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NEURONAL SYNCHRONY AND COGNITIVE FUNCTIONS

ABSTRACT

This paper present a novel reading of ideas on temporal binding as key for cognitive operations by means of fast neuronal synchrony. I advocate a view of binding between widely distributed cell assemblies, transiently locked in a neural hypergraph which serves as a reference point to incorporate (or interpret) other less coherent concurrent, neural events. The paper concludes with some implications for the constitution of a unified cognitive-mental space.

1. THE CONTEXT: CELL ASSEMBLIES AND COGNITION

I wish to present here a new view about cognitive-mental functions based on a large-scale integrating brain mechanism that has been slowly emerging with increasing plausibility. A long standing tradition in neuroscience, dating back to the days of cybernetics, looks at the brain basis of cognitive acts (perception-action, memory, motivation and the like) in terms of *cell assemblies* or, synonimously, of *neuronal ensembles*.

Definition: A Cell Assembly (CA) is a distributed subset of neurons with strong reciprocal connections.

Thus a CA will comprises distributed neuronal populations (very likely neocortical pyramidal neurons, but not limited to them) requiring active connections. Because of their assumed strong interconnections a cell assembly can be activated or ignited from any of its smaller subsets, sensori-motor, or internal. Notice also that the term reciprocal is crucial here: it is one of the main results of modern neuroscience that brain regions are indeed interconnected in reciprocal fashion (this is what I like to call the Law of Reciprocity). Thus, whatever the neural basis for interesting cognitive tasks turns out to be, it necessarily engages vast and geographically separated regions of the brain. Furthermore, these distinct regions cannot be seen as organized in some sequential arrangement as if a cognitive act could emerge from a gradual convergence from various sensory modalities, into association or multimodal regions, and further into higher frontal areas for active decision and planning of behavioral acts. This traditional sequentialistic idea derives from the time of the dominance of the computer metaphor with its associated idea of information flow going in an up-stream direction. Here, in contrast, I emphasized a strong dominance of reciprocal network properties where sequentiality is replaced by reciprocal determination and relaxation time.

The genesis and determination of CAs can be seen as having three distinct causal and temporal levels of emergence.

- 1. First, a very basic *onto-genetic* level which sets the anatomical architecture of a given brain into circuits and subcircuits.
- 2. It has been widely suspected that beyond the basic genetic wiring, neurons develop a variable degree of effective interconnectivity by strengthening or weakening their synaptic contacts. This is a second, strictly *developmental-learning* level and time-scale: sets of neurons that are frequently co-active strengthen their synaptic efficacies. Known generically as Hebb's rule the notion has suffered many theoretical formulations and additions in the recent connectionist movement. More importantly, a substantial amount of evidence shows that Hebb's rule in some form is the case during learning and early life (*e.g.* Ahissar *et al.*, 1992; Bonhoeffer *et al.*, 1989).
- 3. A third and final level of determination for CA is our concern here. This is the faster time scale at the *perception-action* level of fractions of a second when a CA is ignited and it either reaches a distributed coherence or is swamped by the competing ignitions of overlapping CAs. As Braitenberg puts it, the CA must "hold" after its activation (1978). In the language of the theoretician the CA must have a relaxation time. This holding time is bounded by two simultaneous constraints: (1) it must be larger than the time for spike transmission between neurons either directly or through a small number of synapses; (2) it must be smaller than the time it takes for a cognitive act to be completed, which is of the order of fraction of a second (*e.g.* Varela *et al.*, 1981; Dennett, 1992).

In other words: the relevant neuronal processes are not only distributed in space, but they are also distributed in an expanse of time that cannot be compressed beyond a certain fraction of a second.

2. THE HYPOTHESIS: SYNCHRONY AS NEURONAL GLUE

In view of the above, I wish to propose two interlinked (but logically independent) working Hypothesis.

Hypothesis I: A singular, specific cell assembly underlies the emergence and operation of every cognitive act.

In other words, the emergence of a cognitive act is a matter of coordination of many different regions allowing for different capacities: perception, memory, motivation, and so on. They must be bound together in specific grouping appropriate to the specifics of the current situation the animal is engaged in, and are thus necessarily transient, to constitute meaningful contents in meaningful contexts for perception and actions. Further, Hypothesis I predicts that all the physiological correlates associated with CA (*i.e.* multi-unit activity, local field potentials, MEG/EEG scalp recordings, frequency coherences, etc.) should be repeatedly detected for a repeated cognitive act, say, in an odd-ball discrimination task conducted in the laboratory, in an otherwise intact awake human or animal.

Notice that the Hypothesis I is *strong* in the sense that it predicts that only *one* dominant or mayor CA will be present during a cognitive act. We will come back to this below, but it highlights a basic problem opened by Hypothesis I: How is a specific cell assembly selected in successive moments? Although this will be main topic in the rest of this article, I wish to formulate it as the second part of my working Hypothesis. The basic intuition to answer the problem just raised is that a specific CA emerges through a kind of temporal "glue". More specifically, the neural coherency-generating process can be understood as follows:

Hypothesis II: A specific CA is selected through the fast, transient phase locking of activated neurons belonging to sub-threshold competing CAs.

Since in recent literature the notion of neuronal synchrony and binding has received a wide attention, I do not need to provide many empirical details (see Singer, 1993; Varela, 1995).

3. THE MECHANISM: PHASE-LOCKING IN RECIPROCAL CIRCUITS

It is well known that oscillations and rhythms are quite natural to neurons and neural circuits, and they have been explored widely (e.g. Glass and Mackey, 1988; Levan Quyen, Schuster and Varela, 1996). Given that there are finite transmission times in the nervous systems oscillations and cycles are to be expected just on the basis of reciprocal connectivity, as already popularized by Lorente de No in his well-known "reververating" circuits. This entails that one should expect that patterned activity of neurons will display spatio-temporal regularities. A further quite different universal mechanism for generating rhythms of interest to us here is the introduction of inhibition within a population of reciprocally connected excitatory elements, as clearly analyzed by Wilson and Cowan (1973).

A different matter which is my central concern here, is the precise manner in which such coherence can be established. According to Hypothesis II the key idea is that ensembles arise because neural activity forms transient aggregates of phase locked signals coming from multiple regions. Synchrony (via phase-locking) must per force occur at a rate sufficiently high so that there is enough time for the ensemble to "hold" together within the constraints of transmission times and cognitive frames of a fractions of a second. However if at a given moment several competing CAs are ignited, different spatio-temporal patterns will become manifest and hence the dynamics of synchrony may be reflected in several frequency bands. The neuronal synchronization hypothesis postulates that it is the precise coincidence of the firing of the cells that brings about unity in mental-cognitive experience. If oscillatory activity promotes this conjunction mechanism, it has to be relatively fast to allow at least few cycles before a perceptual processes is completed (e.g., head orientation followed by face recognition).

Now, how fast is fast? Consider the following reasoning: There are numerous connections between cortical regions, and a recent study puts their conduction velocities at over 10 m/sec (Aboitiz *et al.*, 1992). This means that, roughly, one cycle of spike exchanges between two hemispheres would be about 40 ms. If we assume that a CA needs at least one round trip of spike to synchronize, this puts the minimum relevant associated frequency at over 25 Hz, that is, in the so-called gamma band (say 35-60 Hz). In other words, if Hypothesis II holds, then large numbers of neurons should give indications of increased activation in local field potentials, EEG/MEG, or single cell in this range, although not necessary at the exclusion of slower rhythms.

This simple reasoning illustrates one of the many avenues one can use to conclude that looking further into these non-classical, fast rhythms may be of cognitive interest. Oscillatory activity in the gamma range was, in fact, already described by Adrian in 1942 in the in the olfactory bulb of the hedgehog, work that was followed by the research line of W. Freeman (1975) using macro-potential in awake animals. Similarly, work with humans, using EEG, MEG and ERPs led Sheer and Galambos early on to similar ideas. Observations from neuropsychology also prompted Damasio and others to select phase locking as crucial (Damasio, 1990; Bressler *et al.*, 1993; Jolliot *et al.*, 1994; Varela *et al.*, 1995). Most recently, work with single units in the visual systems in animals (for review see Singer, 1993; for our own work Neuenschwander *et al.*, 1993; 1996) have made the idea quite popular. I will delve more in detail in this empirical evidence below, but for the moment let us stay at the general level of the Hypothesis itself.

In these studies the main idea is that fast oscillations in the gamma-beta range serve as *carriers* for a phase synchronization of neuronal activity, thus allowing for a process of selection by resonance into a transient coherent ensemble that underlies the unity of cognitive act in a fraction of a second. The substantial experimental support for the hypothesis makes it clear that we are dealing with a *bona fide* candidate for the synthesis of a cognitive space. At the same time I haste to add that the empirical support is far from being limpid, and that the credibility and interpretation of the available observation is not unanimous.

This focus on gamma band, though restrictive, is not meant to imply that fast rhythms are the sole correlates of cognitive processes. The literature provides numerous examples of theta and alpha rhythms in cortex, hippocampus, thalamus and brain stem which are induced by sensory stimulation or motor behavior (see Basar 1992 for a review). It has been show that alpha-like oscillations are present in visual evoked potentials in humans (Mangun 1992; Basar et al., 1992), and alpha-rhythms can desynchronize during complex behavioural tasks, like reading, or planning of finger movements (Pfurtscheller and Klimesch 1992; Pfurtscheller and Neuper 1992). Rhythmic slow activity may operate in the spread of activity over the hippocampus and even facilitate or promote synaptic modifications, ultimately stabilizing memory traces in the limbic cortex (Lopes da Silva 1992). However, slow rhythms generally involve large neural masses, locked in a global state of hyper-synchrony (as in delta sleep or barbiturateinduced spindles). It is hard to conceive how such a slow rhythmic activity could provide the necessary dynamics for attention, perception and purposive motor behavior, which are continually evolving, non-stationary

processes that self-organize into cognitive aggregates in a fraction of a second.

4. THE CORE HYPOTHESIS

I would like to come back to my initial, more general point: what could this large-scale binding do for us? For the sake of stating my ground as clearly as possible, let me now *rephrase* the main idea presented above in Hypothesis I+II this time phrased as the emergence of mental-cognitive states in general.

Core Hypothesis: Mental-cognitive states are interpretations of current neural activity, carried out in reference to a transient coherency-generating process generated by that nervous system.

To clarify, let direct the reader to the following comments:

I am referring to "primary" consciousness only:

I am restricting my discussion here to the kind of mental-cognitive events shared by non-verbal creatures. In all of us, the ongoing constitution of a mental space makes possible a selection and internal evaluation of multiple, concurrent neural events. For example, a visual recognition is surely lived differently depending on conditions related to the overall state of arousal and motivation, and depending on associative memories unique to that individual.

What do I mean by "interpretations":

In this sense it is clear that the neural events accompanying the recognition are not taken at face value but shaped and modified in the context of the rest of the neural events related to, say, limbic and memory activation. This is what I mean by an "interpretation": the generation of a mental-cognitive state corresponds to the constitution of an assembly which incorporates or discards into its coherent components other concurrent neural activity generated exogenously or endogenously. In other words, the synchronous glue provides the reference point from which the inevitable multiplicity of concurrent potential assemblies is evaluated until one is transiently stabilized and expressed behaviorally. This is a form of neural hermeneutics since the neural activity is "seen" or "evaluated" from the point of view of the cell assembly that is most dominant at the time. Dynamically this entire process takes the form of a bifurcation from a noisy background to conform a transiently stable, distributed structure bound by synchrony.

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^{1.} I have been influenced by Chiel (1993) for this unusual approach to neural activity.

Ongoing neural activity assimilated in the dominant assembly:

It should be also clear that the neural events that participate in this process of synthetic interpretation are derived indistinctly from sensory coupling and from the intrinsic activity of the nervous system itself, i.e. levels of activation, memory associations and the like. It is also clear that whatever the mental state thus arrived it will ipso facto have neural consequences at the level of behavior and perception. For instance, if a visual recognition is interpreted in the context of an evasive emotional set and in conjunction with painful memory association, it can lead to a purposeful plan for avoidance behavior complete with motor trajectories and attention shifts to certain sensory fields. This illustrates one key dimension of the view of mental states I am offering here: there is a level-crossing reciprocity in that a mental state as such (i.e. as a global interdependent pattern) can effectively act on neural events (that is, it can have downward causation as the phrase goes). For this to be more than a simple dualistic rehash it is essential that the dominant interpretation be itself an emergent neural event. Whence the odd-looking part of my definition that requires a neural events to be the basis of interpretation of another class (of non synchronous, less coherent) neural events.

Mental events are a distributed hypergraph:

It is also clear that what I am proposing is related to a process which is, by definition, distributed since it involves a variety of dispersed neural activity. Thus a basic cognitive-mental space is topological object, and not topographical one, it is a question of a hypergraph of synchronous relationships rather than one of localization. The process underlying this cerebral hermeneutics itself is, by hypothesis, an ongoing phenomenon, providing a continual emergence. Notice that this process demands that it operates by a distributed coupling of groups of oscillators, it will exhibit a characteristic relaxation time. Thus, we expects that cognitive (and experiential) time will manifest in the manner of discontinuous aggregates over a horizon on ongoing, continuos activity.

Synchronous assemblies are universal:

The key in all of this is, then, that we can identify a neural process which can be a credible support for the transitory coherence from whose vantage point a neural interpretation can happen. The alleged process must be universal enough to be supported and present in a the nervous system of animals at least for all higher vertebrates, and its presence or absence can help identify where sentiency is present in the sense presented here. The evidence discussed above make it plausible that we actually have a good candidate for a neural mechanism. The specificity of a synchronous

hypergraph present for every mental-cognitive state can in principle be studied by the new techniques combining MEG-EEG (see Tiitinen *et al.*, 1993) and fMRI-PET studies. Only a systematic study of this global functional aggregate, followed at the millisecond level during mental experience, will give a definitive answer to the extent to which the Core Hypothesis is valid.

How is this related to our own mental experience?:

By their very nature, mental states make reference to our own experience and thus require a phenomenological account, which we can carry out as sentient humans. That we are both cognitive creatures and self-conscious is both an advantage and a difficulty. Advantage because we can rely on human phenomenology of mental states as valid data. Disadvantage because we have to be careful to address the appropriate primary dimensions of mental life common to all animals, and not those dimensions which are properly human. An adequate phenomenology of mental states in this sense needs to be done by some explicit phenomenological pragmatics, and not just the "It seems to me" method. This has been notoriously lacking in cognitive science, and it is not surprising since it entails a radical turn to examine the texture of our field of experience (see Varela *et al.*, 1991; Varela 1996) for more on phenomenology and neuroscience). I will not attempt to enter into this essential topic here, but let me at least provide some pointers.

Some basic dimensions of mental experience that need to be brought in for this discussion are the following:

- 1. Mental events occur in a unitary space: there is no fragmentation in the manner in which, for instance, different modalities appear to experience or a disjointness between sensations and memories and body tone.
- 2. Mental states are transitory in the most obvious sense that no one state lasts for a sustained duration beyond a limit. Conversely it does not seem possible to experience a mental state without a span of duration which is non-vanishing. Thus, mental states are finite, and have an incompressible and inextendible duration.
- 3. Mental states are always body-bound, embedded in a particular field of sensation. In fact most of the time a mental state has a dominant sensory modality which colors its texture.
- 4. Mental states can be causally triggered by endogenous events. It is also the case that a mental state can be seen as having a distinct perceptual or behavioral consequence. (If this seems strange, think of the classic example of the "voluntary" inversion of the two faces of an ambiguous visual figure). Thus, the kind of neural events underlying a mental state

must be distinct and distinguishable from other kinds of neural events so that this two-relation relationship holds.

These basic phenomenological dimensions of a mental states must enter as an arbiter in the validation of any approach to mental-cognitive processes (Varela *et al.*, 1991; Varela, 1996). In other words, we need to satisfy what we know about neuroscience and come up with a mechanism that is a convincing counterpart to these four dimensions of a mental experience. We need to advance a cognitive science where there is a true circulation between lived experience and the biological mechanisms in a seamless and mutually illuminating manner, as we have discussed elsewhere (Varela *et al.*, 1991), and it has recently been claimed by others from their own perspective (see *e.g.* Flannagan (1992) and his notion of a "unified theory"). Mental states as viewed through the Core Hypothesis provide an explicit avenue to conduct research in cognitive science as if both brain physiology and mental experience mattered.

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