

The roles of gamma-band oscillatory synchrony in human visual cognition

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1. ABSTRACT

Oscillatory synchrony in the gamma (30-120 Hz) range has initially been related both theoretically and experimentally to visual grouping. Its functional role in human visual cognition turns out to be much broader, especially when attention, memory or awareness are concerned. Induced gamma oscillations are thus not related to a single cognitive function, and are probably better understood in terms of a population mechanism taking advantage of the neuron's fine temporal tuning: the 10-30 ms time precision imposed by gamma-band rhythms could favor the selective transmission of synchronized information (attention) and foster synaptic plasticity (memory). Besides, gamma oscillatory synchrony also seems related to the emergence of visual awareness. The recent discovery that gamma oscillations could appear simultaneously in distinct areas at distinct frequencies and with different functional correlates further suggests the existence of a flexible multiplexing schema, integrating frequency bands within the gamma range but also at lower frequency bands. Understanding how and when oscillations at different frequencies interact has become a major challenge for the years to come.

2. INTRODUCTION

Spontaneous brain activity, as measured with electro- or magneto-encephalography (EEG or MEG), is best described by its frequency content, from low (delta range, <3 Hz; theta range, 4-7 Hz) to mid (alpha range, 8-12 Hz; beta range, 15-25 Hz) and high (gamma range, 30-120 Hz) frequencies. The frequency content of EEG signals has long been used as an index (of brain development, of pathological disorders, of sleep stages), with alertness and cognitively active states being characterized by an increase in beta and gamma-range power. In parallel, event-related potentials (ERPs), the neural transient responses to a stimulus, have provided invaluable insights on the temporal organization of the cascade of processing stages involved in any cognitive task. About ten years ago it appeared that visual stimuli elicited not only ERPs, but also deeply affected the frequency content of the EEG, particularly in the gamma range (1-3).

This discovery was directly linked to the proposal that gamma oscillations could play a causal role in visual grouping (4-6). This proposal can be briefly summarized as follows: when an object is analyzed in the visual system,

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dedicated areas process each of its features separately – motion in MT, shape in IT for instance. At some point, those fragmented pieces of information have to be combined in a single coherent percept. The binding-by-synchrony hypothesis postulates that all the neurons distributed in distinct visual areas that participate in the processing of the same object synchronize their firing on an oscillatory mode to signal they are operating on the same object. This theory has a number of theoretical advantages over more classical theories holding that features are integrated by convergence on specialized neurons. For detailed reviews of the theoretical pros and cons of the binding-by-synchrony hypothesis, I refer the reader to the special 1999 issue of *Neuron* on that topic, in particular (7) and (8).

The binding-by-synchrony hypothesis has had a profound influence on human EEG/MEG research. First of all, it led to the characterization of induced oscillatory activities, obtained in response to a stimulus but that are not strictly phase-locked to stimulus onset, as opposed to classical ERPs (figure 1a). This led to a wealth of new experimental results that will be reviewed below. Second, it highlighted the importance of temporal precision for neural activity: whether or not a neuron responds to incoming excitatory post-synaptic potentials (EPSPs) depends on the temporal overlap between the EPSPs, and synaptic plasticity is highly dependent on the relative timing of inputs and outputs (9). The crucial integration window lasts about 10-30 ms, a duration that fits well with temporal patterning imposed by oscillatory synchrony in the gamma range (10, 11). Last, it renewed an interest for emerging population phenomena. Indeed, oscillatory synchrony is fundamentally a population pattern, emerging at the group level. With a few notable exceptions (12), single neurons seldom oscillate, whereas interconnected non oscillating neurons easily produce sustained oscillations (13). As a result, oscillatory synchrony is best observed at the population level: it is easier to detect in multi-unit and than single-unit recordings (14, 15), and can be observed with the naked eye (figure 1A) in local field potentials in monkeys (16, 17) or intracranial EEG recordings in humans (18, 19).

3. WHAT IS MEANT BY "OSCILLATORY SYNCHRONY"?

Most of the electrophysiological data in humans are obtained at the scalp level. Scalp EEG or MEG signals fundamentally reflect the synchronization of weak synaptic currents across a large number of neurons: scalp signals therefore necessarily reflect *synchronized* neural activity. A power increase in a given frequency band at an electrode or MEG sensor is thus considered as a measure of local oscillatory synchrony, probably generated through local, within-area neural interactions. Long-range oscillatory synchrony, thought to arise from between-area recurrent feed-forward / feed-back loops, is best characterized by phase synchronization (20), although some care has to be taken when using this measure at the scalp level (21). Whether local or long-distance, the truly oscillatory nature of a power or phase-synchronization increase might be difficult to assess: are the same neurons engaged at each

cycle? Are there enough cycles to define an oscillation, or is it rather a transient, broad-band phenomenon? In the following review of the experimental literature the equivalence between power or phase-synchrony with local or long-distance oscillatory synchrony will be assumed, but will be further discussed at the end of the paper.

4. OSCILLATORY SYNCHRONY AND VISUAL BINDING

In 1989, the seminal paper of Gray and colleagues (22) showed that anaesthetized cats' neurons synchronized their firing on an oscillatory mode in the gamma range when the stimulus was perceived as coherent by a human observer, without significant effects on their mean firing rate. This highly influential result thus suggested that oscillatory synchrony could act as a "glue" binding together neural activities participating in the same cognitive process.

In human EEG, perceiving a coherent meaningful visual object is consistently accompanied by a burst of induced gamma oscillatory synchrony over occipital electrodes between 200 and 300 ms (1-3, 23-32). When the perceived object spans the vertical meridian, gamma oscillations in both hemispheres become phase-locked (33). Interestingly, the latency of this burst of oscillations correlates with object recognition delays (34). This large amount of convergent results from different laboratories clearly indicates that perceiving a coherent object is accompanied by induced oscillations in the gamma range in humans. They thus lend strong support to the idea that temporally coordinated neural activities, as indexed by oscillatory synchrony measures, are involved in the formation of a coherent percept.

Importantly, in several of those experiments (3, 32, 34) no event-related potential component correlated with the presence of a coherent percept: induced gamma power modulations thus index functional neural properties that are distinct from those revealed by ERPs. These grouping-related gamma oscillations can nevertheless be further modulated by other experimental parameters, such as stimulus spatial frequency (35), speed (36) or contrast (37), or overall task difficulty (38-40).

Where does this activity come from? Topography can be highly informative when care is taken to exclude from the data any muscular artefacts, that preferentially affect peripheral sensors (25, 41, 42). In visual tasks induced gamma oscillations most often peak at posterior sensors, suggesting occipital sources. Attempts at localizing the cortical sources of induced gamma activities from surface data produced surprisingly disparate results: a widespread network, encompassing occipital, temporal, parietal and frontal regions (31) or a focal activation, confined to the occipital pole (43). Such differences may arise from the experimental designs (static object categorization vs. moving stimuli passive viewing), inverse model chosen (discrete spline inverse solution vs. spatial filtering), but a major difference between these two studies probably lies in the different signals used, EEG vs. MEG.

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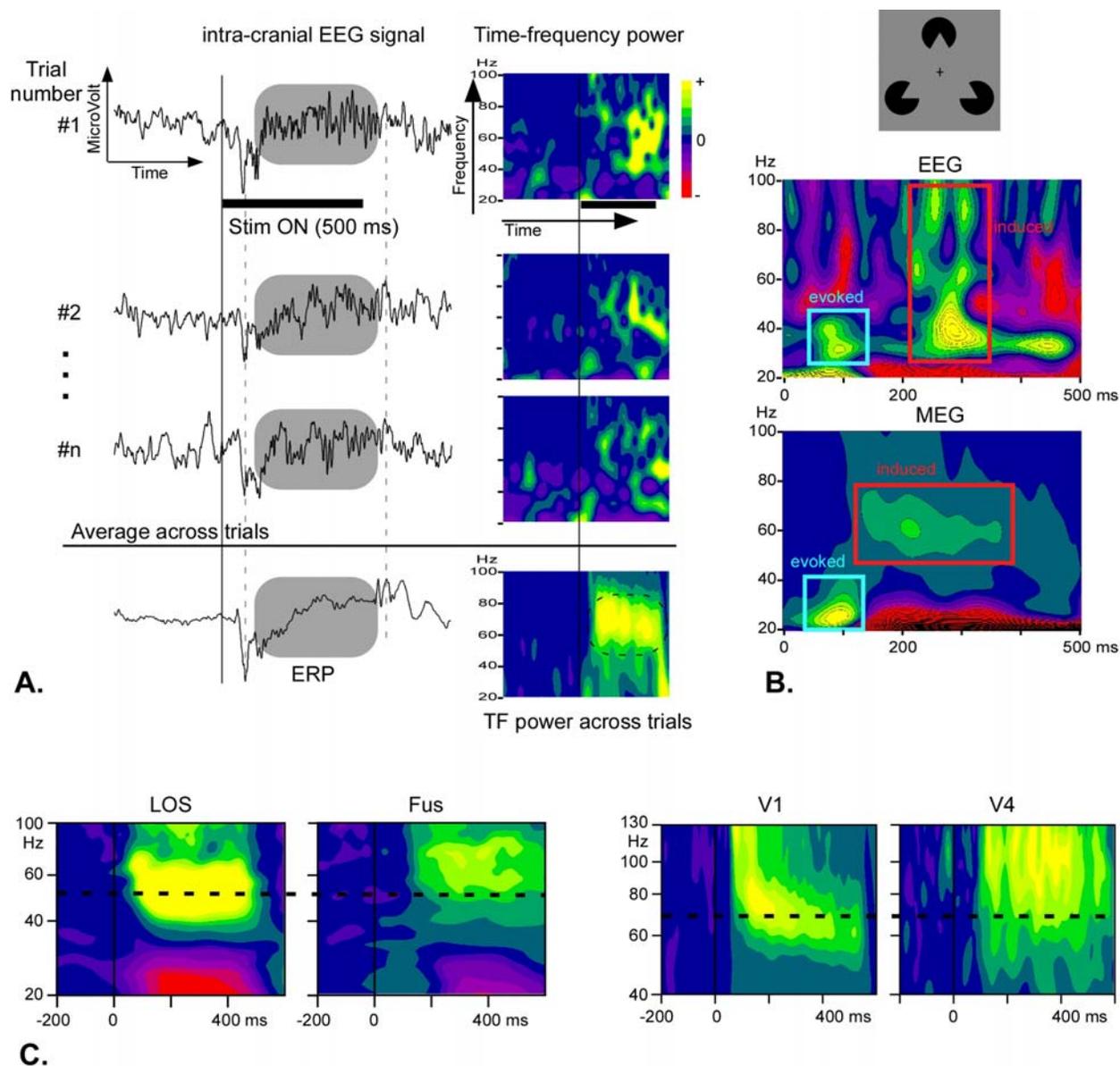


Figure 1. A. Gamma oscillations in single trials. We recorded EEG data at the cortical surface of anesthetized monkeys (17). A transient event-related response, perfectly time-locked to stimulus onset and offset (dashed lines) is followed by a sustained episode of gamma oscillations (shaded area). Because of their loose time relationship with stimulus onset, gamma oscillations disappear from the event-related potential, while they can be easily characterized on the time-frequency power across trials. It should be noted that it is difficult to determine whether gamma-band activity is truly oscillatory in each single trial, although the time-frequency average across trials displays a quite narrow-band sustained gamma power increase. B. A discrepancy between EEG and MEG data. In response to a coherent stimulus, occipital EEG data typically show a transient 200-300 ms enhancement of induced power from 30 up to 90 Hz. The profile of MEG data recorded simultaneously (130) is quite different: induced oscillations appear around 60 Hz, with a more sustained time-course. C. Distinct areas may thus engage simultaneously in gamma oscillatory synchrony at different frequencies. Left: simultaneous intra-cranial recordings the lateral occipital sulcus (LOS) and fusiform gyrus (Fus) of an epileptic patient (19). Right: electrocorticogram over area V1 and V4 in the anesthetized monkey (17).

MEG and EEG data do indeed provide a quite different picture of visually induced oscillations (figure 1B): while EEG data reveal a short-lived burst of oscillatory

synchrony between 30 and 60 Hz and 200 and 300 ms, MEG studies consistently report sustained oscillations at higher frequencies (37, 43-46). This sustained temporal profile is consistent with observations in local field

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potentials in monkeys (17) or in intra-cranial data in human patients (19, 47, 48), that further reveal that distinct recording sites may display gamma oscillations at different frequencies (figure 1C). Another consistent finding, both in LFP and intra-cranial EEG data, is that visually-induced gamma oscillations are observed at multiple focal sites (17, 19, 47). Altogether, these results suggest that a visual stimulus elicits sustained induced gamma oscillations at multiple foci and at different frequencies, that can be observed both intra-cranially and in scalp MEG data.

Why are the temporal and frequential characteristics of oscillatory synchrony so different in EEG and MEG data? Because scalp EEG electrodes integrate brain activity over larger areas than MEG sensors do, the signals from neighboring sources could be combined to generate the short-lived burst of gamma oscillations seen in EEG data. The better spatial resolution of MEG would reveal sustained activities from neighboring sources at distinct frequencies and foci (45, 49). This hypothesis remains to be formally tested, and it should be noted that there are a few reports of gamma oscillations at distinct frequencies (50) or location (51) in scalp EEG data.

5. OSCILLATORY SYNCHRONY AND ATTENTION

Synchronous excitatory post-synaptic potentials (EPSPs) converging on the same target neuron within a short time window, are much more likely to elicit an action potential in this target neuron than the same number of EPSPs arriving in a more distributed manner in time. This implies that information carried by asynchronous EPSPs will not be very efficient on the target structure, while the impact of synchronous EPSPs on subsequent processing stages will be enhanced. This mechanism has all the properties of a bottom-up attentional filter (52): synchronized activities are amplified, while non synchronized activities are filtered out. This line of reasoning opened the way to a number of studies relating gamma oscillatory synchrony to attention, as will be reviewed below.

In line with this idea, it turns out that visually induced gamma oscillations are not only modulated by grouping properties, but are also enhanced by spatial (53, 54), feature-based (45, 50) or object-based (19) attention. These results fit well with the idea that oscillatory synchrony could act as a temporal filter and implement an attentional selection mechanism. However, it should be noted that in most of these experiments gamma oscillations were not the only parameter of the neural response to be modulated by attention.

In addition to bottom-up amplification, oscillatory synchrony could also play a role as an attentional top-down filter: if high-order areas are in a pre-set oscillatory mode, with neurons' membrane potentials alternating between peaks and troughs, only those inputs falling at the peaks of an oscillatory cycle will have an impact. In other words, only those inputs matching with top-down expectancies will be transmitted. This is exactly the pattern we observed in an experiment in which subjects

searched for a specific visual shape in a noisy visual input (41). The role of oscillatory synchrony in top-down attention appears also before stimulus onset, when subjects anticipate the appearance of the stimulus: pre-stimulus gamma oscillations successfully predict the speed of reaction times (55-57), are modulated by the degree of predictability of the stimulus (57-60) or the information content of the warning cue (61, 62). Oscillatory synchrony in the gamma range thus appears as an efficient mechanism to establish a neural state facilitating the processing of forthcoming stimuli – in other words, anticipatory attention.

Anticipating the occurrence of a stimulus implies focusing on a given spatial location or on a specific visual feature, but may also require to predict *when* the stimulus is most likely to appear. Oscillatory synchrony could be related to the temporal orienting of attention: because peaks and troughs of background oscillatory synchrony correspond to epochs of hypo- or hyper-excitability, the phase of background oscillatory synchrony when a signal arrives might determine whether this signal is transmitted or ignored. Although the hypothesis of a role of oscillatory synchrony in temporal orienting is a quite recent one (63-65), there are already a few reports in line with this idea, in particular in the attentional blink paradigm (66, 67). Oscillatory synchrony may also be involved in the discretization of a continuous stream of sensory events into snapshots (68). However, it should be noted that at the moment there is no a priori reason why this hypothesis should be restricted to the gamma-band; rather, it seems plausible that a wide range of different frequencies might be recruited depending on the durations to be estimated.

6. OSCILLATORY SYNCHRONY, LEARNING AND MEMORY

In the influential model of short-term memory proposed by Hebb sixty years ago (69), information is maintained in the system in the absence of sensory input by reverberation of neural activity through reentrant circuits. Because sustained reentrant activity is likely to generate synchronized oscillations, oscillatory synchrony could be a marker of short-term memory maintenance. Besides, in Hebb's model, sustained coincident firing is necessary to enhance synaptic efficiency, a key feature enabling the transition between short- and long-term memory. The mechanisms of synaptic plasticity underlying learning are highly sensitive to the precise timing of neural activity (9) and are more likely to take place upon repeated stimulation. Because oscillatory synchrony offers an opportunity to control precisely the timing of pre- and post-synaptic activities and to repeat this precise temporal pattern at each oscillation cycle, it has long been suspected to reflect a neural state fostering learning and memory (6, 11, 70).

There is now ample evidence in humans that visual short-term memory maintenance is accompanied by sustained occipital gamma oscillations (51, 71, 72), the time-course of the occipital gamma activity varying according to delay duration (73). We could further show using intra-cranial recordings in humans (74) and monkeys

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(75) that distant areas within the ventral stream became phase-locked in the beta range during memory rehearsal, and that the strength of phase-coupling correlated with performance.

Successful episodic memory is also accompanied by oscillatory synchrony: enhanced gamma oscillations have been observed during the presentation of an item when it is subsequently retrieved compared to when it is forgotten (76-80). These results suggest that gamma oscillations at encoding trigger a long-term memory consolidation, that facilitates retrieval. In its simplest form, memory encoding may appear as a modulation of neural activity upon the repeated presentation of the stimulus (81). This so-called repetition effect does indeed affect visually-induced gamma-band scalp EEG oscillations (82, 83) as well as gamma-band oscillatory synchrony in the hippocampus and medial temporal regions in intra-cranial recordings (84). Interestingly, depending on whether the repeated object is meaningful or meaningless, gamma oscillations either decrease or increase (85).

7. OSCILLATORY SYNCHRONY AND AWARENESS

Oscillatory synchronized activity, as an emerging population phenomenon, might capture a non-linear dimension in brain processing, corresponding to the axiom that "the whole is larger than the sum of its parts". Let us first describe in a bit more detail what this axiom means. In a complex system, some properties that do not exist in any constitutive elements of the system can emerge at the population level. An intuitive example of non-linear interactions can be found in the Artificial Intelligence field (86). In this example, "boids" are moving objects following simple local rules: a boid avoids bumping into its closest neighbors, it moves roughly in the same direction and with the same speed than its closest neighbors and it tends to stay close to other boids. These simple local rules are sufficient to produce a group behavior similar to that of a flock of birds, including the V-shaped flight of ducks. Coherent behavior can thus emerge from local rules, without a need for either an explicit global schema or for a group leader. This property – emergence of a global coherent behavior without the need of conductor - is particularly interesting when related to the search for the neural correlates of awareness because of the commonly admitted view that there is not a single anatomical module for awareness (52, 87).

There begins to be some evidence that oscillatory synchrony in the gamma range could be related to visual awareness: conscious recollection (as opposed to the feeling of familiarity) is accompanied by an increase of gamma power over parietal regions and enhanced fronto-parietal coupling (88), both occipital gamma oscillations (89) and long-range phase-synchrony (90) increase when a masked noun is consciously seen, posterior gamma oscillations correlate with awareness independently of performance in hemianopic patient GY (46), transitions between conscious perceptual states are preceded by a burst of oscillatory synchrony in the gamma range (24, 91) and sudden flashes of insight are preceded by a burst of gamma

synchrony in the superior temporal gyrus (92). We recently obtained a clear evidence that mid gamma-band oscillations over retinotopic visual areas not only correlate with visual awareness, but can also be independent of spatial attention (49). Last, it should be noted that altered gamma-band oscillations patterns in autism (28, 93) and schizophrenia (94) might be related to a binding and / or perceptual awareness modification.

8. GAMMA OSCILLATORY SYNCHRONY: TAKING ADVANTAGE OF NEURONS' FINE TEMPORAL TUNING

Modulations of induced gamma oscillations are thus observed in a variety of cognitive tasks, and are without any doubt modulated by visual grouping, attention, learning, memory and awareness. Induced gamma oscillations are thus unlikely to underlie a single cognitive function. Their functional role is probably better understood in terms of a neural implementation that takes advantage of the neuron's temporal properties rather than in terms of cognitive modules. As underlined in the introduction, timing is a crucial parameter determining neural firing: a population code relying on fine temporal tuning is thus likely to be involved in many distinct functions.

One could even argue that the use of similar implementation rules may account for the tight links between conscious perception, attention and memory. Indeed, although these functions have traditionally been studied in isolation, they deeply influence each other. Both attention (95) and short-term memory (96) operate on grouped entities, short-term memory capacity depends on attentional filtering abilities (97, 98), associative memory influences attentional deployment (99, 100) and early visual processing (101), and awareness seems tightly coupled with attention (102, 103) and memory (104).

9. FUNCTIONAL SUB-BANDS WITHIN THE GAMMA RANGE

Oscillatory synchrony in the gamma range should probably not be considered as a single phenomenon, functionally and anatomically homogenous. In response to a visual stimulus, gamma oscillations appear at distinct frequencies in different areas (figure 1C), and there are hints that gamma oscillations might behave differently depending on their location (19, 105). Are these frequency and spatially distinct gamma oscillations engaged in distinct cognitive processes? We recently directly tested this possibility by varying both visual grouping and selective attention within the same experiment, to reveal that grouping and selective attention simultaneously affect gamma band oscillations, but in distinct sub-frequency bands and at distinct locations (45). Similarly, when varying simultaneously attention and awareness, we could show that distinct frequency bands within the gamma range varied separately with visual awareness and spatial attention (49). Distinct frequency components of the gamma-band response may thus support flexibly and simultaneously distinct cognitive functions.

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These recent findings not only show that gamma-band oscillatory synchrony should not be considered as a monolithic phenomenon, they also call for a refined description of gamma oscillations, in terms of frequency content, topographical distribution, latency, etc..., as it has long been done in the ERP literature.

10. FUNCTIONAL CORRELATES IN DISTINCT FREQUENCY BANDS

A number of experiments point at functional correlates of binding, attention and memory outside the gamma range. It is largely beyond the scope of this paper to review the whole literature on human rhythms, but even listing a restricted number of findings suggest that there is no one-to-one relationship between a frequency band and a cognitive function. For instance, grouping can affect oscillatory synchrony in the gamma range, as reviewed above, but also in the alpha range (106); the alerting, orienting and executive attentional networks engaged in many attentional tasks affect oscillatory synchrony in different frequency ranges, from theta to gamma frequencies (61); episodic memory encoding and retrieval typically affects both theta and gamma oscillatory synchrony (77, 80). So while the gamma range remains of particular interest because its frequency range fits well with neuron's integration time constant, obviously the full spectrum of brain rhythms should be taken into account.

The absence of a direct correspondence between a frequency range and a cognitive function raises a fundamental issue: what determines the preferential use of a given frequency? Several factors might be considered. It was initially suggested that frequency depends on the network's size and geometry (107): because conduction delays increase in large network, synchronization takes place at lower frequencies (108). At a more refined spatial scale, the network configuration also seems to influence the frequency range that is used preferentially: *in vitro* experiments reveal that there are distinct frequencies (20-30 Hz vs. 30-70 Hz) in the infra- and supra-granular layers respectively (109, 110). However it should be noted that the same fronto-parietal network can engage in coherent activity at different frequencies (~28 Hz vs. ~42 Hz) depending on the task to be performed (111), suggesting the same anatomical network can modulate its frequency in a task-dependent manner. Indeed the time constant of the task is likely to influence the pace of the system: if there is only 500 ms to complete a visual search for instance, frequencies below 5-10 Hz are unlikely to be relevant, whereas if there is no time constraint to perform a task, then one might use lower frequencies. These two factors – network geometry and cognitive time constant – are of course not mutually exclusive.

11. DISTINCT FREQUENCY BANDS FOR A FLEXIBLE MULTIPLEXING SCHEMA INTEGRATING THE DIFFERENT TIME-SCALES OF BEHAVIOR?

If cognitive visual processing affects oscillatory synchrony simultaneously in different frequency bands, one

may wonder how and when those different frequency band do interact. In the recent years, characterizing cross-frequency coupling has become a major challenge. Three main types of interactions can be considered: co-variations in amplitude, phase coupling between frequencies, or phase-amplitude coupling. Co-variations in amplitude are intuitively easy to understand: as the power of frequency band A increases, frequency B power increases (or decreases). Such amplitude fluctuation coupling between frequency bands can for instance be observed during resting wakefulness (112). Phase-coupling between frequencies refers to the locking of n cycles of one oscillation to m cycles of another oscillation, and is hence also called $n:m$ phase synchrony. Cross-frequency phase coupling links alpha, beta and gamma oscillations in humans during mental calculation and in a working memory task (113). Last, the phase of an oscillation might influence the amplitude of another oscillation. Such nested oscillations have long been suspected to play a role in memory storage (114) and have been observed in the rat hippocampus (115). Recently, the dependence of neocortical high-frequency (80-150 Hz) power on theta phase was revealed in human intracranial data (116). The same authors further show that the strength and topography of the theta/gamma coupling is task-dependent.

What could be the functional relevance of such between-frequency cross-talk? Integrating the different time-scales of behavior is probably an interesting candidate. Indeed the completion of many everyday life tasks requires not only to combine cognitive processes in a correct sequence, but also to relate short-lived sensory experiences to long-term planning. The combination of potentially discrete short sensory events (117) into an experienced continuum might take advantage of a coupling between high and low frequencies. On the other hand, it might be useful to either couple or decouple information in different frequency bands, depending on the task to be achieved.

12. OSCILLATORY VS. TRANSIENT SYNCHRONY

In population signals, an increase of power in a given frequency band is considered to reveal the presence of oscillatory synchrony, i.e. a true reverberation of neural activity. However, it should be noted that a fast succession of neural events in a hierarchical system, without any reverberation, might also show up as a power increase in time-frequency plots. Let us consider a simplified example. Two groups of neurons, A and B, exchange information every 20 ms for 100 ms: this would constitute an example of oscillatory synchrony, with a 5-cycle reverberation, leading to a 100-ms power enhancement at 50 Hz. On the other hand, 5 distinct groups of neurons could be organized in a hierarchical cascade, with a fast feed-forward sweep leading to the activation of A, of B 20 ms later, then C and so on until E is activated. If those five groups of neurons are lying close together, this temporal sequence is likely to generate a power increase at 50 Hz in scalp EEG or MEG data. Distinguishing between these two possibilities might prove difficult solely on the basis of non-invasive

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recordings. Even when intra-cranial recordings can be obtained, whether a power increase reflects a truly oscillatory activity is not obvious, as shown in figure 1A.

Besides, from a theoretical point of view, there are some instances when transient synchrony might be as useful as oscillatory synchrony to constrain neural processing. Let us consider the implication of synchrony to set up an attentional filter, with synchronized inputs being amplified and unsynchronized inputs filtered out. In this particular case, transient synchrony could be as efficient as oscillatory synchrony: a single wave of synchronized outputs might be sufficient to enhance the impact on the target structure. Indeed it has long been known that event-related potentials, that can be considered as waves of synchronized activity phase-locked to stimulus onset, are deeply modulated by spatial attention (118). Besides, the feed-back of an attentional modulation from extra-striate areas to primary visual cortex can be achieved within 200 ms of stimulus processing (119), i.e. only shortly after the onset of gamma-band oscillations.

Obviously a full understanding of how a given function – here attention – operates at the neural level calls for an integration of the findings in ERPs and oscillatory synchrony in a more comprehensive schema. For instance the dependence of visual ERPs on the phase of pre-stimulus alpha rhythms (120) or ongoing gamma local field potentials (121) suggests an interaction between ongoing rhythms and transient evoked responses, although the exact nature of the relationship is a matter of current debate (122, 123).

More generally, this raises the issue of the relationships between the various measures of neural activity that can be obtained in humans, mainly scalp EEG /MEG data and BOLD signals. It appears that gamma oscillations and ERPs are not systematically co-localized (19, 124), nor do they necessarily display the same functional modulations (3, 32, 34). Besides, the BOLD signal seems to correlate better with local field potentials than with spiking activity (125, 126), but whether it corresponds better to ERPs (119) or oscillatory synchrony (127-129) remains unclear.

13. CONCLUSION AND PERSPECTIVES

Induced gamma oscillatory activity has been the subject of intensive research in humans for the last 10 years. Its original status of a marker for binding has been much broadened, with an interesting combination of arguments derived from neuron's physiological temporal properties and cognitive psychology: thinking in terms of a temporal neural code, rather than in terms of cognitive modules, offers an interesting original framework to investigate the neural basis of the relationships between grouping, attention, memory and awareness. The co-existence of multiple frequencies could be integrated in a global multiplexing schema integrating the different time-scales of behavior, but much remains to be done to explore the nature and functional signification of the interactions between rhythms.

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