Resonant cell assemblies:
A new approach to cognitive functions
and neuronal synchrony

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This paper presents a novel reading of ideas on temporal binding as a key for cognitive operations by means of fast (gamma band) phase synchrony. We advocate a view of binding of 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 traces in some detail the empirical evidence concerning the gamma binding process and presents some implications for the constitution of a unified cognitive-mental space.

Key terms: *cell assemblies, cognitive operations, gamma binding, neural hypergraph, phase synchrony.*

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. In order to present this view I need, however, to lay out some context which is the purpose of this Section.

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** (CAs) or, synonymously, of **neuronal ensembles**.

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

Notice that a CA generally comprises distributed neuronal populations (very likely neo-cortical 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 (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: a cognitive act emerges from a gradual convergence from various sensory modalities into association or multimodal regions and 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 emphasize a strong dominance of reciprocal network properties where sequentiality is

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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. 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 coactive strengthen their synaptic efficacies. Known generically as Hebb's rule (Hebb, 1949) 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 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 (1978) puts it, the CA must "hold" after its activation. 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.

THE HYPOTHESIS: SYNCHRONY AS NEURONAL GLUE

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

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 [MEG, magnetoencephalography], frequency coherence, etc) should be repeatedly detected for a repeated cognitive act, say, in an odd-ball discrimination task conducted in the laboratory, but 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 major 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 experienced a wide attention, I need to give some larger context to what I wish to say, in order to unpack this last statement properly. This is done in the next two Sections. The reader will remark that the kind of approach presented attempts to build explicit bridges

between neuronal correlates and cognitive events. This is the spirit of the research direction outlined here.

THE MECHANISM: SYNCHRONY AS NEURONAL GLUE

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). 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 "reverberating" circuits. This entails that one should expect that patterned activity of neurons will display not only a temporal but a spatial pattern as well. 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 is what I wish to focus on now, which is a 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 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 process is completed (*e.g.*, recognition of a face and head orientation).

Now, how fast is fast? Consider the following reasoning[1]: 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 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 in 1942 by Adrian 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. Similar work with humans, using EEG, MEG and ERP (evoked-related potential), led Sheer and Galambos early on to similar ideas (see Sheer, 1970). Observations from neuropsychology also prompted Damasio to select phase locking as crucial (Damasio, 1990). Most recently, work from single unit studies of the visual systems in animals (for review see Singer, 1993) have made the idea quite popular. I will delve more in detail into 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

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[1]   I am indebted to Dr Francisco Aboitiz for suggesting this calculation to me.

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 shown 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 behavioral 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, low rhythms generally involve large neural masses, locked in a global state of hyper-synchrony (as in delta sleep or barbiturate-induced 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. We now turn to examine in more detail some of the empirical evidence.

THE EVIDENCE: MICRO AND MACRO

Macroscopic studies in humans and animals

Studies related to synchronization have used scalp EEG, MEG, or ECoG (electrocorticogram) recorded directly from the brain surface. Wakeful, alert behavioral states are generally characterized by a diffuse desynchronization of ongoing cortical rhythms. This is particularly observable in recordings from the surface, which typically disclose signals of low amplitude with a broad distribution of frequencies (from 10 to 60 Hz). It has been thought that desynchronized EEG signals largely reflect incoherence in the firing patterns of neurons from different cortical areas, which are simultaneously activated during arousal. A body of evidence has questioned this early concept.

It is worth mentioning here that many EEG studies already in the 60's, using a number of different approaches, provided evidence for fast synchronized cortical rhythms during arousal (Dumenko, 1961; Perez-Borja et al, 1961; Sheer and Grandstaff, 1970, reviewed in Sheer, 1970). Sheer, exploiting a fine temporal resolution analysis, has demonstrated that EEG signals recorded epidurally from the visual cortex of the cat show a relative increase in the power spectrum centered at 40 Hz, following a visual stimulus presentation. In his experiments an operant conditioning was employed; the stimuli consisted in a flickering light (at 7 or 3 Hz) and the cat had to press a bar to receive a food reward. The observed changes in the spectrum were closely related to the ongoing behavioral conditions. Oscillations at 40 Hz consistently appeared during the stimulus presentations and motor responses, and decreased during the feeding reinforcements. The shifts in the energy content of the spectrum were rather selective for higher frequencies, as the 20 Hz components persisted at relatively low levels until later after the reinforcements. Another interesting outcome of Sheer's experiments was the observation of an increase in the cross-power at the 40 Hz band between the visual and motor cortex (but not the auditory cortex), coincident with the learned behavioral responses (Sheer and Grandstaff, 1970). These findings attested for a synchronization of spatially separated regions of the cortex in a fully behavioral preparation (see also Dumenko, 1961). On the basis of these results, Sheer has further proposed a link between environmental spatio-temporal patterns and the organization of stable synchronous 'sub-assemblies of electrical activity'. It became clear that the designation *'desynchronized EEG'* indeed hid a variety of different temporal patterns.

More recently, human EEGs have demonstrated the appearance of gamma activity

following sensory stimuli and during cognitive tasks (Sheer, 1989). Galambos *et al* (1981) reported a gamma component in middle latency responses elicited by a periodic acoustic stimuli (500 Hz bursts at a 40 per sec rate). A modulation in evoked potentials in response to a periodic stimuli appeared in recordings of visual and tactile modalities (Galambos, 1992). Gamma oscillations in evoked potentials (at 40 Hz for the acoustic response), as just described, are indeed *induced* rhythms, since they do not depend on the stimulus rate presentation. Recent magnetic field investigations confirmed these results and made possible to infer a precise location and movement of the dipole(s) responsible for the gamma components during acoustic responses (Pantev *et al*, 1991). The oscillatory responses following acoustic stimuli may reflect an essential component of auditory cortex dynamics, and possibly account for the synchronization of different sub-regions of the auditory cortex.

Other studies on cortical dynamics using MEG imaging techniques display gamma activity in humans (Ribary *et al*, 1991; Llinás and Ribary, 1993). Oscillatory activity of cortical origin has been observed globally, extending to large regions over the entire hemisphere. During auditory discrimination the gamma component in the magnetic fields was markedly increased (30-50 Hz), with a peak at ~ 40 Hz. As pointed out by Galambos and coworkers (Galambos *et al*, 1981), stimulus characteristics are not simple determinants for the gamma profiles in the responses. Llinás and Ribary (1993) have directly tested it using single presentations of frequency-modulated tones. An important (and unexpected) result from magnetic field imaging studies was the observation of a systematic phase-shift in the cortical oscillations along the hemisphere. Single sweep recordings, using a 37-channels system, revealed that the oscillatory patterns present for different regions successively rotate the phase, from the superior frontal cortex, to parietal, parieto-occipital, and finally reaching the occipito-temporal areas. The observed oscillatory activity at 40 Hz is indeed highly organized in space and time, yielding an image of a wave traveling over the hemisphere, which can be reset by sensory stim-

ulation (Llinás refers to it as a 'scanning' process). This phenomenon is specific to a narrow frequency band (from 35- to 45-Hz), as other frequency bands do not exhibit phase-shift progressions. A further study of spontaneous magnetic activity during different arousal states showed that gamma oscillations are largely absent from delta sleep (Llinás and Ribary, 1993). In contrast, in subjects experiencing dreams (REM sleep), as in alert wakefulness states, gamma activity is clearly present. Moreover, during REM, sensory stimuli are not capable of resetting an ongoing scanning of activity over the hemisphere. Llinás and coworkers hypothesize that the dynamics of oscillatory activity in the cortex is due essentially to thalamocortical resonance. More specifically, the rostro-caudal scanning of gamma activity should result from a sequential activation of the intralaminary nucleus of the thalamus, which projects to lamina I over the entire cortex. The authors argue that the global scanning process could be essential for bringing unity in perceptual experience under a single temporal frame. This idea has a parallel in the work of Pöppel (1971), who sees gamma activity as a mechanism for temporal unity in conscious experience. It would be of interest to confirm the existence of this scanning activity by other laboratories.

The relevance of gamma oscillations for cognitive processes is evident in studies that account for attentional tasks. In humans, it has been shown that the gamma components in the EEG auditory responses is larger when the subjects paid selective attention to the stimuli (Tiitinen *et al*, 1993). These effects are clearly specific to the 40-Hz range, as the analysis carried for the lower components in the spectrum showed no differences if the stimuli were attended or not. A comparison between unattended stimuli and controls (a reading task) revealed that the 40-Hz responses have the same amplitude in the two cases. This later finding suggests that the mechanisms involved in selective attention are unlikely to arise by suppression (or gating) of activity elicited by unattended stimuli.

In animal models, cortical rhythms related to attentional states have extensively studied by Rougeul-Buser and Bouyer group in behaving cats and monkeys (Rougeul *et al,*

1979; Montaron *et al,* 1979; Bouyer *et al,* 1981). In their experiments, **intracortical** macropotentials were recorded from spatially separated regions of the cortex during focused attentive behavior. Whenever the animal stood motionless, focusing its attention on a target, fast cortical rhythms (ß, ~ 40 Hz in the cat) characteristically appeared in circumscribed foci, at the motor and parietal cortex (for location, see Bouyer *et al,* 1987). Moreover, simultaneous recordings from the thalamus showed a high degree of coherence between activity of a focus in the thalamic posterior group (*pars medialis,* POm) and the posterior parietal area (area 5a, Bouyer *et al,* 1981; see detailed study in Canu and Rougeul, 1992). In analogy to other focal cortical rhythms (*e.g.,* μ rhythm, ~ 14 Hz), it has been suggested that the ß rhythms related to focused attention rely largely on thalamic generators, under control of mesencephalic dopaminergic systems (Montaron *et al,* 1982; Delagrange *et al,* 1989). This hypothesis strengthens the importance of thalamic control for cortico-cortical interactions (Steriade *et al,* 1990); we will return to this issue later. It is important to stress that fast oscillations occur beyond the cortex, at various levels in the nervous system.

Local field potentials in behaving animals

The dynamics of the olfactory bulb and prepyriform cortex provide an interesting example of how gamma oscillations recorded with smaller electrode yielding a localized or so-called **local field** potential were first used to account for olfactory behavior of cats and rabbits (reviewed in Freeman, 1975, 1992). Freeman's studies were pioneering in many respects. First, the experiments were designed to follow the activity of the bulb and cortex in **motivated,** behaving animals. Their central insight was conceiving the study of neuronal dynamics on the basis of a sensory-motor coupling history, including the animal's experiences and present expectancies. Second, new techniques of recording and analysis were developed for disclosing the spatial patterns eventually hidden in the bulbar activity. These studies viewed in the dynamics underneath the activity of ensembles of cells (mass activity) the most relevant

description level of brain mechanisms, which could not be reducible to single cell properties. After many years of research, Freeman formulated a model, making explicit the highly non-linear nature of the olfactory bulb dynamics. To study the spatial pattern in the activity of the olfactory bulb, an array of electrodes was shaped to be chronically implanted over its surface. Local ECoG or local field potential signals could be recorded over a large extension of the bulb in otherwise awake, behaving animals (most of the experiments were done in rabbits). The animals were motivated by food or water deprivation, and trained to respond with sniffs or leaking for certain odorants, under reinforcement.

The olfactory bulb shows a prominent gamma activity, which was invariably present in all recording sites. The gamma oscillations in the bulb appeared during the inhalation phase of the respiration, in alert animals; they consisted in bursts of activity with frequencies ranging from 35 to 90 Hz (in the rabbit). This oscillatory behavior is better understood in terms of network properties. Previous unit recordings from the bulb has shown that in general single neurons have frequencies of discharge ~ 10 Hz, far below the frequency range of the bulbar EEG oscillations (Freeman, 1975). However, the coupling of single elements endows the system with a higher level rhythmicity. It has been shown that the (excitatory) mitral cells are coupled to the (inhibitory) granule cells by reciprocal synapses at the level of dendrites (Rall and Shepherd, 1968). Through these bi-directional connections, the mitral and granule cells behave as coupled oscillators, exerting over each other a negative feedback action.

In Freeman's experiments, the spatial patterning in neuronal activity was followed during the entire conditioning procedures. After proper signal filtering and integration, contour maps were obtained for the amplitude modulation of the gamma bursts over all recording sites. These maps were repeated for the many different behavioral contingencies the animal experienced, like in early familiarization, or during discrimination and recognition of specific odorants. Interestingly, spatial patterns seen in the contour maps were not particular to any specific

odorant and did not appear due to any external stimulation alone and could be followed over months. Changes could be seen only in case of presentation of a new conditioned stimulus. Thus, the establishment of a new sensori-motor coupling, behaviorally *relevant* for the animal, seemed necessary for the appearance of a different spatial pattern. Thus, these findings provided an experimental basis for views that depart from the metaphor of the brain as an information processing device. As remarked in Varela *et al* (1991, p 175): "As in the case of color, smell is not a passive mapping of external features but a creative form of enacting significance on the basis of the animal's embodied history".

More recently, multiple site recordings from the implanted electrodes in a behaving monkey provide evidence for the large scale nature of the temporal processes, beyond the olfactory cortex (Bressler *et al*, 1993). In fact, when a monkey is trained to perform a go-no go task, one observes episodes of increased broad-band coherence among local field potentials from sensory, motor and the association sites of the macaque performing a visual discrimination task. Widely distributed sites become coherent without involving other intervening sites, although the coherence is not restricted to the gamma band exclusively.

Single cell recordings

Oscillatory activity in the gamma range has been reported recently for different brain structures in vertebrates by means of single-cell recordings. A lot of the evidence comes from the visual system in anesthetized cats and awake monkeys (reviewed in Gray *et al*, 1992; Singer, 1993) and in the optic tectum (Neuenschwander and Varela, 1993; Neuenschwander *et al*, 1994). These studies have contributed with a large amount of experimental evidence pointing to temporal relations in the activity of neuronal populations as active components in visual perception. Beyond a purely descriptive account for the oscillatory nature of the signals, a number of predictions and testable hypothesis have been raised in respect of the functional role of gamma activity.

Local groups of cells in the visual cortex of the cat may exhibit a quasi-periodic firing pattern upon activation by a static or dynamic visual stimulus. These stimulus-induced oscillatory patterns are readily observable in local field potential (LFP) and multi-unit activity (MUA)[2] signals recorded from different visual areas, under conditions of light anesthesia (Gray and Singer, 1989; Eckhorn *et al*, 1988). They can also be followed at the level of single cell activity (Ghose and Freeman, 1992; Jagadeesh *et al*, 1992; Bringuier *et al*, 1992). Neurons located mainly in the supra- and infragranular layers show rhythmic firing when activated by an optimal or near-optimal stimulus. Most of the neurons exhibiting oscillatory activity are standard complex cells; in only a few cases oscillatory firing patterns could be observed for simple cells of layer IV (Jagadeesh *et al*, 1992; see also Ghose and Freeman, 1992).

The first detailed studies in adult cats pointed out values ranging from 35 to 50 Hz, which is a quite restricted frequency band. Larger data samplings revealed that oscillations indeed comprise a relatively broad distribution, with frequency values falling between 30 and 80 Hz (Engel *et al*, 1990; Ghose and Freeman, 1992). In kittens, stimulus-induced oscillations have distinct features. A clear bimodal distribution was found for a large proportion of the recordings studied, with peaks centered at 10 Hz (alpha band) and 35 Hz (Schillen *et al*, 1992). The occurrence of alpha and gamma responses in kittens seems to follow independent processes, as they may occur combined to each other or not. Visual alpha responses have also been reported in an intracellular study in the kitten (Bringuier *et al*, 1992), and in EEG recordings from adult behaving cats, in a

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2   Both signals, local field potential and multi-unit activity, can be recorded from a single electrode after proper differential filtering. The LFP is generally obtained through bandpass filtering the compound signal at 1-100 Hz. The exact nature of field potential signals is unknown, but they very likely represent summed up dendritic potentials and action potentials from neighboring neuronal populations (with an integration range of ~600 μm). The MUA, in turn, is obtained after filtering at a higher frequency band (0.5-3.0 kHz), followed by a spike event counting. A group of cells contribute to this signal, the number of cells depending on the characteristics of the electrode.
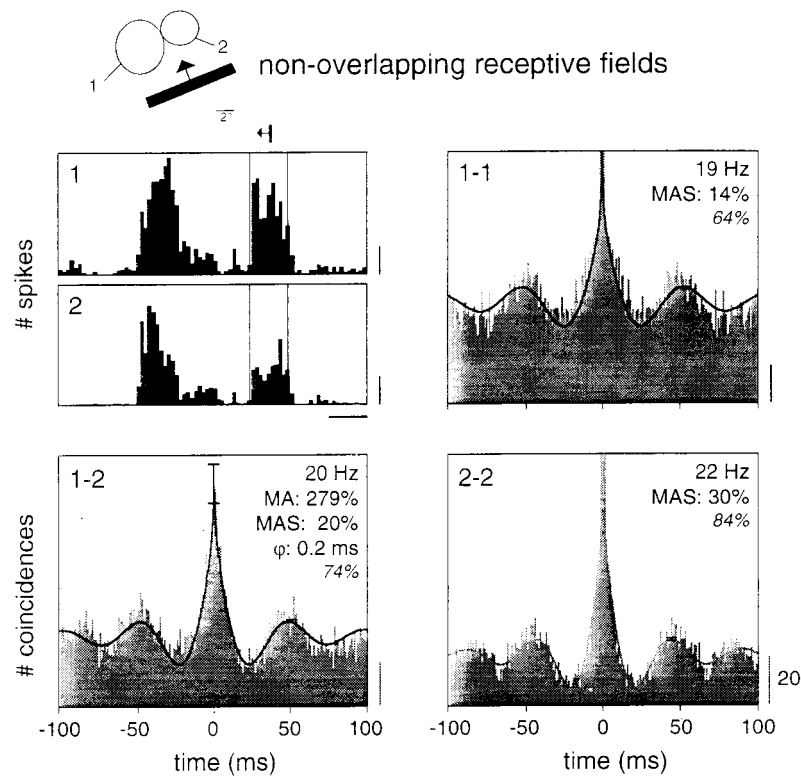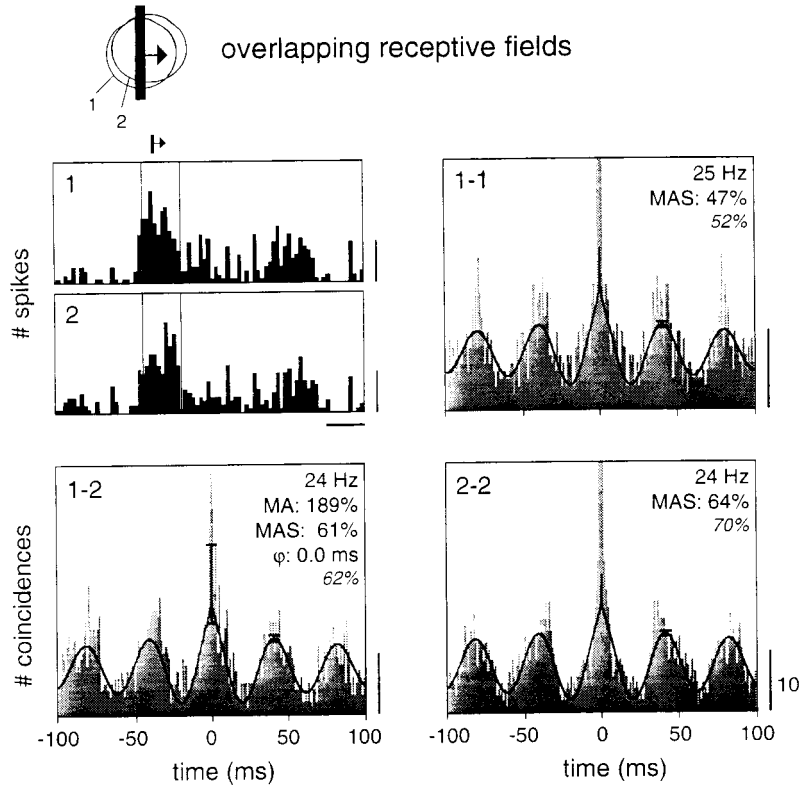
overlapping receptive fields

1	1-1 25 Hz MAS: 47% 52%
2	
1-2 24 Hz MA: 189% MAS: 61% φ: 0.0 ms 62%	2-2 24 Hz MAS: 64% 70%

spikes

coincidences

-100   -50   0   50   100
time (ms)

-100   -50   0   50   100
time (ms)

10

non-overlapping receptive fields

1	1-1 19 Hz MAS: 14% 64%
2	
1-2 20 Hz MA: 279% MAS: 20% φ: 0.2 ms 74%	2-2 22 Hz MAS: 30% 84%

spikes

coincidences

-100   -50   0   50   100
time (ms)

-100   -50   0   50   100
time (ms)

20

Fig 1. Synchronized oscillations in multi-unit activity recorded from cell groups of awake pigeon optic tectum (from Neuenschwander *et al*, 1994). Two clusters of cells coactivated by single light bar crossing receptive fields (inset). Cross- and auto-correlograms, calculated for responses to forward movement of stimulus, shown for each cell group in boxes as indicated (1-2, 1-1, 2-2). Thick line superimposed on each correlogram depicts a Gabor function used for evaluation of synchronization and oscillatory activity (error bars for central peak and first satellite peak are indicated). Peri-stimulus time histograms displayed in upper left; epochs used in computation of correlograms indicated by frames (time scale bar, 500 ms; amplitude, 10 spikes).

    a) Above, for two *overlapping receptive fields*, clear oscillatory modulation present both in cross- and auto-correlograms, with frequency ~ 24 Hz. Notice that central peak in cross-correlogram lies at zero-time lag, indicating no phase difference in oscillatory activity of the two cell groups (φ, phase). MA, modulation amplitude at central peak. MAS, modulation amplitude at first satellite peak. Percentage values indicated below modulation indexes express goodness of fit. Correlation functions are averages across 10 trials. Recordings made with two electrodes separated by 0.3 mm. Analysis window, 500 ms.

    b) Below, synchronization in multi-unit activity recorded from cell groups with *non-overlapping receptive fields*. Strong synchronization evident without accompanying oscillatory activity. Observe that peak in correlogram is roughly centered (φ, time lag). MA, modulation amplitude of central peak. Correlograms calculated for responses to movement of stimulus in forward direction. Light bar oriented in a manner that the two cell groups could be simultaneously activated. In PSTH, time scale bar, 500 ms; amplitude, 20 spikes. Analysis window, 500 ms. Recordings made from two electrodes separated by 1 mm.

situation that involves expectancy (Chatilla *et al*, 1992).

The visual gamma oscillations in the cat are very robust (in kittens even more than in the adult cats). In general, autocorrelation functions averaged over many trials yield one or more satellite peaks, what reflects fairly stable frequencies over the oscillatory events. However, single trial analysis have shown clearly that stimulus-induced oscillations are not strictly periodic, even for intervals as short as tens of milliseconds (Gray *et al*, 1990; Engel *et al*, 1990). A high variability is seen in the frequency and amplitude across different trials, despite the conditions of recording being strictly the same. Also the duration of oscillatory activity is variable (50-400 ms). Oscillatory activity may occur as single or multiple events during the responses, within variable latencies after the stimulus presentation (Gray and Singer, 1989; Gray *et al*, 1992). It is important to notice that the phase of oscillatory events is not locked to the timing of the stimulus[3]. Thus, oscillatory responses can *not* be explained in terms of the spatial organization of receptive fields, or any eventual periodicity present in the stimulus itself.

The above mentioned studies were performed in lightly anesthetized cats. An early study has demonstrated that visual oscillations indeed occur in awake mammals, and they are not merely a by-product of anesthetics (Raether *et al*, 1989). Recordings from

behaving monkeys further ruled out this possibility. In the awake monkey, oscillatory activity has been reported for V1 (Freeman and Dijk, 1987; Eckhorn *et al*, 1993), MT (Kreiter and Singer, 1992), and IT (Nakamura *et al*, 1991, 1992; Young *et al*, 1992). Two studies, however, failed to show oscillatory responses to static stimuli in the inferior temporal cortex (Gawne *et al*, 1991; Tovée and Rolls, 1992). The overall characteristics of the oscillatory activity observed in behaving monkeys are similar to those described for anesthetized cats. Nevertheless, the oscillatory events in the visual cortex of the monkey are lesser robust in comparison to those of the cat. They show greater variability in frequencies and shorter duration (100-300 ms; Kreiter and Singer, 1992).

In fact, gamma oscillations may constitute a rather basic property in the mammalian neocortex dynamics, but are not exclusive to it. This has been clearly shown by the studies in the optic tectum of awake pigeons we have conducted (Neuenschwander and Varela, 1993; Neuenschwander *et al*, 1994). Figure 1 shows an example of this kind of synchrony at the level of spikes between two tectal cells. Interestingly, the results indicate that the optic tectum's oscillations and synchrony resemble strongly the monkey cortex (more than the cats), except in the dominant frequency range which shift down to about 30 Hz. These studies are important since they strengthen the universality of oscillations as a carrier for synchrony. A recent study in an invertebrate olfactory behavior also makes oscillations an essential element of the neural basis for behavior (Laurent and Davidowitz,

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[3] Generally, to control for stimulus-locked responses, a shuffled correlogram (shift predictor, Perkel *et al.*, 1967) is computed over different trials.

1994), raising the possibility that the universality of synchrony as neuronal glue may reach farther than expected.

The occurrence of oscillatory responses are not strictly dependent on stimulus features, as contrast, orientation, and length, given comparable level of firing rates (Gray *et al*, 1992; Ghose and Freeman, 1992). In the visual system, static or moving light bars and gratings are equally capable of inducing oscillatory activity, but the frequency of oscillatory responses is largely independent of the different stimulus parameters. Thus, gamma activity cannot be viewed as an "encoding" mechanism, and *per se* does not constitute a "representation" in the frequency domain (this inference could be also drawn from the studies of the olfactory bulb dynamics).

If orientation tuning curves are computed by taking the energy content of the spectrum at the gamma range, both LFP and MUA signals yield similar profiles (Gray and Singer, 1989; Neuenschwander and Varela, 1993). This suggests that the oscillations in the LFP and the MUA are likely to express the underlying temporal structure in the firing of a local group of neurons. As we have evoked in the case of the olfactory bulb, one cell does not need to fire indefinitely with precise intervals to be synchronized to an ongoing field potential. It may fire *solidaire* to one cycle and skip the next, rather stochastically. This would explain why oscillations are hard to see at the single cell level. It is rather the synchronized activity of the *ensemble* that confers the rhythmicity observed in the macro-signals. In the MUA, oscillatory patterning manifests as recurrent grouped discharges following variable periods of silence. Visual oscillations have not a clock-like periodicity (as certain thalamic neurons do); they can be better described as structured responses, characterized by grouped discharges, which reflect a local synchronization in the activity of the neurons.

In the studies in the visual cortex of the cat and monkey, a stimulus was likely to induce an oscillatory pattern in the activity of the cells, which were, otherwise, spontaneously **non**-oscillating. Interestingly, during cortical somatosensory responses

rather the opposite seems to occur. Ahissar and Vaadia (1990), recording from the area SII of an awake monkey, have shown that half of the cells studied do exhibit oscillations **spontaneously**. During tactile stimulation, however, the ongoing oscillations are either diminished or completely disrupted. These suppressive effects are not dependent on behavioral contingencies, such as alertness, since they could also be demonstrated under anesthesia. These results are rather different from those obtained for the visual cortex of the cat, though gamma oscillations were present in the somatosensory cortex cell discharges. Ahissar and Vaadia (1990) proposed a model based on cortico-thalamic loops, capable of measuring the modulation in frequency of incoming somatosensory signals (the spatial frequency of the surface of objects are transformed to temporal frequency of the cell responses at the receptor level).

Given the density of reciprocal connections in the cortex, it seems unlikely that the synchronization of cortical activity should depend entirely on thalamic interactions. Obviously, cortico-cortical interactions have an extremely important role in perception; and the dynamics underlying cell assemblies formation may also arise from mechanisms intrinsic to the cortex itself. In this respect, the notion of a thalamic **control** may be rather misleading. As studies of interhemispheric functional connectivity (which do not depend directly on a thalamic interplay) show, the cortex is fully capable of large cooperative interactions, apparently without need of a direct thalamic coordination.

CODA: THE CORE HYPOTHESIS

After reviewing in some detail the merits of the gamma binding mechanism, 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 coher-

ency-generating process generated by that nervous system.

To clarify, let direct the reader to the diagram in Figure 2 and 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 the multiple current 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 activation 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 (I have been influenced by Chiel (1993) for this unusual approach to neural activity). 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.

Ongoing neural activity is assimilated in the dominant assembly

It should be also clear that the neural events that participate in this process of synthetic interpretation are both derived 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 among other. 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 of the dimensions of mental states: there is a reciprocity in that a mental state can act on neural events in an effective manner. For this to be more than a simple dualistic rehash it is essential that the dominant interpretation be itself a neural event. Whence the odd-looking part of my definition that requires a neural event to be the basis of interpretation of another class (of non synchronous) 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 the basic cognitive-mental space is topological and not topographical, in that it is a question of a hypergraph of synchronous relationship rather than one of localization. The process underlying this cerebral hermeneutics itself is, by hypothesis, an ongoing phenomenon, providing a continual emergence.

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 an interpretation can happen. The alleged process must be universal enough to be supported and present in the nervous system of animals, at least of all higher vertebrates, and its presence or absence can help identify where 'sentiency' is present in the sense presented here. The above evidence described the neural process which make it plausible. The specificity of a synchronous hypergraph present for every

time

behavior

turns head and foveates   *recognized face*

size of assembly   % of total

coherence in gamma band   1.0

                                        0,5
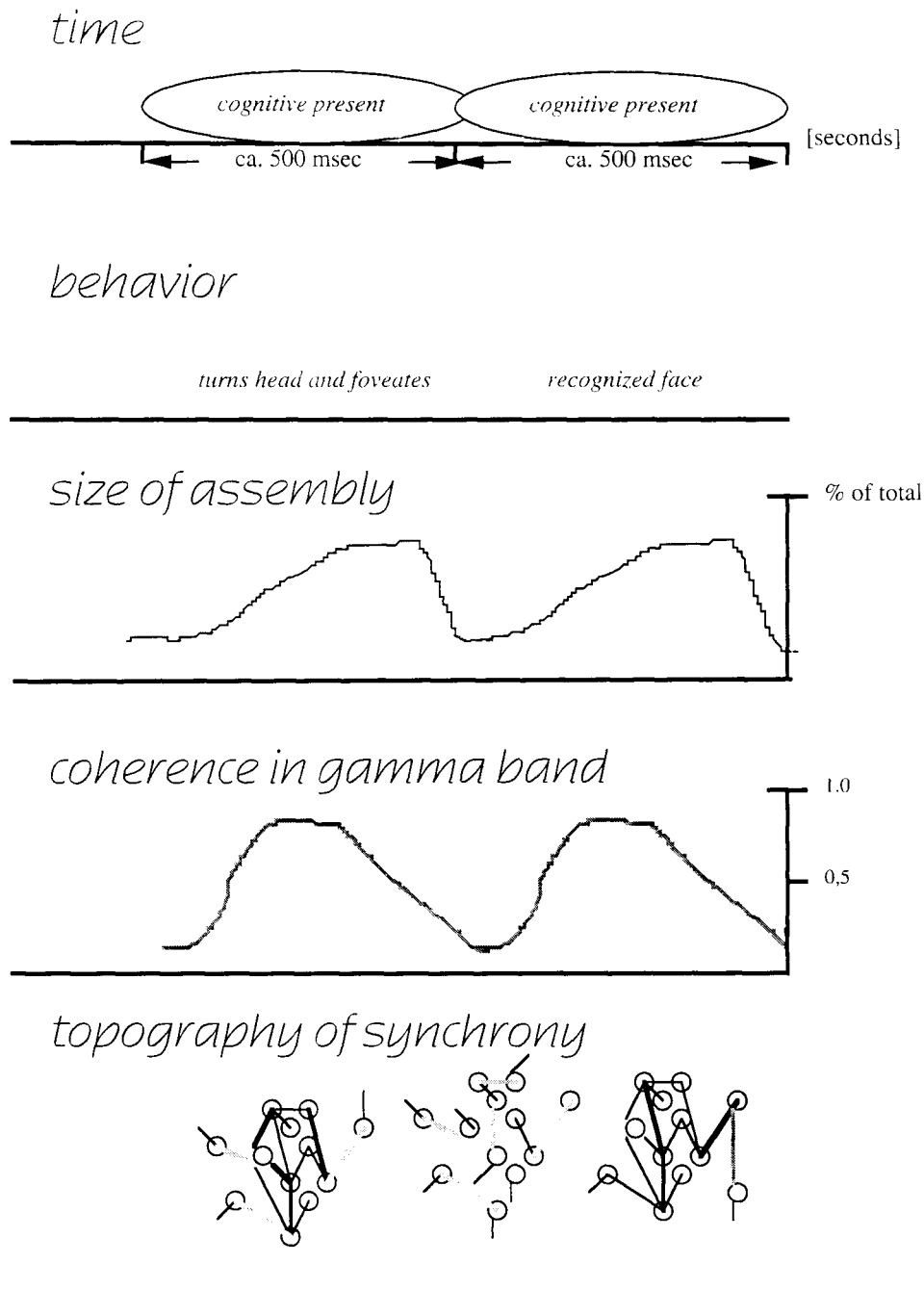
topography of synchrony

Fig 2. Diagram depicting binding hypothesis. Within an incompressible temporal frame (above), a cognitive activity (such as head turning) takes place as result of recruitment of widely distributed ensemble through increased gamma band coherence. Neural correlates of cognitive act presented as synchronous neural hypergraph, wherein other concurrent neural activities can be dynamically incorporated or rejected as indicated in bottom scheme. Circles, brain regions; width of lines, strengths of synchrony.

mental-cognitive state is also made plausible from MEG-EEG studies, but only a systematic study of this millisecond process during mental experience will give a more 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 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:

a) *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.
b) *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 inextensible duration.
c) *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.
d) *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 this approach. 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"; and Searle (1992) and his insistence on irreducible first person accounts]. 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.

REFERENCES

ABOITIZ F, SCHEIBEL AB, FISHER RS, ZEIDEL E (1992) Fiber composition of the human corpus callosum. Brain Res 598: 143-153
AHISSAR E, VAADIA E (1990) Oscillatory activity of single units in a somatosensory cortex of awake monkey and their possible role in texture analysis. Proc Natl Acad Sci USA 87: 8935-8939
AHISSAR E, VAADIA E, AHISSAR M, BERGMAN H, AIRELI A, ABELES M (1992) Dependence of cortical plasticity on correlated activity of single neurons and on behavior context. Science 257: 1412-1415
BASAR E (1992) Brain natural frequencies are causal factors for resonances and induced rhythms. In: BASAR E, BULLOCK TH (eds) Induced Rhythms in the Brain. Berlin: Birkhäuser. pp 425-467
BASAR E, BASAR-EROGLU C, PARNEFJORD R, RAHN E, SCHÜRMANN M (1992) Evoked potentials:

Ensembles of brain induced rhythmicities in the alpha, theta and gamma ranges. In: BASAR E, BULLOCK TH (eds) Induced Rhythms in the Brain. Berlin: Birkhäuser. pp 425-467

BONHOFFER T, STAIGER V, AERTSEN A (1989) Synaptic plasticity in rat hippocampal slice culture. Proc Natl Acad Sci USA 86: 8113-8117

BOUYER JJ, MONTARON MF, ROUGEUL A (1981) Fast fronto-parietal rhythms during combined focused attentive behaviour and immobility in cat: Cortical and thalamic localizations. EEG Clin Neurophysiol 51: 244-252

BOUYER JJ, MONTARON MF, VAHNÉE JM, ALBERT MP, ROUGEUL A (1987) Anatomical localization of cortical beta rhythms in cat. Neuroscience 22: 863-869

BRAITENBERG V (1978) Cell assemblies in the cerebral cortex. In: HEIM R, PLAM G (eds) Theoretical Approaches to Complex Systems, Lecture Notes in Biomathematics N° 21. Berlin: Springer Verlag. pp 171-188

BRESSLER S, COPPOLA R, NAKAMURA R (1993) Episodic multiregional cortical coherence at multiple frequencies during visual task performance. Nature 366: 253-155

BRINGUIER V, FRÉGNAC Y, DEBANNE D, SHULTZ D, BARANYI A (1992) Synaptic origin of rhythmic visually evoked activity in kitten area 17 neurons. NeuroReport 3: 1065-1068

CANU M-H, ROUGEUL A (1992) Nucleus reticularis thalami participates in sleep spindles, not in ß rhythms concomitant with attention in cat. C R Acad Sci Paris 315: 513-520

CHATILA M, MILLERET C, BUSER P, ROUGEUL A (1992) A 10 Hz "alpha-like" rhythm in the visual cortex of the waking cat. EEG Clin Neurophysiol 83: 217-222

CHIEL HJ (1993) Cognitive neuroethology: an approach to understanding biological neural networks. In: STERLING LS (ed) Intelligent Systems. New York: Plenum. pp 143-167

DELAGRANGE P, TADJER D, BOUYER JJ, ROUGEUL A, CONRATH M (1989) Effect of DSP4, a neurotoxic agent, on attentive behaviour and related electrocortical activity in the cat. Behav Brain Res 33: 33-44

DAMASIO A (1990) Synchronous activation in multiple cortical regions: a mechanism for recall. Semin Neurosci 2: 27-296

DENNETT D (1992) Consciousness Explained. New York: Little Brown

DUMENKO WN (1961) Veränderungen der elektrischen Rindenaktivität bei Hunden bei der Bildung eines Stereotyps motorischer bedingter Reflexe. Pavlov Z Höhere Nerventätigkeit 11: 184-191

ECKHORN R, BAUER R, JORDAN W, BROSCH M, KRUSE W, MUNK M, REITBOECK HJ (1988) Coherent oscillations: a mechanism of feature linking in the visual cortex? Multiple electrode and correlation analysis in the cat. Biol Cybern 60: 121-130

ECKHORN R, FRIEN A, BAUER R, WOELBERN T, KEHR H (1993) High frequency (60-90 Hz) oscillations in primate visual cortex of awake monkey. NeuroReport 4: 243-246

ENGEL AK, KÖNIG P, GRAY CM, SINGER W (1990) Stimulus-dependent neuronal oscillations in cat visual cortex: inter-columnar interaction as determined by cross-correlation analysis. Eur J Neurosci 2: 588-606

FLANNAGAN O (1992) Consciousness Reconsidered. Cambridge, MA: MIT Press

FREEMAN WJ (1975) Mass Action in the Nervous System. New York: Academic Press

FREEMAN WJ (1992) Predictions on neocortical dynamics derived from studies in paleocortex. In: BASAR E,

BULLOCK TH (eds) Induced Rhythms in the Brain. Berlin: Birkhäuser. pp 183-199

FREEMAN WJ, DIJK BW v (1987) Spatial patterns of visual cortical fast EEG during conditioned reflex in a rhesus monkey. Brain Res 422: 267-276

GALAMBOS R (1992) A comparison of certain gamma band (40-Hz) brain rhythms in cat and man. In: BASAR E, BULLOCK TH (eds) Induced Rhythms in the Brain. Berlin: Birkhäuser. pp 201-216

GALAMBOS R, MAKEIG S, TALMOCHOFF PJ (1981) A 40-Hz auditory potential recorded from the human scalp. Proc Natl Acad Sci USA 78: 2643-2647

GAWNE TJ, ESKANDAR EN, RICHMOND BJ, OPTICAN LM (1991) Oscillations in the responses of neurons in the inferior temporal cortex are not driven by stationary visual stimuli. Soc Neurosci Abstr 17: 180.18

GHOSE GM, FREEMAN RD (1992) Oscillatory discharge in the visual system: does it have a functional role? J Neurophysiol 68: 1558-1574

GLASS L, MACKEY M (1988) From Clocks to Rhythms. Princeton: Princeton Univ Press

GRAY CM, SINGER W (1989) Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex. Proc Natl Acad Sci USA 86: 1698-1702

GRAY CM, ENGEL AK, KÖNIG P, SINGER W (1990) Stimulus-dependent neuronal oscillations in cat visual cortex: receptive field properties, feature dependence. Eur J Neurosci 2: 607-619

GRAY CM, ENGEL AK, KÖNIG P, SINGER W (1992) Synchronization of oscillatory neuronal responses in cat visual cortex: temporal properties. Eur J Neurosci 8: 337-347

HEBB O (1949) The Organization of Behavior: A Neuropsychological Theory. New York: Wiley

JAGADEESH B, GRAY CM, FERSTER D (1992) Visually evoked oscillations of membrane potential in cells of cat visual cortex. Science 257: 552-554

KREITER AK, SINGER W (1992) Oscillatory neuronal responses in the visual cortex of the awake monkey. Eur J Neurosci 4: 369-375

LAURENT G, DAVIDOWITZ H (1994) Encoding of olfactory information with oscillating neural assemblies. Science 265: 1872-1875

LLINAS R, RIBARY U (1993) Coherent 40-oscillation characterizes dream state in humans. Proc Natl Acad Sci USA 90: 2078-2081

LOPES DA SILVA F (1992) The rhythmic slow activity (theta) of the limbic cortex: An oscillation in search ofa function. In: BASAR E, BULLOCK TH (eds) Induced Rhythms in the Brain. Berlin: Birkhäuser. pp 83-102

MANGUN GR (1992) Human visual evoked potentials: Induced rhythms or separable components? In: BASAR E, BULLOCK TH (eds) Induced Rhythms in the Brain. Berlin: Birkhäuser. pp 217-231

MONTARON MF, BOUYER JJ, ROUGEUL-BUSER A (1979) Relations entre l'attention et le rythme mu chez le chat et le singe. Rev EEG Neurophysiol 9: 333-339

MONTARON MF, BOUYER JJ, ROUGEUL-BUSER A (1982) Ventral mesencephalic tegmentum (VMT) controls electrocortical beta rhythms and associated attentive behaviour in the cat. Behav Brain Res 6: 129-145

NAKAMURA K, MIKAMI A, KUBOTA K (1991) Unique oscillatory activity related to visual processing in the temporal pole of monkeys. Neurosci Res 12: 293-299

NAKAMURA K, MIKAMI A, KUBOTA K (1992) Oscillatory neuronal activity related to visual short-term memory in monkey temporal pole. NeuroReport 3: 117-120

NEUENSCHWANDER S, VARELA F (1993) Visually triggered neuronal oscillations in the pigeon: an autocorrelation study of tectal activity. Eur J Neurosci 5: 870-881

NEUENSCHWANDER S, ENGEL A, KÖNIG P, SINGER W, VARELA F (1994) Synchronous activity in the optic tectum of awake pigeons. Vis Neurosci (in press)

PANTEV C, MAKEIG S, HOKE M, GALAMBOS R, HAMPSON S, GALLEN C (1991) Human auditory evoked gamma-band magnetic fields. Proc Natl Acad Sci USA 88: 8996-9000

PERKEL DH, GERSTEIN GL, MOORE GP (1967) Neuronal spike trains and stochastic point process. I. The single spike train. Biophys J 7: 391-418

PEREZ-BORJA C, TYCE FA, MACDONALD C, UIHLEIN A (1961) Depth electrographic studies of a local fast response to sensory stimulation in the human. EEG Clin Neurophysiol 13: 695-702

PFURTSCHELLER G, KLIMESCH W (1992) Event-related synchronization and desynchronization of alpha and beta waves in a cognitive task. In: BASAR E, BULLOCK TH (eds) Induced Rhythms in the Brain. Berlin: Birkhäuser. pp 117-128

PFURTSCHELLER G, NEUPER C (1992) Simultaneous EEG 10 Hz desynchronization and 40 Hz synchronization during finger movements. NeuroReport 3: 1057-1060

PÖPPEL E (1971) Oscillations as possible basis for time perception. 1st Conference of Society for the Study of Time, Oberwolfach

RAETHER A, GRAY CM, SINGER W (1989) Intercolumnar interactions of oscillatory neuronal responses in the visual cortex of alert cats. Eur J Neurosci. Suppl 2: 72.5

RALL W, SHEPHERD GM (1968) Theoretical reconstruction of field potentials and dendrodendritic synaptic interactions in the olfactory bulb. J Neurophysiol 31: 884-915

RIBARY U, IOANNIDES AA, SINGH KD, HASSON R, BOLTON JPR, LADO F, MOGILNER A, LLINAS R (1991) Magnetic field tomography of coherent thalamocortical 40-Hz oscillations in humans. Proc Natl Acad Sci USA 88: 11037-11041

ROUGEUL A, BOUYER JJ, DEDET L, DEBRAY O (1979) Fast somato-parietal rhythms during combined focal attention and immobility in baboon and squirrel monkey. EEG Clin Neurophysiol 46: 310-319

SCHILLEN TB, KÖNIG P, ENGEL AK, SINGER W (1992) Development of oscillatory neuronal activity in the visual cortex of the cat. Eur J Neurosci. Suppl 5: 3043

SEARLE J (1992) The Rediscovery of Mind. Cambridge, MA: MIT Press

SHEER DE (1970) Electrophysiological correlates of memory consolidation. In: UNGAR G (ed) Molecular Mechanisms in Memory and Learning. New York: Plenum. pp 177-211

SHEER DE (1989) Sensory and cognitive 40-Hz event-related potentials: Behavioral correlates, brain function, and clinical application. In: BASAR E, BULLOCK TH (eds) Brain Dynamics. Berlin: Springer. pp 339-374

SHEER DE, GRANDSTAFF N (1970) Computer-analysis of electrical activity in the brain and its relation to behavior. In: WYCIS HT (ed) Current Research in Neurosciences. New York: Karger. pp 160-172

SINGER W (1993) Synchronization of cortical activity and its putative role in information processing and learning. Annu Rev Physiol 55: 349-374

STERIADE M, JONES EG, LLINAS RR (1990) Thalamic Oscillations and Signaling. New York: Wiley

TIITINEN H, SINKKONNEN J, REINIKAINEN K, ALHO K, LAVIKAINEN J, NÄÄTÄNEN R (1993) Selective attention enhances the auditory 40-Hz transient response in humans. Nature 364: 59-60

TOVÉE MJ, ROLLS ET (1992) Oscillatory activity is not evident in the primate temporal visual cortex with static stimuli. NeuroReport 3: 369-372

VARELA F, TORO A, JOHN ER, SCHWARTZ E (1981) Perceptual framing and cortical alpha rhythms. Neuropsychologia 19: 675-686

VARELA FJ, THOMPSON E, ROSCH E (1991) The Embodied Mind: Cognitive Science and Human Experience. Cambridge, MA: MIT Press

WILSON HR, COWAN JD (1973) A mathematical theory of the functional dynamics of cortical and thalamic nervous tissue. Kybernetik 13: 55-80

YOUNG MP, TANAKA K, YAMANE S (1992) On oscillating neuronal responses in the visual cortex of the monkey. J Neurophysiol 67: 1464-1474