Brain Dynamics across levels of Organization.

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Abstract

After presenting evidence that the electrical activity recorded from the brain surface can reflect metastable state transitions of neuronal configurations at the mesoscopic level, I will suggest that their patterns may correspond to the distinctive spatio-temporal activity in the Dynamic Core (DC) and the Global Neuronal Workspace (GNW), respectively, in the models of the Edelman group on the one hand, and of Dehaene-Changeux, on the other. In both cases, the recursively reentrant activity flow in intra-cortical and cortical-subcortical neuron loops plays an essential and distinct role. Reasons will be given for viewing the temporal characteristics of this activity flow as signature of Self-Organized Criticality (SOC), notably in reference to the dynamics of neuronal avalanches. This point of view enables the use of statistical Physics approaches for exploring phase transitions, scaling and universality properties of DC and GNW, with relevance to the macroscopic electrical activity in EEG and EMG.

Keywords: Metastability, Self-Organized Criticality, phase Transitions, Dynamic Core Hypothesis, Global Workspace, Non-Linear Dynamics, Operational Architectonics, Microstates.

1. Introduction

Neuroscience is being practiced in many different forms and at many different organizational levels. Which of these levels and associated conceptual frameworks is most informative and commensurate to the intrinsic style of brain function is an empirical question and subject to pragmatic validation. It has become customary to speak of Macro-, Meso- and Micro- levels, each defined by the respective method of data acquisition, ranging from brain surface recordings of EEG and EMG, to activity in neuronal assemblies of an extent in the order of magnitude of 1 cm in space, and 100 msec in time, to single neuron activity. In this essay, the emphasis is on the dynamical interdependencies between scales and levels of analysis. This is predicated in the view that dynamics at any scale will affect and constrain the activity across scales and levels of observation, in the spirit of ‘Constrained Multiscale Systems’ of Breakspear and Stam (2005). The investigations which will be discussed in the following have generated several dynamical hypotheses of brain processes which form a kind of “family resemblance”, though also differing in some important aspects and –where applicable- in their respective computational models (for a survey, see Werner, 2006) For clarity of exposition, I will at first trace the various kinds of observations and conceptual reference points at the different levels separately in order to, subsequently, situate their interrelations at the intersection of Nonlinear Dynamics and statistical

Physics. Some aspects of related issues have recently be discussed by Le van Quyen (2003), Chialvo (2006) and Cosmelli at al. (2006).

2. Data and Models

2.1 The macroscopic scale

As standard bearer of this scale, the Electroencephalogram has proven to be a seemingly inexhaustible source of data interpretations. Like the oracle of Delphi, it answers in many voices to the questions it is asked by diverse methods of analysis and data interpretation. However, scale-free dynamics (Freeman, 2005) and phase transitions (Freeman and Holmes, 2005) situate cortical electrical activity as this level in the domain of non-linear dynamics, as do numerous other observations (Freeman, 2000, 2003; Nunez, 1995, 2000; Basar, 2004). Linkenkaer-Hansen (2001) unequivocally established that the amplitude fluctuations in the 10-20 Hz frequency range obey power law scaling behavior in humans. Quantitative fMRI analysis of functional connectivity (Eguiluz et al, 2005, Chialvo, 2004) and EEG analysis of functional connectivity (Fingelkurts & Fingelkurts, 2004) supply additional signatures of brain-style non-linear dynamics.

Different methods of data analysis revealed characteristic discontinuities in the EEG record which, in the view of Fingelkurts and Fingelkurts (2006), are alternative levels of description, complementary to continuous data records. In a series of studies, these authors identified rapid transitions occurring in the amplitude of continuous EEG activity which mark the boundaries between quasi-stationary segments of activity (Fingelkurts and Fingelkurts, 2001, 2004, 2005; Kaplan et al, 1997). It is assumed that each homogenous segment within a particular EEG frequency band corresponds to a temporary stable microstate in the brain's activity, i.e. an 'operation' in the terminology of these authors. The transition from one segment to another is thought to reflect the moment of switching from one neuronal network to another. Moreover, the synchronization of these segments between different EEG channels would indicate the synchronization of spatially separate brain operations: this is the 'operational synchrony' phenomenon of Fingelkurst & Fingelkurts, 2001). This process results in transient metastable states of EEG activity which is sustained by a form of 'operational modules', encompassing a range of distributed cortical areas.

Extensive studies by Lehmann and associates (1984, 1993, 1998, 2006) likewise revealed a segmentation of global brain activity into discrete temporal units: such 'microstates' of discontinuous brain electrical activity occur as chunks of up to 150 msec duration (Koenig at el., 2002), and are detectable as quasi-stable fields, recorded at the scalp of conscious, inattentive subjects (Michel et al., 1999, 2001). During such episodes, the recorded electric field (pictorially conceived as landscape) remains stable, but is punctuated by abrupt changes to new configurations. Lehmann and associates conceive of these stable episodes as "atoms of thought" (Koukou and Lehman, 1987), i.e. particular steps in mental information processing, perhaps comparable to the "mental objects" postulated by Changeux 1983).

Conjectures and implications regarding the dynamics of discontinuous electric activity episodes in the scalp EEG will be developed in Section 3, following the description in the next section of relevant aspects of activity patterns in neural models which emulate perceptual-cognitive functions.

2.2 Models of perceptual-cognitive brain functions

2.2.1 The Dynamic Core Hypothesis (DCH)

Plasticity of synapses and neuron connections afford a causal link between the functional organization of neuron assemblies and the world, adaptive to use and disuse. The Theory of Neuronal Group Selection (TNGS) is an application of this principle (Changeux, 1983; Edelman, 1987,1989, 1993; Tononi & Edelman, 2001]. A primary repertoire of anatomical connections established during development responds to experiential exposure to the environment with differential amplification of synaptic populations. The second central notion is reentrant mapping: this is a dynamic process that is inherently parallel and distributed. It consists of ongoing signaling between separate neuronal groups in a reciprocal and recursive fashion over cortico-cortical, cortico-thalamic and thalamo-cortical radiations. Neuronal group selection and reentrant mapping, together, are considered the prerequisite for establishing new and sustaining existing statistical signal correlations between groups of neurons. Neuronal groups thereby come to reflect spatiotemporal properties of signals arising in the environment, and serviceable for perceptual categorization.

Generalization of this principle to cross-modal perceptual categorization is accomplished by dynamic structures that encompass multiple reentrant local maps (sensory and motor) and interaction with basal ganglia, brain stem and cerebellum; the latter for perception-action coupling. Within such global mappings, long-term changes in synaptic strength favor the formation of neuron groups with correlated activity as basis for memory. Memory in global mappings is procedural, and requires dynamical re-assembly by rehearsal. Note that each re-assembly of a global memory may be constituted by different neuron populations: a consequence of the degeneracy (redundancy) of neuronal groups.

Reentry is instrumental for generating oscillations in the simulated models: Sporns et al. (1991) and Tononi et al. (1992)] established in their respective models the linking of stimulus features by reentrant circuitry, within and between segregated cortical areas. It depends in these studies on the occurrence of rapid changes in efficacy of reentrant connections, and is an aspect of segregation and integration of elementary features into objects and background through temporal correlation and phase relationships among neuronal groups. In a very large computer model of spiking neurons, synchronous oscillations emerged spontaneously, even though the networks was not designed to produce any form of specific dynamics (Lumer et al. 1997)

Conscious experience is in this theory associated with global properties of large but distinct sets of distributed neuronal groups: the Dynamic Core (DC). It consist of distributed clusters of neurons that are intensely interacting with each other (i.e.: integrated) and, at the same time, are quite distinct and differentiated from the rest of the system. Functional segregation is epitomized by stimulus feature detectors in cortical receiving areas; functional integration is expressed in temporal correlations and synchrony in the large-scale, reciprocally interconnected cortical network and thalamic regions. On activation, the neuron clusters of DC achieve high integration within hundreds of msec through reentrant interactions in the thalamo-cortical system. DC must be viewed as a process, creating transiently the clusters of neurons which reflect rapidly shifting long-range functional connectivity among distributed neuron groups, not constrained by anatomical proximity. Suggestion concerning the inter-level dynamics of the distinct spatial and temporal properties of the Dynamic Core will be the topic of Section 2.2.3, following the review of comparable features of the GNW.

2.2.2 The Global Neuronal Workspace Model

The Global Neuronal Workspace hypothesis was described in detail by Changeux & Dehaene (1989) and Deahaene & Naccache (2001), and most recently summarized by Dehaene & Changeux (2004). The hypothesis postulates two computational spaces of distinct patterns of connectivity: 1) a collection of subcortical, automatic processors, each specialized for a particular signal input which is provided via encapsulated local and medium-length connections; and 2) a global neuronal workspace with the capacity for wide-spread, long-range connections for reentrant signal flow between it and the specialized processors. The workspace is a dynamic concept: workspace neurons are not sharply delineated anatomically, but distributed among distant association areas (Dehaene & Changeux, 1997, 2005; Deahaene et al. 1998). The decisive event is the activation of GNW (see Section 3.3). Between episodes of activation, the neurons of GNW are in a state of permanent spontaneous activity, comparable to the intrinsic activity in awake human brains at rest (Reichle, 2006). In the model, this activity is sustained by ascending neuromodulatory input. When of sufficient intensity, the network will display gamma oscillations of thalamo-cortical origin and possibly sudden surges of activation which may be identified with 'vigilance' (Llinas et al, 1998) : they enhance the activation of GNW by sensory stimuli. Activation of GNW also occurs with intense sensory stimulation in the absence of facilitation. The GNW hypothesis postulates that global activation of a GNW is associated with reportability of a subjective experience (Deahaene & Changeux, 2004).

The basic design of GNW was implemented in several Neural Network models, with McCulloch Pitts as computational elements, and proved satisfactory for emulating aspects of human performance in a variety of (effortful) psychological-behavioral tasks (Deahaene et al. 1987,1998). To convey the operational flavor of the theory, I will describe here briefly the most recent model by Dehaene et al. (2003) of a network of single compartment model neurons with explicitly specified ionic conductances and synaptic currents for simulating features of the cortical inter- and intra-columnar connectivity and as cortico-cortical projections. The target of the model was a modified attentional blink paradigm for which conditions for reportability of presence or absence of stimuli were determined in human trials: subjects saw serial visual presentation of distractors, interspersed with two targets T1 and T2; the task was to rate T2 visibility and then to report T1 identity. Typically, reportability of T2 drops at for several hundred msec after T1 presentation. The adequacy of this model compared favourable with human performance in the same task situation.

For the simulation of the human task, the model was placed in a regime of spontaneous thalamo-cortical oscillations. The attentional blink test was simulated by stimulating two groups of thalamic neurons, one coding for T1, the other for T2. The index of model performance was the degree and extent of activity across the cortico-thalamic hierarchy. As to be expected, network activation evoked by T1 stimulation set a long-lasting dynamic brain-state in motion. But the activation elicited by T2 stimulation dependent tightly on its timing: T1 elicited activity prevented T2 activation from propagating to higher cortical levels and abolished part of the top-down amplification in reentrant circuitry, with the global network seemingly acting as a bottleneck (Sigman and Deahaene, 2005). Selective lesions of the long distance connections in the model corrupt the model performance.

2.2.3 Dynamics in Dynamic Core and the Global Neuronal Workspace.

The focus of this section is the nature of the reentrant activity for the transient formation of the neural functional complex described as "Reentrant Dynamic Core" (DC) on the one hand, and "Global Neural Workspace" (GNW) on the other. Although differing in many respects, both models attribute an essential role to the reentrant neuronal activity in circuits connecting cortical with other cortical as well as thalamic regions, and with peripheral processors. Dehaene et al (1998) speak of " distributed neurons with long distance connectivity that provide a 'global workspace' that can potentially interconnect multiple distributed and specialized brain areas in a coordinated though variable manner", and Dehaene & Changeux (2003) characterize it as "self-amplifying recurrent activity". Edelman (2003) speaks of "dynamic reentrant interactions across cortical circuits .. that allow synchronous linking and binding to take place among widely distributed brain areas", and considers reentry "a unique feature of higher brains" (Tononi & Edelman, 2000). Both groups of investigators emphasize the importance of this pattern of connectivity for generation of oscillatory activity.

From their respective publications (see Section 2.2.1 and 2.2.2), it appears that DC and GNW have a somewhat similar temporal pattern of evolving over a few hundred msec, and persisting for several hundred msec, prior to dissolving. Dehaene & Changeux (2004, 2005) who are more explicit about this than the investigators of the Edelman group describe this temporal course as sudden onset of coherent synchronized neuron activity in multiple distant cortical areas and peripheral processors, which is sustained for several hundred msec by reentrant thalamocortical signal flow. They refer to 'phase transition in a metastable dynamic" and use also the apt expression of "ignition" to convey the abruptness of the transition. To assist with gaining an intuitive grasp of the complex dynamics attributed to their Dynamic Core, Tononi & Edelman (2000) offer a helpful model: envision a large cluster of tense springs, variously connected to each other and surrounded by another set springs, loosely coupled to the former cluster; it is then easy to see that even a small perturbation will spread rapidly and effectively throughout a system of this kind.

The suggestion of Dehaene & Changeux to view the natural history of the formation and dissolution of the neural complex that arises transiently in their neuronal models invites an exploration of its dynamic origin. Taking into account that this activity (and the presumed counterpart in the models of the Edelman group) occurs in nonlinear systems far from equilibrium directs attention to the principle of Self-organized Criticality (SOC) of which abrupt avalanche-like transitions are one of its signatures.

As is well known, Bak et al (1987/1988) introduced a theory of SOC to designate the property of systems to exhibit non-equilibrium phase transitions on account of their intrinsic dynamics, without requiring tuning of control parameters by external influences. This was thought to be the distinguishing criterion from the conventional phase transitions in equilibrium systems which require external tuning of control parameters to attain critical state. Systems of this former kind evolve spontaneously to a critical state at which their responses to perturbations display a set of characteristic properties: temporal and spatial scale invariance (i.e. absence of a characteristic scale of length and time, associated with fractals and 1/f noise), drastic reduction of the number of degrees of freedom, and divergence of correlation function as signal for lack of characteristic length. 'Scaling behavior' refers to determining whether the temporal (or spatial) pattern of an observable remains identical under scale transformation; 'scale-free' then signifies the absence of any characteristic scale. Processes based on SOC are characterized by a power law relation between frequency bands and their respective frequency in the record, usually represented as 1/f relation. This is generally taken as a signature of SOC. (Bak, 1996; for an extensive review on scale invariance in Biology: Gisiger, 2001). SOC reflects the process of propagation of long-range interactions based on local effects in the medium (as a kind of domino effect) until the state of criticality is attained at which any further disturbance triggers an abrupt, critical phase transitions (Flyvbjerg, 1996). This sequence of events is sustained by two concurrent processes with different time constants: a faster disturbance of the dynamic stationary state, and a slower relaxation towards its restoration, often referred to as avalanche (a metaphor based on the sand pile of the original model of SOC). The critical state is then maintained until replaced by circumstances that lead to initiation of another process of the same kind.

With the foregoing criteria for self-organized criticality in mind, it is now possible to examine whether measurements of brain activity and structure comply with the stipulations of the theory. Linkenkaer-Hansen (2001) unequivocally established that the amplitude fluctuations in the 10-20 Hz frequency range obey power law scaling behavior in humans. Scale-free neocortical dynamics was also ascertained by Freeman (2005) in the electroencephalogram of rabbits; a computer model also suggested that neodortex is stabilized in a scale free state of self-organized criticality. Quantitative fMRI analysis of functional connectivity (Eguiluz et al, 2005, Chialvo, 2004) and EEG analysis of functional connectivity (Fingelkurts & Fingelkurts, 2006) supply additional evidence. Sporns et al (2004) reviewed recently the numerous literature sources which identify brain neural networks as 'scale free'. The most direct evidence is provided by the work of , Beggs & Plenz (2003, 2004) reported critical behavior in slices of cortical tissue, in the form of "avalanches" of neuronal discharges. This type of activity was subsequently also ascertained in intact cortical tissue of primates, and supports the contention that neuronal avalanches are an organizing principle of cell assemblies in cortical tissue (Plenz & Thiagarajan , 2006; for a discussion, see Vogels et al., 2005). The "avalanches" observed by these investigators meet the criteria for Self-organized Criticality which signifies their scale invariance: thus, the extent of neuron assemblies encompasses spatial dimension at any scale, including very large-range connections, potentially covering major expanses of cortical tissue. Taken together, the evidence suggests that the brain as a whole may be viewed as being in a state of self-organized criticality and, thus, amenable to being studied in terms of principles of statistical Physics (Chialvo, 2006).

In the nearly 20 years since introduction of SOC, critical examination of the claims of Bak et al for universality of SOC have introduced some qualifications in the original theory, and circumscribed the range of its validity (Dickman, 2000; Kadanoff et al, 1989; Jensen, 1998). The conceptual prototype of SOC was originally the 'sand pile model' in which stepwise addition of sand grains on the tope leads in the critical state to propagation of avalanches across the pile, which exhibit the properties of scale invariance. Numerous modifications of the original paradigm were instrumental to characterize the boundary conditions under which the theory of SOC applies while, on the other hand, the signatures of SOC were identified in models not originally considered, such as for instance percolation models (Stauffer & Aharony,1991/1994, Grimmett, 1989). Parenthetically, it is worth noting that one of the extensions of SOC, designed to replicate the sale invariance of earthquakes (Olami, et al, 1992), shares many features with Tononi and Edelman's' (2000) spring model of reentrant activity, referred to earlier. It is now firmly established by the work of Bak's own Group (Paszuski et al, 1996) and many others that SOC is a useful concept for describing systems far from equilibrium that will manifest a phase transition when driven from the outside (Frigg, 2003). Like conventional phase transitions, some forms of SOC are amenable to analysis by Renormalization Analysis (Pietronero et al.,1994; Vespignani et al., 1996); that is: the computational techniques that enables the explicit computation of the critical exponents for scale invariance and other critical properties (Kadanoff et al, 1967; Wilson, 1979; McComb, 2004), thus blurring what was earlier thought to be an essential distinction between SOC and 'classical' (tuning- dependent) phase transitions. The twin concepts of scaling and universality play an important role in description of dynamical systems for elimination of degrees of freedom and scale transformations at points near critical transition (Kadanoff et al, 1989; Kadanoff, 1990). The significance of this lies in the possibility of identifying universality classes (Odor, 2004) which will be pursued in Section 3. Although still lacking a comprehensive theory of SOC, it is now an established part of Dynamical Systems Theory by characterizing (specifically in some instances and in others, in principle) the critical state as the system's attractor, and its fractal structure (Blanchard et al, 2000).

3. Discussion and Conclusions

In their totality, concepts and observations sketched in the foregoing section are intended to give credence to the notion that the transient configurations of neural activity (designated respectively Reentrant Dynamic Core by Edelman et al, and Global Neuronal Workspace by Dehaene & Changeux) are manifestation of SOC in the neuronal reentry circuits of the respective models. As such, they require several hundred msec for constitution of their long-range connections to full criticality at which point the characteristic properties of scale invariance, reduced dimensionality and long-range correlations come to obtain for the critical state's duration. While still on the way to criticality, a metastable regime is in effect. The spatial extent and temporal course of the pattern of activity in the neuronal models under discussion are thought to be essential for their performance in realistic task conditions and, by extrapolation, aspects of neural processes in human cognition and consciousness. It is the purpose of this essay to propose that the dynamics of the "operational synchrony" in the work of Fingelkurts and Fingelkurts and of 'microstates ' in the work of Lehmann and associates are expressions at the macroscale of the recursively reentrant activity in mesoscopic neuronal circuits of DC and GNW. Changeux and Michel (2004) made a similar suggestion. This would then be an instance of the dynamics at one brain organizational level finding expression at another.

What can be gained from pursuing this view ? The answer turns to the notion of Universality classes, mentioned in passing in Section 2.2.3. Permitting oneself some levity, Universality classes may be viewed as God's gift to the Physicist : universality refers in this context to the phenomenon whereby dissimilar systems can exhibit the same numerical indices that reflect the creation of long range correlations from local interactions, and the manner in which disturbances propagate through the system. These indices are independent of physical nature of the system's components, and are solely determined by the properties of the components' interactions (Binney, 1992; Yeomans, 2002). It is empirically established that nonlinear dynamic systems, including those operating far from equilibrium (Odor, 2004), can often be categorized by these critical indices into distinct classes. This means that having ascertained one or the other critical property for a system under study, it is then possible to predict all other critical properties of that system merely on the basis of its class membership. Applying this approach to plausible models of reentry circuitry in the systems of DC and GNW would enable characterizing the nature of their dynamics, and its relation to the potential role in the Operational Architectonis of Fingelkurts & Fingelkurts (2005) and the microstates in the studies of Lehmann ansd associates (2006). Among the various candidates that come to mind is the type of percolation studied by Kozma et al (2005) on models of the neuropil, or one of its several variants. Such computational models of Dynamic Core and the Global Neuronal Workspace would serve as windows for gaining insight into the dynamics of neuronal assemblies with established functions in their respective models. This, so it is thought, would substitute, at least at this time, for the direct observation of the relevant neural assemblies in situ, as it would reveal indirectly the total range of their dynamic properties, on the basis of sharing universality class membership with animate and/or inanimate known substrates.

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