

COMPLEXITY AS SUBSTRATE FOR NEURONAL COMPUTATIONS

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Abstract

Recent discoveries on the organization of the cortical connectome together with novel data on the dynamics of neuronal interactions require an extension of classical concepts on information processing in the cerebral cortex. These new insights justify considering the brain as a complex, self-organized system with non-linear dynamics in which principles of distributed, parallel processing coexist with serial operations within highly interconnected networks. The observed dynamics suggest that cortical networks are capable of providing an extremely high dimensional state space in which a large amount of evolutionary and ontogenetically acquired information can coexist and be accessible to rapid parallel search.

The question that I would like to address is, whether evolutionary increases in the complexity of the cerebral cortex led to the implementation of unconventional computational strategies that have not yet been investigated much in the brain nor implemented in technical systems.

The evolutionary increase in the brain's complexity has led to the emergence of ever more efficient cognitive and executive functions. While neurobiological investigations have been very successful in elucidating the neuronal mechanisms underlying the behaviour of simple organisms such as molluscs, worms and insects, the search for mechanistic explanations of higher cognitive and executive functions, in particular of the human brain, remains a major challenge.

One conundrum is related to the evidence that memories can be accessed nearly equally fast, within fractions of a second sometimes, irrespective of whether they are recent or whether they are from early childhood. This implies that the huge number of memories that have been acquired over a lifetime must be stored in a way that permits equal and fast access. Thus, a space

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must be configured in which all these memories can be superimposed and accessed in parallel. A serial search process as it is realized in digital computer memories is not conceivable because neuronal processes are orders of magnitude slower than electronic computations. Serial search strategies in neuronal systems would consequently be orders of magnitude too slow.

A related conundrum is the fast readout of priors that need to be called upon for the interpretation of sensory signals. There is consensus that perceptions are the result of a reconstructive process. The sparse signals provided by the sense organs can only be disambiguated and interpreted because they are compared with models of the world that are stored in the functional architecture of the brain. This architecture is specified by essentially three processes: Evolutionary selection, epigenetic modification by experience dependent developmental processes, and normal learning. All three processes store knowledge about the features of the embedding world, so called priors, in the brain and this knowledge is subsequently used for the construction of our perceptions. Primates change the direction of their gaze on average four times in a second. This implies that new information needs to be matched with the corresponding priors approximately every 250 ms, the time it takes to interpret a visual scene. How the nervous system is able to retrieve the relevant priors from the immense reservoir of priors within such short intervals is enigmatic. Again, a very large space needs to be configured in order to store these priors and a search mechanism has to be implemented that is capable of retrieving any of these priors with equal probability.

Our ability to explore the huge database of stored knowledge in a surprisingly short time is also revealed by the fact that we immediately know if something is known or unknown to us.

Classical theories on information processing in neuronal networks fall short of explaining how the immense amount of memories and priors can be stored without fusing and retrieved with remarkable speed and accuracy. Here I shall propose a computational strategy that has so far not received much attention by neuroscientists, which goes back to recent theoretical work in the field of non linear dynamics and capitalizes on the extremely rich dynamics of recurrently coupled complex networks. The idea is that such networks are capable of providing a very high dimensional state space that allows the superimposition of an equally large number of dynamic patterns that can be kept separate because of the high dimensionality of the available space.

Options to create high dimensional coding space

Artificial neuronal networks of the Hopfield type are in principle capable of simultaneously representing different objects, i.e. constructs defined by spe-

cific constellations of features and the relations among those features. However, such systems cannot cope easily with the representation of large numbers of superimposed relational constructs, in particular if temporal relations also need to be stored. One reason is their restricted temporal dynamics that limits the dimensionality of states (Hopfield & Tank 1991; Rumelhart & McClelland 1986). Another, more recently developed class of models capable of dealing with relational constructs and providing high dimensional spaces for coding is derived from concepts of reservoir computing, also addressed as echo-state or liquid computing. These networks consist of self-active non-linear units with random recurrent coupling that maintain their own dynamics and are engaged in active processing (Buesing *et al.* 2011; Buonomano & Maass 2009; Jaeger 2001; Maass *et al.* 2002; Lukoševičius & Jaeger 2009).

In this computational framework, the reservoir consists of a network of self-active, randomly coupled neurons (nodes). If a specific input constellation is driving a subset of these nodes, a complex, transient, high dimensional and stimulus specific activity pattern emerges in this recurrently coupled network, the “liquid”, and is then further propagated by waves of recurrent interactions among neurons. Such reverberation provides the “liquid” with a fading memory of recent inputs that allows it to integrate input sequences (e.g. several frames of visual input) while keeping track of sequence order. The readout of the relational code is achieved with conventional machine learning strategies for the classification of high dimensional vectors of activity. This readout function can again be implemented by neuron-like elements, that sample activity from the nodes in the “liquid” and adjust the coupling strength of the sampling lines through supervised learning until they become optimally activated by a particular state of the “liquid” (Nikolic *et al.* 2009). However, the readout stage could also consist of cell assemblies that are in turn ignited by specific states of the “liquid” after appropriate adjustment of the synaptic weights of the connections between the liquid and the readout stage. This strategy increases the robustness of decoding and at the same time generates low dimensional readout patterns that can directly be used to control effectors, e.g. orchestrate the population vector for a composite movement. The principle of this computing strategy is simple and powerful: a low dimensional input configuration is transformed into a high dimensional dynamic representation. In this high dimensional state space stimulus evoked vectors remain compact, cluster in well segregated subspaces and can be more easily discriminated based on their spatiotemporal signatures. The segregation of clusters can be improved further, if the network is endowed with Hebbian synapses and given the opportunity to “learn” in an unsupervised fashion about the features of the

stimulus sample by repeated presentation of the stimuli (Lazar *et al.* 2009). As a matter of principle the performance of the liquid increases with the dimensionality of the space it is able to explore. Thus, if the nodes are configured as oscillators (e.g. relaxation oscillators or damped harmonic oscillators), phase comes into play in addition, which allows for a further expansion of the dimensionality of the “liquid” (see also Wang *et al.* 2011). Because of their high dimensionality, such “liquids” are in principle capable of storing and superimposing very large numbers of “memories” and learned associations that can be accessed and readout nearly instantaneously. The astounding ability of our brains to solve with such ease problems that are still computationally intractable, such as e.g. the fast processing of complex scenes, suggests that the brain might indeed capitalize on computational algorithms which permit parallel storage and fast readout of complex relational constructs.

Analysis of the anatomy and the dynamics of the cerebral cortex suggests indeed that some of the above mentioned strategies might be implemented (for review see Deco & Jirsa 2012).

Developmental studies indicate that the statistics of feature conjunctions in the outer world get translated into the strength of coupling between cells tuned to the respective features. Early evidence for such internalization of contingencies has been obtained in kittens, which had exclusive experience with vertically oriented, unidirectionally moving gratings that had a constant stripe separation of 10 degrees visual angle (Singer & Trepper 1976). As expected, this selective rearing biased the numerical distribution of orientation and direction selective neurons towards the experienced stimulus (see also Blakemore & Cooper 1970). However, most importantly, a substantial fraction (~30%) of the neurons in supragranular layers of area 17 developed multiple, well-segregated receptive fields whose spacing frequently corresponded to the spacing of the experienced stripes. Because intercolumnar connections are shaped by experience according to a Hebbian mechanism (Löwel & Singer 1992) the ectopic receptive fields are most likely due to selective strengthening of intrinsic cortical connections linking those columns that were activated synchronously by the grating. In conclusion the weight distributions of the connections among cortical neurons likely reflect not only evolutionary adaptation to regularities but also the immensely complex statistics of the feature relations experienced throughout life (Heisz *et al.* 2012). Somehow, these countless, content-specific weight distributions must coexist in a very high dimensional space so as to remain flexibly addressable as contextual priors (Rabinovich *et al.* 2001; 2008). As discussed in the following paragraph, the dynamics emerging from cortical networks are indeed high

dimensional, allowing for the coexistence of a large number of potentially realizable states (Schittler, Neves & Timme 2012).

The fingerprints of high dimensional dynamics

The dynamics of complex systems can vary between two extremes. All elements of the system could be active independently and exhibit stochastic activity (high dimensionality) or, alternatively, all elements could be synchronized (low dimensionality). Both extreme states have low computational potential. However, under normal conditions the cerebral cortex operates in an intermediate regime where the emergent dynamics are complex and computational power is high (see below). Interestingly, this is also true for the architecture of the anatomical connections. The connectivity graph constitutes a compromise between randomness and regularity where complexity and dimensionality are high (Sporns & Tononi 2002; Tononi *et al.* 1998).

Analysis of the resting state dynamics of cortical networks suggests that they operate close to a self-organized critical (SOC) state (Deco & Jirsa 2012; Linkenkaer-Hansen *et al.* 2001; Plenz & Thiagarajan 2007; Priesemann *et al.* 2013; Wang *et al.* 2011). The SOC state provides favourable conditions for computations: Its memory capacity is maximal (Bertschinger & Natschläger 2004), the information transfer is most reliable (Shew *et al.* 2009; 2011), it can optimally separate between different inputs (Bertschinger & Natschläger 2004), and it shows the largest dynamical range (Shew *et al.* 2009; Kinouchi & Copelli 2006).

Predictions

If mechanisms posited by the hypothesis formulated above are exploited by the cortex, one can make the following predictions: i) Internal models of the world are stored in the architecture and weights of neuronal connections. ii) The highly complex dynamics that evolve on the backbone of this architecture provide the high dimensional space for the accommodation of an immense repertoire of potential states (memories, priors). iii) The complex spatio-temporal patterns of cortical activity reflect the superposition and coexistence of latent prior distributions, both inborn and acquired. iv) In response to input signals the initially unconstrained, high dimensional internal network dynamics (the internal model) rapidly assume metastable subregions of the state-space. v) These selected substates are distinguished by enhanced coherence (synchrony, covariance) of neuronal responses and constitute the solution of the search process. Hence the transition of the system towards a stabilized substate should be associated with a reduction in dimensionality. vi) The increased coherence of selected substates should

promote their long term stabilization by Hebbian modifications of recurrent connections and this, in turn, should facilitate retrieval of familiar substates in future matching operations and their recruitment by down stream processes. vii) Robustly consolidated substates should be manifest in resting state activity and be detectable as replayed vectors or manifolds. viii) Simple stimuli drive the network in one of its normal modes and thus into states with low dimensional correlation structure while complex stimuli (natural scenes) evoke numerous normal modes simultaneously that superimpose and lead to high dimensional states. ix) Cortical networks should operate in a dynamic range close to Self Organized Criticality (SOC) because the intermediate level of existing correlations and the long correlation distance in SOC states facilitate the rapid relaxation of a dissipative system into coherent substates.

As reviewed recently (Singer 2013), some of these predictions are supported by data. Developmental studies indicate that the statistics of feature conjunctions in the outer world are translated into cortical connectivity according to a Hebbian mechanism (for review, Singer 1995). The anisotropy of this connectivity is reflected by the correlation structure of resting activity (Fries *et al.* 2001a), and the latter can be modified by learning (Lewis *et al.* 2009). Ample evidence is also available for the propensity of cortical circuits to engage in oscillatory activity in a wide range of frequencies and for stimulus dependent changes of correlation structure mediated by intracortical connections. Both features are hallmarks of recurrently coupled networks (for reviews see Singer 1999; Buzsáki *et al.* 2013). The fact that both sensory stimulation (Gray *et al.* 1989; Churchland *et al.* 2010) and top down signals related to attention (Fries *et al.* 2001b; Lima *et al.* 2011) enhance synchronized oscillatory activity in distinct frequency bands is compatible with processes of dimensionality reduction. There are also indications that cortex operates in a SOC state (Linkenkaer-Hansen *et al.* 2001; Plenz & Thiagarajan 2007; Wang *et al.* 2011). Finally, in a recent electrophysiological study (Nikolic *et al.* 2009) in the visual cortex of anesthetized cats we were able to demonstrate features characteristic of reservoir computing. We found that i) stimulus identity can be determined by a linear classifier fed with the responses of 60 randomly selected simultaneously recorded neurons, suggesting that information about stimuli is distributed, ii) stimulus-specific information persists up to a second, which supports the existence of fading memory, and iii) information about the nature and sequence of stimuli is retrievable for at least two successively presented stimuli, suggesting superposition of representations. Most importantly, in these pilot experiments we have obtained indications (unpublished) for unsupervised

learning and replay of stimulus specific vectors in spontaneous activity. Classification improved for frequently presented stimuli because their response vectors became increasingly different and these vectors occurred spontaneously in resting states. Thus, in contrast to liquid state machines, where plasticity is neglected, real neuronal networks exhibit experience dependent long term modifications of their state.

Conclusions

In conclusion, I believe that theoretical arguments and available experimental results now provide sufficient ground to support the hypothesis that neocortex exploits the fantastic computational capabilities offered by complex systems with high dimensional, non linear dynamics in order to i) superimpose information about relational constructs and sequences, ii) perform computations for matching, pattern completion and invariance extraction, and iii) obtain fast results by relaxation into metastable substates of lower dimension, thereby simplifying classification and enhancing stability.

Thus, it appears as if nature had found a way to realize extremely powerful computational strategies by increasing the complexity of neuronal dynamics. The anatomical substrate for this increase in complexity is the cerebral cortex, the most recent invention of evolution. The prevailing principle appears to be dense reciprocal coupling among large numbers of nodes, whereby the nodes already possess highly diverse and non-linear dynamic properties and the connections differ in conduction time and coupling strength. These features generate a maximum of diversity and because of the high degree of non-linearity of the emerging dynamics, such networks provide an extremely high dimensional space for the storage and processing of information.

As is evident from comparisons with artificial intelligent systems, the computational abilities and the energy efficiency of cortical computations exceed by far those of man made systems. If the hypotheses formulated above should turn out to be correct, this is bound to have a strong impact on both neuroscience and artificial intelligence. In neurosciences, it will encourage the incipient paradigm shift from behaviourist stimulus-response concepts towards notions of predictive coding in self-organizing recurrent networks with high dimensional dynamics. It will also provide a new framework for the interpretation of pathological cognitive and executive functions and their experimental analysis, as there is first evidence that diseases such as schizophrenia and autism are associated with abnormal brain dynamics (Uhlhaas & Singer 2012). In the computational sciences it will further encourage and perhaps even instruct the already intense search for novel, biomorphic or

brain inspired computer architectures. Finally, at the epistemic level, it would provide a first hint that evolution, by exploiting complex dynamics, has found a way to realize in a classical system functional aspects like fast parallel search and computation that so far were thought to be realizable only with quantum computers. The analogy with processes known to exist in the quantum world such as the coexistence of a large number of potentialities by the superposition of wave functions and the fast realization of one of these potentialities by the collapse of the wave function is fascinating. As quantum processes cannot play a role at the macroscopic scale at which neuronal network computations occur, this similarity suggests that increases of complexity of classical systems can lead to the emergence of qualities that bear a certain resemblance with features of the quantum world. Thus, the boundaries between the quantum world and the macroscopic world may turn out to be not as sharp as generally assumed.

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