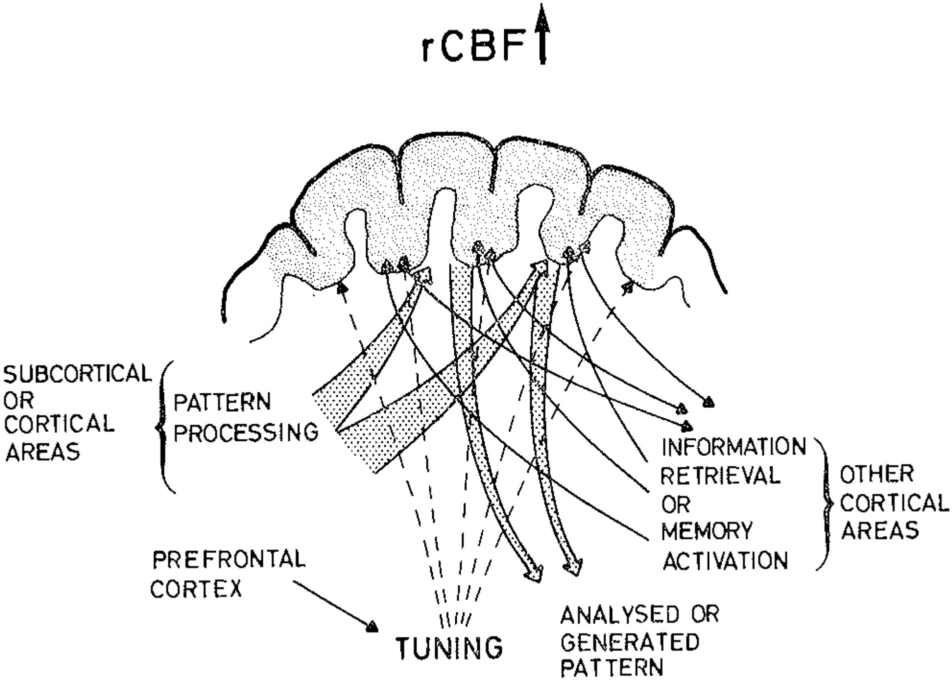

FIG. 10. Summary of the author's present opinion. A cortical rCBF increase is a sign of a net increase in neuronal excitation. During brain work the cerebral cortex of man is activated homogeneously in small fields, usually corresponding to 4-7 channels (4-7 cm^2 in a projection) but sometimes less. Three basic mechanisms were found to activate a cortical field in the posterior zone of the brain (behind the central sulcus). 1) Preparatory tuning for eventual later pattern processing — an effect of a specific direction of attention. 2) Processing of patterns from other cortical areas. 3) Retrieval of information stored in the brain, which primarily passed the cortical field.

30% (Roland and Larsen, 1976). rCBF increases during brain work are confined to single columns in the cortex just as the increase of glucose consumption (Greenberg *et al.*, 1979). The measured homogeneity, consequently, must be an indication that the blood flow does increase in multiple closely spaced points (columns) within a few cm^2 during brain work.

The anatomical correlation of these functionally defined cortical areas is not clear. For obvious reasons cytoarchitectural studies in these subjects are impossible. When a cortical area, for example the posterior superior parietal cortex, participates in different types of brain work it is apparently an activation of the same shape and location in both vertex projections and lateral projections we see in each case. However, when the extent of the posterior superior parietal activation is compared between individuals, there are clearly individual differences in the shape and extent of the superior posterior parietal activations.

One cannot, after the limited number of experiments with cortical activations, exclude that an area, for example the posterior superior parietal might consist of two aeras with partly related functional contributions. The superior prefrontal region, for example, was initially assumed to be functionally homogeneous (Roland and Larsen, 1976), has now proved to be comprised of several functional subdivisions.

The experiments referred to in this chapter have been exclusively confined to the human brain. The approach has been macrophysiologically and may appear primitive in comparison with the single unit studies of the brain of other primates. Such studies are essential if one wants to find out *what* is displayed in these macrophysiologically defined cortical unit areas. The main conclusion of the experiments described has been that a cortical area belonging to one of the three sets of sensory association cortices can be activated in three different modes: 1) as the result of a preparatory tuning process — called differential tuning, 2) as a result of information processing going on in the cortical area during brain work and 3) as a result of reactivation of patterns that once passed the cortical area for reconstruction but now are required to provide memorized information to an actual brain work (Fig. 10).

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VISUAL DEFICITS ASSOCIATED WITH OCCIPITAL LOBE LESIONS IN MAN

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Very much more is known about the functional organisation of the early stages of visual processing in animals than in man. Neuropsychological and neurophysiological experiments in man cannot be planned and are of necessity constrained by arbitrary events that cause structural damage. Nevertheless such accidents of nature can provide the neuroscientist with unique opportunities to observe, document and test behavioural relationships. This approach has yielded rich rewards in our understanding of many higher cerebral functions, especially in skills such as language that are unique to man. Although damage to the striate and peristriate regions in man is not uncommon, relatively few investigations using psychophysical methods have been reported.

Cortical blindness resulting from bilateral occipital lesions is rarely an absolute deficit, except possibly in the acute phase. As the patient recovers some visual capacities appear to be more impaired than others. I shall attempt to review the evidence for the fractionation of the visual functions, acuity, shape, colour and location. First, I wish to argue that two well documented neurological syndromes, achromatopsia and visual disorientation can best be conceptualised as partial or incomplete visual field defects. Secondly, I will describe 5 bilateral occipital lobe cases in all of whom unexpected dissociations of visual functions were observed.

Holmes (1918) both defined visual disorientation and wrote the definitive case reports; descriptions which have never been bettered. He defined visual disorientation as the inability to localise the position and distance of objects by sight alone. The patients he described were unable to reach for objects with any semblance of accuracy, they were unable to judge relative distance or size, they failed to converge, had great difficulty in fixating an object or in following a moving target and the blink reflex was absent. He ruled out an explanation in terms of a motor deficit by observing that these patients had no difficulty in localising a position on their own body, or in blinking in response to menace by their own hand, converging, fixating and following their own hand as stimulus. This syndrome, visual disorientation, presents a much graver handicap in everyday life than would be anticipated by the frequent demonstration of normal acuity contour and colour perception. In an extreme case I have observed a patient (SG) grope her way across a room like a totally blind person, yet on some trials, if her fixation to the screen coincided with the brief flash, she could report strings of letters and words presented tachistoscopically; on other trials she could report nothing (Godwin-Austen, 1965).

Since Holmes' first description of visual disorientation it has been observed that a unilateral lesion can result in unilateral visual disorientation. Riddoch (1935) first described 2 patients with visual disorientation limited to one half field and he concluded that visual disorientation is mapped like a primary visual field defect and that it is only observed in the half field contralateral to the lesion. Cole, Schutta and Warrington (1962) reported two very similar cases, one with a right hemisphere lesion the other with a left hemisphere lesion. Inaccurate pointing was confined to the contralateral half field. That they were equally inaccurate with either hand is further evidence that the motor component of the task is irrelevant.

Holmes and Horrax (1919) noted the high incidence of inferior hemianopic field defects occurring in association with visual disorientation. They in no way intended to suggest that these two neurological deficits were causally related but they did draw the inference that the critical lesion site must be in the region of the occipital parietal boundary. Indeed this localisation has been confirmed in all the more recent cases for whom data is available (e.g. Ross-Russell and Bharucha, 1978). As an aside, I would suggest that this region giving rise to visual disorientation must be intact in those "blindsight" patients described as being able to locate remarkably accurately in perimetrically dense scotomata (e.g. Weiskrantz *et al.*, 1974).

The syndrome achromatopsia is the selective impairment of colour perception such that the visual world is perceived as drained of colour.

In the extreme case only black, white and shades of grey can be differentiated. These patients can have normal visual acuity, location and object recognition. Meadows (1974) wrote a very useful review in which he summarised 14 published cases of achromatopsia drawing inferences about the anatomical correlates of the syndrome from the associated visual field deficits. He noted that there was a high incidence of bilateral altitudinal field defects which implicated damage in the region of the occipito-temporal boundary. There was autopsy data for 3 of these cases and he considered that the critical lesion involved bilateral damage to the fusiform gyrus.

As is the case for visual disorientation it appears likely that retinal topology is maintained for colour perception. Hemiachromatopsia contralateral to the lesion has been documented (Bender and Kanzer, 1939; Albert *et al.*, 1975).

The third component of visual processing I wish to consider is that of shape perception. There has to my knowledge been only one reasonably convincing case in which a selective impairment of shape discrimination has been demonstrated, visual location and colour perception being relatively well preserved. Efron (1968) investigated a patient (Mr. S) recovering from cortical blindness after carbon monoxide poisoning. He observed that light detection was near normal and that Mr. S could discriminate fine differences in hue. The patient's acuity and ability to locate objects in space, though not claimed to be normal, was said to be "adequate". Yet the patient was very handicapped in so far as he was barely able to recognise objects in the real world. He was unable to discriminate (using a same or different judgement) between a square and an oblong that were matched for total flux. The task difficulty was manipulated by varying the ratio of the length to width of the oblong (Fig. 1). Mr. S was barely above chance except on the very easiest discriminations. Efron very reasonably attributed this patient's difficulties to an impairment of shape perception and argued that it was not necessary to invoke the concept of visual agnosia. Weiskrantz (1980) has reported some preliminary data that suggests that shape discrimination deficits like location and colour deficits are retinotopically organised and are observed in the half field contralateral to the lesion.

During the last year or so I have had the opportunity to investigate 5 patients with bilateral occipital lobe lesions that have been referred to me for assessment of their residual visual incapacities. In addition to

FIG. 1. 6 Efron shapes matched for total flux.

recording their minimum separable acuity, in each case some attempt was made to document shape discrimination, colour perception and visual localisation. A brief case history of each of these 5 patients together with a summary of the psychological investigations follows.

CASE REPORTS

Case 1 - JAF a 63 year old teacher of secretarial skills was admitted to the National Hospital on 5.11.80 and again on 2.11.81 for investigation of her visual difficulties. She had had an acute episode of giddyness and visual failure in August 1980 at which time she was noted to be hypertensive with polycythaemia. On examination there was an upper left homonymous field defect and apart from her perceptual difficulties that included impaired object recognition, prosopagnosia and alexia there were no other neurological signs. The C.T. scan demonstrated bilateral asymmetrical infarctions, including the right occipital region, left posterior temporal, right capsular and right frontal regions (see Fig. 2).

Case 2 - RBC a 50 year old civil servant was admitted to the National Hospital on 28.10.79 for investigation of progressive left-sided deafness.

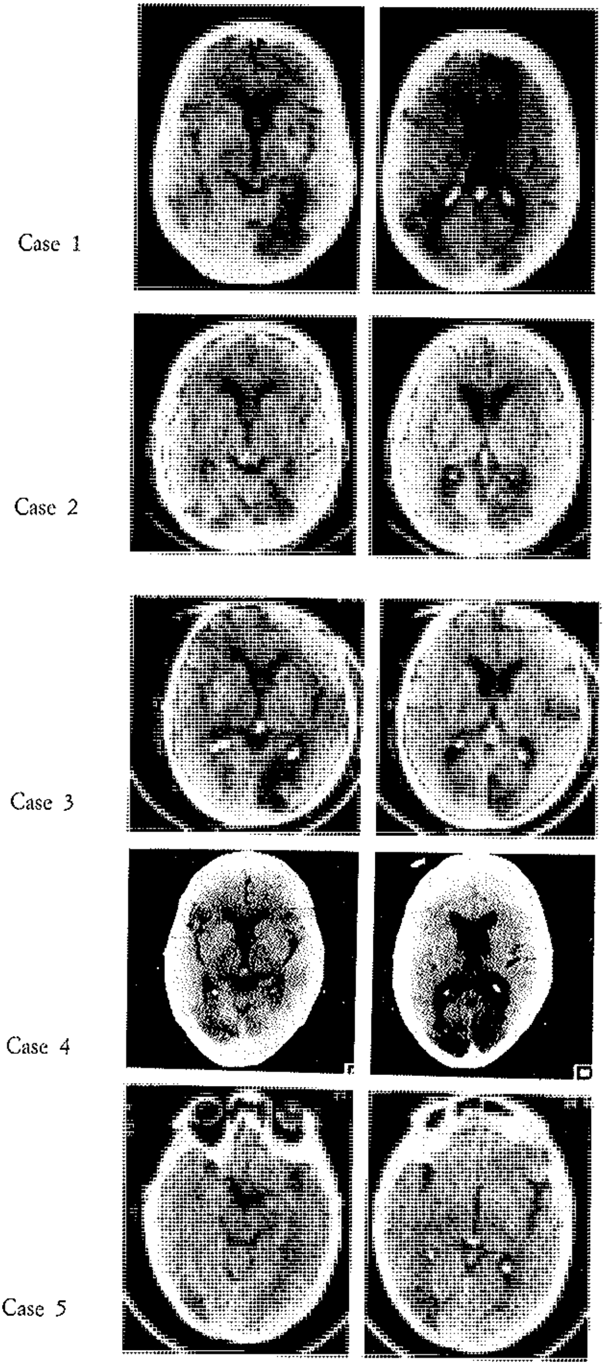

FIG. 2. C.T. scans of cases 1, 2, 3, 4 and 5 showing bilateral occipital lobe infarctions.

At craniotomy an acoustic neuroma was removed. His post-operative course was complicated necessitating 10 weeks in the intensive care unit before being transferred to a medical ward. On examination at this time he had a quadraparesis with sensory impairment to all modalities, the function of his lower limbs being more impaired than his upper limbs. There was a left homonymous hemianopia and a complete deafness in the left ear. His language functions and literacy skills were well preserved but he was acalculic and his object recognition was very impaired. A C.T. scan demonstrated extensive areas of low attenuation in both occipital territories. It was assumed that his basilar artery was thrombosed at the time of the operation resulting in bilateral posterior infarctions (Fig. 2).

Case 3 - COT a 64 year old car examiner was admitted to Oldchurch Hospital on 28.2.83 for investigation of a single episode of loss of consciousness 6 weeks previously. During this time his main complaint was of a fluctuating loss of vision. On examination there were no neurological signs of note apart from very poor visual acuity in both eyes. The only informative investigation was the C.T. scan which showed bilateral occipital infarctions more marked in the right than the left (see Fig. 2).

Case 4 - BRA a 57 year old housewife was admitted to the National Hospital on 18.10.82 for investigation of visual failure of 6 years duration. She had no neurological symptoms prior to an aortic valve replacement for aortic stenosis in November 1976. Immediately after the operation she was confused, unable to move her left limbs and she was unable to see. On examination there was a mild spastic paresis of the left arm and leg. There was a lower altitudinal field defect and very impaired vision in the upper quadrants. Neurological examination was otherwise unremarkable. The C.T. scan showed extensive bilateral posterior infarctions, more extensive on the left than the right which were considered to be secondary to hypoxic damage during surgery (see Fig. 2).

Case 5 - THR a 60 year old housewife was admitted to the National Hospital on 15.10.82 for investigation of headaches and drowsiness for the previous 7 days following a change in her medication for depressive symptoms of many years duration. On examination the patient was drowsy and unsteady and all reflexes were pathologically brisk. Her clinical state fluctuated and one week after admission her level of consciousness deteriorated and she developed a left homonymous hemianopia, a right superior quadrantic field defect and left hemiparesis. She made a slow recovery from this episode and at the time of her discharge there were no neurological signs of note other than a mild visual inattention, impaired object recognition and dyslexia. A C.T. scan demonstrated bilateral occipital lobe infarctions which were considered to be the result of progressive basilar artery thrombosis (see Fig. 2).

PSYCHOLOGICAL INVESTIGATIONS

Intellectual Functions - The patients in this series were tested on the WAIS, their verbal IQ and performance IQs are given in Table 1.

Verbal Memory - A recognition test for 50 words (described in detail by Warrington, 1974) was administered. Each patient's scores expressed as a percentile (corrected for age) are given in Table 1.

Visual Acuity - Corrected visual acuity for distance and near vision for each patient is given in Table 2.

Visual Shape Perception

1. Shape Discrimination: Efron's "squares" test was replicated as closely as possible. The standard was a 2×2 square and the comparison

TABLE 1 - *Verbal Intelligence and Verbal Memory.*

	JAF	RBC	COT	BRA	THR
Verbal IQ	102	129	103	95	95
Verbal Memory	75%	75%	5%	< 5%	25%

TABLE 2 - *Acuity Measurements.*

	1 JAF	2 RBC	3 COT	4 BRA	5 THR
Acuity					
Rt Eye - Distance	6/9	6/5	6/60	< 6/60	6/36
Near	NS	NS	—	> N48	
Lft Eye - Distance	6/9	6/5	6/60	< 6/60	6/36
Near	NS	NS	—	> N48	

stimuli were oblongs matched for total flux. (50×50, 55×46, 65×40, 70×35, 84×30 and 123×21 respectively, see Fig. 1). This squares v. oblong task was attempted either as a forced choice discrimination, a single stimulus being presented, or as a same/different discrimination, the standard square being paired either with the square or with an oblong. All 5 patients were tested in blocks of 20 pseudo-random trials. The % correct for each patient for three levels of discrimination difficulty is given in Fig. 3.

2. Shape Detection: A fragmented shape was superimposed on a fragmented background (described in detail by Warrington and Taylor, 1973), the task being to detect the presence or absence of the stimulus (Fig. 4). The % correct for each patient is given in Fig. 5.

Visual Location

It was possible to test the accuracy of point localisation in 4 of the

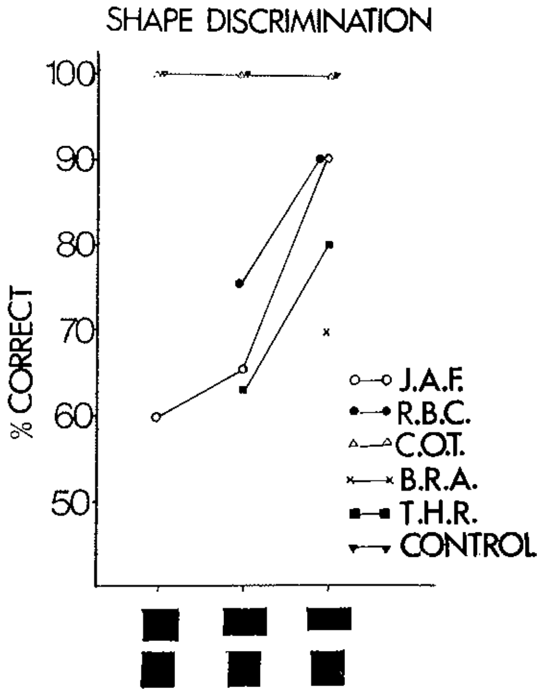

FIG. 3. Per cent correct for each of the patients on Efron's shape discrimination test.

FIG. 4. Example of fragmented X superimposed on fragmented background.

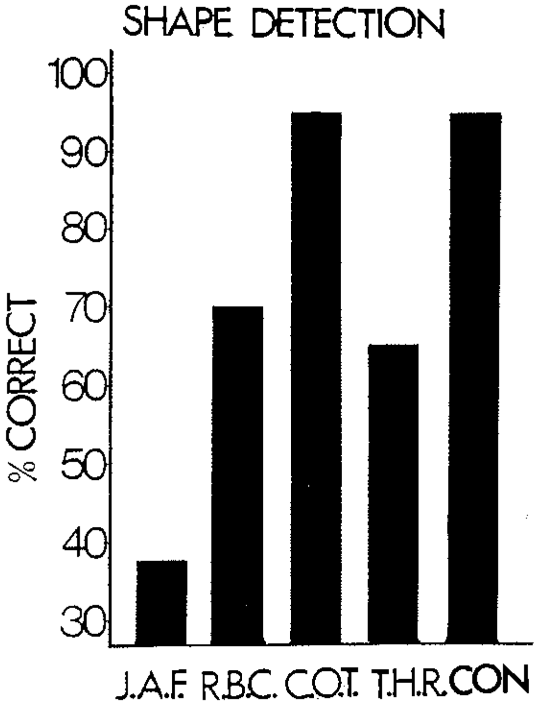

FIG. 5. Per cent correct for each of the patients on the shape detection task.

5 patients in this series using the Aimark perimeter (the procedure is described in detail by Weiskrantz *et al.*, 1974). The mean pointing error for each degree of eccentricity on the horizontal meridian for each patient (the most intact half field was tested) is given in Table 3. RBC was not tested on the Aimark, however it can be inferred from his performance on other visual tasks that his visual localisation was almost certainly normal; for example he was able to follow a line of print and read aloud at a near normal rate.

TABLE 3 - *Visual Localisation Mean Error Scores.*

	Eccentricity Degrees				
	10	20	30	40	50
JAF	1	1	0.5	NT	2.75
COT	0	0.2	0.95	5.1	6.25
BRA	20.8	13.8	15.8	6.1	5.2
THR	10.1	5.7	5.0	2.1	3.5

Colour Perception

Two patients, JAF and COT, were tested on the Farnsworth-Munsell 100 Hue test and their scores are given in Fig. 6. BRA and THR both had a fairly marked degree of visual disorientation and were consequently

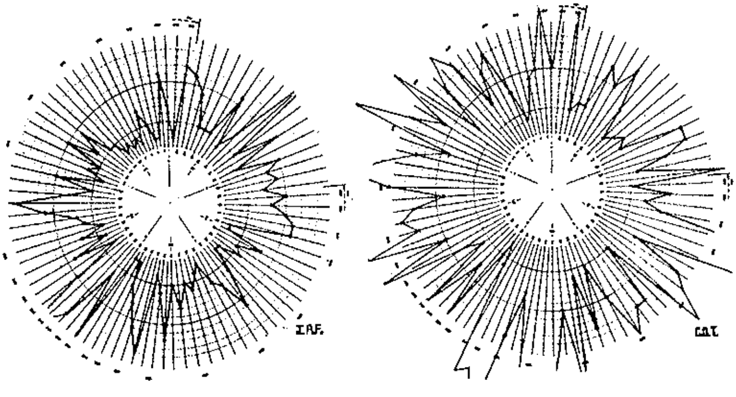

FIG. 6. Farnsworth-Munsell 100 Hue test results for cases 1 and 3.

unable to cope with the task demands of this test, similarly RBC was too spastic to be tested. Instead their colour vision was investigated using the Holmgren wools test. BRA and THR both successfully identified single strands of wool with remarkable accuracy. Not only were the primary colours invariably accurately named but only very occasional errors were recorded for the full range of hues sampled by the test (a more detailed account of these patients' colour perception is in preparation, Ruddock and Warrington). RBC's performance was very inaccurate and he even made errors in identifying primary colours.

SUMMARY

Thus different patterns of visual deficits have been recorded in these 5 patients and a summary of their preserved and impaired visual functions is given in Table 4. JAF and RBC both had normal acuity and point localisation at the same time their shape discrimination and colour perception were impaired. BRA and THR both appeared to have a selective preservation of colour perception, all other visual functions tested were quite severely impaired. COT's pattern of deficit stands in contrast to the above. In spite of very poor acuity and colour perception his performance on a test of shape discrimination and shape detection were entirely normal.

TABLE 4 - *Preserved and Impaired Visual Functions.*

	Acuity	Shape	Colour	Location
1 JAF	–	+	+	–
2 RBC	–	+	+	–
3 COT	+	–	+	–
4 BRA	+	+	–	+
5 THR	+	+	–	+

– Preserved
+ Impaired

CONCLUSIONS

Visual acuity, visual shape discrimination, visual location and colour perception were investigated in a small group of patients all of whom were considered to have made a partial recovery from an acute episode of cortical blindness. The present findings together with well documented observations in the neurological literature suggest that these four functions are all dissociable. Each combination of intact and impaired function for each patient investigated illustrates these dissociations (see Table 5).* Thus JAF was persistently impaired on the Efron's squares test and the test of shape detection, yet most impressively she could read small print and her minimal separable acuity was entirely normal. This same striking dissociation was observed in RBC. It is also worth noting, as has been previously observed (Meadows, 1974) that RBC's colour perception was extremely poor in spite of normal acuity measurements. The opposite dissociation, namely very impaired acuity but normal performance on the Efron's squares test, indicates that this latter test can be performed in spite of considerable visual failure and therefore the more striking dissociation of acuity and shape discrimination cannot be attributed to task difficulty. BRA and THR are of especial interest in so far as colour perception was

TABLE 5 - *Occurrences of Dissociations between Visual Functions.*

	PRESERVED			
IMPAIRED	Acuity	Shape	Colour	Location
Acuity	—	COT	BRA THR	COT
Shape	JAF RBC	—	BRA THR	JAF RBC
Colour	JAF RBC	COT	—	COT
Location	(SG)	(SG)	BRA THR	—

* (SG) from the Godwin-Austen (1965) study completes the matrix.

selectively preserved. This syndrome would appear to be the converse of achromatopsia. BRA was particularly handicapped in everyday life and had virtually no useful vision. Yet she could enjoy television by listening to the sound and perceiving changes in colour.

The significance of these reciprocal dissociations is of considerable theoretical interest. First, these observations are perhaps more consistent with notions of parallel processing than with a hierarchical model at least at this level in the visual system. Secondly, they provide tentative evidence for there being two (at least) distinct codes for processing visual contour information. There would appear to be at least partial independence in the mechanisms subserving the discrimination of an edge (as measured by minimal separable acuity) and discrimination of an edge as an integral part of a shape. However, the more intractable problem of the integration of shape, colour and location is totally unclarified by these observations.

Finally, it is relevant to consider the relationship of these observations to the classical syndrome of apperceptive agnosia. Two bilateral occipital lobe cases, neither of whom could discriminate shapes (and thus appear to be very similar indeed to case 1 and 2 described here), have been claimed to have an apperceptive agnosia (Efron's case Mr. S. subsequently reported by Benson and Greenberg, 1969, and Abadi *et al.*, 1981). However, in order to establish an agnosic deficit, it is necessary by definition to establish adequate sensory functions. These patients were both impaired on one or more simple visual discrimination tasks all of which would appear to be appropriate tests of visual sensory capacities. On these grounds alone one would argue that it would be quite inappropriate to identify their object recognition difficulties as an apperceptive agnosia. But more importantly there is very strong evidence to suggest that apperceptive agnosia, a failure of categorical perception, can be identified in patients with unilateral lesions of the right hemisphere. Such patients misrecognise complex visual stimuli while performing *normally* on simple tasks of visual discrimination of the type described in this paper. It has previously been postulated that the early stages of visual analysis resulting in a structured percept are achieved by the visual cortices, there being no lateralisation of function at this level of analysis (Warrington and Taylor, 1978). The evidence from patients recovering from cortical blindness provides support for this view; namely that systems subserving visual acuity, visual form perception, visual location and colour perception are retinotopically organised. The patients described here and other similar patients described in the literature all had evidence of bilateral occipital lobe lesions. All the indications are that such visual deficits in patients with unilateral lesions are restricted to the contralateral half-field of vision, lateralisation of function only occurring at the level of categorical perception.

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RECOGNITION AND THE SELF: REMARKS ON POPPER'S EPISTEMOLOGY

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a) *Towards the self.*

"Pattern Recognition Mechanism": in each of the three words which give the present Conference its title, and in their union, can be read the enunciation of a problem. What is "pattern", and in what way can this "something" be proposed as an object of "recognition"? And what activity does "recognition" imply? Furthermore, is this an operation that should be seen as the effect, the simple product of a purely mechanical connection, as the choice of the term "mechanism" would seem to indicate? As one can see, what scientific inquiry can and must take as the starting point which is meant to circumscribe the ambit of its experimental activity is instead a source of embarrassment and questions for philosophical quest. Indeed, in this lies the peculiar characteristic of philosophical speculation — and for this reason philosophy has often been accused of being "useless" — that the innocence of truth is never for the philosopher a starting point, but always a goal. It is not by chance that the symbol of philosophy is the bird of Minerva, which awakens at sunset.

"Pattern Recognition": a philosophical problem is already implied here. It is not the unity and meaning of what is indicated by "pattern" (and which can by connotation be extended to include the more traditional concepts of "figure" and "form"), nor the act of "recognition" as a purely psychological process that stimulates a philosopher's interest. Rather, it is the unity and solidarity of the two, the fact that one cannot talk of "pattern" without mentioning "recognition" and vice versa, that has always constituted the basic ground for meditation and enquiry. Long before the modern theory of knowledge took these problems as its favorite ones, classical thought gave them a central place within the frame of its epistemological conception. One need only think of Plato, for whom "recognition" and "recollection" represent the two bases of the doctrine of knowledge as reminiscence. For Plato, to know means to re-cognize something in its truth. For man this means to remember, to collect oneself (also in the ethical sense) thanks to what had once already been seen and known in its truth (the "idea"). Even outside the mythical framework of Plato's thought, recognition is an essential element also for Aristotle's more realistic epistemology. Here, reminiscence is out — though Aristotle was the first to devote a special treatise to the problem of memory — but knowledge can be seen as an activity by which one returns to the heart of the known object passing from superficial apprehension to a radical recognition of the object's true nature. The famous formula with which Aristotle tries to express this central concept (*to ti ēn einai*) indicates, by using the imperfect (*ēn*), a "having-to-be-what-a-thing-is", that is to say the ultimate nature of all reality to which human intelligence tends as to the final stage of a true recognition. Taking up in his own way his teacher's terminology, Aristotle, too, calls this central nucleus *eidos* — "form".

This brief reference to classical thought is not meant to be just a learned parenthesis, for indeed it potentially comprises a problem which the theme of our Conference invites us to face. The crucial point lies in what seems to be suggested by the adoption of the term "mechanism". There is no doubt that even though it is very general, this word seems to point to a consideration of the phenomenon of recognition as a simple effect of a complex of brain processes. With the different perspective it indicates, classical thought gives us, then, an opportunity for meditating on what our culture takes as an inevitable conclusion. Of course I do not want to question the experimental framework, which needs restrictive hypotheses in order to operate on a solid, circumscribed ground. What I would like to discuss is rather the idea — which is widespread today — that a hypothetically exhaustive description of cerebral processes can constitute a sufficient explanation of the activity of consciousness at all its levels. In other words, the question is to see whether from a general point of view the fact that — as Socrates said in the *Phaedo* — I have bones and nerves is not only the necessary condition but also the sufficient cause of my sitting here still without getting up to go somewhere else.

Thus, our question could be put in the following manner: apart from the opportunity of experimental proof, can one maintain that a virtually complete analysis of cerebral processes can exhaust the meaning of a phenomenon such as "pattern recognition"? Once we put the question in these terms, we can but see it as a particular chapter of the better known mind-body problem, and it is in this context that it must be treated as a philosophical question. A special reason brings us to this conclusion, too. This Conference is meant to celebrate the eightieth birthday of Sir J. Eccles. Now, taking as starting point the remarkable book that Eccles wrote in collaboration with K.R. Popper, *The Self and its Brain* [1], I will try to develop some speculations on the original and stimulating response that this book has prompted against the prevailing contemporary inclination towards a monist solution of the mind-body problem, to which also the choice of the word "mechanism" for the title of the present Conference seems to refer.

Let us ask the question brutally: is man more than a mechanism (body), not only for what he does or is able to do, but also for what he is to himself (mind and self), or does everything in him equal the operation of a machine, however wonderfully complex it may be? In sum, which is right — monism or dualism? Or — and I only hint at it here — is there also a third possible solution? At a time when, as Lord Adrian pointed out in this very place some twenty years ago in his paper *Consciousness*, "modern metaphysicians of all shades have shown a notable unanimity in rejecting the dualist position" [2], Popper and Eccles become courageous defenders precisely of the dualist thesis. To what extent is it possible to share their argument? And where is it weakest — not through a lack of materialistic monism, but rather because it fails to recognize the real ground of the spiritual nature of the self (at least in the case of Popper, to whom I shall from now on confine myself)?

We might appreciate the issue better if we begin with a quotation from Pascal, cited by Eccles at p. 357 of SB. "When I consider the short extent of my life, swallowed up in the eternity before and after, the small space that I fill or even see, engulfed in the infinite immensity of spaces unknown to me and which know me not, I am terrified, and astonished to find myself here, not there. For there is no reason why I should be here, not there, why now rather than at another time. Who put me here? By whose order and design have this place and time been allotted to me? (...) The eternal silence of those infinite spaces strikes me with terror" [3]. Indeed whereas to Pascal that inner discomfort was the starting point of a deeper and really striking quest, some modern scientists seem to feel very much at ease with it, to the point of taking it as a good and true basis upon which a new ethics of knowledge should be built up. I am referring, as one can easily gather, to Monod's well known *Le hasard et la nécessité* (1970). Despite his dualism, this may be assumed to be to some extent also Popper's position. Thus one might wonder whether such an outcome has its roots in a specific epistemological conception or whether it is just a matter of personal and indeed unquestionable inclinations and beliefs. The latter seems to be the answer which emerges from a reading of the last pages of SB, where the Authors, though sharing to a large extent the same epistemological assumptions, come on this very point to quite a sharp disagreement. But behind Popper's position there is too much philosophy for us to be content only with the objection that faith (or non-faith), too, must have its own rational basis (*fides quaerens intellectum*). In fact, Popper's dualism expresses a precise philosophical view. And so does his peculiar notion of the objective "spirituality" of the self, which leads him to offer a historical rather than personal evaluation of it, with all the consequences which derive from it and which I cannot here examine in any detail (personality, survival and so forth).

b) *Monism, dualism, and the theory of the three Worlds.*

The problem is, as we have seen, the mind-body problem, or to put it better, the problem of the relationship (and "emergence") between the mind and the body — its restatement in terms of self-brain problem is mainly meant as an anthropological specialization of it. Since the age of the Cartesian separation of a *res cogitans* and a *res extensa*, this relationship has become a very acute problem for modern thought. Like Descartes, Popper is a dualist. Differently from him, however, Popper claims that mind and body do not indicate two different substances, but rather states and processes.

Now, the main purpose of the dualistic hypothesis is to avoid that thought be interpreted in terms of an epiphenomenal outcome of physical or material processes, and, on the other hand, that all reality be reduced to thought, in the sense of Berkeley's *esse est percipi.* These two opposed aspects of monism are widely criticized by Popper in the first section of SB. The asserted dualism is further specified by him as *interactionism*: this means the unacceptability of the idea of a parallelism between mental and physical states — as it happens to be in Descartes, Malebranche and Spinoza. Moreover, interactionism is claimed to justify or describe the deep relationship or better, the mutual ownership [4], namely the evident capacity of both sides to act and react causally upon each other, without the possibility of being thereof reduced to each other. Incidentally, regarding this relationship we find a further hypothesis both in Popper and in Eccles which can undergo methodical criticism. The matter in hand is the need of finding out some preeminent localization for the interaction. For Eccles this link is supplied by the liaison-brain, while for Popper by language. The difficult point in this matter seems to be the following: either this element belongs to either (i.e. body or mind, self or brain) and in this case there would be no real intermediation, or supposing it is a really intermediate third thing, it would be possible to raise an endless demand for further intermediations. This may sound a sophistical objection, but it is not so. On the contrary, it is meant to show the main weakness of any dualism whatsoever (also to be found in parallelism), where starting from two entities (no matter what their nature may be), the result is that the intermediating factor eventually becomes the most important thing. This is an old, well known story in the history of philosophy, a story which culminates in Hegel's dialectic and is basically due to the philosopher's incapacity to disentangle the order of the analysis from the things analyzed, or, in other words, of conceiving a unity that comes before its constituent elements. To make all this clearer: this idea of a topological determination of the relationship of mind and body is reminiscent of Descartes' hypothesis of the pineal gland as the place of the soul, and indeed betrays a somewhat substantialistic preconception of mind and body as two a-priori separate entities. This suspicion is strongly corroborated by Popper's appreciation of Plato's metaphor of the helmsman and the ship to show the relationship between mind and body. One might perhaps try to avoid such an extrinsic picture of this relation, by appealing to the functional character of the elements, thus coming near to the Kantian doctrine of a "schematism" between the concepts of the intellect and the forms of intuition (another way of stating the same eternal problem). In any case my criticism is not in the least a plea for monism: all it intends to do is to recall something that has remained ignored for many centuries now, and ignored, needless to say, also by Popper's historical account of the mind-body problem. I mean the idea of a fundamental unity of man, that from Aristotle to Aquinas went under the name of "hylemorfism", a unity which needs not to be explained in terms of an addition or interaction of elements, but which explains the elements in terms of the line of reciprocal reflection (*horizon*) of two metaphysical conditions that cannot be thought of apart from each other (i.e. matter and form). This is the only serious attempt in the whole history of the mind-body problem that comes close to an evaluation of the inner spiritual principle of man without a priori separating it from the body, or reducing it to a sheer outcome of brain processes.

On the contrary, in Popper's dualism this evaluation is entrusted to the conception of the self as connected with the three-worlds epistemological model. Before moving to further perplexities, let us very briefly summarize this three-world model. The interactionist interpretation of dualism presupposes two levels of reality, physical reality and mental reality. These are called by Popper World 1 and World 2. Previous to its interactionist role, World 1 plays in Popper's epistemology a very important function. It constitutes the realm of the last evidence for existence and reality. First of all come the physical bodies, and these are assumed to be the very first referent for the ordinary use of the word "real": "the most central usage of the term 'real' — says Popper — is its use to characterize material things of ordinary size" (SB p. 9). "Ordinary size" has obviously to be interpreted as the possibility for something to be the object of a normal perception under normal conditions. Solid material bodies become thereafter the ultimate referent of the reality of all those things that, though not perceptible and even not material, nonetheless manifestly produce some effect upon the world of physical reality (a pretty much Kantian idea). In Popper's words, "we accept things as 'real' if they can causally act upon, or interact with, ordinary real material things" (SB p. 10). This is not a "deduction" of reality in the Kantian sense of this word, namely a philosophical demonstration of its necessity, nor are physical bodies taken by Popper to be the ultimate level of reality. We are dealing rather with what Popper would call a "conjecture", in this case a sort of nominal definition. And yet it is not such an innocent definition as it appears to be. In fact it states the possibility of inferring the existence of everything that interacts with the bodies without committing oneself about what reality and existence are to be (Berkeley would have had no difficulty in criticizing the issue). But Popper manages to avoid such "quibbles" because of his programmatic refusal of what he calls the "what is" questions.

In any case, Poppers claims to have established a sound basis in World 1 which can guarantee not only the reality of its hidden states and processes, but also the reality of a second level World 2, the realm of mental states, which is real because it interacts with World 1, and real in itself because on the sole account of World 1 we could not possibly understand such an interaction (we could not make of the effect the cause of its cause, as it were; i.e. World 2 is not a simple epiphenomenon of World 1).

Moreover, there is another world, World 3, which is to be distinguished from both World 1 and World 2. Again, this is real because it interacts with World 1 via World 2 and it is real in itself because it cannot be reduced to being an epiphenomenon of World 2 (or of World 1). To sum up, we have "first the world of physical objects and of physical states; secondly the world of states of consciousness, or of mental states, or perhaps of behavioural dispositions to act; and thirdly, the world of objective contents of thought, especially of scientfic and poetic thoughts and works of art" [5]. This tripartite scheme entails for Popper not only a structural heuristic import, but also an evolutionary meaning. Indeed it is clear that numbers 1, 2 and 3 are not given at random, and that, as in the succession of numbers, they imply the (temporal) priority of the lower stages. Furthermore, as for numbers, the succession is not continuous. This means that evolution from the lower to the higher stages, at least for some of its steps, is creative: the higher stages cannot be reduced to being the simple outcome of the increasing complexity of the lower ones. Rather we should admit that at a certain evolutionary point something new "emerges", something that is totally unpredictable and even most improbable on the sole account of the lower levels. Thus we can say that World 2 emerges above World 1, and World 3 above World 2 (there are for Popper at least three other sub-levels of emergence — but epistemologically they can be resolved in the tripartite model).

Popper describes World 3 as the realm of objective knowledge. He claims that it is necessary to discriminate from an epistemological point of view the psychological processes of knowing (World 2) from the object of knowledge itself. The last cannot be explained in its real value and meaning simply in terms of mental processes. This may seem to be very sound and even unquestionable: indeed the objective import of knowledge has very little to do with psychological processes. But one may begin to wonder whether the very opposition between subjective and objective knowledge is real and unavoidable, or if the defence of an objective knowledge that at times arises in modern philosophy (Popper quotes Bolzano, Frege and Husserl, though also other names could be mentioned) is prone to a failure that is parallel to the one it criticizes, being in fact rooted in the same — false — initial opposition, which is the epistemological equivalent of the dualism we have already noted between mind and body.

Let us now sketch very briefly Popper's account of World 3, in which, as he says, the self is "anchored". First of all Popper refers explicitly to Plato's doctrine of a world of ideas. The objects of World 3 are very much akin to Plato's ideal paradigms. The main difference lies in the fact that whereas Plato's ideas are divine in nature and eternal in being, the World 3 objects are man-made and changing. Still, they may be regarded as separate or independent from physical and mental reality and activity or, what is equivalent, they are not to be seen as the product of a generalization of experiences nor of induction. Being separate, however, they are not essences, but problems and prohlem solutions that call for a purely intellectual trial and error. Thus World 3 can be seen as the store of the tradition of the highest (hut why so?) intellectual achievements of humanity, but such a store that continuously applies for reassessment and restatement.

At this point it is possihle to show the meaning of the three-world model for Popper's anthropological dualism and for his notion of the self. Of course if it were possible to establish an immediate equivalence of body, mind and self with the three-world series, our analysis would be far easier. Yet, things are not as simple as that, even though that kind of parallel is not after all very far from being true. What is most important, in any case, is to throw light on the meaning of World 3 in order to evaluate what Popper calls the "self". For him the self is a moment — a higher stage — of the mind, but it does not entirely coincide with the mind itself. There is much in "mind" that cannot be recognized as "self": automatic psychic processes and more or less conscious instinctual mechanisms cannot be part of the self's higher sphere, which implies on its side a real detachment from the purely psychic processes. This detachment is given in self consciousness, i.e. the consciousness of one's own personal identity, which therefore constitutes the basic mark of the self. Animals undoubtedly show a certain awareness of their condition — and hence cannot be considered as mere machines — but they have no feeling of a personal uniqueness and cannot therefore be seen as "selves". In short, the self implies certain prerequisites which simple conscience (mind as phenomenon of World 2) cannot guarantee. It is in fact in the mind's capacity to transcend itself that Popper finds the specific nature of the self. Now, what does this act of transcending mean but the mind's capacity — as self — to enter World 3? The self is not World 3, nor is World 3 the self; but the possibility both have of being what they are arises from their acting and reacting each upon the other. On the one hand, the possibility the self has to "emerge" above the flow of psychic processes, to recognize itself as an objective, durable reality, is offered by the retroactive effect of World

3 upon World 2 — that is to say, the self is the "precipitate" of a series of objective, linguistic or theoretical, processes, and hence a reality which can be apprehended only within the background of those processes (Medieval philosophers had already recognized this "secondary" nature of self-consciousness and called it *intentio secunda*). On the other hand, World 3 presupposes, at least as a condition for its existence, an activity which has its roots in World 2, though World 3 itself keeps, as far as its meaning is concerned, a position of objective autonomy vis-à-vis World 2.

It will be now clear, then, that the epistemological theory of the three worlds, and specifically the "discovery" of World 3 as the world of objective knowledge, are used by Popper to re-define the overall picture of the body-mind relationship, with special reference to the two questions of interaction and emergence of the self. In particular, the full evaluation of the self is due not so much to self-consciousness, but to the self's own capacity to face and solve problems, to concentrate upon and comprehend theories, in short to find and keep its place in World 3.

This point deserves further enquiry, for indeed it might seem that here we meet with one of those occasions — rare for modern epistemology — where the significance and spiritual value of intellectual activity are rooted not so much in the supposed "spontaneity" of intelligence, but rather in its capacity or readiness to be measured by (or to measure itself upon) a world of objectively autonomous realities. Unfortunately, this is not the case. The originality of Popper's position towards modern rationalism does not in this case go beyond the apparent autonomy he acknowledges to an objective world, the fundamental function of which lies in its providing a framework or an appropriate context for the formation and production of new knowledge.

One can undoubtedly purge this function of all possible psychological connotations, but this is not enough to make of it a real objectivity and to obtain the complete elimination of the "knowing subject". It is after all obvious that Popper's whole treatment of World 3 is but a positivistic variation of what Kant called the transcendental conditions (for the subject) of an objectively valuable knowledge.

c) *Intentionality, spontaneity and the emergence of the self.*

We may now return to the initial point of "recognition". Indeed this is a very good basis for appreciating the real meaning assigned to the appraisal of the spiritual value (or "emergence") of the self. Here, before sketching the modern rationalistic background in which also Popper's position must be understood, it can be very much to the purpose to develop for a while the solution that classical philosophy gave to the problem. I take Aristotle as the most representative figure of Antiquities not only because of his more developed technicality, but also because, in opposition to his master Plato, he tries to avoid as far as he can any kind of opposition between body and mind in evaluating the spiritual import of the act of knowing. For Aristotle every genuine act of knowing can be said to be an act of recognizing reality such as it is. This must not be interpreted as bare empiricism. On the contrary, here we face the idea of man's plunging into reality, an idea which, without denying the value of cognition through the senses, nevertheless represents a true going beyond this initial level. Aristotle's teleological conception of nature and reality, which was so strongly influenced by his biological researches, shows the need of an explanation of reality in terms of the inner agreement of each being with its own hidden nucleus of organization. Each being is supported (up-held) by its essence (or form) as by a sort of internal objective memory, the same that echoes in the Greek imperfect tense (*ēn*) cited above. This ancient idea has been given new life in our times by the discovery of the DNA's genetic memory. To know is to approach as closely as possible that hidden nucleus, and the final step of all this is the clear recognition one gains of the nucleus itself in its (ideally) perfect definition. Thus recognizing, recollecting, knowing is but the result of an act of *intentionality*, i.e. man's disposition to be filled by the very form of the thing. The act of intelligence is therefore at the same time active and passive: it is the intellect's openness to receive and to be informed, but only in its own particular way — that of the universality. One does not know reality in the passive mode of a print upon wax (to recall Locke's celebrated metaphor, which was in fact proposed by Plato for the first time and adopted by Aristotle himself), but rather is in-formed (i.e. knows) so long as he enters the paths of the hidden intelligibility of reality. The ultimate apprehension (*noēsis*, *apprehensio*) is form.

But this notion of form, as the intimate condition of being for each reality (*forma dat esse rei*), manifests a double aspect as far as the act of knowing is concerned. Besides the fact that form is the object of the final apprehension of the true nature of reality, we must also acknowledge the fact that the character of form is also shared by man's intelligent mind (in the sense of Popper's self). Mind or soul is the form of the body, the inner condition for the body itself to be. But it is a form that in itself has no form, apart from the capacity of being informed by reality. Now what is more important for us is that it is precisely in this idea of a "formless form", as the true nature of man's intelligent mind, that Aristotle rooted his evaluation of the absolute openness and spirituality of the intellect without being forced to exclude it from the body. What is most poor and in itself absolutely bare, is for this very reason most rich and pure. Intentionality and receptivity is for Aristotle the mark of human spirituality. It is clear then, that with this superaddition of an ontological and a noetic character (mind as the form of the body and mind as the receptivity of forms) we are supplied with both a substantial and a functional description of the human mind. Here we cannot deal with all the subtleties and difficulties of this doctrine. Let us rather take this brief account of what spirituality meant for Aristotelian (and indeed scholastic) anthropology as a mere device against which to measure the radical shift that the notion of form has undergone in modern thought, and the import of this upon the notion of the spirituality of the mind.

This crucial modification of the notion of form took place in philosophical tradition when knowledge began to be interpreted as nothing more than a relationship between a knowing subject and an external object, and such a relationship that could adequately be accounted for by means of the same principle of causality which is used by physics (i.e. in terms of efficient cause and effect). By the time of Descartes — I consider him as the most outstanding figure of this new trend, though the story can be traced back to earlier Nominalism — the very sensible warning of Caietanus, a Dominican philosopher of the early 16th century, was completely lost. I would like to quote this warning here: "it would be awkward to give an account of sense and of the formal object of sense, of intellect and of its formal object, and also of the act of sensing and understanding in the same way as we do of other things. One must learn to elevate one's mind and to enter a higher order of reality" [6]. Since Descartes, then, thanks to the generalization of the model of efficient causes, knowledge began to be considered as a type of production either in the subject or of the subject.

The first direction (production in the subject) was chosen by empiricism, the second one by rationalism, but both led to a complete dissolution of metaphysics. Let us follow this second path for a short while: indeed it is the one which is relevant for understanding Popper's position. Popper's claim that his theory's goal is the foundation of an "epistemology without a knowing subject" does not weaken in the least his strong dependence on modern rationalism. As a matter of fact rationalism, at least from Kant on, has never spoken of the "subject" in such psychological fashion as the one Popper criticizes. We must therefore admit that his criticism is mainly directed against the empiricist's notion of the knowing subject. On the contrary, Kant's Transcendental Subject (and even Descartes' Ego) goes back to at least such a strongly objective foundation as the one Popper seeks for his notion of the self. Moreover, Kant's example and suggestions are so deep and widespread throughout Popper's epistemology from its very beginning, that it seems difficult to deny the same patronage on this very point.

To summarize Kant's position: let the subject be the producer, i.e. the "legislator" of nature thanks to what Kant calls the "spontaneity of the understanding" (*Spontaneität der Verstand*) then in order not to fall into arbitrariness (such as the psychological "habits" or "beliefs" of empiricism result in) we have to find out some kind of rule, as an objective standard (already internal to the subject) of the act of legislation. This standard, according to Kant, may be found through a work of transcendental reflection upon those branches of knowledge which already exhibit the requisites of the necessity and universality of their statements. Thus from mathematics and Newtonian physics (in other words from World 3's objects!) Kant draws the idea of a synthetic a priori judgement, and by combining this assumption with formal logic, he "deduces" his famous table of the categories, i.e. of the internal intellectual objective conditions of human scientific knowledge. Needless to say, with his *Kritik der reinen Vernunft* (1781, 2nd ed. 1787) he supplies a philosophical foundation of nothing more than those very branches of science he had started with. All the rest is left to a form of psychological experience ("judgement of perception") devoid of any kind of necessity. Ten years later, when Kant came to enquire about other forms of scientific activity (that he called "empirical sciences", namely all the classificatory sciences, plus biology) he was bound to seek for a somewhat looser principle of knowledge. This was the outcome of his *Kritik der Urteilskraft* (1790), where Kant shows how in order to account for the scientist's choice among different explanatory models of description of an empirically given material, as well as for the very first featuring of these models, we have to assume a sort of aesthetic activity, a first creative draft of what is later to become an object of scientific systematization.

It seems to me very clear that Popper's World 3 is meant to play the same epistemological role as Kant's "transcendental principles" in both the *Kritik der reinen Vernunft* and the *Kritik der Urteilskraft* — that of securing an objective screen for the acts of the self without prejudice to its claimed creativity. Indeed Popper criticizes the sclerosis of the Kantian "table of the categories", while totally ignoring the new perspectives opened by the "third" *Kritik*. When Popper, in an attempt at rectifying Kant, maintains that "theories are seen to be the *free* creations of our own minds the result of an almost poetic intuition, of an attempt to understand intuitively the laws of nature", this is not in the least a "modification of Kant's solution" as Popper believes. On the contrary, without being aware of it, he is speaking in the same spirit of the *Kritik der Urteilskraft*. Popper adds, in terms that must not deceive us, "we no longer try to force our creations upon nature. On the contrary, we question nature, as Kant taught us to do; and we try to elicit from her *negative* answers concerning the truth of our theories: we do not try to prove or *verify* them, but we test them by trying to *disprove* or to falsify them, to refute them. In this way the freedom and boldness of our theoretical creations can be controlled and tempered by self-criticism..." [7]. This prudential statement, with its reminiscence of Popper's well known "falsificationism", does not lead us any closer to an objective conception of reality, such as the one shown in the classical notion of form. Reality is already silent and subject to be forced by us, when objectivity is taken as a mere guarantee of human knowledge. When Popper claims that it is not possible to assert that things "are so", but only that things "are not so", does this make any difference as to the import of reality upon knowledge? Furthermore, what kind of an objective function of control is ensured by reality, if any hypothesis and experiment, as Popper maintains, is alive and meaningful only within a context of theories? If the act of formation and reassessment of theories is but a process of *making-matching-making*, the middle term, corroborating or falsifying, does not indeed face any reality, but always and only a theory.

Neither the innovating audacity nor the prudential flexibility of scientific creativity is unknown to Kant, who in fact anticipates many of Popper's solutions in this matter. Here, however, I am not looking for philological details. I have introduced this reference only to clarify the nature and function of World 3 as the world of objective knowledge. Popper says he wants to abandon the subject-object polarity in the theory of knowledge, and for this he appeals to a knowledge without a knowing subject. But this refusal affects only the subject as psychological entity, not at all the subject as transcendental principle of the laws of nature.

This is precisely what Popper tries to found "objectively". Popper's objectivity, then, indicates above all the impersonal character of theories, but never an objective connotation of the theories themselves. Popper completely neglects what the scholastics called the "formal object", that is to say the delimitation, founded upon the object's nature, of a certain ambit of "knowability". He in fact fully shares with rationalism (and partly with idealism) the prejudice towards the objectivity of form which necessarily follows from establishing the subject as "legislator" of nature.

The function of that curious blend of Plato, Hegel, Comte and a few elements of Darwinian evolutionism which is World 3, becomes fully clear as an answer to the need of ensuring an objective stimulus and control to the free "Copernican" creativity, which is the source of the making-matching-making process. Once you reject the rigidity of categories the risk presents itself of giving way to epistemological arbitrariness such as that theorized by Feyerabend's anarchism. Feyerabend at least has the merit of having unmasked the inevitably irrational outcome of a rationalism brought to its extreme consequences. Being, as a "moderate" rationalist, convinced of the *Wertfreiheit* of science (i.e. of its independence from all those alien conditionings which are for Feyerabend its real principle), Popper must in any case establish an "objective" limit in order for creativity not to become gratuitous and for science not to become a prey to all sorts of external conditioning. This limit, however, is still within the dynamics of knowledge and never aims at a real objective determination of it (we have already seen how even the *ultima ratio*, the physical world, is no more than an hypothesis). Here we really see the perverse mechanism (human, all too human!) of any genuine rationalism at work: the theoretical stage requires its meta-theoretical stage, and so on endlessly. This happens when one totally ignores the sense of the fundamental affinity which prepares human intelligence to accept, in the act of knowing, any intelligible form. Form is in fact the ever renewed seal of that intellect's readiness to consent to being. When scientific creativity roots only in the (transcendental) subject its own fundamental norm, it is inevitable for it to recognize its highest moment of expression in an "aesthetic" almost poetic act. Here scientific creativity comes closest to what Kant called "intuitive intellect" or "archetypal intellect". Before this extreme possibility, however, a "critical" rationalist, though longing for it, must pause: he cannot share it. Creativity must still be "reasonable" and hence acquire a system of self-control without ever being forced to reach something beyond itself. Whether it be called World 3, or complex of theories, or paradigm, or meta-theoretical complement of the self, the context of "objective knowledge" offers but a series of projecting stages, each of which postulates a successive one as its own indispensable condition of interpretation. In this endless discursiviness man, like a new Midas, can never touch anything that has not been already contaminated by his intemperate "creativity".

d) *What is the self?*

"Recognition mechanism": the major effort of Popper's dualistic hypothesis is directed against any form of reduction of the superior activity of the mind to a bare outcome of a mechanism. Something higher "emerges" above the levels of the physical and psycho-biological mechanisms. This is the self. And to this extent we must appreciate Popper's dualism as a bold effort against the trend overwhelming nowadays of materialistic monism. But this is all.

The self "emerges": what is the self? I have chosen this way of putting the question (that Popper most dislikes) on purpose. A "what is" question is in fact to him a question about essences, and therefore a meaningless question. At one point in SB, however, Popper admits that "the talk about a substantial self is far from being a bad metaphor" (p. 146). The image of the "ghost in the machine", in which he, despite all Ryle's arguments against it, claims to believe is not for him a bad metaphor either. But a ghost and a substance are not quite the same thing, even though they are used as metaphors! Again then: what is the self? A ghost, a kind of substance in process, a helmsman, a pure function? Alas! everything goes! Or rather: there is no answer, just because what is questioned coincides with the question itself. It is not just because we are facing a "what is" question that there is no answer, but because we are questioning the self, i.e. the possibility itself of asking questions (the universal legislator of all questioning), in such a way that if we take the question seriously we are immediately involved in an endless circle.

As we have seen, it is precisely this kind of "principality" of the self, its autonomy or "spontaneity", that hinders the demand for a really objective foundation of it. What Popper offers to us instead is the so called objectivity of World 3. In other words: there is no real objectivity (a demand which to Popper is a myth due possibly to an equivocal overevaluation of the import of perception upon knowledge): the objectivity for him is rooted in language and is manifested by those human products (problems, theories, works of art) that appear to be nothing more than a specialization of language.

We go back to Pascal's dilemma: in the solitude of infinity what sense has this trifle — ourselves? Is Popper's "self" enough of an answer? It does not look like it. The self "emerges", is a superior function, it is anchored in World 3. Hence it is always (at least virtually) in touch with the highest conquests of intelligence; it is an unforeseeable, indeed altogether improbable, event, but above all it is the critical ruler of any perspective we might have of reality. "Reality", the "universe" — are not these concepts, acts of the self, impulses of World 3 to back-act on it? But then the significance of the self is the self itself (as object of World 3), and all questions lose strength and taste. For Popper in fact the world of values (and within it the value of the self) is always a stage of World 3. Kant, who wondered most at the starry sky above him and at the moral world within him, had, with this distinction, tried to save the reciprocal autonomy of facts and values thanks to a schizophrenia of worlds (nature and freedom) which is difficult to uphold. For Popper a consequential rationalism cannot rightly allow this distinction to be made. The value of the self coincides with its being, i.e., with its function. And this "coextensivity" once more makes any non-psychological distinction between fact and value vain, so that in the end we cannot distinguish in this matter between value and non-value. This is exactly the original source of Pascal's *pari*, equally distant from yes and no. A rigorous rationalism (and such was Pascal's) allows no more than this — we may find no convenience in either pole, no external suggestion might come from without ourselves, from the world that surrounds us and of which we are a part. We only have the loneliness of risk and of absolute freedom. Popper, removed as he is from Pascal's tremblings, looks at all this skeptically. Of the three traditional characteristics of the soul — spirituality, immortality and personality — he accepts the first as a mere hint of "emergence", is inclined to discard the second (which he finds simply fearful), and considers the third as a specialized function of the consciousness. There is nothing in them that might constitute a real basis for the appraisal of the self. It is highly significant that, in this *pari* situation, Eccles, though starting with the same epistemological presuppositions, should often come, with equal right, to opposite conclusions (SB part III).

Recalling Pascal, we asked ourselves at the beginning whether the alternative imposed on men by the "sense of heing" between looking after their own business (as Voltaire suggested) or opening themselves up to higher hopes (Pascal's choice), can be solved by recurring to philosophy, or whether it is a question of merely personal beliefs. What, at the end of the enquiry, we can say, is that Popper's critical rationalism (like any form of rationalism) excludes any possibility for the self to appraise its value, in that the self coincides with the totality of possible experiences without any space being left to its contrary determination (against which alone can something be qualified as value). Hence Popper's position leads to the conclusion that the problem must be solved on the level of personal belief, but it also strengthens the unavoidability of that *pari* situation which is itself vitiated right from the beginning hy the rationalistic divorce between the I and the world that surrounds it.

And yet, with its prefix of reiteration, the word "recognition" invites us to meditate precisely on the singular complexity of the act of human knowing which, the more it opens itself up to embrace reality, the more it stays within itself — the more it knows the form of being, the more it recognizes itself and its spiritual breadth. Indeed, it is only in the "potentiality" of the self as its formal determinability that the meaning and value of a genuine objective "emergence" projects itself. In this determination lies the appeal of the depth of form — a depth which is not just the kernel of a concealed thing in the sense of Heraclitus' "nature loves to hide", nor the opacity of form's being always intertwined with matter as far as man's experience is concerned. Far more than that: it is the depth of what in revealing the measure foreshadows at the same time the ontological ground in which a thing is rooted — and gives room to the real question.

Why is there being instead of nothing? It is only within such question that one discovers the sense of an objective value. Since — as Leibniz saw very well — "nothing" is simpler and more logical than "being", the very source of objective value is being. The spread of its roots in being measures for each being its objective value. Surely the improbability or the unforeseeability is not enough of a token of the value of the self, as Popper would maintain it to he. On an absolute scale, such as the one commanded hy Leibnitz's question, there is no more improbability for a self to be than for a pebble to be. If something is there, instead of nothing, then this "something" must have a meaning. This "must" is no longer an invocation which is pressing out of an existential anxiety, in front of which philosophy has nothing to say. Silence is allotted to philosophy whenever the self is torn up from its consent to the intelligibility of being. When the experience of reality no longer prompts man to face the depth and radicalness which alone can pave the way to a meditation on his spiritual dimension, then the self prepares for itself that loneliness which either makes it a slave of its own image or forces it to expect that immediate contact with the root of all "whys" that is the denial itself of all grace. "When a man is truly lonely — says Lamartine — God sends him a dog". What, then, if the dog, and all that comes with it is but the shadow (be it called conjecture or concept or whatever) that the self casts upon reality, and each form is imposed on being thanks, as it were, to a right of "projection"? Man can no longer escape his circle, nor can he avoid to make inevitable the dilemma between the *credo quia absurdum* and Wittgenstein's icy statement, "what one cannot speak of, one must keep silent about" [8]. It will be the task of philosophy to unmask that dilemma, once Aquinas' warning will again be taken seriously "amongst all errors the most indecent seems to be that because of which we err about the intellect, thanks to which [i.e. the intellect] we are born to know the truth, after having avoided all errors" [9]. That is, only through the poverty of the self can its real wealth emerge.

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THE ROLE OF NATURE, NURTURE, AND INTELLIGENCE IN PATTERN RECOGNITION

INTELLIGENT PATTERN RECOGNITION

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ABSTRACT — It is argued that the brain acquires knowledge of the patterns it recognises in three ways: by genetic inheritance, by learning or precept, and by intelligence — the detection of unexpected orderliness in sensory messages. This paper is mainly concerned with the third of these, but progress in understanding the neural mechanism of directional selectivity is reviewed, since this is probably the example of pattern selective neural logic we are closest to understanding at a biophysical level.

To illustrate the acquisition of patterns as unexpected orderliness, psychophysical experiments on the detection of order in arrays of random dots are described. These have confirmed ideas about band-pass spatial frequency filtering in primary visual cortex, and have provided some information about symmetry detecting mechanisms. The high efficiency of utilisation of the statistical information in these tasks shows that the visual system is good, on an absolute scale, at detecting order in chaos. The paper concludes with some speculations about the advantages of band-pass spatial frequency filtering, about the importance of knowing the statistical structure of sensory messages, and about the organisation of the visual system required to achieve this.

According to the Oxford English Dictionary the word *pattern* comes from *patron* in Middle English, and means *an archetype to be copied or emulated.* Now *patron* was used for both things and people, as is still the case in French, but in English *pattern* came to be used chiefly for inanimate objects. This raises a question whose answer affects one's attitude to the whole problem of pattern recognition: *patron*, the person, must obviously be recognised for his or her excellence, or for authority gained in some other way, but what gives an inanimate pattern its importance? How can an object be excellent or authoritative? Neither adjective seems appropriate, and yet I am convinced that patterns are important by virtue of a quality they themselves possess, not simply by qualities conferred on them by association. In order to lead you to this conclusion I shall start with an imaginary dialogue[1] between a Nativist (N), an Empiric (E), and myself on a simpler, more direct question. The view that I am espousing about the importance of redundancy in perception and thought goes back to Ernst Mach (1886) and Karl Pearson (1892) in the last century, and has been advanced more recently by Fred Attneave (1954) and myself (1961, 1984).

Dialogue on innate and learned acquisition of pattern

ME. "Can you detect a pattern without having any previous knowledge of it?"

N. "Why certainly you can: we all have born in us the capacity to detect certain outstanding and excellent qualities, such as female bodily beauty and elegance of behaviour."

ME. "But I think I learned to appreciate these qualities at my mother's breast or knee, and I am not at all sure that they were born in me. What say you, Empiric?"

E. "I could not agree with you more; the appreciation of these qualities depends entirely upon early experience and education, as you can easily tell by observing the savage and uncouth tastes of those who have been deprived of a satisfactory bonding relationship in early life. That is why it is so important to provide generous subsidies..."

ME. "Quite so, quite so, but..."

N. "Well I don't agree with you at all. I have seen a chick newly hatched from a seagull's egg peck affectionately and in an entirely decorous manner at the elegant red spot on its mother's bill, thus proving beyond all reasonable doubt that it had a natural taste for female beauty."

E. "That proves nothing, for I have seen newly hatched goslings behave in the most ridiculous and perverse manner, all as a result of what they experienced shortly after hatching. Instead of showing natural love for their mother goose, and total obedience to her, they rushed with a single mind to a man in breeches while their mother waddled pathetically in the background."

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[1] At the meeting Professor Elisabeth Warrington very kindly read the part of the Empiric and Professor Lamberto Maffei that of the Nativist.

ME. "You are both referring to fascinating observations made thirty or forty years ago, and confirmed repeatedly since. I think they establish without doubt that a pattern, which is afterwards to be recognised, can be implanted in the brain either by experience, or by the same developmental processes that generate the bodily patterns of an animal. So the question whether you can detect a pattern without having previous knowledge of it is still unanswered: all that we have discovered is that knowledge of a pattern can be acquired genetically as well as by experience."

At this point I am going to interrupt the dialogue in order to review what is known of the neural mechanism of a simple example of innately determined pattern recognition. After doing this I shall return to the dialogue, for my main point in this paper is to argue, as above, that there is more to a pattern than what it is associated with, and to try to show that this intrinsic property is orderliness, the opposite of chaos or randomness. Now intelligence has been defined as the ability to detect order, and I therefore think that intelligence ranks with nature and nurture as a means of detecting pattern. These ideas are closely related to some I have written about before (Barlow, 1961, 1974, 1984) in terms of information theory and reduction of redundancy, but here I shall avoid this technical approach and shall use more qualitative arguments. First, however, consider the observations referred to by N and E above.

Innate pattern detection

About thirty years ago the interesting results already referred to by "Nativist" were becoming widely known, largely through the work of N. Tinbergen (1953). By constructing various models of a herring gull's head and testing their effectiveness, the red dot on the lower mandible was shown to be important in eliciting the pecking response of the young by which they obtain the regurgitated food held in their parent's bill. Was this simply because the model with the red dot was a better match to the chick's memory of a real herring gull's head than models with the wrong coloured dot or none at all? The answer must be "No" because the experiment works with chicks newly hatched by incubation that have never seen an adult gull. Furthermore a stimulus can be found that is actually better than the best imitation of a real gull's head.

These results were not the first of their kind, but they became widely known and opened my eyes to "innate releasing mechanisms" — the idea that quite simple features of sensory stimuli can trigger important items of behaviour. At that time I was working on the frog's retina and had been impressed by the fact that it did a good deal more than simply transduce light into nerve impulses: because of lateral inhibition a ganglion cell responds better to a small stimulus than to a large one (Barlow, 1953), and Hartline (1938) had emphasised many years previously that it responds better to a moving stimulus than a stationary one. Was it possible, then, that the ethological and neurophysiological approaches met in the retina? Might certain ganglion cells act as locks which, when opened by the appropriate key stimuli, admitted signals to the brain that triggered particular items from the animal's behavioural repertoire?

With this in mind I tried playing about with various optical stimuli, trying to find out how to elicit the maximum number of impulses from ganglion cells of various types. For the on-off type a piece of black or white paper mounted on a wire and twiddled or agitated in front of a lens casting its image on the ganglion cell's receptive field proved very effective. From the optics one could calculate what would be the equivalent stimulus for an intact frog, so I armed myself with the appropriate paper disks on wires and visited the tanks in the basement where the frogs were kept. The first tank held a few English frogs (*Rana temporaria*), and they did nothing whatever I twiddled or jerked in front of them; perhaps they were sick or on strike. But the second tank had some *Rana esculenta* recently imported from Hungary, and they were quite different: the sight of my twiddling and jerking bits of paper transformed them from a passive mass into a den of ravenous beasts jumping and snapping at these lures. I cannot claim to have established that the optimum twiddle-rate and paper-size were identical for the intact frogs and their retinal ganglion cells, but it was certainly impressive to find that a stimulus chosen on physiological grounds should be so effective behaviourally.

It is unfortunately not easy to see how this kind of anecdotal evidence can be put on a sounder footing. Possibly there is enough variation between the properties of retinal ganglion cells in different species for one to establish convincing parallels with feeding habits, but I rather doubt if the crude optimisation I did would have given a very different answer even for some of the ganglion cells of the cat. Another trouble with extending this line of argument is that excitation of the appropriate ganglion cell can, at best, only be the first condition for eliciting a specific response. The frog must, presumably, also be hungry, and not frightened by large moving objects in other parts of the visual field. Such complicating factors become obvious soon enough in a behavioural experiment, and they make it difficult to provide anything approaching a complete account of pattern recognition in neurophysiological terms. But selectivity for pattern is the important property, and this can be investigated physiologically.

Neural mechanism of pattern selectivity

The directionally selective ganglion cells of the rabbit's retina provide one of the simplest examples of pattern detecting mechanism. When Levick and I analysed their properties in 1965 (Barlow and Levick, 1965) we showed: a) that the mechanism could distinguish the sequence of excitation of just a single pair of points in the ganglion cell's receptive field; b) this pair did not have to lie one on either side of a fixed dividing line in the receptive field or anything simple like that, but could occupy a wide variety of positions: we therefore thought that the ganglion cell must be pooling information from many sub-units, each with the sequence selective property; c) many facts fitted a model of the mechanism in which inhibition prevented responses to the wrong sequence, rather than a more obvious model with a coincidence detecting mechanism that responded only to the correct sequence. Many of these observations have been confirmed and extended (Wyatt and Daw, 1976; Ariel and Daw, 1982), and evidence for the importance of inhibition for pattern selectivity has been found elsewhere (Sillito *et al.*, 1980). Thus it seems likely that the brain makes extensive use of what we called VETO logic (perhaps better called NOT AND, or NAND logic), and it may never use AND for the restrictive logical condition. However to assess progress it is more instructive to look at what we got wrong rather than what we may have got right.

Because it is the bipolar cells that feed the ganglion cells we naturally suggested that these were the anatomical sub-units that possessed the sequence selective property, and the horizontal cells, from what was then known, seemed to fit the bill for the inhibitory veto-ing elements. This interpretation is shown in fig. 1, but it was cast in doubt by the electron-microscopy of Dowling (1968) and Dubin (1970), for they showed that retinae in which complex information processing takes place tend to have complex synaptic structures in the inner, rather than the outer, plexiform layer. As Levick and I ought perhaps to have realised, the synapses between receptors, bipolars, and horizontal cells must be mainly concerned with gain control and lateral inhibition, which are required to enable the retina to work over the vast range of luminances that it encounters. Our

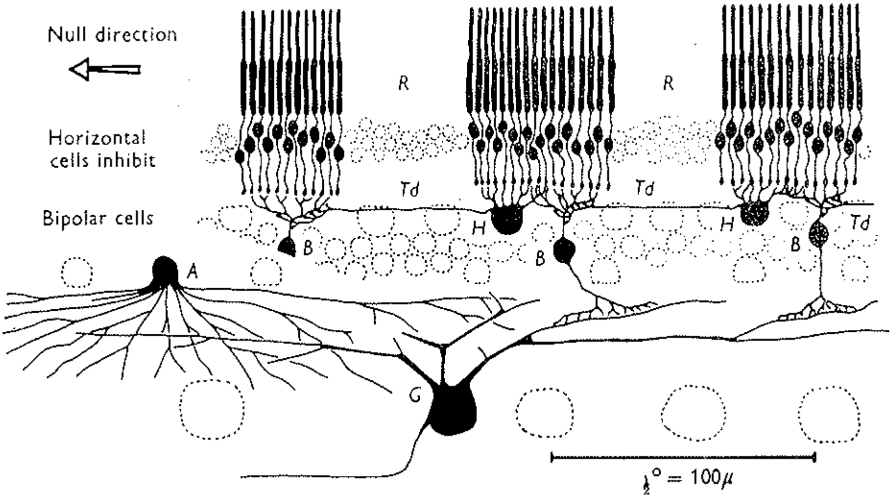

FIG. 1. The scheme for directional selectivity in "on-off" ganglion cells of the rabbit retina proposed by Barlow and Levick (1965). A process of a horizontal cell was thought to inhibit a bipolar cell lying in the null (i.e. non-preferred) direction. Cells were thus thought of as the logic elements, but later theories suggest that synapses and synaptic complexes can act as separate elements (see figs. 2 and 3).

scheme finally died when Werblin (1970) looked for the sequence selectivity it predicted in bipolar cells and could find no evidence for it.

If bipolar cells are not directionally selective one is forced to look elsewhere for the sequence selective sub-units Levick and I had found evidence for. Fig. 2 shows the suggestion made by Dowling (1970): the excitatory terminals of one set of amacrine cells are presynaptically inhibited by the terminals of another set of amacrine cells. Thus synaptic complexes he calls *serial synapses* take the place of bipolar cells in our scheme. With the demonstration of numerous chemo-transmitters in the retina, and the elucidation of the actions of some of them as modulators, this suggestion is looking increasingly plausible.

A third suggestion, illustrated in fig. 3, comes from Torre and Poggio (1978). They postulate an interaction on the dendrite itself, pointing out that an inhibitory transmitter could exert a powerful local shunting effect without necessarily causing much change in the intracellular potential. This was very much what our VETO model required, and in subsequent papers Poggio and his colleagues have shown how the effectiveness of this type of inhibition is dependent on the proximity of the inhibitory synapses to the excitatory ones they shunt, how the shape of the dendritic tree

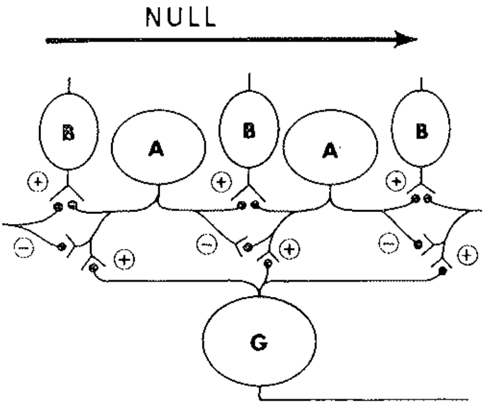

FIG. 2. The scheme for directional selectivity proposed by Dowling (1970). Amacrine cells presynaptically inhibit the excitatory endings of another amacrine cell lying in the null direction.

influences the degree to which sub-units are isolated from each other, and how the precise timing of excitatory and inhibitory synaptic release influences their interactions (Koch *et al.*, 1982). This is theoretical work and has not so far been experimentally confirmed, but Amthor, Oyster and Takahashi (1983) now have pictures (fig. 4) of the dendritic trees of known directionally selective cells, and it should not be too hard to find out if the inhibition is presynaptic of postsynaptic. I think this is as close as we have come to giving a biophysical account of how a cell does pattern selective logic.

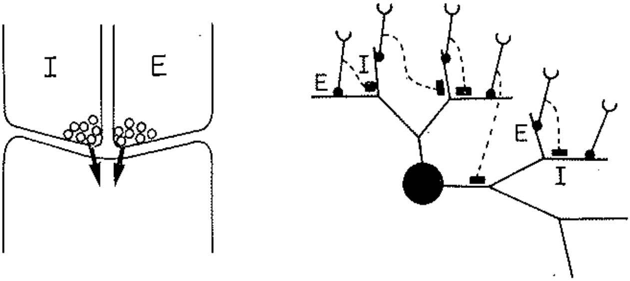

FIG. 3. The proposal for directional selectivity by Torre and Poggio (1978). If an inhibitory ending lies close to an excitatory ending it can reduce its epsp's by shunting, without necessarily contributing an ipsp or having much effect on epsp's from more distant excitatory synapses. This means that a dendritic tree can be functionally subdivided into more or less independent compartments, each acting as a sub-unit; this is indicated at right.

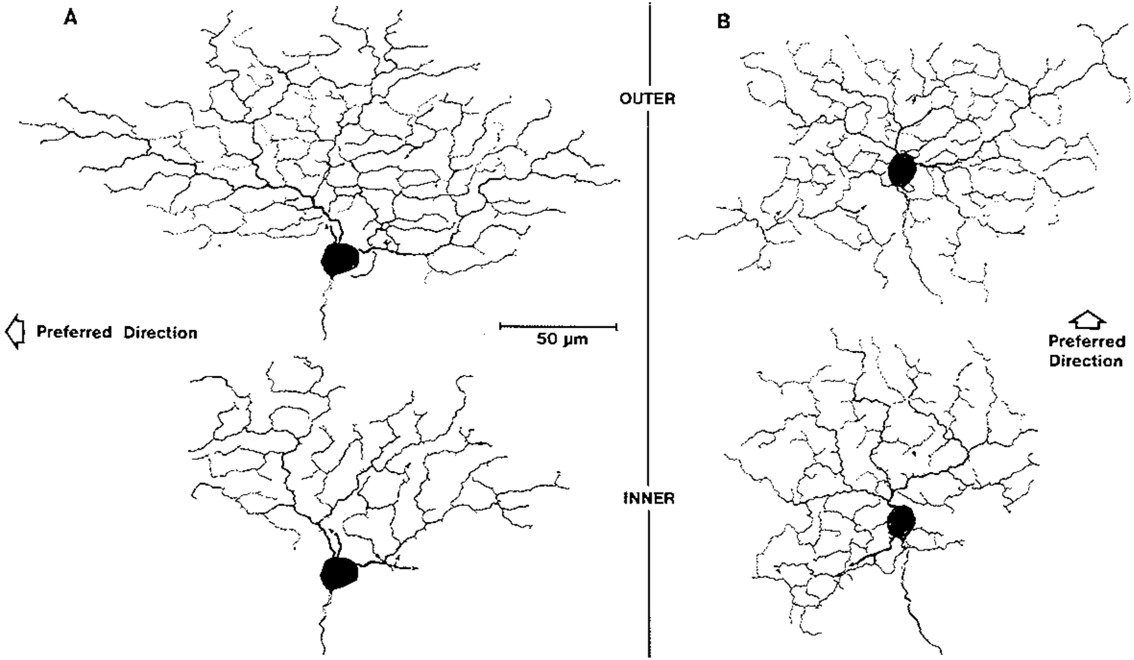

Fig. 4. Dendritic trees of identified directionally selective cells ("on-off" type) in the rabbit retina (from Amthor, Oyster and Takahashi, 1983). The dendritic trees are probably strongly compartmentalised, but there appears to be no asymmetry associated with the preferred direction.

Notice that on either of these last two schemes what we first assumed to occur in two synaptic stages actually occurs in one, and synapses or synaptic complexes take the place of cells as the logical elements. Now cells are packed in the brain at a density of about 10^5 to 10^6 per mm^3, whereas synapses occur at packing densities of 10^8 to 10^9 per mm^3. Thus regarding synapses rather than cells as the logic elements increases one's estimate of their number 1000-fold. Another way of putting it would be to say that we now realise that a single cell can compute a very much more complicated logical function than we previously thought.

Pattern recognition by precept

It was suggested by Empiric that all knowledge of patterns was derived from experience, and although this extreme view must be wrong, there is of course no doubt that some such learning occurs. But it is far from certain that it could ever be very effective by itself; in the early days of artificial intelligence many claims were made for devices like the Perceptron (Rosenblatt, 1962) which learn by precept, and the principle is often appealed to by theoreticians of associative nerve nets (Palm, 1982), but few of these claims have actually been substantiated. What was not appreciated is the necessity of taking the structure of patterns into account before they can be handled effectively, and I shall return to this.

The imprinting of young birds referred to by Empiric is certainly one of the best biological examples of learning by precept. As with innate releasers, this phenomenon became widely known about thirty years ago, in this case largely as a result of the writings of K. Lorenz (1952) and his dramatic experiments on the grey-lag goose in which he showed goslings becoming imprinted on him rather than the mother goose, and following him wherever he went. Unfortunately we do not know how goslings classify the things they see, nor how this enabled them to distinguish Lorenz from other objects, nor the mechanism whereby they came to prefer him. Presumably the pattern selectivity of certain neurones must be changed during the imprinting experience, but so far these changes have escaped detection in spite of much work on the behavioural, anatomical and neurochemical basis of the phenomenon (Bateson, 1966; Horn, 1981).

The mammalian visual cortex has proved a better place to study the effects of experience on single neurons. It is still not entirely clear how ontogeny and experience interact to produce the adult cortex, and this topic cannot be reviewed here. But it is important for the subsequent argument to make one point about it: the general effect of experiencing a particular pattern of excitation is to preserve, and probably increase, both the responsiveness and the selectivity of the cells that respond to that pattern. It will be shown later that this fact fits in with the view that patterns can be recognised even if their nature has not been transmitted to the brain by the genetic code or by experienced precept. Let me explain this by resuming the dialogue with my Nativist and Empiricist friends.

Dialogue on Pattern as unexpected order

ME. "I maintain that patterns have a property that enables them to be distinguished from non-patterns without any prior knowledge at all."

N. "How can that be so? Without specific patterns to match our experience against, surely all would be chaos and confusion in our minds?"

ME. "Not necessarily. You think of patterns like flowers in a garden, and suppose that without planting there would be nothing but weeds and barren soil. But let me ask you where you think the flowers came from? Were they not bred from the very weeds that would be there without them?"

E. "I thought that many of our garden plants grew wild in foreign lands."

ME. "Well yes, you are right about that. But you must not misunderstand me, for I am not denying that some knowledge of patterns comes into the mind genetically or by precept, only that patterns can also be recognised by an intrinsic property which they all have. In the same way not all flowers come from exotic lands or by purchasing a seed-packet in a super-market; some have been produced from weeds by a process of selection and protection, and I think this is similar to what happens in the mind: patterns are cultivated from the chaos and confusion that would otherwise reign."

E. "But you must know what to select and protect before you can get anything different from the weed, surely?"

ME. "Not so. If you start from the weed, anything that is unusual, unexpected, or surprising is worth preserving and protecting. And that same characteristic, unexpectedness, is just what I think enables us to detect patterns without prior knowledge."

N. "You have diverted the argument into distinguishing flowers from weeds, but I originally spoke of chaos and confusion; surely weeds have more distinct characteristics than chaos?"

ME. "I believe you are probably right, but you have played into my hands, for it is the very lack of distinct characteristics of chaos that persuades statisticians to base their tests upon it. The distinction between pattern and chaos is even clearer than the distinction between flowers and weeds."

N. "Well that is too technical a matter to follow up here, but there is another difficulty I see in your approach. You have indicated that you can find one pattern, because it departs from chaos. But surely our minds are full of so many myriads of patterns that it is not much use claiming to find one single pattern hidden in chaos? Experience seems to consist almost entirely of a great diversity of different patterns, and we can find little of the chaos you say underlies it all."

ME. "In the same way a well cultivated garden is full of flowers and you see little of the weeds or the soil. But I must admit that you have a point to make, for it is not enough simply to detect a departure from chaos: the direction or type of departure must also be determined, for it is only after we have specified this first pattern that we can go ahead and find if this one pattern plus chaos is enough to explain experience. If not, then we can find a second pattern, and so forth."

E. "This sounds like slow and hard work."

ME. "Indeed it is, but so it must be, for just as it takes many years to cultivate a garden, so it takes many years to cultivate one's perceptions. And I ask you what work is being done by the mind in all these years if it is not as I say?"

My main point in the rest of this paper is to argue, as above, that there is more to a pattern than what it is associated with, and to try to show that this intrinsic property is orderliness, the opposite of chaos or randomness. On this view the logical step is to explore pattern recognition starting from chaos; instead of starting with a known pattern and considering how it might be distinguished from other patterns, and perhaps from a noisy background, let us start with the problem of distinguishing non-chaos from chaos, and see how knowledge of patterns might be built up from this basis.

Detecting order in chaos

To talk clearly about chaos, and to illustrate what I am saying, one needs to realise it in some concrete form. A convenient starting point is an array of random dots such as that illustrated in fig. 5 (centre). This picture is not as chaotic as it might be, for each dot has the same size, shape, and luminous intensity, and the dots can only occur at a finite number of specified positions. But they are arranged to occur, as nearly as possible, independently of each other so that the dot density is the only non-stochastic parameter determining the array. If you look at such an array, and particularly if it is dynamic so that the randomly chosen dots are continuously being replaced by new ones, then you begin to see patterns where none exist. I presume this is a phenomenon rather like seeing faces or butterflies in Rorschach figures or the patterns Fergus Campbell (1984) has shown us. One rapidly comes to recognise the character of these spurious patterns and, though interesting, I shall not spend more time on them here, for I think that what one detects that does have a basis is more interesting. The thesis is that you will successfully detect any departure from pure chaos, for this will constitute some type of pattern.

The first such departure is to change the average dot density over part of the array. As you might expect you see this very clearly as a patch containing more dots, as shows in fig. 5 (left and right). This confirms in a rather obvious way the hypothesis that one detects departures from chaos, but on this problem one can go further than just saying one can detect it, for one can measure how well it is detected; furthermore the result of the measurement is an absolute figure comparable with mechanical or thermodynamic efficiency.

The importance of absolute measures

This ability to measure the absolute efficiency of a person's perceptual performance is a very important feature of the type of task we are considering. If you feed an animal a known diet you can study its balance for various constituents of the food, such as nitrogen, and thus if you are fattening it for the market you can find out how efficiently it is converting the nitrogenous food you give it into the protein that enables you to get a good price for it. Likewise if you use the animal for mechanical work you can calculate how much of the energy you feed it comes back to you in the form of useful work. Both these efficiencies would be

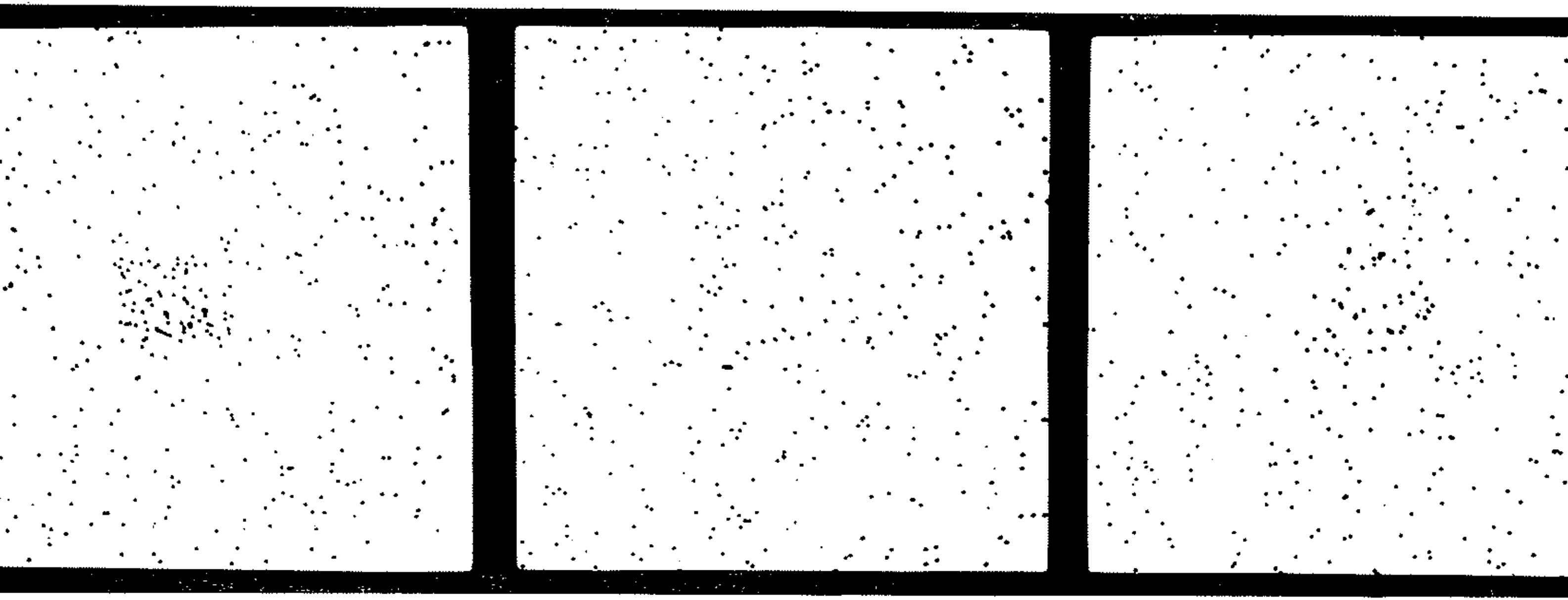

FIG. 5. The centre panel shows 400 randomly placed dots. A central square has 1/25th the area and contains 16 dots on average, subject to variation with a standard deviation of + or − 4 dots. On the left 80 additional dots have been placed in this square, corresponding to a signal/noise ratio of 20 which is very easily visible. On the right 20 additional dots have been added, and at this signal/noise ratio of 5 the excess is becoming harder to detect.

astonishingly low, but if you want to find out about the metabolic pathways that yield protein or mechanical work, then you must trace the balances of nitrogen or energy through the system. I think that in perception the task before us is rather similar to the one that has been largely solved in metabolism, but it is information, not energy or nitrogen, that we need to trace through the system. So let me go back to the problem of distinguishing a patch with a higher dot density in a nearly random array in order to outline how one can find out the fraction of the available information that is used.

Dot density defines the mean number of dots in a patch, but in different examples the actual numbers will be distributed around this mean value. If one raises the density in a patch, the numbers will be distributed around the new mean, but there is no guarantee that the number in a particular array will be shifted above the old mean value. One thus has the familiar situation in which two bell-shaped distributions overlap, and it is impossible to decide which of them a particular example belongs to without making errors. It is by counting these errors, and comparing their number with the expected number calculated from the known parameters of the two distributions, that one can find out how efficiently the subject has used the information that was available to him. The technicalities will be familiar to many of you through Signal Detection Theory, and I shall simply show you some results.

First, the efficiencies at this simple task are of the order 10% to 50% (Barlow, 1978); these are very much higher than for a bullock converting food-stuff into protein or for a mule converting it into mechanical energy. Furthermore these efficiencies remain high in spite of wide variations in the parameters such as patch size or dot density, so the visual system is quite a versatile detector of non-chaos, at least as far as simple changes of dot density are concerned. Though no very complicated mechanism is required for this task it would have been disappointing for the hypothesis if the efficiencies had been low.

What is the best pattern?

I originally hoped that one could find out important properties of the pattern detecting system by finding out what types of patch one could detect with highest efficiency. There were two good reasons for this hope: first, what one does best in a sense reflects the "design" of the system, which would be interesting; and second, some suggested

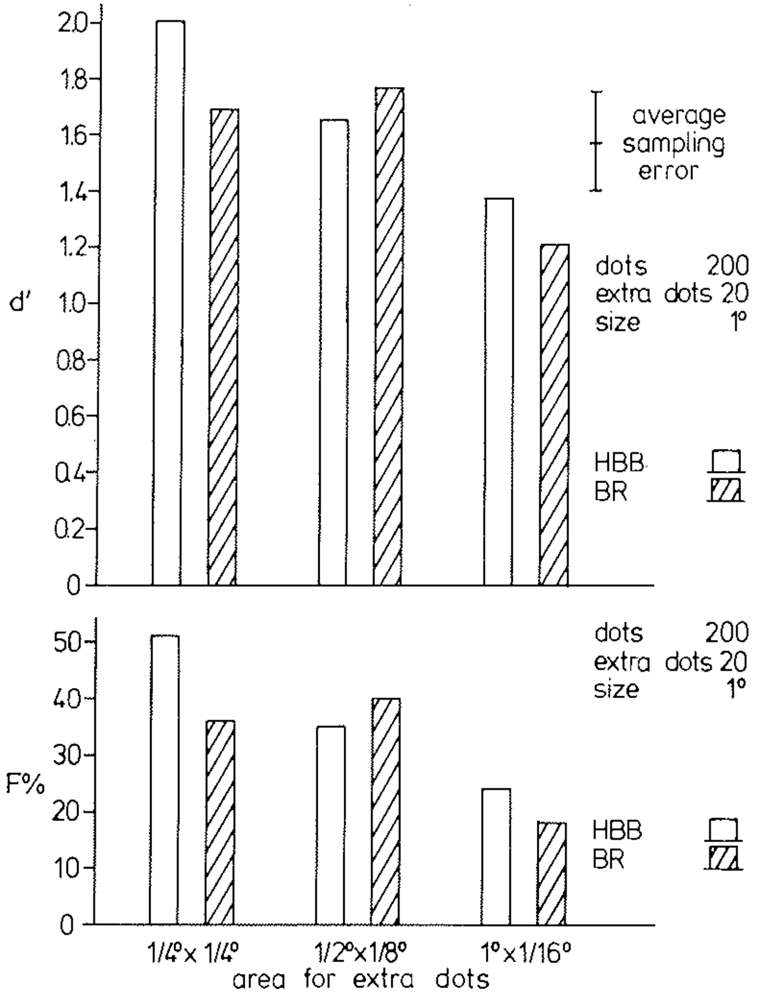

FIG. 6. When the shape of the patch containing extra dots is changed from a square subtending 1/4 × 1/4 deg to a rectangle subtending 1 × 1/16 deg the efficiency of detection decreases slightly (from Barlow, 1978). This experiment failed to show evidence of bar-detectors.

mechanisms of pattern detection would simply not be good enough to perform as well as we do and could therefore be excluded. The results were disappointing at first, for nothing seemed better than a simple square patch of moderate size (see fig. 6). But recently this has changed dramatically so I shall give the argument in more detail.

If the energy of a foodstuff is to be utilised later for producing mechanical work one expects it to be retained in energy-rich intermediate metabolites, and it certainly must not be dissipated as heat by breaking the material down into low-energy fragments. In the same way if there are information-rich features of visual patterns one expects them to be preserved and represented by activation of specific intermediate neurons in the visual pathways, for if this is not done the information is in danger of being lost. Now in order to detect a pattern optimally, and thereby preserve information about it, one needs to match its spatio-temporal characteristics to the pattern exactly; I therefore hoped one could use this argument in reverse, and by finding out what information was optimally preserved one might find what pattern-features the visual system specifically catered for. Because we already know a little about the receptive fields of cells in the visual pathways I was of course looking for evidence of movement sensitivity and bar- or edge-detectors, hut the early results were most unpromising in this regard (fig. 6). However I thought this might be simply hecause my dot patterns were too coarse-grained to test the details of the structure of the receptive fields of cortical neurones, so I suggested to Watson and Robson that we measure quantum efficiencies for the range of patterns they could produce on their high-performance oscilloscope display. No noise was added, and as expected the quantum efficiencies we found are very low compared with the statistical efficiencies obtained with random dots; some additional source of errors must be responsible for this degradation of performance, and we do not yet know what this is. But it is still interesting to compare efficiencies for different spatio-temporal patterns discriminated from this intrinsic noise, whatever its origin, and the question "What pattern does the eye see best?" must surely have some interest for this conference in its own right.

The result was clear (Watson, Barlow and Robson, 1983): gaussian-envelope sinusoids of 1/2 to 1 octave bandwidth, about 4Hz temporal frequency, about 6 cycles/degree spatial frequency, and about 1/6 sec duration, are detected some 3 times better than the best rectangular section (in space and time) stimulus we could find. Such a pattern is shown in fig. 7. At ahout the same time A. Burgess *et al.* (1981) were also interested in the problem of finding spatial patterns that were well matched to the natural pattern detectors of the human visual system, but in these experiments noise was added. In this version of the experiment we did not follow such an extensive optimisation program as

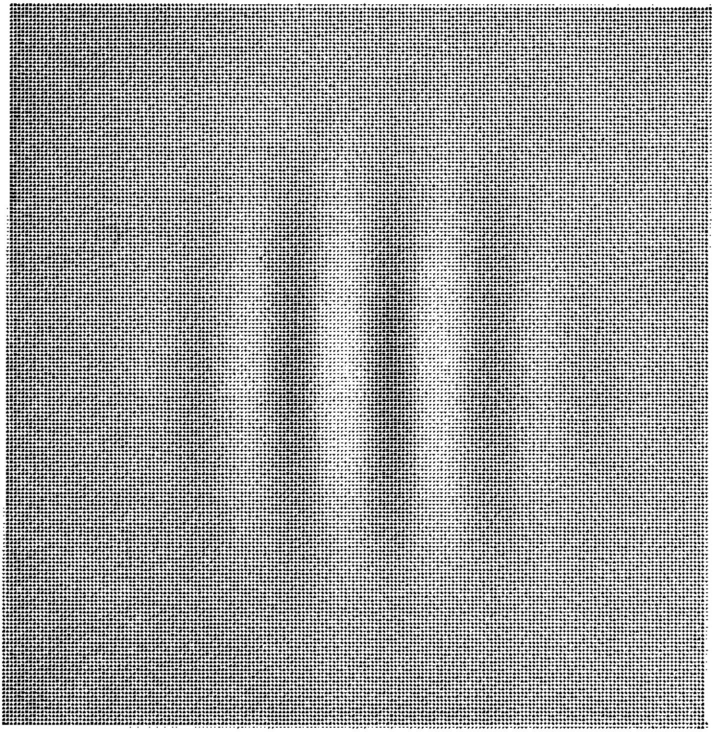

FIG. 7. A gaussian-envelope grating patch. This is the pattern subjects see best when it is viewed from a distance such that its spatial frequency is about 6 cycles/degree, when it is flickering at about 4 Hz, and when its gaussian temporal envelope lasts about 200 msec.

Watson *et al.*, but as we now know these optima are rather flat. We were able to obtain efficiencies of almost 80% using gaussian-envelope sinusoids not very different from the later-established optimum. Thus the type of pattern that is best detected against intrinsic noise is also detected against external noise at an efficiency that leaves very little room for improvement.

What is fascinating about this result is that these stimuli do seem to match the receptive fields of the simple type of cortical neurone (Movshon, Thompson and Tolhurst, 1978; De Valois, Albrecht and Thorell, 1982), and there are reasons for believing that the appropriate collection of such neurones can represent economically all the information reaching a small patch of the visual cortex (Sakitt and Barlow, 1982). They also fit much other evidence on the representation of the image at a fairly early stage in the visual pathway (Watson, 1982). I have always been surprised by the evidence that the visual system performs something like a local Fourier transform, so this evidence for quite finely tuned spatial frequency filters was a bit of a puzzle to me: What conceivable use could they be for vision? Allow me to speculate about this.

I think that V1 is concerned, first, with the interpolation mechanisms required to achieve high precision estimates of position, especially of moving objects; and second, that it detects those local characteristics of the image that offer presumptive evidence of a common origin in the external world (Barlow, 1981). Guzman (1968) called these "linking features", and they correspond pretty well both to the local characteristics that gestalt psychologists pointed to as causing segregation of figure from ground, and to the characteristics, such as motion, colour and disparity, that we now know V1 neurons to be selectively sensitive to. Now a straightforward record of the spatial pattern of light in a region of the image is not at all suitable for this purpose, for it is not likely to be particularly characteristic of the object causing that part of the image, nor can it be readily interpreted in conjunction with similar records from other parts of the image. But the presence of a dominant orientation or a dominant spatial frequency is another matter, for these are both possible identifying features of an object, and are characteristics that can be shared or not shared by other parts of the image. These views of the functions of V1 have other implications which I shall return to.

Second-order orderliness

So far I have only discussed the detection of departures from pure chaos that are characterised by non-uniformity of the dot density. As we have seen these changes are efficiently detected over a wide range of parameters, and the patterns that are best detected show a remarkable concordance with the neurophysiological expectations derived from the receptive fields of cortical neurons. But one can impose other types of departure from pure chaos, and perhaps the next simplest is to perturb the second-order probability distributions in the dot arrays. If all dots are positioned independently, the presence of a dot at a particular location has no influence on the probability of other dots occupying neighbouring locations, but this need not be the case. A very intriguing way of changing the second-order probability distributions was devised by L. Glass (1969), and examples are shown in fig. 8. To generate such figures half the dots

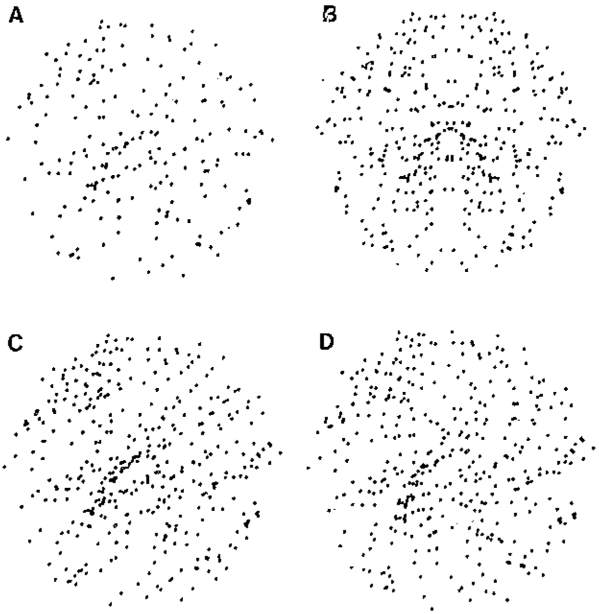

FIG. 8. Examples of second-order orderliness. In A the dots are placed at random positions and there is no second-order pattern. In B each of the first set of dots has a mate placed at a position mirror-symmetric with the first about the vertical mid-line. In C the mate is placed a short distance up and to the right. In D it is displaced out from the centre and rotated anti-clockwise. In such arrays (Glass, 1969) the regular feature is noticed much more than the initial irregular array (A), which is the same in all.

are first placed completely at random, as shown in fig. 8A; then, for each of these dots, another is placed at a precisely defined position. In fig. 8C the second dot is displaced upward and to the right; in fig. 8D it is displaced outward and rotated about the centre in a clockwise direction; in fig. 8B it is placed at a position mirror symmetric with the first dot about the vertical mid-line of the figure. I find it very intriguing to see how these regularities completely dominate one's perception of the arrays. The same selection of random dots (fig. 8A) was used as the starting point for all these figures, but most of you probably failed to notice this fact, for the regular, non-chaotic, features of each pattern grabbed your whole attention.

Reeves and I (1979) did an analysis of the detection of symmetry of the type shown in fig. 8B. Among the interesting results were the speed with which it was detected, indicating that eye movements are not required, and the fact that the axis of symmetry could be at different positions and orientations in the visual field. This seems to imply a versatile mechanism for symmetry detection that is extensively replicated to cater for the different possible positions and orientations of the axis. It was possible to estimate absolute efficiencies for the performance of this task, and although they were not as high as for simple changes of dot density they reached above 25% when the task was well-adapted to the mechanism, as shown in fig. 9. We do not understand this mechanism, but the fact that highest efficiencies were reached when there was considerable latitude in the accuracy of placing the mirror-symmetric dots indicates that, though versatile, the symmetry-detecting mechanism is not at all precise. Here then is another case where regularity emerging from chaos is efficiently detected, and where we can find out something about the mechanism by measuring these efficiencies.

If one pursues the analogy with metabolism, the demonstration that one can detect non-uniformity of dot density, and symmetric components of the second-order statistics, with high efficiency is rather like showing that amino-acids, or energy-rich carbohydrates, are transported into the blood stream without being dissociated into smaller, low-energy, fragments. The preservation of information-rich messages must be very important steps in the perceptual metabolism of patterns, but it is obvious that there are many undisclosed steps ahead. Perhaps it is worth briefly speculating about these in the light of what we have already discovered through the approach from chaos, and in the light of what we know about cortical neurones and organisation.

Intelligent pattern recognition

The thesis I am advancing is, 1st that the main task for any sensory system is to sort out what is significant and important from the largely random mass of messages that strike the sense organs; 2nd that much of this task can be done without reference to any external source of knowledge, simply by selecting out what is unusual and unexpected in these messages themselves. The essential step for what I have called *intelligent* pattern recognition is the detection of *significant coincidences.* These are coincidences in the detective story sense — i.e. the associated occurrence of two or more events that would have been unlikely to occur by chance alone, but I am thinking of the occurence of elements of the sensory messages, not of the complex events in the external world that

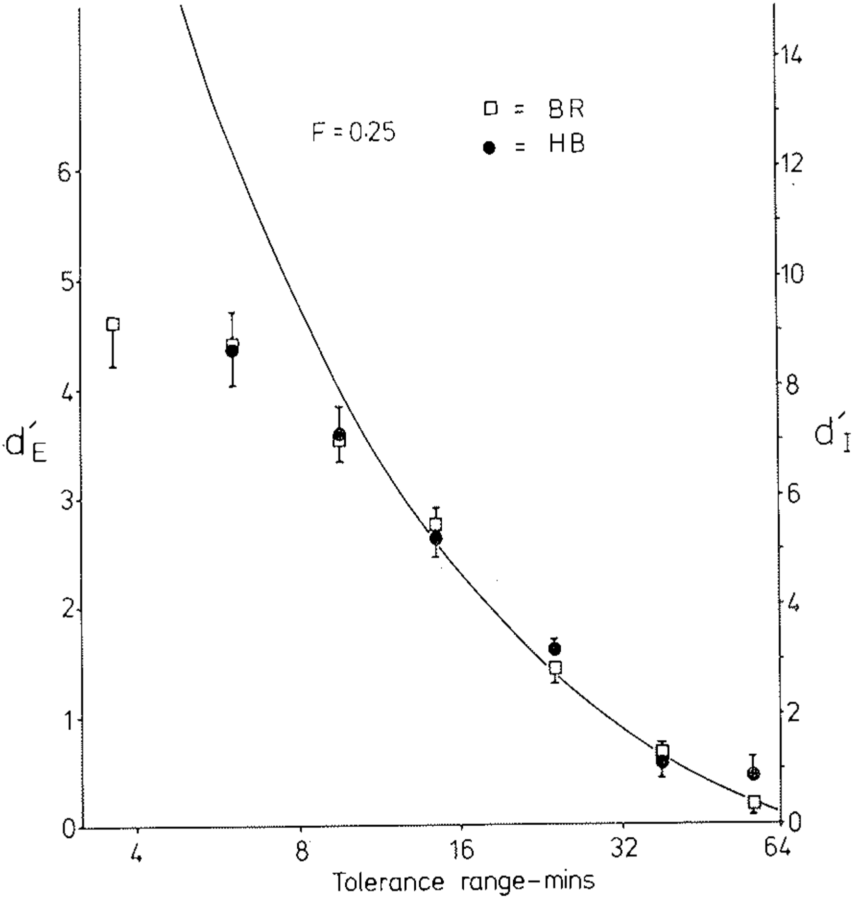

FIG. 9. Instead of placing a paired dot in the exactly mirror symmetric position it is placed at a random position in a box, or tolerance area, centred on the symmetric position. The dimensions of this square box are plotted as abscissa, and the ability of two subjects to discriminate such an array from a completely random one is plotted as ordinate. The continuous line shows the calculated (and simulated) performance of an ideal model utilising 25% of the available information. The subjects' performance is much worse than this model if the tolerance box is small, but matches it when large. Absolute efficiency of symmetry detection is less than for gaussian-envelope sinusoids or simple changes of dot density, but reaches a respectable value for large tolerances (from Barlow and Reeves, 1979).

the detective deals with. The detection of such external coincidences is obviously crucial for intelligence in the accepted cognitive sense, but there is also evidence that the coincident occurrence of elementary messages is important neurophysiologically in the cortex, which is after all the organ that is supposed to underlie intelligent behaviour. Berlucchi (1984) referred to one example of this, namely Innocenti's (1978) work showing that callosal connections are initially very widespread and diffuse, but only persist in regions where the information they convey "agrees with" the information already represented in that region. Presumably it is the occurence of coincidences between the activation of the callosal connexions and the activation of the other afferents to that area that determines the survival of the callosal connexions. Another well known example is from the work of Hubel and Wiesel (1965): they showed that if a kitten was prevented from using its eyes together by covering one on one day, the other on the next, and so on, then the number of neurons in the primary visual cortex that received an input from both eyes was drastically reduced. Apparently if cortical neurones receive coincident input from two sources, then they continue to be responsive to these two inputs, whereas if such "significant coincidences" do not occur they lose their responsiveness to one or other of them.

Thus an idea that has something to commend it is that the basic operation of a small region of cortex is to detect that certain "significant coincidences" are occuring among the inputs to that region, and then to signal to other parts of the brain when these significant events occur (see Phillips, Zeki and Barlow, 1984). Perhaps it is this coincidence-detecting proclivity that determines which survive among the innately determined possibilities for pattern detection in cortical neurons.

If this view is correct it may throw some light on the multiplicity of visual areas that we have heard so much about. V1 has an accurate topographical map, and therefore the coincidences it can detect must be purely local ones. We have seen that the characteristics it detects are potentially useful for identifying objects in the external world, and we already know that this is done by the system as a whole: regions are associated or grouped together if they have the same colour, or the same disparity, or move in the same direction, or have the same "texton" structure (Julesz, 1984). There must be anatomical arrangements making the detection of such coincidences possible, and the accessory sensory areas seem likely candidates.

Detection of novelty and familiarity

If a thorough analysis of what is usual and unusual in sensory messages has been carried out, then the remainder of the task of pattern recognition is enormously simplified and perhaps becomes almost trivial. Let me try to illustrate this point.

Suppose that a goat forages for food in its meadow succesfully and uneventfully for several days and then encounters a tempting shoot of purple foxglove (*Digitalis Purpura*); it tentatively nibbles a leaf or two of this highly poisonous plant, and shortly thereafter becomes indisposed. Now it can only benefit from this experience and avoid foxglove in future if it has a rather extensive knowledge of the botany of its meadow, and it is in a position to have acquired this by storing up memories of the usual and unusual tastes, smells, and sights during its previous foraging expeditions. Of course it cannot attach names to the various species, but it should come to recognise the ordinary and the extraordinary, and hence the young shoot of foxglove should have been tagged as new and unusual; if this was done, the cause of its indisposition would have been fairly obvious, but if it was not then I think it would be extremely difficult for it to identify what made it sick. Of course goats probably have many powerful detoxifying enzymes, and perhaps some of their botanical knowledge is either innate or taught to them by their nannies, but I do not see how herbivores can survive the pharmacological hazards they confront unless they have a natural ability to classify the sights, smells, tastes and habitats of the plants they eat, along the lines I have suggested.

Notice that the last step of this goat scenario was the detection of an association of two rare events, feeling indisposed and eating an unusual plant: that particular pattern was, if you like, taught by precept — a negative one in this case. But the foundations upon which its detection was based were the myriads of previous associations of taste, smell and sight by means of which the goat recognised that the foxglove shoot was something new and unusual. I think this shows that the potential importance of detecting associations is not confined to associations with positive and negative reinforcing stimuli; an intelligent animal must know the structure of associations in the sensory stimuli it ordinarily encounters, for otherwise it will not be able to do a good job of distinguishing the unusual from the usual.

Any global notion of how patterns are detected and stored is unlikely to be correct in the present state of knowledge because we simply do not have enough evidence, but that does not make speculation worthless; there is an obvious dearth of sensible hypotheses to test, but they are certainly needed if one is going to make the best use of hard-won experimental evidence. I think it is very encouraging how close to experimental testing some of the ideas I have talked about are: for instance if the interpolation required to achieve high positional accuracy is done in V1, then lesions of V1 will dramatically impair performance on such tasks; this does seem to have been born out by the experiments of Berkley and Sprague (1979). The hypothesis about linking features clearly implies that tasks requiring figure/ground segregation should also be abolished by V1 lesions, and Berlucchi (1984) seems close to testing for this. Finally it is encouraging to hear that the monkeys Rolls (1984) has told us about have single neurons with a keen sense of the expected and unexpected among the objects in its laboratory, and this is just what I postulated for my goat browsing among the plants in its meadow. The time scale for these effects is obviously unlike that for the critical period in V1, so the mechanism may well be quite different, but if a phenomenon can be recorded reliably in a physiological preparation, it ought to be possible to find out the mechanism.

Pattern recognition in higher mammals is an extraordinarily complex matter, but we are perhaps approaching some of the answers at an accelerating rate.

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RECOGNITION-MEMORY AND CONSCIOUSNESS

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The contributions to this conference on recognition memory have been almost entirely visually orientated with neglect of the acoustic and somatosensory systems, which corresponds to the overwhelming scientific concentration on the visual system. This is in contrast to our ordinary life experience where communication by language and by touch are so important. Moreover in a recognition of objects or situations we often utilize more than one sensory modality. Despite these reservations I will begin by reference to visual recognition.

The prestriate cortex

There is general agreement that in the prestriate cortex there tends to be at least four areas with specific recognition features as reviewed by Cowey (1981, 1982) in his valuable comparison between human visual defects arising from clinical lesions and primate visual defects produced by precise operative resections.

In this topological study the colour deficiency, achromatopoia, produced by lesions of the ventral aspect of the prestriate, corresponds to the colour deficiency produced in monkeys by lesions of V4 and the lateral bank of the superior temporal sulcus (Zeki, 1977). Other correspondences are for disorders of movement perception, of positioning of objects, and of stereoscopic depth (Cowey, 1982). Apparently in these prestriate regions there has been separation of these visual qualities for analysis and synthesis. Hence there arises the problem of the further synthesis at a higher hierarchical level in the process of visual recognition. Cowey (1981) seems to be ambivalent on this problem stating that:

"... there is no *necessity* that these cells should provide convergent input to cells in another visual area. Such an arrangement smacks of the homunculus inside the head 'looking at' the combined activity of cells in a network ... Yet the cells in the temporal lobe, which have enormous receptive fields and complex trigger features and which are known to receive information from several prestriate visual areas, appear to play this redundant role. There may be one reason for such an arrangement. The analysis of the visual world is only a prelude to our response to it, which includes recognition, actions, ideas, emotions, etc. And the response must vary with learning. The same stimulus may provoke different responses according to its learned significance". He wisely states that: "... It does not imply that any single cell can 'recognize' a complex shape, and there is no physiological evidence that it can. A single cell in the temporal lobe that is maximally excited by the outline of a monkey's paw (Gross, Rocha-Miranda, and Bender, 1972) nevertheless does respond to other shapes. Its tuning is not, and cannot be, sharp enough to give an unambiguous percept, which presumably still requires the combined activity of thousands of cells".

He finally argues against: "... that model of perceptual processing in which individual stimulus features are isolated and coded in parallel and then put together again in a hierarchical fashion to achieve a final percept", though he admits its limited usefulness.

At a higher hierarchical level Warrington (1982) concentrates on visual recognition of objects and faces when distorted by orientation at unusual angles or by fragmentation or in confusing overlaps. There is severe impairment with post-Rolandic right hemisphere lesions. It is a valuable concept that there are stored in memory elemental shape descriptions (Marr and Nishihara, 1978), which would correspond to the stored motor programs (Brooks, 1979), and that these are used as a general basis for more specific identifications. All of this computation and recognition would proceed at a level hierarchically above the prestriate as is diagrammed by Mishkin (1982). Yet strangely there is no reference to a possible role of the prefrontal cortex in the process of conscious recognition of visually observed objects.

The prefrontal lobe

Roland has already described the manner in which the radio-xenon technique is employed for discovering the cerebral regions of raised meta-

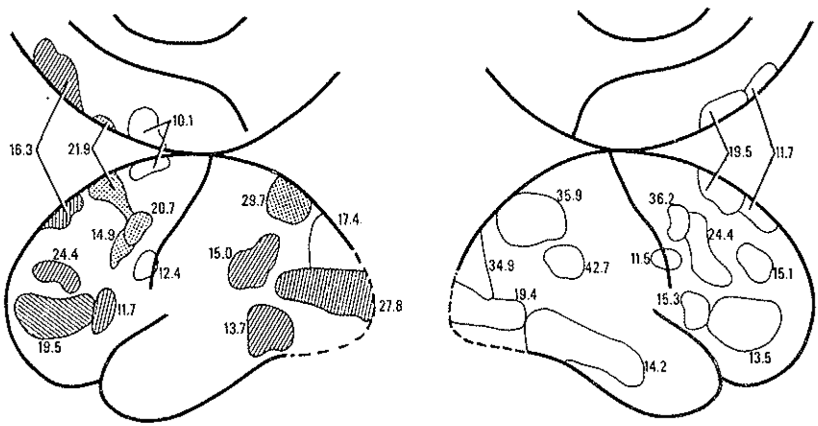

FIG. 1. The mean increases of rCBF in percent and their average distribution during visual discrimination. Left: Left hemisphere, 6 subjects. Cross-hatched areas have rCBF increases significant at the 0,0005 level (Student's t-test, one sided significance level); hatched areas, $P < 0,005$; other areas shown, $P < 0,05$. The mean hemispheric blood flow went up from 52,8 to 58,1 ml. 100 g.$^{-1}$ min.$^{-1}$ No decreases in rCBF. Right hemispheric, 2 subjects. Mean hemispheric blood flow increased from 51 to 59 ml. 100 g.$^{-1}$ No decreases in rCBF. (Roland and Skinhøj, 1981).

bolic activity. When carrying out some discriminative recognition, there is always a significant neuronal activity in the prefrontal cortex in addition to the areas specially involved in that sensory modality. For example when judging the eccentricity of two elipses presented on the screen (Fig. 1) there are, in addition to areas of the occipital, temporal and parietal lobes, increases of up to 20% in the superior and mid-frontal areas on both sides including the frontal eye field (Roland and Skinhøj, 1981). Likewise during auditory discrimination of rhythms, in addition to the large increases in the temporal and posterior parietal lobes of the right hemisphere, there are highly significant increases of up to 20% in the prefrontal lobe, particularly on the right side (Fig. 2; Roland, Skinhøj and Lassen, 1981). The prefrontal increase is also well displayed in most interesting tests on somatosensory attention in the absence of stimulation (Fig. 3; Roland, 1981). To a remarkable extent these zones of rCBF increase in the prefrontal lobe are in overlapping areas in the superior and midfrontal zones.

These zones are hierarchically superior to the early stages of sensory processing. Can we regard them as being concerned in the integration of information from the various sensory modalities, vision, hearing and touch, as is so often experienced in perception? Furthermore are these

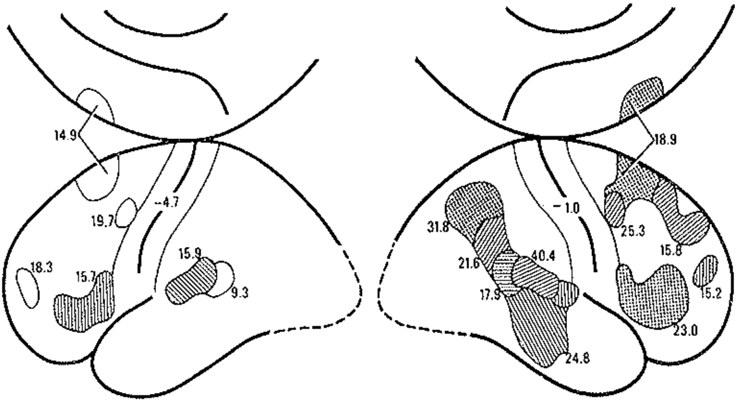

FIG. 2. Mean increases of rCBF in percent and their average distribution during auditory discrimination of temporal tone patterns. Inputs to contralateral ears. Crosshatched areas have rCBF increases significant at the 0,0005 level (Student's t-test, one sided significance level). Hatched areas: P < 0,005, other areas shown: P < 0,05. Left: left hemisphere of six subjects. No change in blood flow outside the focal activations. Right: right hemisphere of six subjects. The blood flow increased by 4,7% in the rest of the association cortex outside the focal activations. (Roland, Skinhøj and Lassen, 1981).

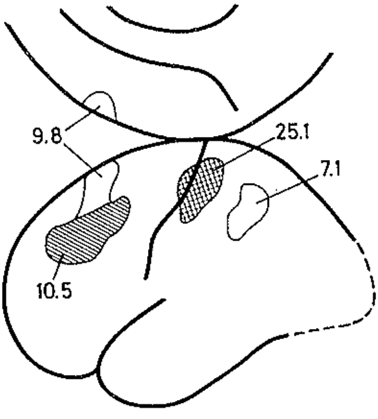

FIG. 3. Mean increase of rCBF in percent during pure selective somatosensory attention; that is, somatosensory detection without peripheral stimulation. The size and location of each focus shown is the geometrical average of the individual focus. Each individual focus has been transferred to a brain map of standard dimensions with a proportional stereotaxic system. Data from the right and left hemisphere have been pooled because there were no differences in their respective activation patterns except for the auditory region. The crosshatched area has an increase of rCBF significant at the 0,0005 level (Student's t-test, one-sided significance level). For the other areas shown the rCBF increase is significant at the 0,05 level. Eight subjects. (Roland, 1981).

prefrontal zones concerned not only in sensory integration, but also in recognition memory and consciousness? This question leads to a consideration of the role of the hippocampus in laying down cognitive memories.

The hippocampus and memory

The role of hippocampus in memory has been a controversial topic ever since the bilateral hippocampectomy performed by Scoville in 1953 on HM. Scoville also removed other adjacent medial temporal structures, the uncus, the amygdala and the hippocampal gyrus, so there have been claims that damages to these other structures of the medial temporal lobe are the key factors in causing the amnesia, not the hippocampectomy. For example Horel (1978) has contended that the amnesia arises not from the hippocampal resection, but from damage to the medial temporal lobe, the essential structure being its connecting pathway, called the temporal stem. However, his thesis has now heen disproved by a study of monkeys with lesions restricted to the temporal stem in comparison with monkeys with a hippocampal-amygdala lesion (Zola-Morgan, Mishkin and Squire, 1981; Squire, 1982a). The temporal stem lesioned monkeys displayed no amnesia in contrast to those with the hippocampal-amygdala lesions (Squire, 1982b). Mishkin (1978, 1982) has also called into question the significance of the hippocampus in memory by claiming that memory of monkeys is severely impaired only when the hippocampectomy is linked with amygdalectomy, which of course was the case in the Scoville operation on HM. The experimental testing certainly shows that the hippocampal lesion alone gives a memory deficit for both visual and tactual inputs (Mahut, Moss and Zola-Morgan, 1981; Squire, 1982b). The addition of an amygdalectomy may add to the amnesia (Mishkin, 1978), but this is not yet certain (Mahut *et al.*, 1981; Squire, 1982a, 1982h). The conclusion certainly is that the hippocampus is most importantly concerned in memory.

By serial degeneration techniques Jones and Powell (1970) showed that the somatosensory, visual and auditory inputs to the primary sensory areas projected after several relays to the limbic areas, and particularly to the entorhinal cortex and so into the hippocampus. Fig. 4 is a diagram showing the principal connections from the somatosensory (3, 1, 2) and visual areas (17, 18, 19). The downward projecting arrows indicate the connections made to the limbic system. The auditory area projects to the limbic system in much the same way as does the visual area (fig. 4B). Fig. 5 gives a more anatomical diagram of the left cerebral hemisphere,

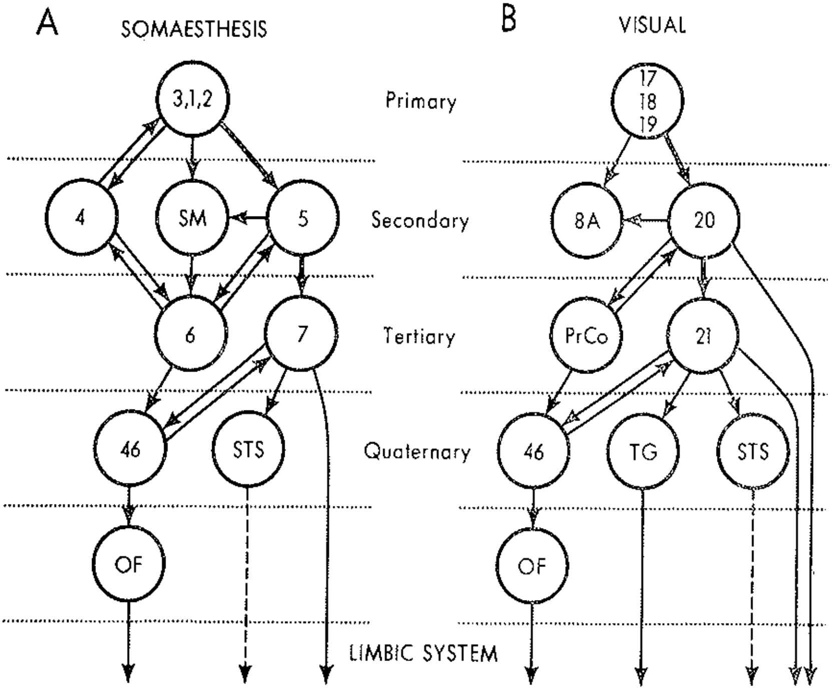

FIG. 4. Diagrammatic representation of cascade of connectivities for the somaesthetic (A) and visual (B) systems in the cerebrum. The numbers refer to the Brodmann areas; the other areas are: *SM*, supplementary motor; *STS*, superior temporal sulcus; *PrCo*, precentral agranular; *TG*, temporal pole; *OF*, orbital surface frontal lobe. (derived from Jones and Powell, 1970).

where for convenience of illustration the medial structures are translocated above the hemisphere as seen from the side (Kornhuber, 1973). The arrows show the projection from the visual area (Vi) to the cingulate gyrus and so to the hippocampus via the parahippocampus (the entorhinal cortex). Similarly arrows from the somatosensory area (S) and from the auditory area (A) project to the hippocampus via the cingulate gyrus. In Fig. 6 the inputs into the hippocampus (HI) from the entorhinal cortex (EC) are shown diagrammatically for the right hemisphere viewed from the medial side with the sectioned corpus callosum shown dotted. There are connections from the cingulate gyrus (CG) as in Fig. 5, from the prefrontal area 46 (cf. Fig. 4A, B) and from the cortical sensory areas. Other cortical areas project to the entorhinal cortex, area 20 of the temporal lobe and OF from the orbital frontal cortex are shown, but there are many others.

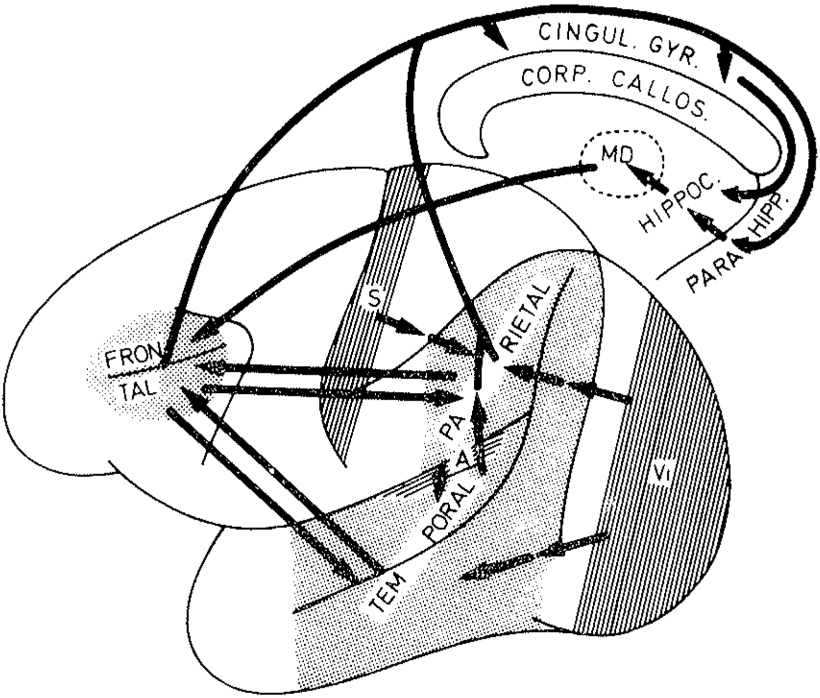

FIG. 5. Scheme of pathways in the monkey brain involved in the flow of information from primary sensory areas via the sensory association areas of the temporal and parietal lobe and the cortex of the frontal convexity to the limbic system and then the loop back via the medio-dorsal nucleus of the thalamus (*MD*) and the frontal cortex to the temporal and parietal areas for long-term storage. Primary sensory areas: *Vi*, visual; *A*, auditory; *S*, somatosensory; the vestibular area is the lower part of S. (Kornhuber, 1973).

In summary there is a wealth of cortical inputs to the hippocampus via the entorhinal cortex, that would relay all sensory inputs.

The block diagram of Kornhuber (1973) (Fig. 7) gives an excellent illustration of the pathways whereby the hippocampus is inserted into the circuitry involved in cerebral memory. It summarizes the input connections that have just been described and illustrated. The sensory associations areas project via the cingulate gyrus through the parahippocampus (the entorhinal cortex) to the hippocampus (cf. Figs. 4, 5). There are two outputs from the hippocampus: to the MD thalamus and the prefrontal cortex via the fornix and the septal nucleus; and to the mammillary bodies (MB) via the CAI output to the subiculum. The mammillary bodies are

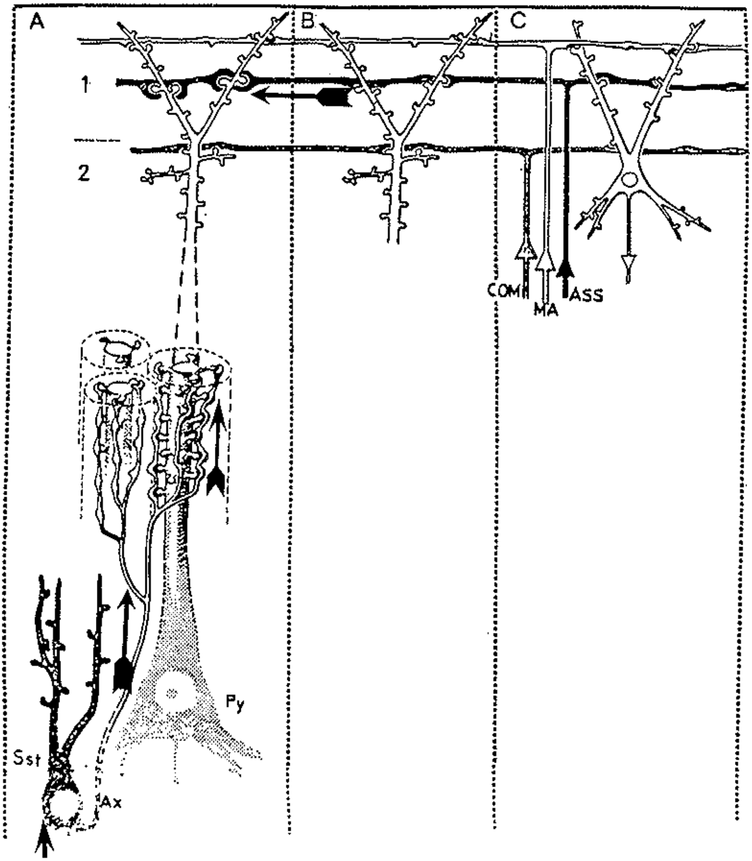

FIG. 8. Simplified diagram of connectivities in the neocortex that is constructed in order to show pathways and synapses in the proposed theory of cerebral learning (cf. Eccles, 1981). The diagram shows three modules, A, B, C. In lamina I and II there are horizontal fibres arising as bifurcating axons of commissural (COM) and association (ASS) fibres and also of Martinotti axons (MA) from module C. The horizontal fibres make synapses with the apical dendrites of the stellate pyramidal cell in module C and of pyramidal cells in modules A and B. Deeper there is shown a spiny stellate cell (Sst) with axon AX, making cartridge synapses with the shafts of apical dendrites of pyramidal cells (Py). Due to conjunction hypertrophy the association fibre from module C has enlarged synapses on the apical dendrites of the pyramidal cell in module A (Eccles, 1981).

stimulation provided by the contralateral entorhinal cortex to these same granule cells (Fig. 9B), a finding that is attributable to the failure to depolarize the cells sufficiently for causing a calcium influx. However, when the conditioning repetitive stimulation was applied simultaneously to the ipsi- and contra-lateral entorhinal cortices there was an LTP of the

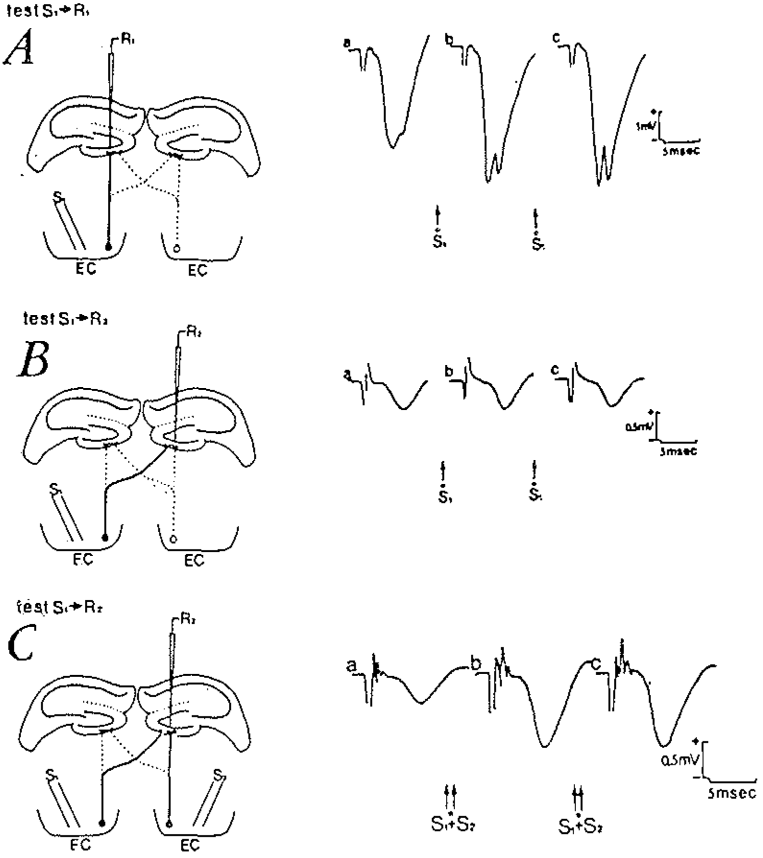

FIG. 9. Effect of entorhinal conditioning stimulation S_1 or S_2 on testing responses evoked by a testing entorhinal cortex (EC) stimulation, S_1 Extracellular recording from dentate granule cells gives population excitatory postsynaptic potentials (EPSPs). In A, S_1 stimulation of EC excites the perforating path to the ipsilateral granule cells for both testing and conditioning stimulation. The conditioning was by 8 trains of 8-10 pulses at 400 Hz delivered every 10 sec. (a) shows the population EPSP recorded by microelectrode R_1 before conditioning and (b) at about 2 min after the conditioning tetanus. A second conditioning tetanus was applied at 16 minutes after the first and (c) gives the population EPSP about 2 minutes later, revealing a slight further increase in LTP. In B there were the same EC stimulation procedures by S_1, but the recording by R_2 was for the population EPSP of the contralateral side. Note absence of LTP in b and c. In C there was recording by microelectrode R_2 as in B, but there was now conditioning by a conjoint stimulation of both entorhinal cortices, S_1 and S_2, as indicated. As a consequence there was, b, c, a large LTP of the testing contralateral response S_1 alone in great contrast to the absence of LTP in B. (Levy and Steward, 1979).

contra-lateral response (Fig. 9C). Presumably the contra-lateral entorhinal synapses are potentiated because they take advantage of the raised intracellular calcium produced by the strong ipsilateral stimulation. The finding illustrated in Fig. 9C provides a good model for the conjunction hypothesis of Marr (Fig. 8). The powerful cartridge synaptic excitation of the apical dendrite of the pyramidal cell causes by the calcium influx a long-term potentiation of those horizontal fibre synapses activated at about the same time (Fig. 8). The selective potentiation is a most important feature of the conjunction hypothesis, and a necessary basis for the subtelty and diversity of cognitive memory. The selection would be for a very few out of the 1000 or more horizontal fibre synapses on the dendrites of that pyramidal cell.

Generation of module patterns in relation to memory and retrieval

Fig. 8 illustrates symbolically the selective synaptic potentiation that occurs when there is conjunction of the cartridge activation of the pyramidal cell in module A with the horizontal fibre arising from association fibre bifurcation in module C. We have to ask: How far that selection can have a meaningful influence on the pattern generation? This question is particularly relevant to pattern generation by virtue of the module to module transmission by the cortico-cortical fibres.

The most important cortico-cortical communication system was discovered by Goldman and Nauta (1977) and is illustrated in Fig. 10. By selective projection of cortico-cortical fibres, the immense sheet of the neocortex is subdivided into a mosaic of quasi-discrete space units which are the modules forming the basic units in the functional design of the association cortex (Szentágothai, 1978).

The immense communication system from the cortical modules from and to the thalamus (TH) is indicated by the reciprocal arrows of Fig. 10. It is this input from the MD thalamus (Fig. 7) that activates the spiny stellate cell (SSt) in Fig. 8, and so the cartridge synapse (Szentágothai, 1978a). The reciprocity of the thalamo-cortical connections would give reverberatory circuit action and so provide a continued activity which would be of particular significance in enhancing the excitation of cartridge synapses that are postulated to be the effective agents in producing the large depolarization required for the Ca^{++} influx. Hence the thalamo-cortical input plays a key role in the conjunction hypothesis of synaptic

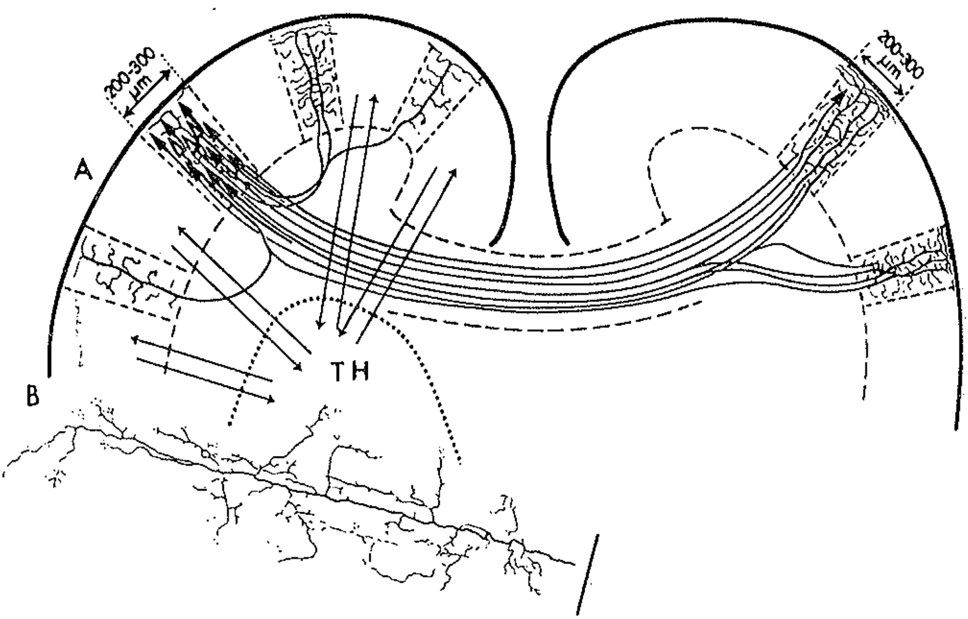

FIG. 10. The general principle of cortico-cortical connectivity is shown diagrammatically in a nonconvoluted brain. The connections are established in highly specific patterns between vertical columns of 200-300 μm diameter in both hemispheres. Ipsilateral connections are derived mainly from cells located in layer III (cells shown at left in *outlines*), while contralateral connections (cells shown in *full black*) derive from all layers II-VI. The diagram does not try to show the convergence from afferents originating from different parts of the cortex to the same columns. TH, thalamus. B. Golgi-stained branching of a single cortico-cortical afferent, oriented in relationship to the module with a single afferent in A, but at several times higher magnification. It illustrates the profuse branching in all laminae. Bar = 100 μm. (Szentágothai, 1978a).

potentiation (Eccles, 1978, 1979, 1980, 1981). The thalamo-cortical input is also of great significance because it provides an input from the limbic system (Graybiel and Berson, 1981) that would give emotional overtones to memory and also provide motivation (Kornhuber, 1973; Eccles, 1980).

In Fig. 11 the modules are shown in plan as seen from the surface, each being enclosed by a circle of 300 μm in diameter. In this pattern two modules with cortico-cortical inputs are shown at about 600 μm apart with outward radiating horizontal fibres, and around both are modules with a gradually diminishing horizontal fibre activation, as indicated by the progressive decrease in the density of horizontal fibre distribution.

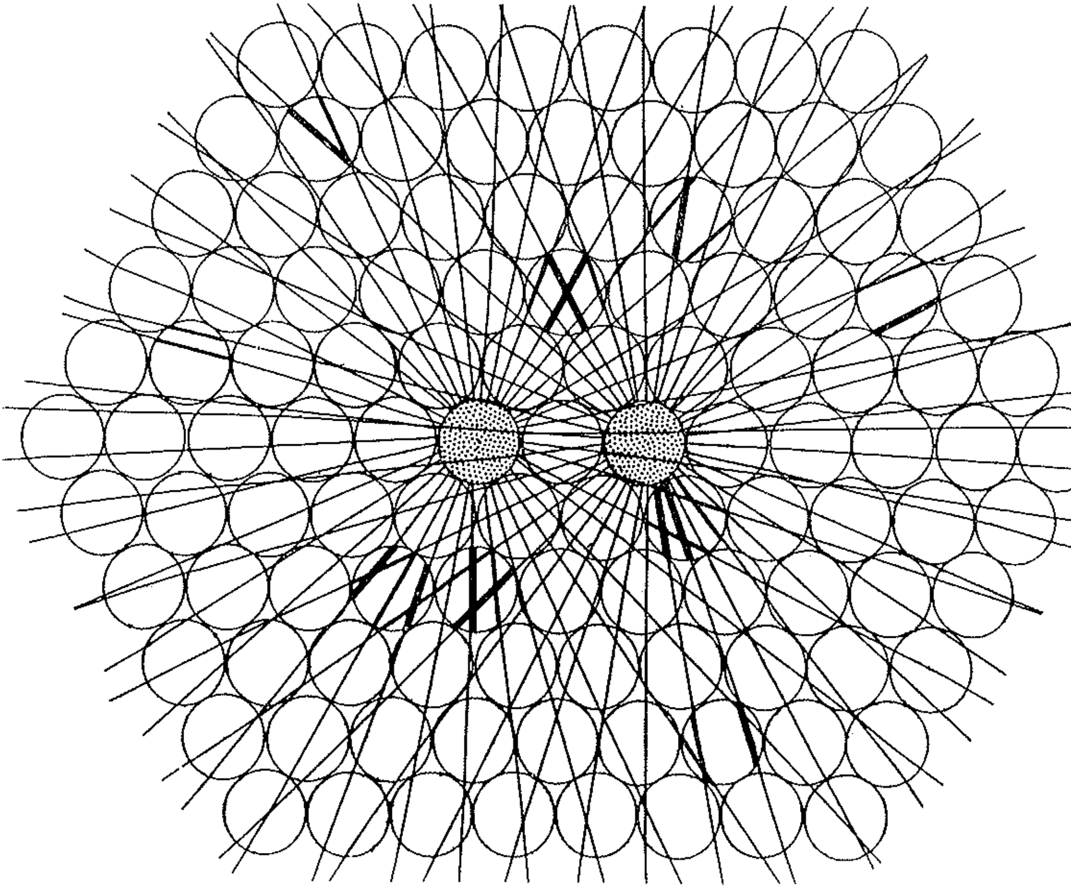

FIG. 11. Diagram of a large assemblage of modules as seen in plan, each outlined by a circle. From two modules there are seen 38 radiating horizontal fibres that would travel far beyond this illustrated zone. Each of course bifurcated in laminae I and II (cf. Fig. 8), so the number of radiating fibres is twice the numbers of fibres of origin — association, callosal and Martinotti (cf. Fig. 8). In several modules there has been hypertrophy of the synapses made by the traversing horizontal fibres as shown in Fig. 8, and this is shown by thickening of the lines. Further description in text. (Eccles, 1981).

Potentiation of the horizontal fibre synapses to several modules, as illustrated in Fig. 8, is shown in Fig. 11 by the convention of a thickening of some lines as they traverse these modules. It can be seen that around the two excited modules there will be a constellation of modules with an augmented input to pyramidal cells from horizontal fibre synapses, and that consequently in the memory process these pyramidal cells could be excited to initiate via a modular discharge the development of a spatio-temporal pattern that could form the neural basis of the remembered experience. The augmented discharge of these pyramidal cells will have opened up new lines of modular communication that were hitherto ineffective. We might term the situation illustrated in Fig. 11 as "modular jumping". It could provide a very simplified model of the changes in modular patterns that are responsible for the storage and retrieval of the cognitive memory.

A simple model of cognitive memory

As a consequence of the synaptic potentiation, the horizontal fibres would be able selectively to activate the pyramidal cells involved in the conjunction potentiation (cf. Figs. 8 and 11) and this could occur in the absence of the initiating thalamo-cortical input to the focal Sst's (cf. Fig. 13B). The laying down and retrieval of a memory will now be considered in more detail in relation to Figs. 12 and 13.

In Figs. 12 and 13 an attempt is made to diagram the conjectured development of modular patterns during a cognitive memory, and the associated mental events. In the lowest row of Fig. 12 there are five modules (A-E) that are serially connected by association fibres in the conventional cortico-cortical manner (Fig. 10). For diagrammatic simplicity only 2 pyramidal cells are shown for each module, a thousand fold reduction. Further association fibre projections shown by a downward arrow from each module would contribute to the spatio-temporal patterns developed in response to thalamo-cortical and cortico-cortical inputs into modules A and B. Each connecting arrow for modules A to E would represent a bundle of up to 100 association fibres. The on-going activation is indicated by the punctate shading of modules. Modules F and G and those sequential therefrom are inactive in the absence of inputs into F and G.

Fig. 13A depicts the modular connectivities at the time of *conjunction* of the TC inputs to modules F and G with the TC inputs into modules A and B. These latter inputs excite the horizontal fibre (H) projections to modules F and G. When there is conjunction between on the one hand

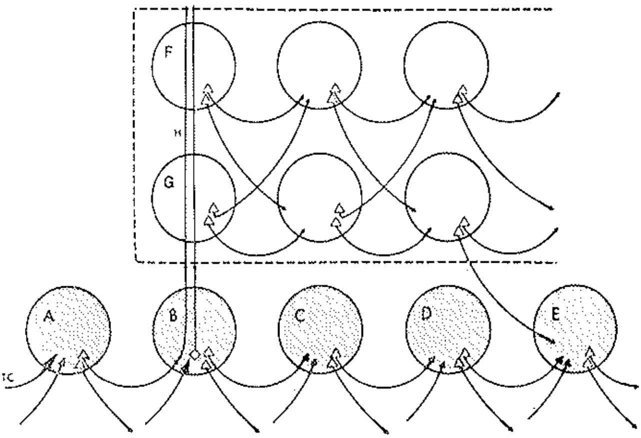

FIG. 12. Diagram of modular arrangement looked at from above with the modules separated so as to allow drawing of the cortico-cortical fibres. Modules A to E represent a basically connected sequence of modules (cf. Figs 10A, 11). Only two pyramidal cells are shown for each module and input and output lines in part connect to modules out of the diagram. In A and B thalamo-cortical (TC) input lines are indicated by large arrow heads. Pyramidal cells project by cortico-cortical fibres to other modules (small arrow heads) that are activated, as indicated, by the punctate shading. From module B there are projecting upwards two horizontal fibres (H) as in Fig. 8, one being the continuation of a cortico-cortical fibre, the other the projection of a M Martinotti cell (diamond). In the absence of inputs to modules F and G, the H fibre input is ineffective, as is shown by the empty modules, F and G and onwards. (Eccles, 1981).

the cartridge activation of pyramidal cells by the TC inputs into modules F and G and on the other hand the horizontal fibre activation from module B, there is conjectured to be an enduring hypertrophy of the horizontal fibre synapses (Fig. 8) and this is shown by the convention of thickening in Fig. 13B (cf. Fig. 11). As a consequence of this hypertrophy, even in the absence of TC inputs to modules F and G, the pyramidal cells of modules F and G would be excited to discharge by horizontal fibre activation from module B (cf. Fig. 8) as illustrated in Fig. 13B, which is in contrast with Fig. 12. There has been module jumping from module B to modules F and G with the consequent initiation of on-going spatio-temporal activation of the upper two rows of modules, as indicated by the weaker punctate shading. Thus the patterned development inside the box (outlined by broken lines) is a weak replica of that initiated in A by the normal TC input into F and G modules, but it now occurs in the absence of this input. This pattern is conjectured to be the neural correlate of the cognitive memory and the associated conscious experience.

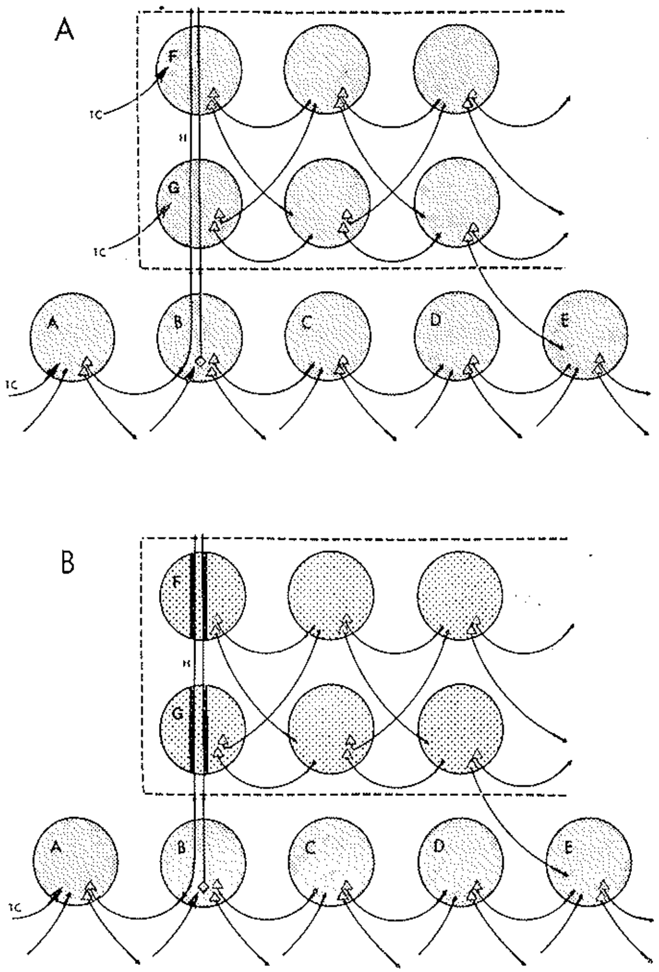

Fig. 13. As in Fig. 12, but in A there are thalamo-cortical inputs into modules F and G at the same time as the inputs into modules A and B with the activation of the H inputs to modules F and G. The spread of activation from modules F and G to the next modules in sequence is indicated by the punctate shading. The conjunction between the horizontal fibre input to modules F and G and the TC input into these modules is postulated to result in an enduring hypertrophy of the horizontal fibre synapses on the apical dendrites of some pyramidal cells (cf. Fig. 8), which is shown in Fig. 13B by thickening of the H fibres as in Fig. 11. As a consequence, even when there are no TC inputs into modules F and G, there will be discharge of impulses from their pyramidal cells in response to the inputs into modules A and B, as is indicated by the punctate shading. Thus by the connecting pattern of cortico-cortical fibres there can be activation of the modular pattern enclosed by the broken line, that otherwise (cf. Fig. 12) would not have been activated in the absence of the TC inputs into F and G. (Eccles, 1981).

Thus Fig. 13B illustrates the retrieval of the memory laid down in the conjunction process of Fig. 13A. It also illustrates that memory retrieval is best secured by some related sensory input (the TC inputs to A and B) or by a deliberate mental effort to conjure up related signals, as when trying to remember a name.

As an aside, I find the simplest exemplar of a cognitive memory is provided by the learning of a name for a perceptual experience, for example of the picture of some person. After repeated display of the picture plus name, the subject has to remember the name when presented by the unnamed picture. This would be the situation in Fig. 13B where the "picture" inputs into modules A and B activate by modular jumping the on-going modular pattern from F and G that gives the memory of the name. This is a standard memory test that can be applied years later, if there has been a sufficient training.

It must be recognized that in Fig. 12 and 13 there has been a tremendous diagrammatic simplification. There should be an amplification of at least 1000-fold in the pyramidal cell population and in their axons, the cortico-cortical fibres. Moreover instead of the two output lines from each module there sbould be connectivities to up to 50 other modules. It would seem that with this transformation into many parallel modular connectivities the diagram could represent both the distributed system of Mountcastle (1978) with modular elements in echeloned parallel and serial arrangment, and the modular operation of superstructures suggested by Szentágothai (1978b, 1979) and by Sperry (1980) in his nested hierarchies.

Self-consciousness and memory

It has been argued (Popper and Eccles, 1977) that without memory we would not experience self-consciousness, and that all experiencing is tinged with remembering. On the basis of the generalization that cognitive memory and self-consciousness are intimately related phenomena, *the conjectured modular patterns subserving memory on the conjunction hypothesis should also be the modular patterns correlated with self-consciousness in all of its manifestations.*

As shown in the information flow diagram of Fig. 14, mental events in World 2 and neural events in World 1 are independent entities that interact across the interface in the manner indicated by the reciprocal arrows which signify transmission of information, not energy. The neural

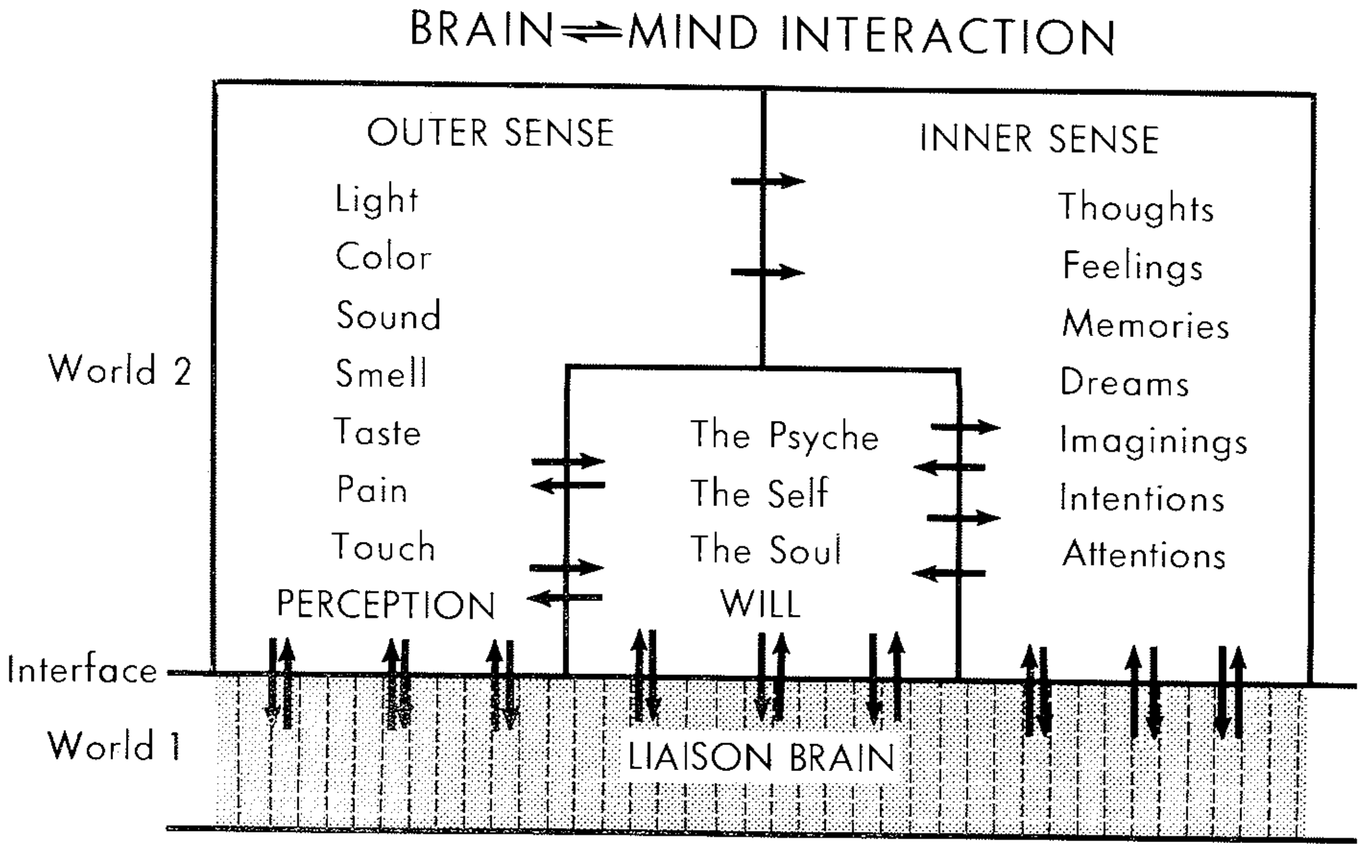

FIG. 14. Information flow diagram for brain-mind interaction. The three components of World 2: outer sense, inner sense and the psyche, soul or self are diagrammed with their communications shown by arrows. Also shown are the lines of reciprocal communication across the interface between World 1 and World 2, that is from the liaison brain to and from these World 2 components. The liaison brain has the columnar arrangement indicated by the vertical broken lines. It must be imagined that the area of the liaison brain is enormous, with open modules numbering over a million, not just the two score here depicted.

correlates of the conscious experiences are in the neocortex — the liaison brain with its modular columns.

Since each cognitive experience is embedded in memories that are being retrieved, the modules in the boxed area of Fig. 13B would contain the neural correlate of the conscious experience. This experience is for giving as well as receiving. It is here that we have the most subtle and sensitive dynamic operations of the neocortex. The voluntary retrieval of a simple memory, for example of a name or a number, involves the initiation of a cerebral action that is designed to deliver the required information from the data banks, for example the boxed-in area of Fig. 13B. That information is then evaluated for correctness by what can be called a recognition memory in the mind, that appears under Inner Sense in Fig. 14. It may be judged erroneous — perhaps a slight error in a name or in a number sequence. This leads to a renewed attempt at retrieval, which may again be judged faulty — and so on until the retrieval is judged to be correct, or until the attempt is abandoned. It is therefore conjectured that there are two distinct kinds of memory: 1. brain storage memory held in the data banks of the brain, especially in the cerebral cortex as in Fig. 13B; 2. recognition memory that is applied by the self-conscious mind in its scrutiny of the retrievals from the brain storage memories.

In a voluntary memory retrieval the input to modules A and B in Fig. 13B must somehow be influenced by the mind so that it activates the modular operations in the punctate shaded modules F and G and onwards that is the neural correlate of the memory. As suggested above, this influence is exerted initially by the potentiated synapses of the horizontal fibres from module B, so that they become more effective in exciting some of the modules they traverse. In this way modular jumping is initiated with the consequent development of the unique patterns of modular activity that are conjectured to be the neural substrate of the memory. The retrieved memory is momentarily encoded in the spatio-temporal patterns of the boxed-in area. According to dualist-interactionism all interactions between neural and mental events are reciprocal (cf. Fig. 14). Hence it can be conjectured that the neural events in the whole modular ensemble are in reciprocal relationship to the mental events of the experienced memory. At this simplest level, name or number retrieval, conscious experiences can be identified with conscious memory. However at all levels of self-conscious experiences it would seem that there is a matching level of memories.

Though the potentiated horizontal fibre synapses may be the first target of the mental influences in retrieval, it is postulated (cf. the reciprocal arrows across the interface of Fig. 14) that the whole of the spatio-temporal pattern stemming from that origin is also recognized and controlled by the mental influences in attention, in interpretation and in the quest for meaning. It can be further proposed that at any one instant not all modules in the cerebral cortex have this transcendent property of being "open" to mental influences (World 2) and thus being the World 1 components of the interface of Fig. 14. For example they would have to be at the appropriate level of activity. Fig. 15 gives a diagrammatic illustration of the conjectured relationship of open and closed modules as viewed by looking down at the surface of the cortex. A convenient diagrammatic liberty is to show the columns as separate discs, and not in the close contiguity that is the actual relationship (Szentágothai, 1978a). Furthermore, it has to be recognized that the normal intensely dynamic situation is frozen in time. The convention is that open modules are shown as open circles, closed as solid and that there are also partly open modules. It can be conjectured that the self-conscious mind probes into this modular array, being able to receive from and give to only those modules that have some degree of openness. Fig. 15 has been designed to show several zones of

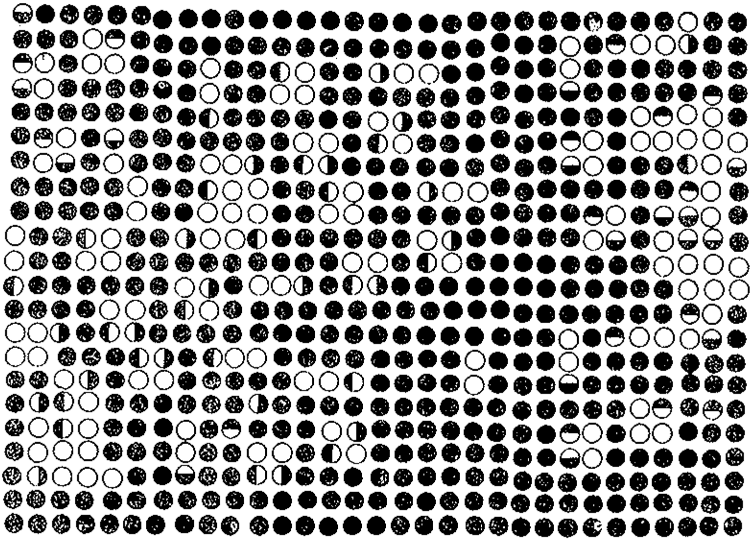

FIG. 15. Diagrammatic plan of cortical modules as seen from the surface (cf. Fig. 11). As described in the text, the modules are shown as circles of three kinds, open, closed (solid black) and half open.

excited modules interspersed in large dark areas. Also there are smaller patches of excitation. Fig. 15 represents just a fragment of a coded representation in a moment of time. The complexity of the real situation can be appreciated when it is recognized that the modular assemblage of the neocortex would be represented by increasing the area of Fig. 15 almost 5000 times. When in memory retrieval by modular jumping there is activation of the boxed-in area of Fig. 13B, for example, there will be a change in the modular pattern of Fig. 15 that in its developing dynamic patterns is the neural counterpart of the remembered experience.

It is important to realize that the separateness of the two modular systems of Figs 12 and 13 is related to some specific TC input. With another input there would be a complete rearrangement. The modules A to F could be triggered by an appropriate horizontal fibre system, and so be the neural correlates of some other memory. Any one module could participate in the spatio-temporal patterns for an indefinitely large number of memories with their embedded conscious experiences.

It is difficult to understand how the self-conscious mind can relate to such an enormous complexity of spatio-temporal modular patterns as in Fig. 15. This difficulty is mitigated by three considerations. *Firstly*, we must realize that our self-conscious mind has been learning to accomplish such tasks from our babyhood onwards, a process that is colloquially called "learning to use one's brain". *Secondly*, by the process of attention the self-conscious mind selects from the total ensemble of modular patterns those features that are in accord with its present interests. *Thirdly*, the self-conscious mind is engaged in extracting "meaning" from all that it reads out. This is well illustrated by our experiences with ambiguous figures, for example a drawing that can be seen holistically either as a staircase or an overhanging cornice, but never with some compromise solution.

So it can be concluded that pattern recognition would ultimately depend on the reading out from the scintillating spatio-temporal patterns of modules at various degrees of activation from moment to moment. An analogy would be tbe manner in which we derive a meaningful picture from a TV screen, where the signal is from patterns of brightnesses displayed by the million or so units.

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PRECONSCIOUS AND CONSCIOUS PROCESSES IN VISION

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1. *Unconscious (Preconscious or Preattentive) Processes in Vision*

The notion of unconscious mental processes usually conjures up in the layman's mind Sigmund Freud's insights about suppressed thoughts. Freud's notions of the unconscious are related to mental processes that were once conscious, but suppressed, or never reached consciousness, but could be made conscious after major, time-consuming, efforts. In this article, however, I am concerned about quite different unconscious processes — I prefer to call them preconscious processes — which are so fundamental and occur so early in the processing chain that by their very nature no internal effort could ever reveal their workings.

Indeed, as we watch our hand from an outstretched distance, and bring it closer to, say, 25 cm, the best viewing distance, we will notice that the size of our hand did not appear to increase, in spite of such large change in physical size of the image projecting on our retina. This well-known perceptual phenomenon is called *size constancy*, and the neural circuitry performing this size invariance, is not yet fully known, and without sophisticated psychological experiments, no amount of introspection would permit us to make conscious this automatic, hidden mental process.

There are many perceptual constancies that are the result of effortless, automatic processes, probably at the earliest stages of our central nervous system, that are "file protected" against internal scrutiny. For instance, perceptual *color constancy*, that in spite of dramatic changes in the spectral composition of illumination the appearance of the color of surfaces of objects stays remarkably invariant. Another well-known example is perceived *positional constancy* of objects as we move our heads and eyes. Tbat this constancy is closely related to our preconscious intent of our eye and head movements can be easily demonstrated if we wiggle our eyes by finger pressure, that causes a breakdown of the positional constancy, and objects in our perceptual world seem to wiggle around, too.

Here I do not want to dwell further on the considerable amount of vision research on these important problems, but instead, I turn to my own research — spanning over two decades — that reveals a novel operation of human vision based on a preconscious (preattentive) process that detects in parallel some conspicuous, local feature differences, I named differences in *textons*, and, in turn, directs a serial, conscious process of *focal attention* to these loci of texton differences (Julesz, 1981; Julesz and Bergen, 1983).

2. *The Definition of Textons*

Before I review our texton theory and clarify how our preattentive/attentive dichotomy differs from the many "two-visual systems" of others, let me give some historic account. The work reported here started with preattentive texture discrimination in 1962 and during the next two decades has been carried out in collaboration with many colleagues, mostly mathematicians, who helped me invent the sophisticated stochastic processes I needed. From 1962 till 1975 David Slepian, Mark Rosenblatt, Ed Gilbert and Larry Shepp were instrumental in creating random texture pairs whose elements in isolation appeared conspicuously different, yet as texture pairs could not be told apart without element-by-element scrutiny. In 1977-78, colleagues Terry Caelli, Ed Gilbert and Jonathan Victor helped me in finding stochastic texture pairs with global constraints that yielded preattentive texture discrimination based on some local conspicuous features I later called textons. Finally, two postdoctoral fellows of mine, Peter Burt and particularly Jim Bergen, conducted experiments with me that *extended* the texton theory of preattentive vision to preattentive vision *in general*, and led to the novel two-visual system model to be outlined here.

Luckily, now that we know what textons are and their role in vision is clarified, I can save the reader the torturous mathematical path that led to their discovery. Here I follow an axiomatic treatment that does not require mathematical knowledge to be understood (except for the next few paragraphs till the end of this section, that can be skipped). Our main findings are presented as *heuristics* (similar to *axioms*, but not necessarily independent of each other), immediately followed by many demonstrations. The reader can test the power of these newly acquired heuristics, by being able to predict and then verify which texture pairs will be perceived to be different, and which will appear as a single texture. As a matter of fact, the same heuristics can predict preattentive texture discrimination of a few patterns presented in a brief flash followed by masking. However, this generalization can only be demonstrated in the laboratory. So I regard texture discrimination as an excellent way to demonstrate our findings on the printed page. Indeed, texture discrimination serves as a "royal road" to preattentive vision of any pattern.

In the next section I will provide these heuristics that will define our theory of human vision. But before doing so, I am now outlining the basic mathematical ideas that led to the discovery of textons. The reader who is allergic to mathematical concepts can skip the remainder of this section, but has to pay a price. Without understanding the statistical ideas that led to the discovery of textons, the local, conspicuous elements of preattentive vision, the mere postulates of Heuristic 2 are misleading. Indeed, learning that elongated blobs (line segments) or the ends (terminators) and crossings of line segments are textons, the reader will assume that textons are similar to the many ad hoc features of the psychologists (e.g. Beck, 1972) and artificial intelligence researchers (e.g. Marr, 1982) who borrowed and renamed some of the "trigger features" of single microelectrode neurophysiologists (e.g. Hubel and Wiesel, 1968). This assumption, however, is incorrect. Textons are precisely defined entities in their own right, and that some of them resemble the local features of psychologists and neurophysiologists is most gratifying, but not a matter of course. (For instance, the texton of crossing line segments has not been described by the neurophysiologists, to my knowledge).

In order to explain how textons were discovered, I must introduce two concepts (Julesz, 1962): a) preattentive texture discrimination, and b) texture pairs with identical second-order statistics.

Preattentive texture discrimination is illustrated by Fig. 1. In my research textures are composed of many similar elements either randomly (or regularly) spaced in random (or regular) orientations, usually without overlap. In Fig. 1 the area composed of "+"s clearly stands out from the surroundings "L"s, and this immediate, parallel process will be called *preattentive texture discrimination*. On the other hand, it requires element-by-element scrutiny to notice the texture composed of "T"s hidden in

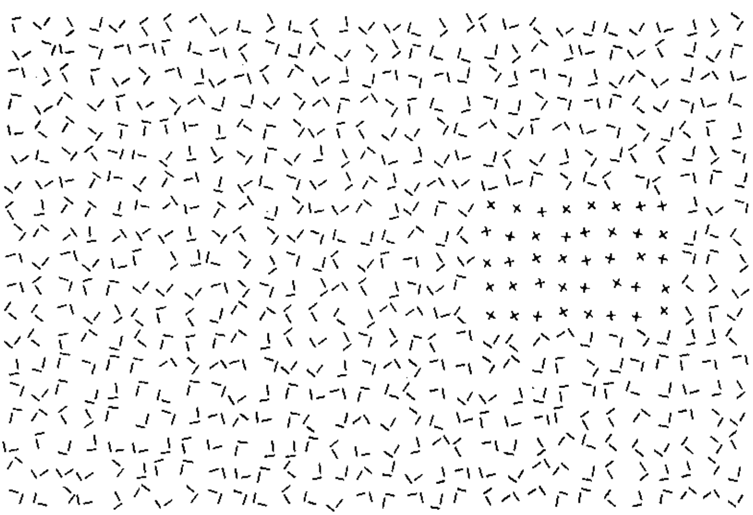

FIG. 1. *Preattentive texture discrimination* versus element-by-element scrutiny (called *focal attention*). [From Julesz and Bergen, 1983].

the "L"s. This serial, element-by-element search will be called *focal attention*. At the moment, we are interested only in preattentive texture discrimination.

The second concept, of generating texture pairs with identical second-order (hence first-order) statistics, requires the notion of *n*th-order statistic (or *n*th-order joint probability distribution). Although the reader can find the definition in any advanced textbook in probability or stochastic processes, I give here a brief account: If we throw dots on a texture in a random fashion, the frequency (probability) that the probing dot will fall on a certain color (e.g. black, white, gray, red, etc.) is the first-order statistic (or probabily distribution). Similarly, if we throw randomly needles (i.e. line segments, 2-gons, or dipoles) on the texture (where the needles have certain lengths and orientations) the probability that the endpoints (vertices) of the needles will land on certain color combinations (e.g. white and white; or black and white; or black and black, etc.) is the second-order statistic (or joint probability distribution of two events). Iso-second-order textures thus have identical needle- (hence dot-) statistics, but usually different third- and higher-order statistics. The third-order statistic is the probability that the three vertices of a triangle (3-gon) of a given shape when randomly thrown will fall on certain color combinations (e.g. black, black, black or white, black, white, etc.).

For instance, we have shown (Julesz, Gilbert, Shepp and Frisch, 1973) that textures composed of the same elements (e.g. "R"s) in random orientations, and their *mirror-images*, respectively, have the same second- and first-order statistics, but different third- and higher-order statistics. Figure 2A shows such a texture pair, and without element-by-element scrutiny the texture pair is preattentively indistinguishable. In the same paper we also proved that a texture pair composed of the same elements having the same orientation (e.g. "u"s) and their *upside-down images* ("n"s), respectively, are also having identical second-order statistics, but different third- and higher-order statistics.

Figure 2B shows such a texture pair, which again is preattentively indistinguishable. We found several hundred such texture pairs, where the individual elements appeared very different, but their aggregates could not be told apart without lengthy, element-by-element scrutiny. Since all these indistinguishable iso-second-order texture pairs have different third- or higher-order statistics, one could conjecture that the preattentive visual system cannot process statistical parameters of third- or higher-order. Furthermore, if preattentively discriminable textures were ever to be found, discrimination *could not be* the result of *statistical* (i.e., *global*) computation, but by definition must be based on either *topological* or *local* feature dif-

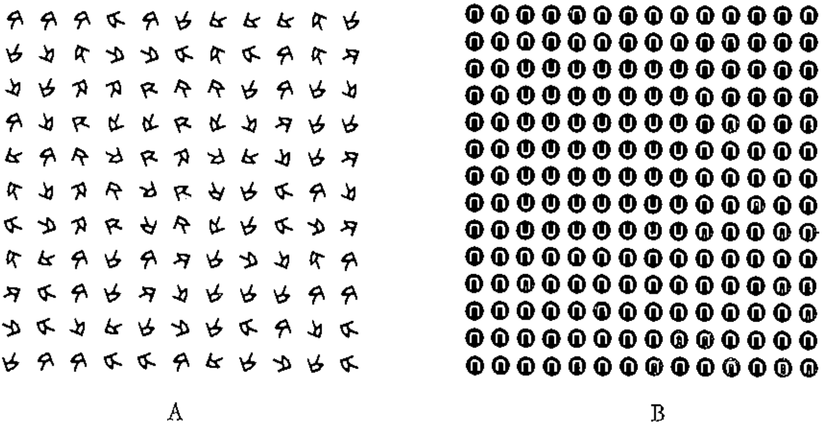
A B

FIG. 2. Preattentively indistinguishable texture pairs (having identical second- and first-, but different third- and higher-order statistics, as described in text): *A*) Texture pair composed of "R"s and "mirror-image R"s respectively, having random orientations; and *B*) Texture pair composed of "u"s and "n"s respectively, having the same orientation. [From Julesz *et al.*, 1973].

ferences. Indeed, since the second- and first-order statistics were kept identical, and the third- and higher-order statistical parameters were shown to be beyond the processing power of the preattentive system, in case of texture discrimination, the cause cannot be statistical, hence must be topological or local. As we will see, topologically identical features (e.g. narrow or wide elongated blobs) are discriminable, hence the basic feature must be local. I called these putative conspicuous local features "perceptual quarks" which I later renamed *textons.* So, *textons are the local cospicuous features that yield preattentive discrimination in iso-second-order textures.*

One of the highlights of my scientific life was the discovery of the first textons in 1978 (Caelli and Julesz, 1978; Caelli, Julesz and Gilbert, 1978; Julesz, Gilbert and Victor, 1978). As a matter of fact, in the latter publication we created texture pairs with identical third- (hence identical second- and first-order statistics) that were preattentively discriminable, as shown in Fig. 3. Indeed, it is most unlikely that the preattentive system could process differences in the fourth- and higher-order statistics, but instead discrimination must be based on textons, the local elongated black and white blobs that have different widths, lengths and orientations in the two textures.

After this detour, let us turn to the heuristics of the texton theory of human vision.

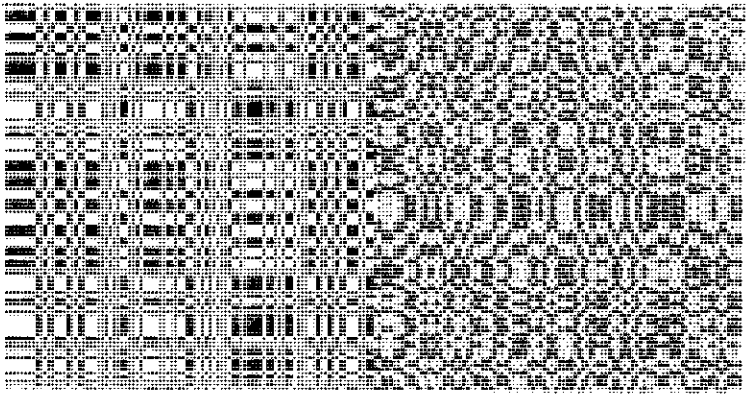

FIG. 3. Preattentively discriminable texture pair with identical third- (hence identical second- and first-) order statistics. Discrimination is based on differences in local elongated blobs (called textons). [From Julesz, 1981].

3. *The Heuristics of Preattentive and Attentive Vision*

Now I state three axioms (heuristics) that will permit an explanation of our new theory of vision, and give several demonstrations. The purpose of the demonstrations is to clarify the concepts underlying the axioms defined, and to illustrate how the axioms enable the reader to predict which patterns in aggregates yield texture discrimination. As mentioned earlier, these axioms are not all necessarily independent, so it might be more proper to call them heuristics.

Heuristics 1: Human vision operates in two distinct modes:

A) *Preattentive vision* (parallel, [i.e. independent of the number of patterns,] instantaneous, without scrutiny, covering a large visual field; as in texture discrimination).

B) *Attentive vision* (serial search by focal attention in 50 msec steps [4 times faster than scanning by eye-movements] limited to a small aperture; as in form recognition).

Heuristic 2: Textons:

A) *Elongated blobs* (e.g. rectangles, ellipses, line segments) with specific colors, angular orientations, widths and lengths.

B) *Terminators (ends-of-lines) of line segments.*

C) *Crossings of line segments.*

Heuristic 3: The role of textons:

Preattentive vision directs attentive vision to the locations where differences in textons, or in the density (number) of textons occur, but ignores the positional relationships between textons.

Only very elongated blobs, such as line segments are used to define the "terminator" and "crossing" textons. Indeed, for wide elongated blobs it is not easy to define what their terminators and crossings might be. While I do not want to mix this psychologically motivated theory with neurophysiology, nevertheless, even terminators of line segments could be thought of as being detected by complex neural units that combine "on" and "off" type detectors with elongated blob-shaped receptive fields (perhaps perpendicular to each other). While elongated blobs are the primary textons, their terminators and crossings serve only as useful heuristical concepts in case of patterns and textures composed of line drawings. This is the reason why the above given rules are only heuristics and not axioms. On the other hand, the inclusion of terminators and crossings as memhers in the texton class has great advantages. With their help we can see how local concepts can replace (at least in the case of line drawings) complex global topological properties such as closure or connectedness.

At this point I have to clarify the difference between the perceptual notions of textons and trigger features of neurological analyzers (detectors). The texton of, say, a vertical elongated red blob in a blue surround is a perceptually well defined psychological entity. How such a texton is actually extracted by some cortical detector is not our concern. Of course, it is gratifying that our textons — identified after many years of careful psychophysical research — show resemblance to the trigger features to which cortical detectors are tuned, as discovered by Hubel and Wiesel (1968) and other neurophysiologists. Nevertheless, as I pointed out years ago (Julesz, 1971) the trigger feature of a Kuffler-unit (Kuffler, 1953) or a Hubel and Wiesel-type of simple unit is not a perceived dot, or slit (i.e. an elongated blob texton), respectively. Indeed, such neural units fire equally for a small blob with high contrast, or a larger blob with corresponding lower contrast, while we can easily *perceive* these two cases as being quite *different* entities. Obviously, the percept of a slit (or dot) is encoded by several neural detectors optimally tuned to different sizes. Two or more such detectors properly interconnected can easily discriminate between blobs of different extent and contrast.

Furthermore, in this article only static and flat images are demonstrated. With the help of random-dot stereograms and cinematograms (Julesz, 1960, 1971) it can be shown that binocular disparity, movement parallax (velocity), and flicker are conspicuous features that yield preattentive pattern discrimination and are also powerful textons. For instance, binocular disparity difference in random-dot stereograms can yield depth discrimination in 50 msec (Julesz, 1964; Julesz and Chang, 1976), and the extraction of these "textons" must occur at an early stage. Indeed, as Gian Poggio found using dynamic random-dot stereograms (Poggio, in press), there exist pure binocular disparity detectors (in the absence of any monocular contrast difference) as early as in layer IVB and IVC in Area 17 of the monkey cortex. So, in addition to the texton properties of color, width, length and orientation of elongated blobs, one has to add binocular disparity, velocity, and flicker as well.

We have shown that the preattentive system is not sensitive to relative position. How is it then possible that texton properties of velocity and binocular disparity can be extracted with great precision by the preattentive system? The answer is that highly puctiform subsystems exist for movement and binocular disparity detection, however, in the preattentive system these various pools of detectors tuned to different velocities and disparities are not coupled to each other.

Before we discuss the implications of these heuristics, let us apply them to a few pairs of elements and *predict* whether the texture pairs formed from these elements will yield preattentive discrimination or not. This application of the rules also helps the reader to clarify them. I will mainly use textures composed of line segments, since I want to show the importance of terminators and crossings.

Obviously, differences in line segment number of the elements will cause these elements to be preattentively discriminated (in a brief flash, with presentation time limited to 160 msec or briefer by a successive masking stimulus). Such a preattentively discriminable texture element pair with different line segments (2 vertical line segments in one, missing in the other) and 6 terminators versus zero terminators, is shown in Fig. 4A. As predicted by the texton theory, even the aggregates of these elements will yield preattentively discriminable texture pairs (Fig. 4B). Whether the elements are presented in parallel (Fig. 4B) or in random orientations (Fig. 4A) does not affect the strength of discrimination.

In the next examples we stress the importance of terminator textons. For instance, in Fig. 5A the two elements are composed of three identical line segments (i.e. same orientation, width and length). The only difference is in the number of their ends-of-lines (terminators). The triangle-shaped element has no open ends, while the "dual" element has *3* ends-of-lines. One should expect texture segregation, given such a large difference in terminator number, and as Fig. 5B demonstrates, this in the case. Furthermore, the triangle-shaped elements stimulate different shaped white elongated blob textons flanked by the black line segments than the three-pronged shaped elements do.

As a matter of fact, discrimination is so strong that a *single* element can be preattentively detected among 35 "dual" elements, as sbown in Fig. 5C. This arrangement is now routinely used by us in studying pattern discrimination in preattentive vision, as will be discussed later. Here we note only that when there is a texton difference (as in Fig. 5C) detection of one element in the midst of 35 other elements is almost as easy as

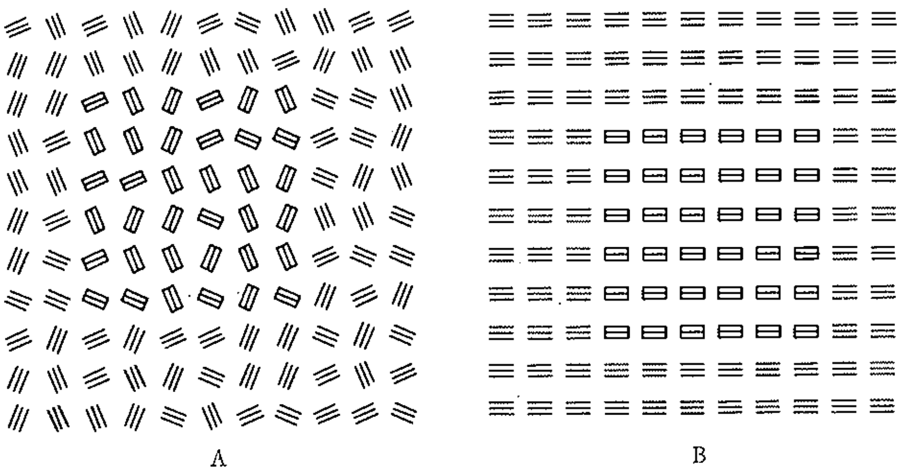

FIG. 4. Preattentively discriminable texture pair: *A* based on different textons (line segments) and different number of ends-of-lines; *B* same as *A*, except orientation of elements is not randomized.

detecting the difference between two elements (shown in Fig. 5A) for presentation times as brief as 100 msec.

In the next example, both members of the element pair of Fig. 6A are again composed of the same five line segments (each corresponding line segment in the two elements has identical width, length and orientation, respectively) but one element contains only two ends-of-lines, whereas the other contains five. This large difference in terminator numbers should yield texture segregation, and inspection of Fig. 6B demonstrates that it does.

Figure 6C consists of the same arrangement as Fig. 5C except that the target contains the five terminators and the surround (also called "ground") is composed of dual patterns having two terminators. As predicted, the large difference in terminator numbers again makes the target stand out from its surround.

The next example, shown in Fig. 7A, consists of the "S"- and "10"-shaped elements, that in isolation appear quite different. However, the two contain the same number of line segment textons (three identical horizontal and two identical vertical line segments) and both contain two ends-of-lines. The fact that the positional relationship between these textons is different (as it is in Fig. 4B) can be perceived only by the attentive visual system (yielding the percept of an "S" versus a "10"). How-

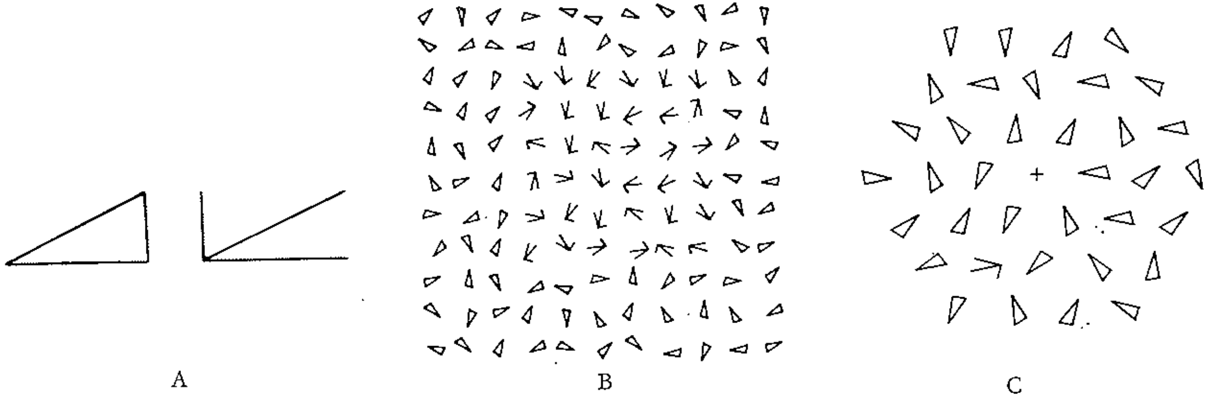

FIG. 5. Preattentively discriminable texture pair *B*, where the two elements, shown in *A*, have identical line segment textons, but differ in their ends-of-lines (terminators). *C* Preattentive discrimination is so strong that a *single* element can be detected among 35 dual elements in a 100 ms brief flash terminated by a masking stimulus. [From Julesz and Bergen, 1983].

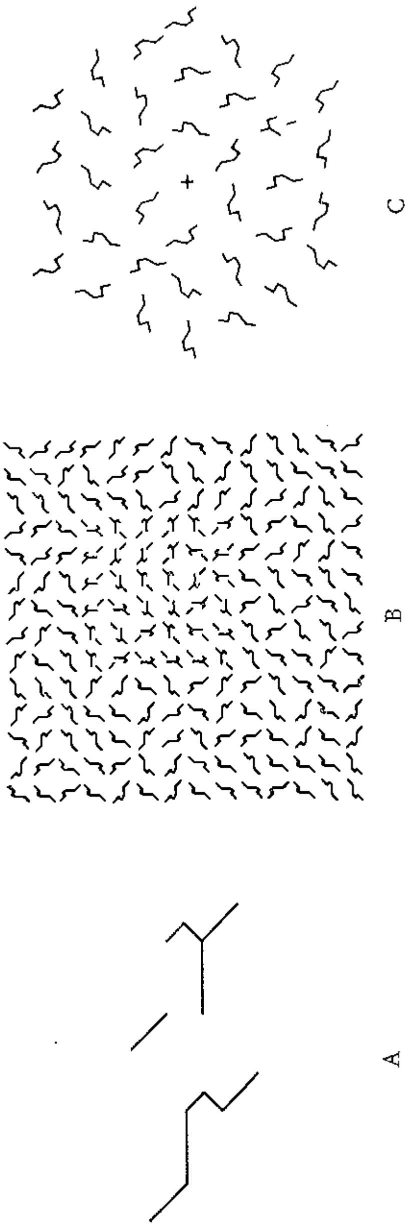

FIG. 6. Similar to Fig. 5, except the elements contain 2 versus 5 terminators. [Julesz and Bergen, 1983].

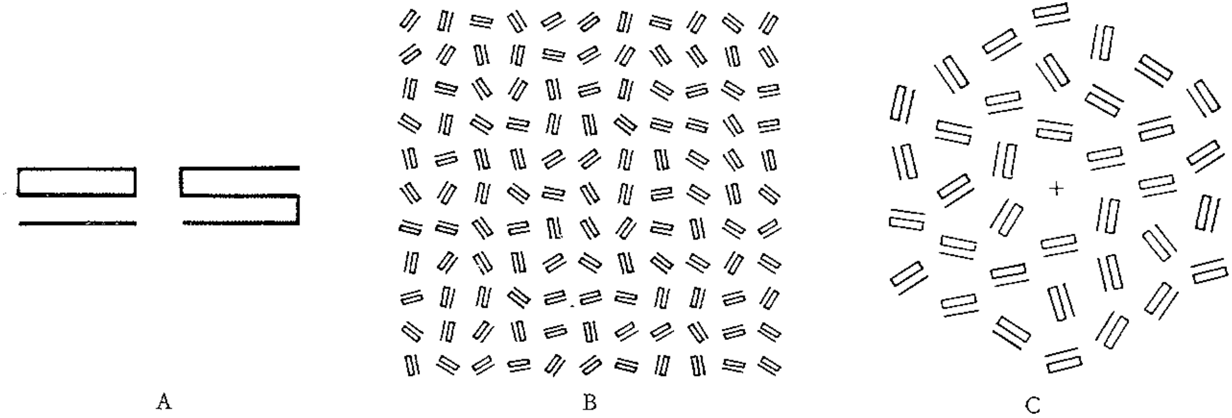

FIG. 7. Preattentively indistinguishable texture pair *B*; and indistinguishable target *C*; although the elements themselves appear very different *A*. [From Julesz and Bergen, 1983].

ever, according to *Heuristic 3* the preattentive system can count only the density (number) of textons and ignores their relative positions. So, according to our rules, a texture pair composed of these elements contains the same average density (number) of textons, and thus should be indistinguishable. Surprising as it may seem, the texture pair is indeed preattentively indistinguishable as demonstrated by Fig. 7B. [Readers who find this demonstration of the distinction between preattentive and focal vision not adequately convincing without brief presentation, should note the contrast between the attentively different percepts of Fig. 7A, and the corresponding texture pair in Fig. 7B that cannot be distinguished without element-by-element scrutiny. However, in Sec. 4 detailed numerical data of discrimination by the preattentive and attentive systems will be provided using brief exposures with erasure.]

Let me note that as long as the dual elements that constitute the texture pair have all their line segments of identical orientations, the texture pair remains indistinguishable even if the elements are not randomly rotated (Fig. 8A).

However, in these examples with line segments one must not lose account of the large white blob textons that are flanked by two or more black line segments. I mentioned these briefly when discussing Fig. 5B. What is surprising is the extent these dual textons can be disregarded, but not always. For instance, one would assume that the indistinguishable texture pair composed of "S"s and "10"s has to be composed of very much longer horizontal line segments than vertical ones. Indeed, for any very elongated white blob detector flanked by two parallel horizontal line segments it should be unimportant whether their ends are flanked by zero, one, or two short vertical line segments. On the other hand, this should be more important when the horizontal and vertical line segments become of equal length. Interestingly, the square shaped "S" and "10" shaped elements in aggregates (Fig. 8B) are still at threshold of texture discrimination, but require less scrutiny tban Fig. 7B. The importance of large white (black) blobs formed by black (white) line segments will be discussed in the next few examples.

If the texton theory is correct, one could mix linearly two elements in one texture so that the sum of line segments and terminators should be identical to that element (or elements) that form the other texture, and obtain indistinguishable texture pairs. Of course, one should not mix elements with very different textons (e.g. a "dummy" element such as a blank) since the preattentive system might detect *fluctuations in mean*

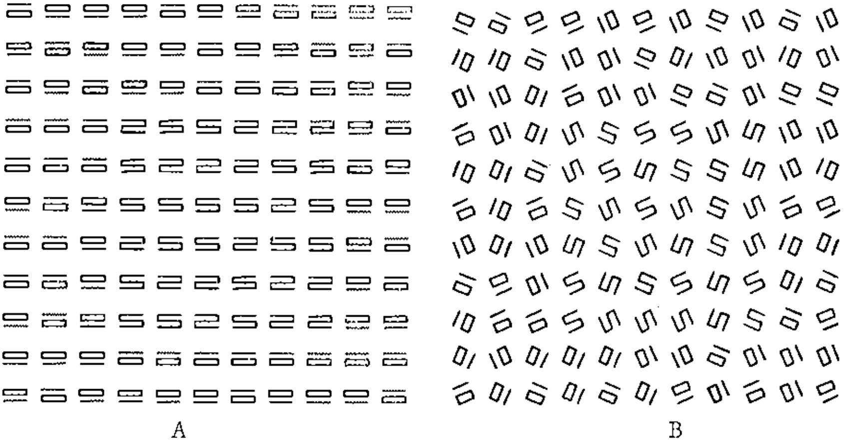

FIG. 8. *A* Same as Fig. 7B, except that the elements have identical orientations. [From Julesz, 1981]. *B* Same as Fig. 7B, except that the elements are square shaped.

densities even when the texton count is kept identical. One example of such a texture mixture is shown in Fig. 9A following an idea of Howard Resnikoff. Here a "10" and an "8" shaped element are mixed with equal probability, whose sum of textons is equivalent in color (line segments) and terminators to a "6" shaped element. Indeed, as predicted by the texton theory neither Fig. 9B, nor 9C yields distinguishable textures. Figure 9B is similar to 9C, except that the elements are elongated.

Figures 4A and 4B demonstrated the strength of discrimination between an "8" shaped element and one composed of three horizontal lines. Therefore it is interesting that the equal mixture of these two elements yields a indistinguishable texture from another formed by "E" shaped elements, as shown in Fig. 10B. The elements themselves are shown in Fig. 10A.

However, if these elements are less elongated, and have a square shaped convex hull, as shown in Fig. 10C, then the white elongated blobs flanked by the line segments start to modulate the mean densities in the two textures in different ways, resulting in weak texture discrimination.

Finally, let us demonstrate the third texton, the crossing of elongated blobs (line segments). Figure 11A shows the conspicuous difference between a texture pair that segregates based on the presence or absence of elements having crossing versus not crossing line segments. If the elements have identical textons, including crossing (or not crossing line

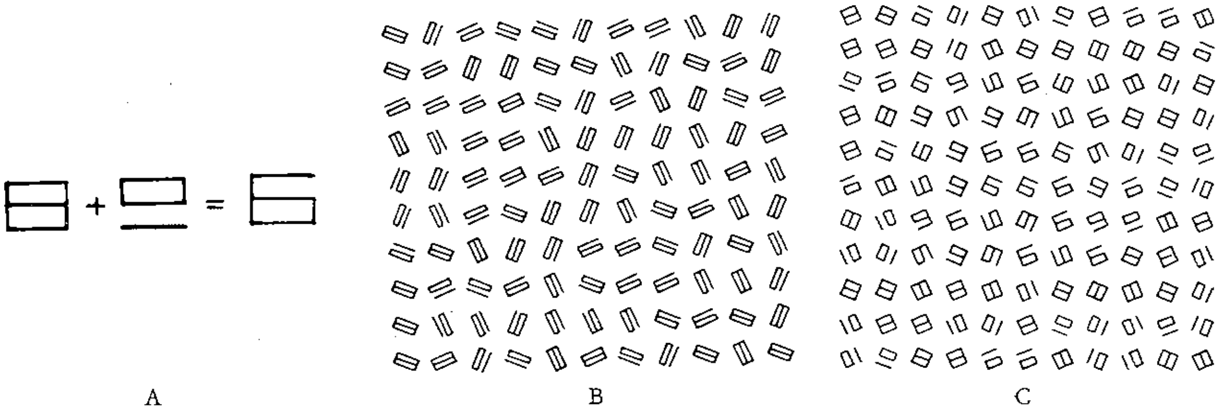

FIG. 9. Combination of elements with identical textons A) yield indistinguishable textons B), even when elements are square shaped C).

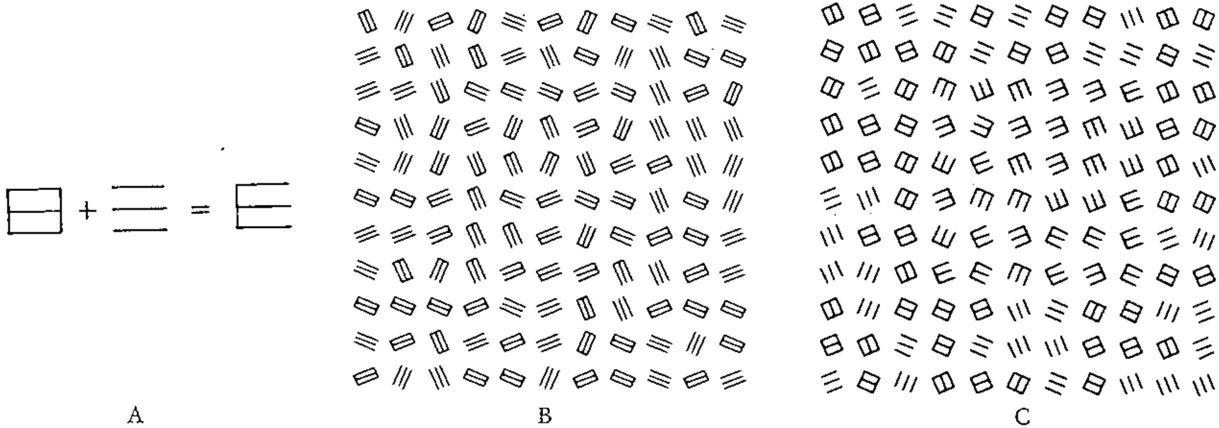

FIG. 10. Similar to Fig. 9, except that the white elongated blobs (flanked by the black line segments) modulate the texton density and yield weak texture discrimination in C) but not in B).

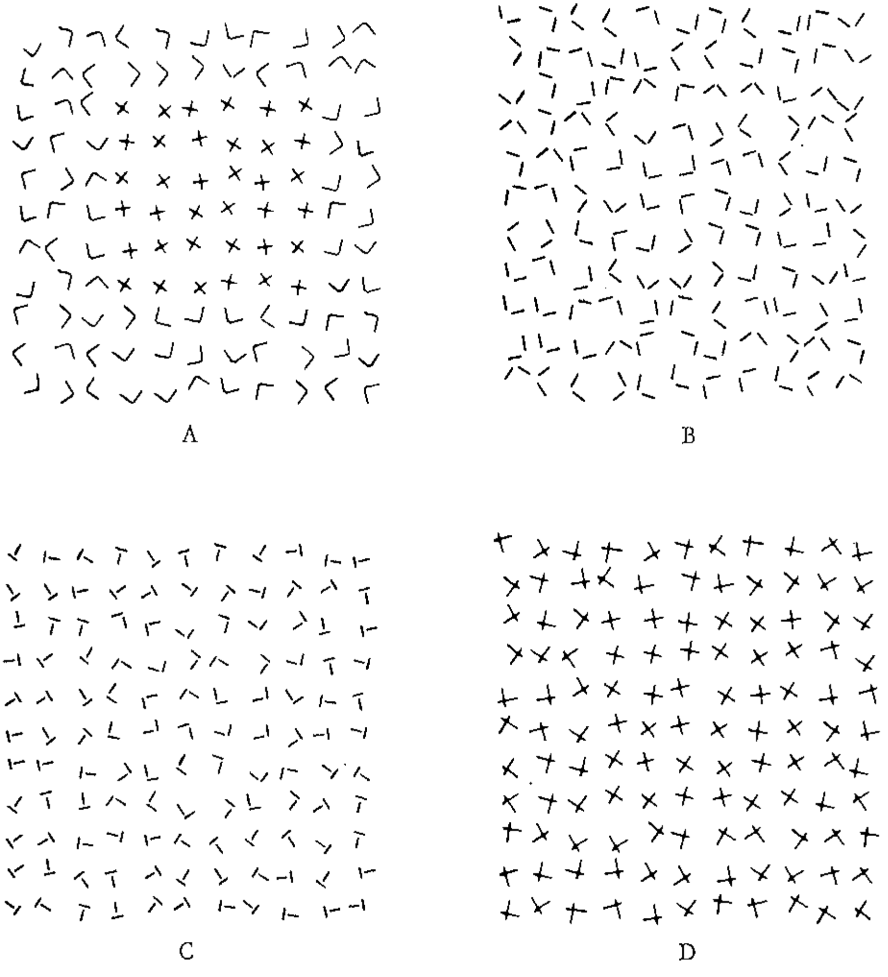

FIG. 11. Role of the texton of crossing. A) Preattentive texture discrimination based on presence and absence of crossings, and indistinguishable texture pairs because pairs either have no crossings B, C; or have both crossings. [From Julesz and Bergen, 1983].

segments) the texture pairs become preattentively indistinguishable. The positional relationship between the line segment textons is unnoticed by the preattentive system. The difference in gap-size between the "L"-shaped elements in Fig. 8B yields a preattentively indistinguishable texture pair. Particularly interesting is the demonstration in Fig. 8C where T-versus L-shaped elements yield an indistinguishable texture pair. Although we have kept a small gap between the perpendicular line segments that make up the "L"s and "T"s, preattentive discrimination of texture pairs composed of these elements is impossible even when the gaps are not resolvable. Apparently, the difference of a single end-of-line terminator is not adequate to yield texture segregation. Finally, 8D depicts a preattentively indistinguishable texture pair, where, with scrutiny, it is obvious that the elements contain line segments that either cross at midpoint or cross far from the midpoint.

4. *Texton Differences Direct Focal Attention*

The success of the texton theory in accounting for texture perception is the result of the spatial complexity of patterns. This complexity over a large area exceeds the capacity of focal attention and thus allows the preattentive system to dominate. This same overloading of focal attention can be achieved in simpler patterns by using very brief presentations. Jim Bergen and I have shown that under these conditions the same texton theory can be applied. [The interested reader might consult Julesz, 1982; Julesz and Bergen (1983); and Bergen and Julesz (1983) for further details.]

We used the hexagonal array of 35 elements plus 1 target element as in Fig. 5C. Observers first focused on the center marker, then the hexagonal stimulus was flashed for 40 msec duration followed by a masking array (where the elements were the union of the two being discriminated and overlapped the elements of the first array). The duration between the onset of the stimulus and masking arrays (called SOA, or stimulus onset asynchrony) was varied. The 40 ms presentation time cast a sharp stimulus on the retina and even if eye movements could be initiated, the afterimage of tbe stimulus remained stabilized on the retina. In half of the presentations the hexagonal test field consisted of identical elements, and observer's task was to discriminate between these two conditions. The results can be predicted from the heuristics and are shown in Fig. 12. If the target "L" was embedded in 35 "+"s, thus differed in a texton

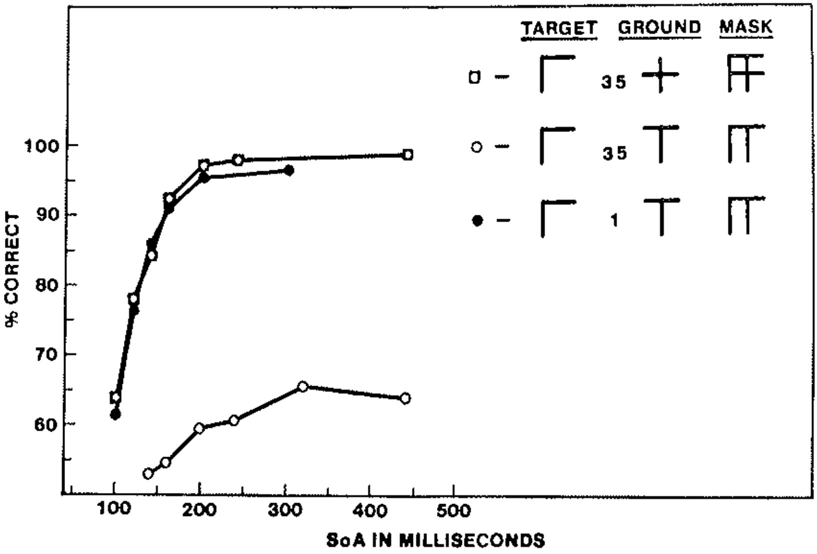

FIG. 12. Target detection as described in text. Abscissa: stimulus onset asynchrony (SOA), ordinate percent of correct response. [From Julesz and Bergen, 1983].

(crossing) performance reached 100% correct responses within 200 msec. This is about as good as if only a single "+" and single "L" had been presented. On the other hand, a "T" target in 35 "L"s, (e.g. no texton difference, since a small gap was exerted in a perpendicular line segment, as in Fig. 1) gave almost chance performance in 200 msec. We varied the number of elements (being all the same or one element being different) and *without* texton difference it required about 50 msec for each added element to scan it step-by-step using focal attention shifts. This shift of focal attention is about four times faster than saccadic eye-movements.

With Bergen we also found an interesting fact about the size of the aperture of focal attention. It has been known for more than a century (Aubert-Foerster law, as referred to by Helmholtz, 1909), that if a pattern is resolved in the periphery, then moving closer or farther away will not affect its resolution. In all our experiments we selected the farthest element in the hexagonal array from the fixation marker to be resolvable. Then we experimented with scaling up or down our test arrays, so the whole array had a diameter from 14 deg arc down to 2.8 deg arc. If the target element and its six surrounding elements had no texton difference, performance (70% correct at 140 msec) remained invariant with zooming, as shown in Fig. 13. Thus, when the entire stimulus array had been confined within the fovea, the aperture of focal attention was also diminished to a tiny fraction of the fovea, extending only a few min of arc. In summary we found that a texton difference can guide focal attention almost instantaneously to this locus. On the other hand, without a texton difference attention wanders aimlessly until by chance the target is found.

The essence of our findings is illustrated in Fig. 14. The left array contains a texture composed of "L"-shaped elements, except for one "+" shaped and one "T" shaped element. The "+" shaped element (target) differs from the many surrounding "L"-s in one texton (crossing) and perceptually stands out immediately. On the other hand, the "T"-shaped target can be detected only after time-consuming search, after the aperture of focal attention happens to fall on the target.

The right array is identical to the left, but illustrates our model of vision. The parallel preattentive system instantly detects the location of texton differences and directs the aperture of focal attention to this location as indicated by the dotted disc around the "+". Since the T contains the same textons as its surround, its detection requires the aperture of attention (symbolized as a cone of a searchlight) to scrutinize the texture elements in sequence. Obviously, this serial search for the T-shaped target depends on the number of texture elements and may take considerable effort and time. However, after the "T" has been found, and the aperture of focal attention surrounds it, both the "+" and "T" targets are seen with the same clarity. Obviously, form recognition, restricted to the aperture of focal attention, does not depend on the way attention has been directed to the targets.

In summary, the reason that texture discrimination is the royal road to preattentive vision is that textures usually cover wide areas of the visual field, while the texture elements are a small portion of the textural area. When the observer is inspecting an extended field, there is an "uncertainty region" in which the relative spatial position of local features is ignored. This is very different from a resolution limit due to visual acuity. In all of the indistinguishable texture pairs, the line segments that make up the texture elements are clearly resolved; nevertheless if these textons fall within this uncertainty region, it is impossible to tell a T from an L. Only by shifting the small aperture of focal attention to the T and L elements can we perform the magnificent feats of form recognition.

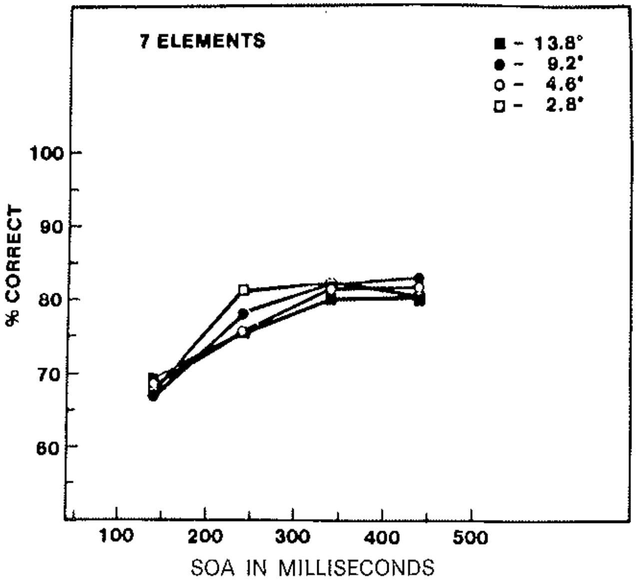

FIG. 13. Finding of size constancy for detecting one T among six Ls (or vice versa) for SOA = 100 msec, indicates that the aperture of focal attention can be a minute portion of the fovea. Diameter of targets around fixation marker varies from 13.8 to 2.8 deg arc. [From Julesz and Bergen, 1983].

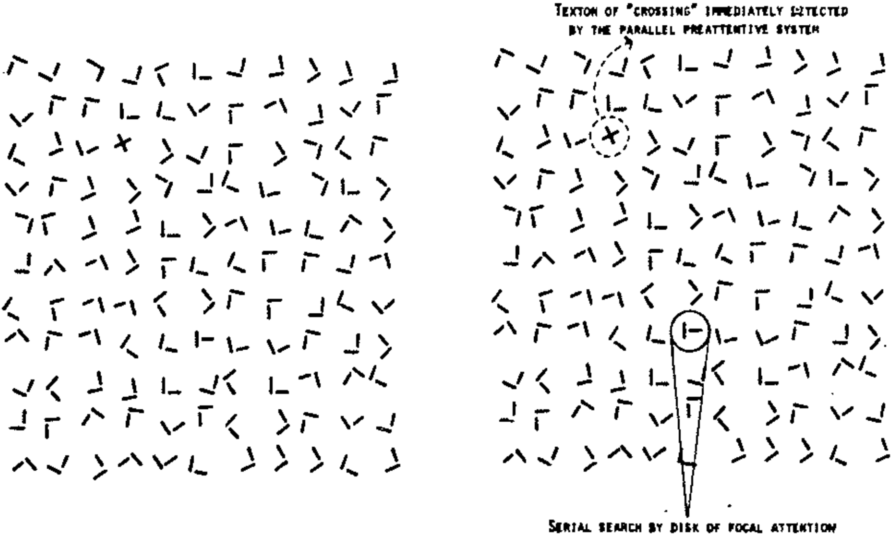

FIG. 14. The preattentive-attentive visual system, as described in text. [From Julesz and Bergen, 1983].

5. *The Texton Theory and Other Two-Visual-System Theories*

The texton theory of preattentive/attentive vision as outlined here should not be confused with the many other "two-visual systems" ideas proposed in recent years. It is certainly very different from the often mentioned foveal versus peripheral dichotomy of vision, since the aperture of focal attention can be a minute portion of the fovea and can be shifted to any position of the retinal afterimage (that persists on the retina as a stabilized image) at four times faster speeds than eye-movements (Julesz and Bergen, 1983). It also differs greatly from the "two-visual systems" of Held, Ingle, Schneider and Trevarthen (1967-68) who introduced this term to distinguish failures in locating versus discriminating patterns when lesions in the striate cortex, superior colliculus, or pulvinar were anatomically present. The ambient/focal dichotomy of Trevarthen (1968) observed in monkeys with split cortical hemisphere but intact subcortical midhrain connections seems also very different from our dichotomy that most likely represents dual processing hy an intact visual cortex.

Even the dichotomy within the cortex between occipito-temporal pathway (for identifying *what* an object is) and occipito-parietal pathway (for locating *where* an object is) as proposed by Mishkin (1972) and Ungerleider and Mishkin (1982), is very different from ours. In their work "landmark" objects localization requires learning and long-term memory, while our preattentive localization of texton differences requires merely short-term (iconic) memory. Also the sustained versus transient dichotomy (attributed to X and Y cells, respectively) of Breitmeyer and Ganz (1976) is very different from our dichotomy (Julesz and Bergen, 1983), since our findings of preattentive vision apply both for briefly presented figures or for sustained texture pairs.

Perhaps our preattentive/attentive dualism is closest to the concepts of Treisman (1978) and Treisman and Gelade (1980), but differs from theirs significantly (as discussed elsewhere, Julesz, 1983). Here I note only that we postulate a priori the textons, while Treisman's "features" are not explicitly defined, hence her theory cannot be falsified. In spite of the difference between Treisman's theory and ours, the fact that her cognitive studies and our perceptual studies found the same parallel/serial dichotomy is most gratifying.

Let me note that our texton theory of preattentive vision also resembles the "primal sketch" model of Marr (1976). However, the two theories greatly differ (as discussed in detail by Julesz, 1983). Here I only note that David Marr assumed that elongated blobs and their terminators would form higher order entities, he called "place tokens", that might be the elements of texture perception and attentive vision. Here I have shown that except for crossings no other place token is used in texture discrimination, since the preattentive system merely counts the textons (of elongated blobs, their terminators and crossings). But more importantly I am not convinced that the basic elements of preattentive vision, the textons, are also the elements of attentive vision! When in the preattentive (preconscious) mode of vision, the visual world fragments into textons and differences in textons or in texton densities are quickly detected. However, when the preattentive system does direct the small aperture of focal attention to these loci of texton changes, there is no compelling reason to assume that in this aperture the same textons are utilized. Indeed, the essence of the aperture of focal attention is that in this small zone the textons are coupled to each other (e.g. a T and L can be told apart), permitting the prodigious feats of form recognition. When our entire visual machinery is concentrating on a small aperture, it can holistically process the entire visual information in this aperture, as a Gestalt. While it could be that characters of the Chinese alphabet or familiar faces are constructed from textons, the positional relations between textons (that are sensed by the attentive system) form countless patterns, rendering the concept of "elements" impractical.

So, it is my contention that the structuralist concept of perceptual elements does exist for preattentive (preconscious) vision, but when we switch to the conscious (attentive) state, then the Gestaltist psychologists' belief might be true. In conscious vision Gestalten are formed that probably cannot be expanded into textons or it is unlikely that some simple interactions between textons will be found. It could be that the elements of form vision will be identified in the future, but I do not believe that these elements would resemble textons and probably might interact with each other in complex ways and from a distance.

6. *Conclusions*

Even if it turns out that textons are only the building blocks of preattentive vision, the knowledge of those conspicuous features that grab our attention wherever they occur is of interest to everyone who wants to understand human vision. Indeed, the texton theory as outlined here can explain the strategic problem of vision: the perception of the world into conscious *figures* and ignoring the rest as unconscious *ground*. According to my view, figures can be perceived only at areas of texton differences in fast changing environments. In steady scenes, of course, one can scrutinize the visual world at length and look attentively at any spot. It is of importance that this scrutinizing does not require scanning eye-movements, but can occur much faster by looking around with the "mind's eye".

This research for perceptual elements and their interactions occurs in the first split seconds of image presentation. It resembles research in modern cosmology where the briefest initial time of the "big bang" is studied for finding a few basic elements and discovering a "unified field theory" that connects these elements. After this brief initial time the elements multiply and their interactions become very complex. This analogy to vision research fits very well. There is increasing evidence (e.g. Zeki, 1978) that the various stimulus features such as color, orientation, movement, depth, etc. are encoded by special areas (modules) in the brain. This finding parallels our psychological observations that the textons in preattentive vision are not coupled to each other, that is, they are independent dimensions. Only after some time, that is required to shift the minute aperture of focal attention to certain loci, do the textons become coupled in this aperture. A strategic problem for brain research is: how can an aperture scan each brain module simultaneously and place in exact registration (without eye-movements) those various stimulus features that the modules contain?

Perhaps the reason why textons, identified by psychological methods, resemble so much the trigger features of cortical neurons is that most of the neurophysiological studies were carried out on animals under anaesthesia, or the animal was not paying attention to the stimulation; these conditions favor the preattentive mental state. But regardless of whetber our perceptual findings have direct relevance to neurophysiology, they suggest that the brain researcher must take into account both the conditions of the stimulation and the mental state of the animal under study. Of course, workers in psychobiology, particularly in dream research, are aware of the importance of the mental alertness of their subjects, and characterize their various mental states by the observed patterns of eye-movements. Here I stress only that conscious mental states of "figure" and unconscious states of "ground" can be shifted around without any accompanying eye-movements. Of course, it could be that eye-movements always follow cortical attention shifts when they are not prevented.

It is also interesting that in the light of the texton theory, we can shift attention to one patch at a time. Perhaps this single, undivided concentration on one thing is the most characteristic manifestation of the enigmatic phenomenon we call consciousness.

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