Oscillatory synchrony and human visual cognition

Catherine Tallon-Baudry *

INSERM U280, 151 cours Albert Thomas, 69003, France

Abstract

Oscillatory synchrony could be used to establish dynamic links between the various cortical areas participating in the same cognitive process. Is it possible to detect oscillatory synchrony in humans, and is it relevant to behavior? There is now converging evidence for the existence of a transient oscillatory activity in the gamma range (30–60 Hz), obtained in response to static visual objects, and having only a loose temporal relationship to stimulus onset. This so-called "induced" gamma response is much larger in response to coherent static or moving objects. However, functional variations of gamma and/or beta (15–20 Hz) oscillations are not restricted to perceptive, bottom-up mechanisms, but are also observed during visual imagery or short-term memory maintenance. Oscillations at the scalp level thus seem to reflect large-scale neural cooperativity in a variety of task-dependent networks.

Human intra-cranial recordings in a short-term memory paradigm further reveal the existence and the task-dependency of oscillatory synchrony in the beta range, between focal sites separated by several centimeters and with a few milliseconds time-lag. These findings thus confirm experimentally the hypothesis of a functional role of synchronized oscillatory activity in the coordination of distributed neural activity in humans, and support Hebb's concept of short-term memory maintenance by reentrant activity within the activated network. In addition, the intra-cranial data obtained in humans and monkeys also help to better understand the neural mechanisms generating scalp-recorded oscillations.
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1. Introduction

Our understanding of vision has progressed by identifying many functional areas, dedicated to some particular visual process. As pointed early by Lashley [1], "the classical concept of cerebral localization is of limited value, because of its static character and its failure to provide any answer to the question of how specialized parts of the cortex interact to produce the integration evident in thought of behavior. The problem here is one of the dynamic relations of the diverse parts of the cortex, whether they be cells or cortical fields". A series of theoretical papers suggested that integration was performed within a distributed assembly [2], and that relations within this assembly could be tagged by oscillatory synchrony [3–5]. The findings that neurons in area 17 of the anesthetized cat synchronize their discharges on an oscillatory mode in the gamma range (25–80 Hz) when responding to the same object [6] was the first experimental contribution to the hypothesis of assembly coding signaled by oscillatory synchrony. This result, together with a series of others in anaesthetized or awake animals (see [7] for review), motivated a number of study in humans, aiming at observing oscillatory synchrony at the scalp level and at relating this collective neural behavior to perception and cognition.

Addressing the issue of the functional role of oscillatory synchrony in humans, several groups assessed the existence of synchronized oscillatory activity at a large spatial scale, in scalp EEG or MEG recordings. Indeed, only synchronized patterns of activity in large neural ensembles are strong enough to be picked up at the scalp level by volume–conduction effects. Oscillations in EEG or MEG signals thus always reflect an underlying oscillatory synchrony, whose precise anatomical extent cannot be directly assessed from scalp measures. In the last decade, these non-invasive techniques not only revealed the existence of induced oscillations in the gamma and beta (15–20 Hz) ranges but also offered unique hints on their functional role.

* Tel.: +33-472-68-16-12; fax: +33-472-68-19-02.

E-mail address: tallon-baudry@lyon151.inserm.fr (C. Tallon-Baudry).

2. Induced gamma oscillations at the scalp level in humans: existence and functional variations

2.1. How to detect induced oscillatory activities and synchrony

Any signal showing a peak in its frequency spectrum in the 20–100 Hz range has been considered to contain gamma oscillations. However, very different types of oscillations have been gathered under this label. So far, only one type of oscillations (called ''induced'' oscillations) has been repeatedly related to information integration. As opposed to transient or steady-state evoked responses, induced activities are characterized by a loose temporal relationship to the stimulus. Because an induced activity appear with a jitter in latency from one trial to the other, it tends to disappear in the averaged evoked potential. Induced patterns of activity thus require specific methods to be extracted from EEG/MEG signals. All the methods used so far have in common the transformation of the potential or magnetic field into spectral power prior averaging. Different techniques, with different time and frequency resolutions, have been successfully applied, such as bandpass filtering and signal rectifying [8], short-term Fourier transform [9], or wavelet-based time–frequency decomposition of single trials [10–12].

Comparison between these various methods is not straightforward. In addition, scalp data may be contaminated by muscle artifacts in the gamma range. Last, it was often not stated in the literature whether the results dealt with evoked, steady-state or induced patterns of activity, resulting in apparently conflicting results. The combination of these three issues added confusion to this new field of research, and some authors even denied the possibility of ever observing gamma oscillations at the scalp level [13,14]. However, different groups that used various stimuli and methods of analysis now agree on the existence and characteristics of the scalp-recorded induced gamma activity.

2.2. Converging evidence: existence of a transient gamma response, larger in response to coherent stimuli

Several groups presented static visual stimuli while recording EEG and analyzed their data in the time–frequency domain [10,15–20]. All report the existence of a transient induced gamma response peaking between 230 and 330 ms, and between 25 and 45 Hz.

There is much variability in the topography of this response, some reporting an occipital or parietal distribution [10,15,16,18] while others observe either a frontal maximum [19,20] or a more homogeneously distributed pattern [17]. This stimulus- and task-dependent variability may be accounted for if scalp oscillations reflect a mechanism of neural cooperativity in the particular subset of areas engaged in the task.

A more prosaic interpretation of the frontal or occipital distribution is that the recordings were contaminated by either neck or forehead muscle activity. However, Lutzenberger and co-workers [21] provided a strong argument against muscle artifacts by showing that the topography of the occipital gamma response followed the retinotopic organization of V1/V2. In addition, the spectral distribution of muscle activity and of the scalp gamma response differ, muscle activity spanning a much wider range of frequencies [15].

Different studies addressed simultaneously the issue of the existence of induced oscillations at the scalp level in humans and of their functional relevance: if gamma oscillations reflect binding by oscillatory synchrony, they should be larger in response to a stimulus leading to a coherent percept. Using the paradigm developed by Gray et al. in the cat, Müller and colleagues [9,22] showed that scalp gamma oscillations were larger when the subject passively viewed a long moving bar than when observing two independently moving stimuli. In a discrimination task, we compared the responses to coherent stimuli (illusory and real triangles) with the responses to a non-coherent stimulus, a Kanizsa triangle [23] in which the inducing pac-men had been rotated to suppress the illusion [10]: a larger induced gamma response was observed over occipital electrodes in response to a stimulus eliciting a coherent percept. Csibra and colleagues [19] showed further that Kanizsa stimuli elicit a frontal induced gamma increase in eight-month-old infants, but not in younger infants whose visual system is not mature enough to construct such illusory percepts. Other groups showed that inverted faces, that do not elicit a face percept, generate a smaller induced gamma response than upright faces [17,20,24]. An increase in gamma oscillations also seem to accompany the transition from a meaningless two-dimensional stereogram to an illusory three-dimensional percept [25], as well as switches in the perception of the Necker cube [26].

All these results are in agreement with the hypothesis that an object elicits a coherent percept by the oscillatory synchronization of the neurons encoding the different parts and features of this object. The assembly thus defined is probably large: if only a small group of neurons were involved, the signal would be too weak to reach the scalp. In addition, in some of these studies, the induced gamma response was shown to have different functional variations than activity in the alpha range (8–12 Hz), or than the classical evoked potential. The functional role of gamma oscillations thus seem different from the one of transient evoked responses or slow oscillations.

2.3. Beyond bottom-up feature-binding: oscillatory synchrony and visual object representation

Presenting a coherent stimulus is only one possibility to elicit an object representation, characterized by the

bottom-up processing of the information contained in the stimulus. Is it possible to generalize the functional role of high-frequency oscillations to other types of object representation [27]? We addressed this issue in experimental paradigms in which the construction of an object representation is driven by an internal process rather than by the stimulus itself.

We used a modified version of the Dalmatian Dog picture (Fig. 1). When naive subjects were presented this picture, they perceived it as meaningless black blobs on a gray background, and produced only a very weak induced gamma response. Once the subjects were informed of the presence of a hidden Dalmatian dog, and trained to detect it, they actively searched for the dog in any picture containing black blobs. In other words, they activated a mental representation of this dog and checked it against the picture presented. As a correlate of the activation of this internal representation, we observed a large induced gamma response in trained subjects searching for the Dalmatian dog in the stimulus [15].

Other internal representations are those held in short-term memory. We recorded scalp EEG while subject performed a delayed-matching-to-sample task [16,28]. A first shape was presented, and after a delay of 800–1600 ms a second one. The task of the subject was to respond when the two shapes were perfectly identical. Subjects were instructed to try to keep a visual image of the first shape during the delay. To promote the active maintenance of visual information in short-term memory, the shapes we used were difficult to describe verbally, and a new shape was randomly generated at each trial. Sustained gamma and beta (15–20 Hz) oscillations appeared when the picture of the first shape was rehearsed in visual short-term memory, and disappeared in a control condition in which no mnesic process was involved. Both gamma and beta oscillations appeared at occipital and frontal electrodes, in keeping with the known functional anatomy of visual short-term memory in monkeys [29–31] and humans [32,33].

2.4. Oscillations and oscillatory synchrony in scalp data

2.4.1. Functional interpretation of oscillations

Induced high-frequency oscillations are thus not only observed in response to a coherent object, but are also present when the subject activates or rehearses an internal representation. This suggests that induced high-frequency
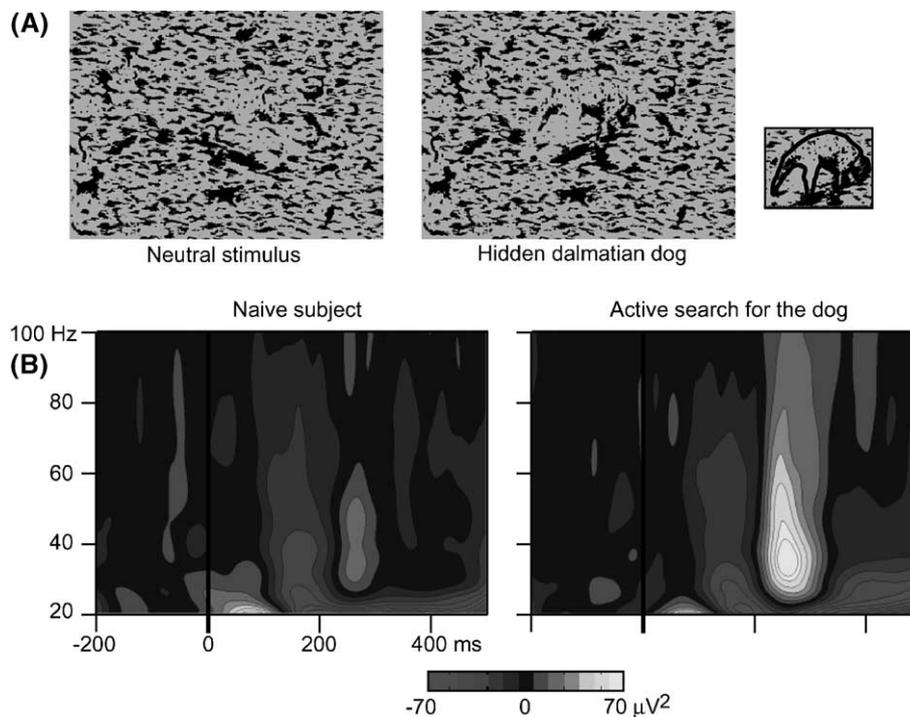

Fig. 1. Dalmatian Dog experiment. (A) Stimuli. In the first recording session, naive subjects were presented such pictures, experienced as meaningless stimuli. They were then trained to detect the hidden Dalmatian dog whose outlines are shown in the rightmost panel. (B) Time–frequency plots at electrode O1, grand-average across 13 subjects. Time is presented on the x-axis, frequency on the y-axis. Time–frequency resolved power is color-coded, white indicating large values of power. The transient induced gamma response peaks at about 280 ms and 30 Hz. It is much larger in trained subjects (right) than in naive subjects. This gamma activity was increased not only in response to the Dalmatian dog, but also in response to the neutral stimulus, though to a lesser extent. This suggests that part of this gamma response reflects the activation of the internal representation of the dog the subject was actively looking for. The earliest difference in the evoked potentials between naive and trained subjects peaked later than the gamma response. Induced gamma activity and evoked components thus seem to reflect distinct processing modes, with possibly different functional roles.

oscillations underlie the activation of the neural representation of the object in mind. In addition, the topography of gamma and beta oscillations is highly task-dependent, suggesting that depending on the task to perform, different functional areas are dynamically and flexibly bound by oscillatory synchrony. Indeed, oscillatory synchrony should not be considered as dedicated to a particular cognitive process, but rather as a mechanism that could bind together the sensory and cognitive properties of an object into the experienced entity.

An alternative explanation of the functional variations of the induced gamma response is that it reflects an attentional mechanism. Indeed, scalp-recorded gamma oscillations have been shown to be modulated by spatial attention [34,35]. This modulation has been interpreted in the light of the proposal that oscillatory synchrony may serve to amplify relevant signals [36]. This apparent conflict between the "representational" hypothesis and the "attentional" hypothesis sends back to the hard question of attentional selection [37,38]: does attention precede stimulus selection—and if so what does attention select? Direct evidence for feature- or object-based attentional selection has been obtained in classical evoked potential studies [39,40]. However, the question of whether correlates of object-based attention in the evoked potentials precede or follow the induced gamma response has not been addressed experimentally yet.

2.4.2. Neural interpretation of scalp-recorded oscillations and oscillatory synchrony

The exact interpretation of oscillations recorded at the scalp level in terms of neural mechanisms and sources remains difficult to establish. Because only those electrophysiological components that are synchronousover large enough cortical areas can be picked up at the scalp level [41–43], scalp-recorded oscillations necessarily reflect some degree of underlying oscillatory synchrony. But is this synchrony limited to a small cortical region, or does it encompass several functional areas? The signal recorded at one scalp electrode is likely to be a compound from several active sources, whose respective orientation, frequency and phase will determine the amplitude of the resulting signal. Whether scalp-recorded oscillations are related to the amount of synchrony within a small cortical region or to the amount of synchrony between distinct functional areas separated by a few centimeters remains an open issue.

Relationships between regions widely apart can nevertheless be studied at the scalp level by looking at synchrony between electrodes. There again, different methods have been used, like coherence [44] or phase synchrony [45,46]. Several problems related to the application of these methods to scalp data are still only partially solved, like the choice of the reference electrode or the discrimination between volume conduction effects and physiological synchrony [44,45,47].

Using these methods, a common pattern of increased coherence between temporal and parietal electrodes was observed independently of the modality used to present objects (pictures, written or spoken words) [48]. As scalp oscillations do, synchrony between scalp electrodes in the gamma range increases in response to coherent object: the comparison between upright and inverted faces showed an increased between-electrode synchrony at the latency of the induced gamma response [17], and the presentation of coherently moving gratings spanning the vertical meridian increases the interhemispheric coherence between occipital and parietal electrodes [49].

3. Oscillations and oscillatory synchrony in intra-cranial recordings

We recorded the activity of depth electrodes implanted in the occipital and temporal cortices of epileptic patients suffering from pharmacologically resistant partial epilepsy. These intra-cranial recordings in humans offer a unique opportunity to study between-area oscillatory synchrony in direct relationship with behavior. Patients performed the delayed-matching-to-sample task already studied at the scalp level in normal subjects.

3.1. Memory rehearsal and synchrony in the beta range

Visual short-term memory is a function that is particularly interesting to consider in the light of the possible roles of oscillatory synchrony. This function is relying on activity in the visual and prefrontal cortices [29–33]. It is usually considered that activity in this distributed network must be coordinated, but no direct experimental evidence of such coordination has been obtained yet. Collective behavior of the mnesic network could be ruled by oscillatory synchrony. Another puzzling feature of short-term memory is that sustained neural discharges are maintained during the delay, in the absence of sensory input. Hebb [2] originally proposed that the maintenance of information was due to reverberating activity enabling sustained neural outliving the sensory stimulus. Such reverberatory loops could be established by oscillatory synchrony. In addition, because oscillatory synchrony could impose a temporal relationship between pre- and post-synaptic spikes, it could also induce modulations of synaptic efficiency [50] related to storage in long-term memory.

In two epileptic patients, we could show the existence of a sustained synchrony in the beta band between distinct extra-striate visual areas [51], during the rehearsal of information in visual memory (Fig. 2). Synchrony occurred between small cortical regions extending on a few millimeters but separated by several centimeters,
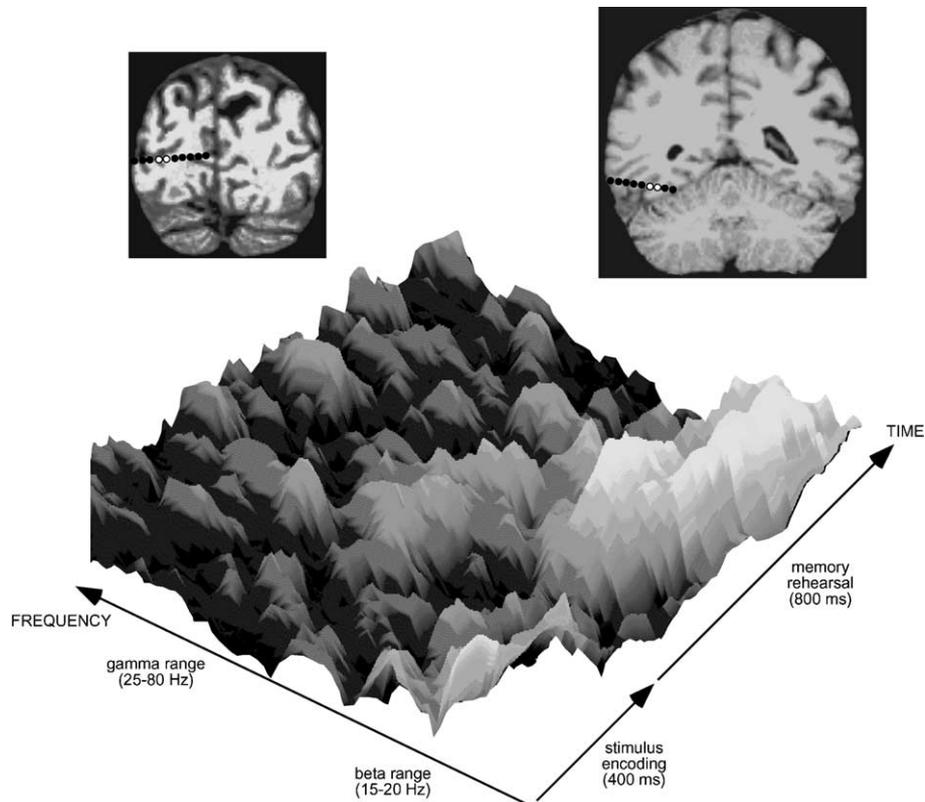
Fig. 2. Between-area oscillatory synchrony in humans during memory maintenance. Local signals were obtained from the lateral occipital sulcus (left MRI) and the fusiform gyrus (right MRI) of a patient whose epileptic focus was located in the amygdaloid complex, away from these structures. The two sites were located in the visual extrastriate cortex and were separated by more than 3 cm. Phase synchrony between these two sites is described in the time–frequency domain: a large synchrony (in white) appears during memory rehearsal in the beta range. This synchrony drops to baseline level in a control condition that had a similar time course and the same attentional demand, but that required no maintenance of information in memory.

located in extrastriate visual areas that have been shown to be activated during visual object perception [52,53] or imagery [54] as well as during visual short-term memory [55] in humans using positon emission tomography or functional magnetic resonance imaging. The between-area synchrony observed during memory rehearsal nearly completely disappeared in a control condition that did not involve any mnesic process. Both experimental conditions were matched for difficulty (implying a similar level of attention in both conditions) and timing (in both conditions, subjects had to wait for the end of the delay to be able to give their answer). The synchrony we observed in the memory condition only is thus not likely to reflect an attentional increase or an expectancy process during the delay. Memory rehearsal could thus be based on re-entrant loops established by oscillatory synchrony between distinct functional areas, as suggested by Hebb more than 50 years ago.

3.2. Characteristics of local gamma and beta oscillations

The between-area synchrony during memory maintenance was preceded by large gamma oscillations during stimulus encoding. These oscillations lasted for the

400 ms of stimulus presentation, and peaked at different frequencies in different areas. Such long-lasting oscillations had already been reported from the calcarine sulcus in human epileptic patients [56]. These results are also in keeping with data obtained over V1 and V4 in the anesthetized monkey [57]: large-amplitude gamma oscillations could last up to 3 s, the longest stimulus presentation time we tested, and peaked at different frequencies in V1 and V4. Neither in the intra-cranial data in humans nor in the electro-corticogram in the anesthetized monkey did we find convincing evidence for between-area synchrony during stimulus presentation, maybe because of the different frequencies observed at each site. However, between-area synchrony in the gamma range has been observed during stimulus encoding between the hippocampus and the rhinal cortex [58].

In human intra-cranial data, local gamma oscillations disappeared after stimulus onset and were replaced by a between-area synchrony in the beta range during memory rehearsal. This beta synchrony could be accompanied by local beta oscillations, but the existence of local oscillations did not seem to be a pre-requisite for the establishment of between-area synchrony. The transition

from local gamma oscillations to between-area beta synchrony observed in human intra-cranial data closely matches the pattern obtained in rat hippocampal slices after tetanic stimulation, a pattern that has also been related to memory formation [59,60].

3.3. Interpretation of scalp-recorded oscillations

Scalp-recorded oscillations could a priori reflect two different types of synchrony: a local one, restricted to a single area located close to the recording electrode [61], or an oscillatory synchrony spanning several distinct functional areas separated by a few centimeters. Comparison between the scalp and data described above strongly advocate for the latter interpretation. Indeed, between-area synchrony and scalp oscillations displayed similar temporal and functional properties during the delay of the short-term memory task in the beta range. Both scalp beta oscillations peaking at occipital electrodes and beta synchrony between extrastriate visual areas were sustained during the delay, and both disappeared in the control condition. While there is a strong parallel between intra-cranially measured between-area synchrony and scalp-recorded oscillations, the local oscillations reflecting within-area synchrony showed somewhat different properties. In particular, intra-cranially measured beta oscillations were not systematically larger in the memory compared to the control condition.

The transient gamma response observed in scalp EEG data is also more likely to between-area synchrony than within-area synchrony. Indeed, at different sites in intra-cranial recordings, the local oscillatory response peaks at different frequencies in different areas and shows a sustained time-course, in both humans and monkeys. The transient scalp-recorded induced gamma activity could thus rather reflect a short episode of between-area synchrony. However, because the frequency of local oscillations differ a lot from one area to the other, this "synchrony" probably occurs between distinct frequency bands. It may be more related to some non-linear phase interactions than to the intuitive notion of synchrony between signals at the same frequency. If a such a transient between-area "synchrony" exists, it could correspond to the fundamental recognition event described in a spiking neural network-based on template matching between input and output patterns [62]. However, it remains to be determined whether the transient gamma increase observed at the scalp level is related to a brief event of between-area synchronization (Fig. 3).

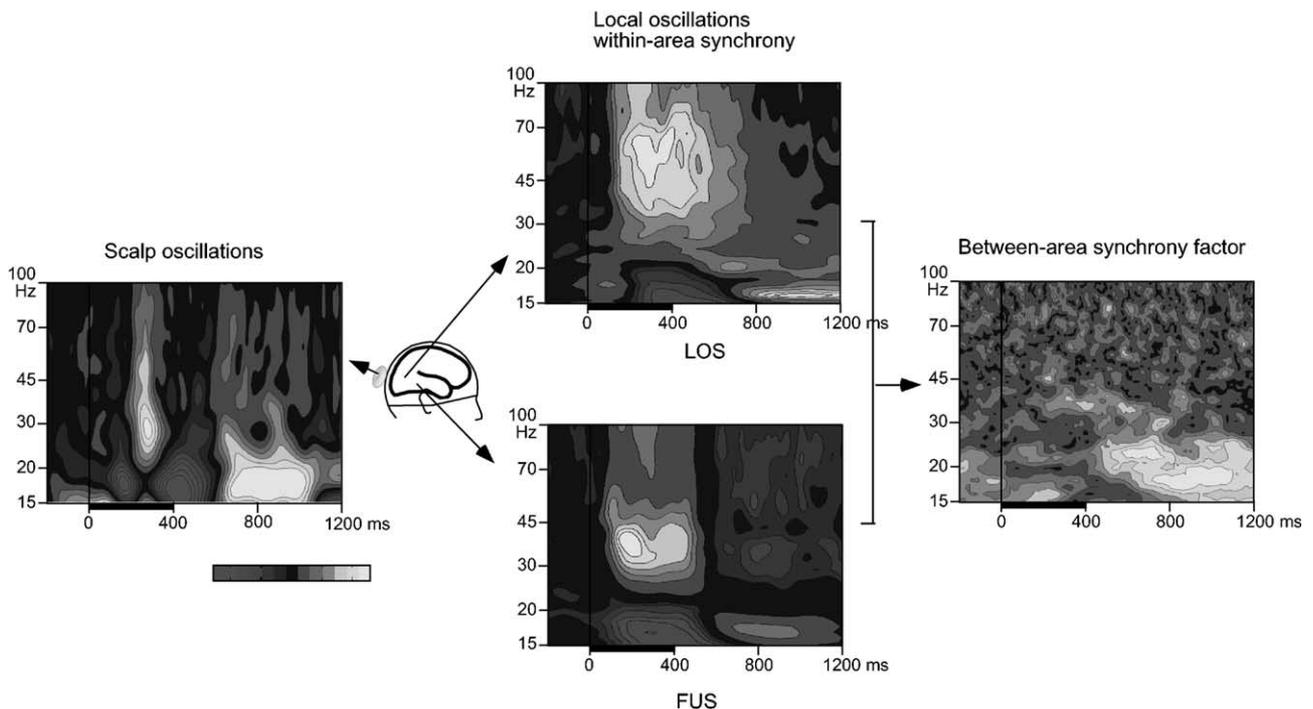The temporal course of induced gamma activity measured in MEG recordings is very different from the

Fig. 3. Oscillations and oscillatory synchrony at different recording levels in the same short-term memory task. At a scalp electrode located over the occipital lobe (left), a transient increase is observed in the gamma range during the 400 ms of stimulus presentation, followed by beta oscillations during memory rehearsal (from 400 to 1200 ms). High power values appear in white. In local signals obtained intra-cranially (middle) in the lateral occipital sulcus (LOS) and in the fusiform gyrus (FUS), sustained oscillations reflecting within-area synchrony are observed for the 400 ms of stimulus presentation. Synchrony in these areas peaks at different frequencies. During the delay, no strong beta oscillations are observed. However, synchrony between these two areas (right) reveals a strong coupling in the beta range, during memory rehearsal (up to 1200 ms). Between-area synchrony in the beta range and scalp-recorded beta oscillations have the same temporal course and display the same functional modulations.

one observed in scalp EEG recordings. A recent re-appraisal of MEG data [63] showed the existence of weak but long-lasting induced gamma oscillations over the occipital cortex of subjects viewing Kanizsa figures. As opposed to EEG oscillations, MEG oscillations could thus be directly related to within-area oscillatory synchrony.

The comparison between recording scales thus shows that the terms "oscillations" and "synchronization" are only loosely defined and that their neural interpretation in terms of between- and within-area synchrony probably depends on the recording level considered. A better definition of these terms may become particularly relevant if it turns out that within- and between-area synchrony underlie distinct cognitive functions.

4. Discussion

4.1. Scalp EEG oscillations

There is now a growing body of evidence for the existence of a transient increase of scalp EEG power in the gamma range, in response to a visual stimulus leading to a coherent percept. Scalp gamma and beta oscillations have further been shown to involved in the construction of object representation via top-down processes or in the rehearsal of an object representation in visual short-term memory. Taken altogether, these data point toward a role of oscillatory synchrony in the activation of a coherent object representation. There are obviously interactions between object-based attention and object representation, and oscillatory synchrony can be interpreted in both attentional and representational terms in many experiments. These two interpretations could meet if the transient burst of gamma activity observed at the scalp level and tentatively interpreted as a transient between-area synchrony reflects a pattern-matching operation between bottom-up computations and top-down expectancies, object-based attention being only one of the possible top-down bias.

Though this will require further investigations, scalp EEG oscillations are likely to reflect between-area synchrony. Local synchrony, within a single area, shows a more sustained time-course, and peaks at different frequencies in distinct functional areas during stimulus presentation. The existence of these distinct frequencies may seem to challenge the hypothesis of frequency tagging within a distributed assembly. However, if one admits the possibility of interactions between-areas and between distinct frequency bands, the existence of different frequencies may be a way to nest a local assembly inside a larger one to enable the system not only to integrate but also to retrieve object parts, a problem that might have received too little attention [64].

4.2. Two modes of visual processing

If assembly-based processing seem to have been used by the subjects in all the experiments described above, it should not be forgotten that the visual system can in some instances achieve complex tasks much faster. It has been shown that the first difference between target and non-target stimuli peaks as early as 150 ms in the classical evoked potential in an animal/non-animal categorization task [65] (see also van Rullen, this issue). This early difference in the evoked potentials is likely to be due to a feed-forward propagation of information, spreading quickly from the primary visual cortex to ventral areas. The feed-forward mode can be extremely fast: a face-specific response has been observed as early as 80 ms after stimulus onset in the infero-temporal cortex [66]. Synchrony takes longer to get established in early visual areas (more than 100 ms in areas V1 and V4 in the anesthetized monkey [57]), and even longer (at least 250 ms) in the case of between-area synchrony as indexed by the transient burst of scalp gamma oscillations.

If these two processing modes are considered to co-exist [67], experimental data showing directly the transition from one mode to the other are still lacking. It could be that any stimulus elicits both a fast sweep of feed-forward activation and a series of locally synchronized activity. The fast feed-forward mechanism would enable a coarse and unconscious identification of some specific features of the stimulus, probably sufficient in most of everyday life situations. Local oscillations in early visual areas would maintain, for a few hundreds of milliseconds, an information on scene segmentation. If ever needed, these local activities could get strongly synchronized between-areas to provide a much more detailed representation of the stimulus, along maybe with the conscious experience of it.

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