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COGNITION, CONSCIOUSNESS, AND CULTURE: UNDERSTANDING HUMAN COGNITION AND ITS GROUNDING IN A PRIMATE BRAIN

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One of the key outstanding scientific questions for the 21st century concerns the evolutionary origins of human cognitive competence. How is the human brain architecture organized to support our cognitive abilities? And how did this architecture appear?

The human species is primarily characterized by its remarkable cultural competence – the capacity to acquire, from its peers, a great variety of mental tools that were not anticipated by evolution. This competence rests, in the final analysis, on the plasticity of the developing brain which authorizes the laying-down of novel 'neuro-cultural' circuits. Within the space of a few years, the child's brain acquires new specializations and competences unique to the culture in which it is embedded. Thanks to education, a spoken language, a writing system, and many other motor, mathematical or artistic competences get inscribed in the brain for the rest of one's life.

This emphasis on cultural learning does not, however, imply that the human mind is detached from its evolutionary origins. The standard social science model used to consider the brain as the proverbial 'blank slate', an isotropic learning device that places little constraint on the patterns of human thought. This view is now obsolete. It is giving way to a new paradigm that considers human brain function in an evolutionary perspective. Even in domains such as mathematics, it is possible to identify precursors of human abilities in non-human primate brains. Cultural learning does not emerge entirely *de novo*, but operates by the transformation or *neuronal recycling* of evolutionarily older brain pathways that served a related role in other primates.

In the present chapter, based on recent cognitive neuropsychological evidence, I shall briefly review our current understanding of this interplay between evolution and culture in three areas where the specificity of the human species seems most evident: language development, cultural transmission of reading and mathematics, and consciousness. In each case, we begin to understand how human mental functions arise from a complex anatomical and functional architecture of nested neuronal networks, largely inherited from our primate evolution, yet importantly reorganized to support flexible symbolic manipulations unique to humans.

ORIGINS OF LANGUAGE

Language was rightly seen by Descartes as one of the defining features of the human species. Since Broca's original description of aphasia, numerous studies in neuropsychology and neuroimaging have questioned whether a particular organization of this part of the brain might explain the language faculty in our species, and its special relation to the left hemisphere (for review, see G. Dehaene-Lambertz, Hertz-Pannier, Dubois, & Dehaene, 2008).

In the adult human brain, leftward structural asymmetries are observed, both at the macroscopical and cytoarchitectonic levels, such as a longer sylvian fissure and a larger *planum temporale*. The white matter volume underlying the primary auditory area, Heschl's gyrus, is larger on the left than on the right side. Bigger pyramidal cells are noted in the left auditory cortex, associated with thicker myelinated fibers. It is argued that these structural features might allow the left hemisphere to code the rapid and complex acoustic transitions characterizing speech more accurately than the right. Indeed, the *planum temporale* is less asymmetric in children with specific language or reading impairments relative to the normal population.

Developmental studies indicate that these structural asymmetries are present early on in infancy and may guide language acquisition. During the last trimester of human gestation, sulci appear first on the right hemisphere. The right superior frontal, superior temporal and Heschl's gyri are detectable one or two weeks earlier than their left-sided homologous (Dubois *et al.*, 2008). This asymmetry in sulcation development is not reported in macaque fetuses. At birth, the sylvian fissure is longer on the left side and is associated with a larger left *planum temporale* while the superior temporal sulcus is larger on the right. Twin studies reveal a strong genetic influence in these areas. The volumes of both left *planum temporale* and Heschl's gyrus are similarly larger in hearing and congenitally deaf adults. Contrary to the hypothesis of an equipotential brain at the beginning of life, these observations point to evolutionary genetic changes in the human lineage which favoured a differential development between the left and right hemispheres in a systematic way across humans. Genetic studies have indeed begun to reveal asymmetrical gene expression in the peri-sylvian regions, specific to the human lineage. These genes that either regulate cell signalling or control other genes or protein expression are expressed at an early developmental stage (especially between 12 and 14 weeks of gestation), a critical time for cortical regionalization. LM04, for example, is expressed more on the right side than on the left in humans. For this gene, asymmetry is also present in mice but not biased systematically to the same hemisphere across individuals as in humans.

Functional brain activation also indicates that language acquisition does not initially cause a broad and unspecific pattern of brain activity, but recruits a specific, evolved brain network. My laboratory, under the leadership of Ghislaine Dehaene-Lambertz, has obtained some of the first images of the brain organization for language in 2-to-3 month-old infants (G. Dehaene-Lambertz & Dehaene, 1994; G. Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002; G. Dehaene-Lambertz *et al.*, 2006). Remarkably, a circuit similar to adults is already in place and can be activated by listening to short sentences. It seems to be hierarchically organized and involved a progression from the bilateral auditory areas towards the left posterior temporal lobe, the bilateral superior temporal sulci, the temporal poles, and Broca's area in the left frontal gyrus.

Anatomical precursors of this hierarchical organization are already present in the monkey brain – there is already a hierarchical synaptic organization leading from the primary auditory cortex to both the anterior temporal region and to selected areas of the frontal cortex (Romanski *et al.*, 1999). However, the middle temporal gyrus is considerably more expanded in humans and a massive bundle of temporo-frontal connections, the arcuate fasciculus, has seen a large expansion and lateralization towards the left hemisphere (Rilling *et al.*, 2008). In a nutshell, the human cortical organization for language can be seen as an extension, expansion, and lateralization of temporal-frontal networks that are present in other primates, in ways which are beginning to be explored. Just after birth, the infant's brain is already biased for language acquisition through the presence of lateralized and hierarchically organized circuits. These early biases precede any overt production of language, even in the elementary form of babbling. However, they shape the early processing of language inputs from the child's environment.

ACQUISITION OF A WRITTEN AND MATHEMATICAL CULTURE

Cortical specialization exists not only for language, but also for many other domains of cultural competence of the human species. For instance, recognition of written words is systematically associated with the left ventral occipito-temporal cortex, and mental arithmetic with the bilateral intraparietal sulci (for review, see Dehaene & Cohen, 2007). This reproducibility of the brain's major cognitive circuitry is remarkable, because although there might have been a specific evolution for language, reading and arithmetic are clearly too recent inventions to have exerted any selective impact on the evolution of specific brain circuits.

My proposal is that cultural inventions such as reading invade cortical circuits that initially evolved in a very different context, but are capable of partially 'recycling' for novel uses unique to the human species. Each cultural object must thus find its cortical niche, a neuronal circuit which is already structured but exhibits enough plasticity to be reconverted to a novel use.

Neuro-imaging and neurophysiological findings support the 'cultural recycling' hypothesis by showing precursors of the human adult specialization in infants and even in primate brains. For instance, in 3-month-old infants, the ventral occipito-temporal pathway already activates during visual object recognition, and the dorsal occipito-parietal pathway during the extraction of the numerosity of a set of dots. A similar ventral/dorsal distinction also exists in the macaque monkey, including the presence of inferotemporal neurons responding to an 'alphabet' of elementary visual shapes, and parietal neurons responding to numbers. Human education radically expands these abilities by allowing them to become activated, not only directly (e.g. by seeing a set comprising five objects), but also indirectly through the use of cultural symbols (e.g. by seeing the Arabic digit 5 or hearing the word 'five').

In the past twenty years, a particularly detailed evolutionary argument has been developed for the sense of number – a foundational sense upon which the specifically human development of mathematics largely rests (for review, see Nieder & Dehaene, 2009). The first imaging studies of calculation, using SPECT, PET and fMRI, quickly pointed to a reproducible bilateral activation in the intraparietal suclus of both hemispheres. The advent of single-subject fMRI demonstrated that, although inter-individual variability is somewhat larger than in studies of reading, the banks of the intraparietal sulcus are always consistently activated whenever adults compute simple comparison, addition, subtraction or multiplication with Arabic numerals. The intraparietal region seems to be associated with an abstract, amodal representation of numbers inasmuch as it can be activated by numbers presented as concrete sets of visual or auditory objects and events as well as in various culturally learned symbolic notations such as Arabic numerals and spelled-out or spoken number words. It is active in adults from various countries and cultures including France, UK, USA, Austria, Singapore, China, and Japan.

The parietal activation associated with 'number sense' occupies a fixed location within an overall map of sensory, motor and attentional functions in the parietal lobe, including finger pointing, manual grasping, visual attention orienting, eye movement, written word processing and calculation (Simon *et al.*, 2004; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). This layout in humans bears considerable similarity with the anatomical organization of areas V6a, LIP, PRR and AIP in macaques. Although details of this homology remain debated (Culham, Cavina-Pratesi, & Singhal, 2006; Orban *et al.*, 2006), the human map predicted that, if a precursor of human numerical abilities existed in monkeys, it might lie in the depth of the intraparietal sulcus. Indeed, awake-monkey electrophysiology uncovered number-coding neurons distributed within and near the intraparietal sulcus (Nieder & Miller, 2004; Sawamura, Shima, & Tanji, 2002).

Several parallels between monkeys and humans suggest that the monkey intraparietal neural code for numerosity may be the evolutionary precursor onto which the human invention of arithmetic encroached (Nieder, 2005). First, numerosity-tuned neurons are mostly found in the depth of the intraparietal sulcus and often show visual flow-field responses, compatible with a location in area VIP. Likewise, human fMRI studies have located a plausible homolog of area VIP at a location remarkably close and overlapping with that of number-related responses (see Hubbard, Piazza, Pinel, & Dehaene, 2005). Second, monkey intraparietal neurons are each tuned to a particular numerosity and show Gaussian variability on a log scale, similar to inferences derived from behavioral and fMRI adaptation studies in humans. Third, in some neurons at least, the code is abstract enough to respond to both sequential and simultaneous presentations of number. Fourth, distinct but intermingled populations of neurons code for number and line length, again parallel to inferences drawn from human fMRI.

Developmental evidence from human infants and toddlers suggests that higher-order arithmetical competence builds upon this foundational parietal 'number sense'. Even infants show a sensitivity to numerosity and to concrete addition and subtraction operations performed on sets (for review, see Feigenson, Dehaene, & Spelke, 2004). Number-related parietal activation, particularly in the right hemisphere, is already present in 4-year-old children and even in infants as they attend to the numerosity of sets. Thus, the parietal mechanism of numerosity extraction identified in monkeys seems to be already functional prior to arithmetic education in humans. A recent behavioral study shows that, prior to any explicit instruction, preschoolers possess a spontaneous capacity for approximate symbolic arithmetic whose variability is predictive of subsequent success in the math curriculum (Gilmore, McCarthy, & Spelke, 2007). Furthermore, children who suffer from dyscalculia, a disproportionate impairment in learning arithmetic which cannot be imputed to general intelligence, sensorimotor deficit, or deficient social or educational background, frequently exhibit a parietal hypoactivation and anatomical disorganization. These alterations are often due to genetic, pre- or peri-natal pathologies, suggesting that they may represent plausible causes rather consequences of dyscalculia.

In brief, the origins of human arithmetic abilities rest upon a functional parietal quantity system that is shared with monkey and probably many other species, and that we co-opt for higher-level arithmetic with specifically human symbols. A similar argument has been developed for the case of reading, where our cultural competence capitalizes on pre-existing circuitry for invariant visual recognition of elementary shapes of objects (Dehaene, 2007).

EVOLUTION OF PREFRONTAL CORTEX AND ORIGINS OF CONSCIOUSNESS

Both arithmetic and reading rely on the linking of arbitrary symbol shapes with meanings. Symbolic linkages seem to be unique to humans – as is the ability for metaphor, which implies the *de novo* creation of innovative links between otherwise distinct domains. Symbols and metaphors may reflect a particular capacity of the human brain for flexible thought – the ability to recombine, at will, various elements of thoughts into novel combinations. Various neuroscientists such as Luria, Fuster or Goldman-Rakic have emphasized the behavioral flexibility of the human brain and its link to the huge expansion of the frontal lobes (which occupy close to one third of all gray matter in humans). The frontal lobe can be considered as a major cortical site that contributes primarily to non-automatic, flexible reflection and imagination (Fuster, 1989). Thus, its expansion in the human lineage may betray a particular evolution towards greater rationality and ‘free thought’ detached from external sensory and motor contingencies.

White matter bundles underlying the prefrontal cortex, in particular, seem to have expanded considerably in humans (Schoenemann, Sheehan, & Glotzer, 2005). Guy Elston and his colleagues have described anatomical correlates of this massive increase in connectivity at the dendritic level, where pyramidal cells exhibit a considerably larger number of branches and synaptic contacts in humans than in other species, particularly in prefrontal cortex (Elston, 2003). Jean-Pierre Changeux and I have explored the theoretical proposal that this connectivity increase, although made possible by small genetic changes, led to a major alteration of the cognitive processing style associated with human prefrontal cortex. In our ‘global workspace’ model, prefrontal cortex is seen as a hub for information exchange that already exists in other non-human primates, but has expanded in the human species and serves to break the processing modularity of other cortical regions, thus allowing for information exchanges that would not otherwise be possible by direct point-to-point connections.

We further propose, speculatively, that prefrontal cortex plays a specific role in the evolution of human consciousness. What we subjectively experience as a conscious representation would be a global availability of information, resulting from its entry into this neuronal ‘workspace’ with divergent long-distance axons (Dehaene & Changeux, 2005). According this view, although considerable specialized processing can occur non-consciously, access to consciousness is specifically associated with the entry of information relevant to the goals of the organism into a capacity-limited workspace system that serves to dispatch information to other processors.

While the theory is clearly speculative, a variety of neuroimaging experiments have now begun to pinpoint the neural correlates of conscious experience (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Koch, 2004). Such an empirical research program has become possible thanks to the design of simple experimental paradigms in which identical or very similar stimuli do or do not lead to conscious perception, thus opening a window into the minimal differences that separate conscious and non-conscious brain states. Whenever information accesses consciousness, neuroimaging experiments reveal the sudden ignition of a distributed parieto-prefrontal system and the simultaneous top-down amplification of relevant posterior networks. Long-distance causality relations and phase-coherent oscillations are temporarily established across the relevant cortical areas, thus creating a transient metastable brain-scale assembly. This capacity to transiently link otherwise distant areas may have been a key ingredient in the emergence of human cognitive flexibility and symbolic competence.

A recent line of research has examined the 'resting state', 'default mode', or 'baseline' activity of the awake human brain at rest. This research has evidenced a broadly distributed network of areas active during rest, including dorsal and ventral medial prefrontal, lateral parietotemporal, and posterior cingulate cortices (Mason *et al.*, 2007; Raichle *et al.*, 2001). This network is not static and strictly confined, but constantly fluctuates in synchrony with changes in EEG spectral content. Furthermore, prefrontal, parietal, and cingulate areas show the greatest drop in metabolism during various types of transitions away from the awake state, whether during anesthesia, sleep, coma, or the vegetative state (Boveroux *et al.*, 2008).

In summary, long-distance neural networks linking associate brain areas with prefrontal cortex exist in all primates but have seen a particular expansion in the human brain. Their state of activation appears to systematically vary whenever the state or the contents of consciousness is altered, both as the result of stimulus changes in normal subjects, or as the result of brain insults and pathologies in non-communicating patients. The exact nature and reliability of this correlation between conscious states and distributed brain states remains a matter of some debate (Boly *et al.*, 2008). If reliable neural correlates of consciousness could be found, leading to a theory of its origins, it would not only provide a remarkable intellectual advance for our understanding of the relation between mind and brain, but also offer important hopes for the diagnosis, classification and potential treatment of pathological conscious states such as coma, vegetative state, minimally conscious state, and locked-in syndrome (Bekinstein *et al.*, 2009; Owen *et al.*, 2006; Schiff *et al.*, 2008; Voss *et al.*, 2006).

Conclusion

At first sight, human cognitive abilities appear radically different from those of other animals and may even suggest a unique status of the *Homo sapiens* species. However, the main conclusion of this rapid review of the origins of human cognitive abilities is that, although they are uniquely expanded, upon closer scrutiny none of them is devoid of evolutionary roots. The architecture of the human brain is that of a primate with additional evolutions regarding brain size, differential expansion of prefrontal cortex and other associative areas, long-distance connectivity, lateralization, and emergence of specialized regions such as language areas (as well as areas specialized in the representation of congeners, the 'social brain', which could not be reviewed here for lack of space). The uniqueness of humans does not seem to originate from a radically novel brain design – but rather, from the capacity to re-utilize or recycle its existing brain architecture for novel cultural uses such as reading or arithmetic. By granting the human brain a capacity for cultural invention and transmission, our biological evolution allowed for a massive change in the speed with which our mental life evolved, now based primarily on cultural rather than biological transmission.

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