

The Formation of Global Neurocognitive State

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Abstract I propose in this chapter that the formation of global neurocognitive state in the cerebral cortex is central to the mammalian capacity for assessment of organismic state. I consider a putative mechanism for the formation of global neurocognitive state from interactions among interconnected cortical areas. In this model, each area makes a local assessment of its own current state, representing a partial assessment of organismic state, through the generation of packets of high-frequency oscillatory wave activity. The spatial amplitude modulation (AM) pattern of the wave packet is proposed to represent the expression of an area's current state in relation to the other areas with which it is interacting. Through their interactions, sets of cortical areas mutually constrain the AM patterns of their wave packets. It is proposed that this process leads to the manifestation of wave packets having cognitively consistent patterns, and the formation of globally unified consensual neurocognitive states.

1 Introduction

An essential function performed by the cerebral cortex is to dynamically assess the state of the mammalian organism on a moment-by-moment basis. This dynamic assessment plays a critical role in adaptive behavior by allowing the organism to perceive and act in a manner consistent with the context of the changing situation in which it exists [15]. It requires the monitoring of sensory inputs in multiple modalities that inform the cortex about the states of the external and internal environments, including the state of the musculature. The states of numerous brain systems, e.g. the preparatory, postural, and kinematic states of the motor system, must also be monitored. The assessments of these diverse states must further be integrated to create a global neurocognitive assessment state in the cortex from which judgements may be formed and actions planned and executed. Since the external and internal environments are in continual flux, the cortex must be highly flexible in its ability to monitor and integrate the plethora of data concerning organismic state to which it has access in order for the organism to behave adaptively.

It has long been recognized that no single area of the cerebral cortex serves as a central supervisor that performs all of these monitoring and integrative functions.

Although the functions of many areas of association cortex are considered to be primarily executive in function [37], there is no single “supreme” executive area. The cortex consists of a large number of areas profusely interconnected by long-range pathways in a complex topological structure [3, 24, 40, 41, 56, 73, 83, 87]. An important aspect of cortical connectivity is that each cortical area has a specialized topological position within the cortex, i.e. a unique pattern of interconnectivity with other cortical areas [10, 60]. To a large degree, the function of every cortical area, including executive areas, is determined by its unique patterning of long-range connectivity. Furthermore, in spite of the well-known cytoarchitectonic distinctiveness of certain areas [20, 21], the short-range interconnectivity of local circuits within cortical areas is generally similar throughout the cortex, implying that no area has a specialized monitoring function by virtue of its internal organization. In sum, these considerations suggest that cortical monitoring and integrative functions are a result of cooperative interaction among many distributed areas, and not the sole property of any one area or small group of areas.

The goal of this chapter is to attempt a reasonable explanation of how the cortex dynamically generates global neurocognitive states, representing the assessment of organismic state, from interactions among its areas. Evidence will be considered for the generation of local states by neuronal populations within cortical areas, and for the interaction of cortical areas in the generation of global neurocognitive states. The effect of short- and long-range patterning of interconnectivity within the cortex on the generation of local and global states will be considered [16, 72].

2 Coherent Local Cortical Domains and Their Interactions

This section considers the local organization of population activity in the cortex. There is ample support for the existence of locally coherent domains of high-frequency (13–100 Hz) oscillatory activity in the cortex. The evidence comes largely from recordings from the pial surface of sensory cortices of rabbits, cats, and monkeys by high-density electrode arrays [4, 7, 8, 25, 26, 31, 35]. The observed activity is spatially coherent, indicative of a common waveform, across spatial extents on the order of tens of square millimeters [27]. The spatial coherence arises largely as a result of mutually excitatory synaptic interactions among the excitatory neurons of the cortical area [22]. Within the spatial extent of a coherent domain, which has been termed a “wave packet” [27], the wave amplitude and phase are both spatially modulated.

The spatial pattern of amplitude modulation (AM) of the wave packet in sensory cortices has been found to correlate with the categorical perception of conditioned stimuli in the corresponding sensory modality [4, 31, 35, 58]. The spatial AM pattern changes reliably with behavioral context, conditioning, and the animal’s cumulative experience of the sensory environment, but does not reflect the specific features of sensory stimuli. Wave packets have been observed to recur intermittently with rates in the delta-theta frequency range (2–7 Hz), each recurrence resulting from a state transition in the population activity of the local area [34]. The spatial

pattern of phase modulation of the wave packet has not been found to correlate with perception or behavior, but is a useful indicator of the spatial extent of the wave packet. Since the spatial extent of coherent domains can exceed the size of the primary sensory areas [28, 30, 33], it remains an open question as to what degree the coherent domains are confined by the boundaries of cortical areas as defined anatomically.

Extrapolating from these considerations, it is reasonable to infer that each area of the cerebral cortex, whether sensory or non-sensory, generates a sequence of wave packets during normal cognitive behavior, and that interconnected areas concurrently generate wave packets that may result in their undergoing conjoint local state transitions. Generation of the spatially patterned wave packet arises from the local circuitry in each cortical area. The spatial AM pattern of the wave packet generated in an area depends on the interaction of pulse inputs from other areas with the local synaptic matrix acting as an associative memory formed by Hebbian learning [1, 53]. The spatial extent of the wave packet is limited by such factors as the spatial distributions of mutually excitatory connections and of the terminal arborizations of incoming axonal projection pathways.

From this perspective, the generation and transmission of spatially patterned activity between areas is central to cortical communication. Given that the anatomical interconnectivity of the cortex is largely bidirectional at the population level [24], areas typically receive feedback from the same areas to which they transmit, and in this sense cortical processing is considered to be “reentrant” [79]. By providing feedback inputs to the circuit elements in sets of interacting cortical areas, reentrant interactions mutually constrain the spatial AM patterns of wave packets generated by those areas.

In this process, each cortical area generates a spatial distribution of pulse activity whose density conforms to the spatial AM pattern of its wave packet. These pulse density patterns are transmitted between cortical areas over inter-areal fiber pathways, some of which have a degree of topographic specificity, but which in general have a high degree of divergence and convergence in their projection to other cortical areas. Thus wave packets undergo spatial integral transformations in transmission from one cortical area to another [4]. The pattern of postsynaptic potentials produced in an area by pulses transmitted over inter-areal fiber pathways depends further on the pattern of synaptic transmission strengths at the axon terminals that have been modified by transcortical Hebbian learning [36, 63]. The overall effect of multiple reentrant interactions among cortical areas is mutual constraint of the spatial AM patterns of the wave packets that they generate [12].

3 The Emergence of Global Neurocognitive State

In the awake state, cortical areas have been found to generate wave packets lasting on the order of 100–300 msec, interrupted by nonlinear state transitions [29]. Each time the wave packet is regenerated, its spatial AM pattern may change. The spatial AM pattern of the wave packet may be considered as an expression of a given

area's own current state in relation to the other areas with which it is interacting. It is thus reasonable to suppose that, as reciprocally interconnected areas undergo reentrant interactions, the spatial AM patterns of the wave packets they generate are conjointly constrained. In that case, the wave packets in interconnected cortical areas may thereby undergo pattern constraint in conjunction with one another.

The conjunctive generation of wave packets by interconnected cortical areas represents a possible mechanism for the assessment of organismic state by the cortex. I hypothesize that the spatial AM pattern of the wave packet generated in each area represents an expression of the contribution by that area to the overall assessment of organismic state by the cortex. Each area's contribution arises from its own unique memory store, embodied in its local synaptic matrix, under the influence of inputs from other areas with which it interacts. Each area's spatial AM pattern may be expressed in conjunction with others in sets of interacting cortical areas as they conjointly undergo state transitions and co-generate wave packets. The mutual pattern constraint exerted by those areas is expected to promote the expression of consistent contributions to the state assessment, creating a "consensus" interpretation of available evidence concerning the state of the organism within the context of its current situation [15].

Although it is currently unknown what cellular mechanisms are responsible for the expression of consistent spatial AM patterns in interconnected cortical areas, there is evidence that they involve the (partial) phase synchronization of high-frequency oscillatory activity. The wave packet itself is a locally phase synchronized oscillatory event, and evidence suggests that high-frequency oscillatory activity in different cortical areas becomes phase synchronized in relation to cognitive state [13, 17, 18, 65, 75, 84]. The rapid emergence of large-scale patterns of phase-synchronized cortical sites at specific stages of cognitive task performance suggests that creation of the cognitive microstate [55] depends on the transient coordination of specific sets of areas by long-range oscillatory phase synchronization [9, 13, 14, 16]. It is thus likely that phase synchronization serves not only to coordinate local neuronal populations in wave packets within cortical areas, but also distant populations in different areas.

A neural process that produces long-range phase synchronization of neuronal populations in interconnected cortical areas has several attractive features for the creation of a global state of the cortex representing the ongoing assessment of organismic state. First, the possibility exists for both the transient inclusion and exclusion of cortical areas from large-scale phase-synchronized networks. Areas whose wave packets achieve the co-expression of consistent spatial AM patterns may be linked by long-range phase synchronization, whereas others may be excluded due to a lack of phase synchronization. Oscillatory activity in different cortical populations is called "coherent" when there exists a high level of phase synchronization between them, and "incoherent" when the degree of phase synchronization is low (Fig. 1). By a terminological coincidence, the term "coherence" has also been used to refer to the satisfaction of consistent cognitive constraints [76]. In this second sense, areas generating wave packets with consistent spatial AM patterns may be considered to express cognitive coherence with one another, and those with inconsistent patterns may be considered to express cognitive incoherence.

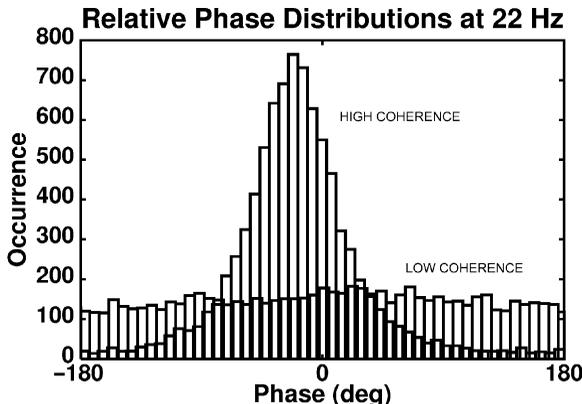


Fig. 1 Relative phase distributions between local field potentials recorded from two posterior parietal electrode sites in the macaque monkey. The 22 Hz frequency, in the mid-beta frequency range, represents the center frequency of oscillatory activity manifested by neuronal populations at both sites. The two distributions were computed from different time intervals as the monkey performed a visuomotor pattern discrimination task. The first distribution, labeled “HIGH COHERENCE”, was from a prestimulus interval when oscillatory activity at 22 Hz was highly synchronized. The second distribution, labeled “LOW COHERENCE”, was from a poststimulus interval when the phase synchronization at 22 Hz was very low. In general, high coherence indicates a highly concentrated relative phase distribution, and low coherence a weakly concentrated distribution

A second benefit of such a process is the possibility of maintaining the global coordination dynamics of the cortex in a state of metastability [10, 14]. A metastable system of interacting components preserves a balance between states of global coordination of the components and of component independence. In a system of

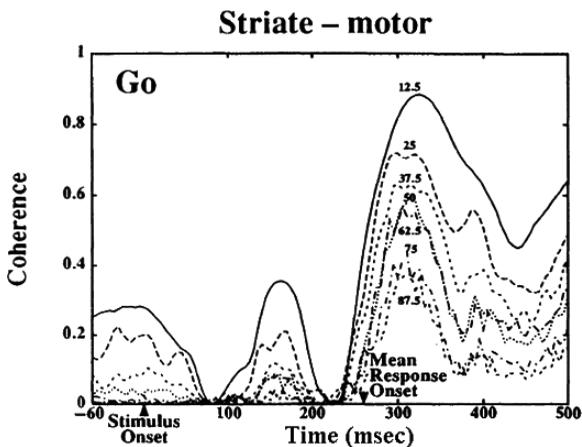


Fig. 2 Episodic increases in phase synchronization between local field potentials from electrodes sites in primary visual and primary motor cortical areas of the macaque monkey. Phase synchronization is measured by coherence, which varies from 0, representing no synchronization, to 1, representing total synchronization. Adapted from [13]

interacting oscillatory neuronal populations in interconnected cortical areas, metastability implies the coexistence of the tendency for these populations to be globally coordinated balanced by the counteracting tendency for them to be independent. A metastable system displays intermittency in coordination: the components may alternate between periods of coordination and uncoordination [14]. The concept of intermittent coordination dynamics is consistent with the experimentally observed intermittency of elevated phase synchronization among widely distributed cortical neuronal populations (Fig. 2), as well as the intermittent state transitions that separate wave packets [29, 32]. For both phenomena, the intermittency occurs roughly on the order of 100–300 msec.

4 Implications for the Study of Cognition and Consciousness

In essence, the proposal presented here is that an assessment of organismic state occurs in the cerebral cortex as the result of interactions among interconnected cortical areas, while they are receiving inputs from thalamic and other subcortical structures that convey the raw data about the internal and external milieus. By each cortical area making a local assessment of its own current state, it provides a partial assessment of the entire state of the organism. Depending on its position in the large-scale connectivity structure of the cortex [38, 56], each area expresses a different aspect of the total state.

A potential mechanism for the creation of a global neurocognitive state, representing the assessment of organismic state, involves the generation of packets of high-frequency oscillatory wave activity in cortical areas. The spatial AM pattern of the wave packet is proposed to represent the expression of an area's current state in relation to the other areas with which it is interacting. Through their interactions, cortical areas exert modulatory influences on one another that mutually constrain that expression. Cortical areas generate wave packets at rates of several times per second [29], each generation being initiated by a nonlinear state transition.

Mutual pattern constraint may lead sets of interacting cortical areas to achieve unified consensual states that are consistent according to cognitive coherence and incoherence relations [76]. It is proposed that such sets become coordinated in large-scale cortical networks by the phase synchronization of high-frequency oscillatory activity. Support for this idea comes from the observation of large-scale phase-synchronized cortical networks in relation to different cognitive functions [9, 65, 66, 75, 82, 84]. A example from the sensorimotor region of macaque monkeys monitoring the state of their limb position as part of a visuomotor task is shown in Fig. 3.

Depending on the location and extent of the areas involved, the emergence of unified consensual states may represent the assessment of organismic state in different cognitive forms [56]. Within perceptual systems, these states may lead to the recognition and identification of perceptual entities. Between perceptual and motor systems they may provide behavioral adaptation within the perception-action cycle [38]. Through integration across executive systems, they may establish

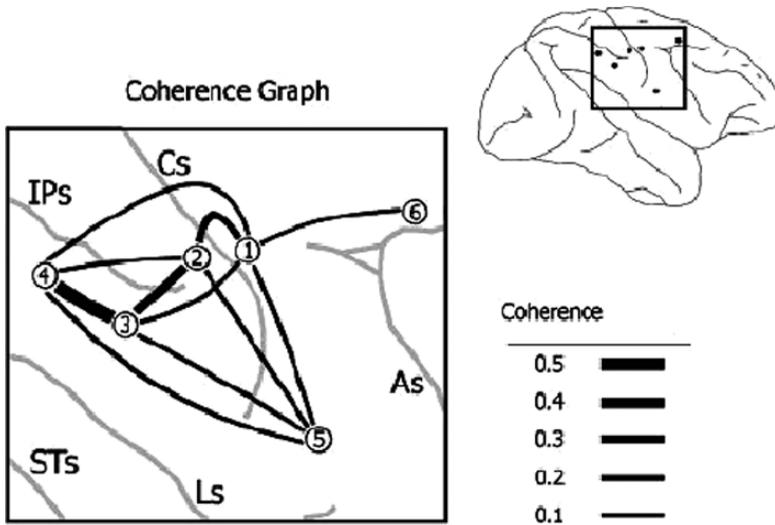


Fig. 3 Phase synchronized network in sensorimotor cortex of the macaque monkey. Lines connecting electrode sites represent significant coherence in the beta frequency range. Adapted from [17]

neurocognitive contexts [15] that allow the anticipation of impending events and the recognition of those events when they occur.

Of course, the assessment of organismic state is rarely perfect. A fundamental indeterminacy exists in the process of evaluating the states of sensory environments [12] and brain systems. Furthermore, sensory data may be incomplete, ambiguous, or contradictory. These considerations suggest that multiple clusters of consensual cortical areas may concurrently arise in the cortex, representing competitive assessments of organismic state, in much the same way as has been proposed for the competition among perceptual entities within [23] and between modalities [54]. Through increased consistency of expressed spatial AM patterns, as well as the recruitment of additional consistent areas, some clusters may be come better established over successive state transitions, whereas others may die out. Clusters may also coalesce if they express consistent interpretations of the organismic state. Through an on-going process of recurring assessment, it is expected that the cortex may achieve neurocognitive states representing the globally consistent assessment of organismic state.

The framework proposed in this chapter is consistent with dynamical approaches in cognitive science that focus on the evolution of cognitive state on a sub-second time scale [5, 71]. The spatial AM pattern of a wave packet in a cortical area may be represented as a vector in high dimensional space [29]. As the wave packet of the area undergoes sequential generation, the vector follows a trajectory in state space, and its interactions with other areas modulates the state vector trajectory. Furthermore, the conjoint spatial AM patterns of interacting areas may also be represented as state vectors in high dimensional space. At the level of the global neurocognitive

state, a cortical system trajectory is envisioned that is equivalent to cognitive state space trajectories described in the literature [45, 62, 70, 85].

The proposed assessment of organismic state is also similar to the appraisal process postulated to mediate the interplay of cognitive and emotional states [52]. The creation of global neurocognitive states in the cerebral cortex is likely to have important effects on subcortical brain structures with a wide variety of consequences [19]. Subcortical structures may feed influences back to the cortex by direct pathways using neurotransmitters or neuropeptides [59], as well as by more indirect paths involving circulating hormones. Several studies have demonstrated an interrelation between neurocognitive state and circulating hormones [48, 49, 64]. Thus, the cortical system trajectory described above is likely to be influenced by a number of sources elsewhere in the brain and body.

Disruption of the proposed organismic assessment process may be responsible for many of the symptoms observed in neuropsychiatric disorders. There is growing agreement that schizophrenia is a disease characterized by a disturbance of coordinated cognitive processes [2, 42, 57, 61, 78], and that this disruption occurs as a result of abnormal phase synchronization of high-frequency oscillatory neuronal population activity in the cortex [6, 11, 50, 51, 69, 74, 80, 81]. Evidence exists also for similar disruptions of phase synchronized cortical oscillations in Alzheimer's disease [47] and autism [86]. The impairment of organismic state assessment, in different forms, may be common to all these pathologies.

5 Conclusions

The global neurocognitive state discussed here as a means by which the organism is able to assess its own state may also be related to the state of conscious awareness. Although the process by which cortical areas become coordinated may largely be unconscious, it may possibly become conscious when a threshold is crossed in terms of the number of coordinated areas, the overall strength of coordination, or the recruitment of particular areas [44, 46, 67]. If, then, global neurocognitive assessment states are a prerequisite for consciousness, the latter should be considered as an emergent property of the interaction of distributed cortical areas [68, 77]. To view consciousness as a dynamic property of brain function that emerges from the interactions of cortical areas in relation to the assessment of organismic state suggests that it may endow mammals with enhanced survival value [39, 43]. By augmenting the assessment of organismic state, consciousness may provide mammals with greater flexibility in their ability to distinguish environmental entities and a greater behavioral repertoire. It further suggests that all mammalian species possess consciousness with a level indexed by the number of differentiated cortical areas and the complexity of their interconnectivity.

Acknowledgment Supported by grant MH64204 from the National Institute of Mental Health.

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