

Object representation and gamma oscillations

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1 Introduction

It is now well established from lesion patient studies, neuroimaging studies, or animal and human electrophysiological studies, that any sensory or cognitive process involves a network of distributed neural structures. How do these different structures cooperate to allow the emergence of a percept, or more generally a coherent representation required for a specific action? On which neural mechanism are based the interactions within and between brain areas underlying these cognitive processes?

An influential theoretical proposal [1, 2] suggests that these structures are dynamically bound by the oscillatory synchronization of their neural activity. More specifically, neurons responding to different features of the same object would synchronize their discharge on an oscillatory mode. In case of multiple objects, each cell assembly would synchronize at a distinct frequency [3].

In the last decade, unit recordings in animals have shown that oscillatory synchronization in the gamma range (20-100 Hz) appears preferentially between neurons responding to the same object (see [4] for a review). These studies, essentially undertaken in the visual modality, concerned animals that were either anaesthetized or performing a simple passive fixation task. They provide experimental evidences for a functional role of neural synchronization in low-level visual areas during perceptual grouping (bottom-up spatial binding). A striking characteristic of those oscillatory synchronizations is their variability in latency from one trial to the other. In humans, the existence of gamma-band (or 40-Hz) oscillations in EEG or MEG recordings has been occasionally reported in the literature since the 50's in a variety of modalities and tasks (among many others: [5-14], see [15] for a review). At first glance, these observations may appear rather disparate. Two major factors contribute to this impression: 1) different electrophysiological phenomena have been very often gathered under the same appellation "40-Hz activity" in an undifferentiated manner, 2) a common framework for interpretation is somehow lacking.

In this paper, we will present the different types of 40-Hz responses reported in the literature, and show some evidence for a role of induced gamma oscillations in sensory information processing (both visual and auditory) and memory rehearsal, in other words, in brain processes requiring the activation of a coherent object representations. The neural substrate of those gamma oscillations observed on the scalp will also be discussed.

2 Different types of "40-Hz" activities

Different types of gamma oscillatory activity have been described in the auditory, visual, and somatosensory modalities, as well as during motor tasks. While these different gamma activities are often referred to using the general term '40-Hz activities', they actually include different categories of neural activity that need to be precisely distinguished before we can attempt to relate them to the representational hypothesis presented in the introduction. Two main categories of 40-Hz, or gamma, responses can be considered according to their stimulus phase-locking properties: evoked or induced oscillations.

2.1 Evoked 40-Hz responses (steady-state or transient)

Evoked responses will refer here to components that are phase-locked to the stimulus onset, and that could be usually detected by averaging single-trial responses of EEG or MEG signals.

A stimulus (auditory, visual or somatosensory), periodically modulated at high frequency, elicits a nearly sinusoidal response at the driving stimulus frequency, phase-locked to the stimulus onset, and showing a maximum amplitude in the gamma range (usually when the stimulus rate is around 40 per second). It has been interpreted in terms of natural resonance frequencies of the brain [16], or more prosaically considered as the linear superposition of the early transient components of the classical evoked response [8, 17]. As the classical transient ERPs, it depends on certain physical characteristics of the stimulus, and therefore has been considered as a useful indicator of early sensory processes.

Nevertheless, this 40-Hz steady-state response does not seem to be specifically related to the representational or binding hypothesis.

Galambos and his coworkers [8] were the first to notice that the series of peaks that appears in the evoked response 8 to 80 ms after an acoustic click resemble 3 or 4 cycles of a 40-Hz sine wave. This transient oscillatory response, strictly phase-locked to the stimulus, can be clearly detected by a narrow band-pass filtering of the average evoked potentials. It has been repeatedly observed both in the auditory and visual modalities, in EEG and MEG signals [9, 10, 18-20]. In the auditory modality, the underlying neural sources of this transient 40-Hz response were found in the auditory cortex [9], but did not follow a tonotopic organization, as opposed to the sources of the low-frequency evoked components in the same latency range [21]. Indeed, this highly filtered transient response may reflect the superimposed activity of several evoked-response sources each having a distinct tonotopic organization [22]. An alternative view suggests that this response is initiated in the thalamus and propagates through cortico-thalamic loops from occipital to frontal areas [23]. This interpretation was proposed because a fronto-occipital phase-shift of the oscillating waves was observed over the head. However, these data may be explained as well by several active sources in or near the auditory cortex and slightly delayed in time. This 40-Hz evoked response disappears during deep and REM sleep [10], and is enhanced when the subject is paying attention to the acoustic input [24]. It has also been suggested that the 40-Hz evoked response is related to the temporal integration of two successive brief acoustic stimuli [25]. However, in none of these experiments was the 40-Hz response compared to the wide-band auditory evoked components occurring in the same latency range, namely the middle-latency components (30-70 ms). Its functional specificity as a unitary event thus remains to be established.

2.2 Induced gamma responses

As opposed to the transient or steady-state evoked responses, induced activities are characterized by a loose temporal relationship to the stimulus onset. Oscillatory gamma oscillations, appearing on the scalp with some jitter in latency from one trial to the other, tend to cancel out in the stimulus-locked average response. They received more attention in the late 90's, in relation to the binding hypothesis, following the observation that oscillatory synchronization were found also with a jittering latency in animal multi-unit recordings [26].

Such non-phase-locked activities require specific methods to be reliably detected. All of them have in common the transformation of the single-trial potential or magnetic field into spectral power prior averaging. One simple possibility is to estimate, on each single-trial, the time-variation of gamma power in a particular frequency band around 40 Hz [27]. However, as latency and frequency of gamma activities are not known a priori, a time-frequency approach should be preferred. This can be achieved for instance by computing the time-varying spectra of the EEG/MEG signals tapered by a moving window of fixed duration [12] (Gabor's transform). We propose an alternative method that estimates the time-frequency power of the signals by means of a complex Morlet's wavelet transform which provides a better compromise between time and frequency resolutions (Fig. 1).

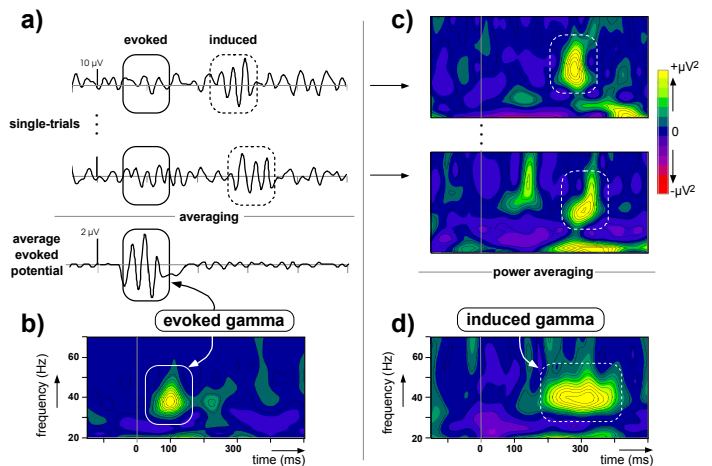


Figure 1: *Principle of wavelet analysis of evoked and induced gamma responses. a) Successive simulated EEG trials with a small amplitude gamma response phase-locked to stimulus onset (full-line boxes) and a gamma burst jittering in latency (dashed-line boxes). Averaging across single trials leads to the conventional evoked potential. b) Time-frequency power representation of the evoked gamma response obtained by wavelet transform of the average evoked potential. The x-axis represents time, and the y-axis, frequency. The color scale codes the variations of power (positive or negative) with respect to a pre-stimulus baseline. The non-phase-locked activity tends to disappear. c) Computation of the time-frequency power for each single-trial, and d) averaging across trials, which allows detecting the induced gamma response.*

When this analysis is applied to the averaged response, the phase-locked gamma activity can be clearly identified (Fig. 1b). When this method is

applied to each single trial, followed by averaging of the powers across trials (Fig. 1d), it becomes possible to identify non-phase-locked activity as long as the signal-to-noise ratio is high enough and the latency-jitter does not exceed the duration of the oscillatory bursts (for more details see [15]).

While the transient or steady-state 40-Hz evoked responses have been tentatively related to the binding hypothesis, there is a growing body of evidence indicating that induced gamma activities is more likely to be relevant for high-level cognitive processes [28], and more precisely in tasks requiring the activation of visual or acoustic object representations (for a review see [15, 29]).

3 Functional role of induced gamma activities

Induced gamma activity has been observed in response to sensory stimuli and during motor tasks in a variety of human EEG and MEG experiments. Although gamma oscillations have been shown to be relevant in motor preparation and sensory-motor integration [11, 30-32], we will focus here our presentation on the role of induced gamma oscillations in visual and auditory processing.

3.1 Induced gamma oscillations and coherent visual representations

In a series of studies from different groups [14, 19, 33-36], it has been shown that when a visual stimulus leads to a coherent percept, a transient increase in the gamma-band is observed at occipital leads, compared to meaningless stimuli (between 200 and 400 ms after stimulus onset, and very often between 30 and 50 Hz). In addition, in several of these studies, the coherence of the stimulus was not reflected directly in the classical ERPs, or in the alpha band (8-12 Hz). Last, variations of gamma power at particular recording sites can be accompanied by episodes of gamma synchronization between distant electrodes, suggesting that areas wide apart can get synchronized [34]. Altogether, these results provide arguments in favor of a specific role of induced neural synchronization in the gamma range in the integration of visual information into a coherent object representation, probably through bottom-up processes.

In addition, induced gamma oscillations also increase when the object representation is not directly triggered by the sensory input itself. Indeed, a transient increase in gamma power appears when the subject has to activate an internal representation of a target, to detect it in a picture where it is hidden, irrespective of its actual presence or not [37].

Moreover, sustained gamma and beta (15-20 Hz) oscillations were shown to be also present during the rehearsal of an object in short-term memory in a visual delayed-matching task [38]. The topography of this sustained activity was this time emerging at both occipital and frontal leads. This suggests a role of oscillatory neural synchrony in bringing together pieces of information, probably activating distinct functional areas, into a meaningful and coherent representation that is perceptually experienced and rehearsed in short-term memory.

3.2 Induced gamma oscillations and auditory representations

So far, induced gamma oscillations have been much less studied in the auditory modality. An induced gamma response was first observed on the human scalp during a simple acoustic detection task [39]. Its amplitude around 40 Hz increased between 200 and 400 ms after stimulus onset in subjects who reacted rapidly, whereas it increased before stimulus for subjects who reacted more slowly.

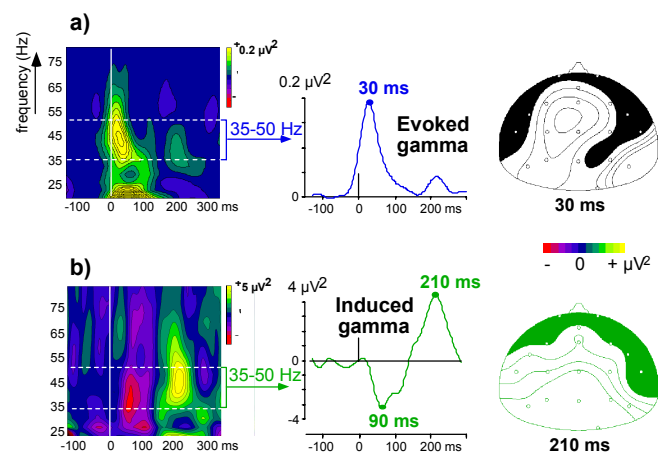


Figure 2: Auditory gamma responses during passive listening. Stimuli: 50-ms and 1000-Hz tone burst presented to subjects watching a silent video movie. a) Time-frequency power representation at electrode Cz of the average evoked response, with the time-course of the mean 35-50Hz power, and its topography at the latency of the maximum (30 ms). b) Mean across trials of the time-frequency power representations (induced activity) with respect to a baseline level in the pre-stimulus (-200 to -50 ms), with the time-course of the mean 35-50 Hz power, and its topography at the latency of the maximum (210 ms). Note the difference in amplitude between the induced ($4\mu V^2$) and the evoked ($0.2\mu V^2$) gamma responses.

In an experiment where subjects were passively listening tone-bursts (1000 Hz and 50-ms duration)

[29, 40], we detected an induced oscillatory response in the EEG, characterized by a reduction (before 150 ms) followed by an increase (peaking between 150 and 300 ms) of gamma power (30-50 Hz) with respect to the pre-stimulus level (Fig. 2b).

This temporal pattern of activation is similar to that observed on an epial electrode array placed over the auditory cortex of anaesthetized rats after acoustic click presentation [41]. Furthermore, the scalp topography of the induced gamma response, with a maximum spreading over parietal electrodes, clearly differs from that of the evoked 40-Hz response (Fig 2a), as well as later auditory evoked components (N100 and P200), thus suggesting different neural sources.

A frequency discrimination paradigm was used to test for a possible role of induced gamma activity in acoustic object representation [15, 29]. Frequent standard tones (1000 Hz) and rare deviant tones (targets at 1040 Hz and distractors at 1080 Hz), were presented to the subjects who had to detect targets by pressing a button. The differences in tone frequency were chosen such that the task could not be performed automatically (85% of correct responses). The inter-stimulus interval was constant (1.4 s), and subjects were aware that at least 3 standard tones were delivered between 2 deviants. The induced gamma response to standard tones showed again a decrease/increase temporal pattern, although the amplitude was 5 times higher than in the passive listening situation (Fig 2b).

The gamma response to the second standard tone (2nd STD) following a deviant was compared to that of the last standard tone (last STD) preceding a deviant (when the subjects were highly expecting a target to occur soon). We found (Fig. 3a) that the induced gamma response peaks significantly later for the last STD (around 500 ms) than for the 2nd STD (around 200 ms) and remains longer (up to 1000 ms). Furthermore, following deviant tones (target or distractor) the gamma activity does not show any increased in power but rather a transient decrease followed by a return to baseline.

The classical averaged evoked potentials after the 2nd and last STDs showed a very clear difference characterized by a large parieto-central positive component between 200 and 400 ms (Fig. 3b). These evoked responses start to differ in the same time period as the induced gamma responses that have different onset slopes. However, while the ERP differences are rather restricted in time (200-400 ms), the gamma response to the last STD remains sustained for a much longer time (200 to 1000 ms). These different time-courses and slightly different

topographies suggest that induced gamma oscillations and ERP components reflect distinct neural processes.

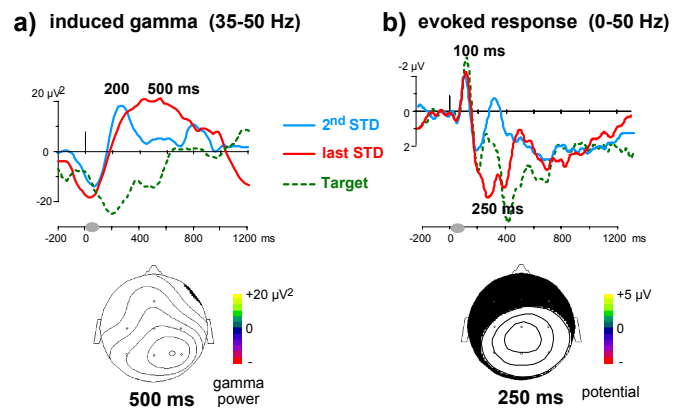


Figure 3: *Frequency discrimination task. Stimuli: 50-ms pure tone-burst delivered binaurally at constant ISI (1.4 sec) in an odd-ball task (see details in the text). Induced gamma and evoked responses were computed separately for the second standard (2nd STD) following a deviant and the last standard (last STD) preceding a deviant. a) Time-course of the mean 35-50 Hz power (induced gamma response) for the different tones. The baseline level is the same for the 3 curves: -250/-50 ms pre-stimulus period of the 2nd STD tone. Bottom: topography of the sustained gamma response at 450 ms. b) Evoked responses of the same tones showing clear differences between the 2nd and the last STD tones between 200 and 400 ms. The response to the target shows a P300 component around 400 ms. Bottom: topography of the increased positivity after the last tone (250 ms). In the time period when the induced gamma response of the 2nd and the last STD are significantly different (400-800 ms), the corresponding evoked responses are identical.*

The prolonged induced gamma activity after several standard tones could be interpreted in terms of increased attention oriented towards an expected target. The subjects reported that, because of the difficulty of the task, they had to actively maintain in memory the pitch of each standard tone to be able to detect small stimulus frequency differences. The sustained gamma could thus also reflect the rehearsal in short-term memory of the pitch representation required to correctly perform the task. Furthermore, after presentation of a deviant tone (target or distractor), the gamma activity is no longer increased, suggesting that the frequency discrimination is performed by distinct and faster processes. This result in the auditory modality is in line with our working hypothesis proposing that

gamma oscillations should emerge during tasks requiring activation of an object representation.

4 Origin of induced gamma activities

Where do these induced oscillations recorded on the scalp originate? How could they be related to oscillatory synchronization observed in animals at a microscopic level? These questions still remain largely unsolved. Nevertheless, several attempts have been made to address the issue of their neural substrate.

4.1 MEG recordings

In collaboration with C. Pantev from Münster, Germany, we repeated the Kanizsa illusory triangle experiment [19] and recorded simultaneously EEG and MEG signals over occipital areas [20]. This experiment requires building up a coherent percept of a triangle, either real or illusory. The transient 40-Hz evoked response at 100 ms was detected both in EEG and MEG recordings, whereas the induced 30-60 Hz gamma activity at 250 ms was observed in the EEG signal only. Preliminary results in the auditory modality showed a similar discrepancy between EEG and MEG recordings for the induced gamma activity during passive listening. It should be noted that almost all the observations of visually or acoustically induced gamma activity reported in the literature concerned EEG recordings. The absence of such induced gamma activity in MEG signals could be explained by deep or radially oriented neural sources which gives rise to a weak magnetic field, or by an unusual source configuration.

4.2 A possible dipole source model

In support of this EEG/MEG discrepancy, we proposed a ring-shaped distribution of current dipoles (Fig. 4) as a source model of the induced gamma oscillations [42]. This dipole configuration creates an electric potential field but no or only weak magnetic field on the scalp surface. Moreover, it generates a field potential that does not reverse through cortical depth as observed in animal studies [43, 44]. This ring-shaped source model could mimic the activity of synapses located on horizontally oriented dendrites all around the soma. Such a geometry is consistent with the idea that interneurons might be involved in a network generating a coherent oscillatory activity [45-47]. However, a possible contribution of pyramidal neurons (basal dendrites for example) to this network cannot be ruled out [48].

4.3 Intracranial recordings in human and monkeys

Preliminary results have been obtained by recording epileptic patients prior to surgery with depth intracranial electrodes. The frequency discrimination paradigm designed for scalp recordings (see section 3.2) has been used in these patients. The case presented here (Fig. 5) shows that on electrodes located in the auditory cortex, crossing Heschl's gyrus and superior temporal gyrus, clear gamma activities can be observed: a first peak of evoked gamma power at 50 ms is followed by an induced activity between 150 and 250 ms, in the 23-43 Hz band. These gamma oscillations were localized rather focally in the auditory cortex: they both vanish laterally within 6 mm.

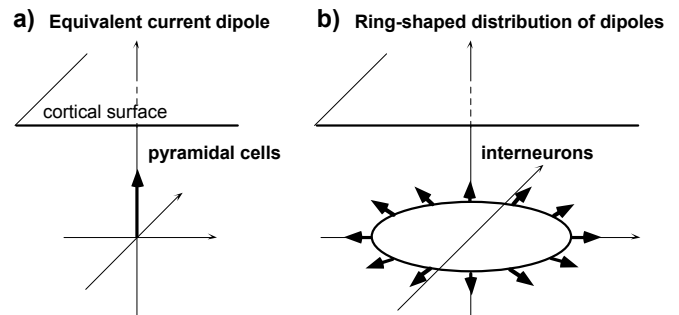


Figure 4: Possible source model of induced gamma activity. a) An equivalent current dipole source model, oriented perpendicular to the cortical surface, is usually proposed for the pyramidal cell synaptic activity underlying the early evoked components. This source model fits with the polarity reversal often observed in cortical depth for such components. It generates a recordable scalp potential distribution and a magnetic field if oriented parallel to the scalp surface (along folded sulci for example). b) This ring-shaped distribution of dipoles creates a field potential that does not reverse through cortical depth, and generates a potential distribution, but no, or weak, magnetic field on the scalp surface. Such ring-shaped sources could explain the discrepancy in EEG/MEG observations, and could mimic the activity of synapses located on horizontally oriented dendrites (interneurons).

The induced gamma activity was found to be more prolonged for the late STD compared to the 2nd STD, as it has been observed in the scalp EEG (see section 3.2). However, this induced intracranial gamma activity was not lasting as long as on the scalp, thus suggesting that oscillatory sources located in other areas might also be involved.

To bridge the gap between unit recording at the cell level and macroscopic recordings on the scalp, we also recorded multichannel EEG signals directly over the surface of the visual cortex of anaesthetized monkeys. This work done in collaboration with J. Bullier from Toulouse, France, allowed to map the electrophysiological activity over areas V1 and V4 after presentation of flashed stimuli (white squares) located at different positions of the visual field. It was possible to clearly identify in both V1 and V4 areas a very focal induced gamma activity, sustained during the stimulus duration [49]. These activities followed the retinotopic organization of V1 and V4.

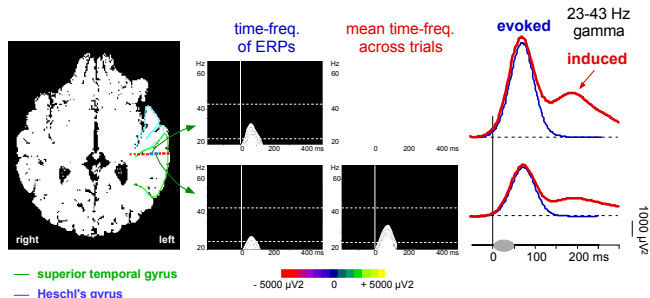


Figure 5: *Intracranial recordings of gamma oscillations in the auditory cortex. The horizontal MRI slice shows the location of the different contacts of the intracranial electrode in the auditory cortex. Time-frequency representations of average ERPs and of the mean power across trials are presented for the electrode contact showing the largest gamma amplitude (top row) and a neighboring electrode 3 mm apart (bottom row). Gamma power time-courses between 23 and 43 Hz are drawn in all cases. They show that early transient evoked gamma activity is still visible on the mean time-frequency power averaged across trials because of the large amplitude of this response. However, an induced gamma activity, well localized in time and frequency, peaks around 200 ms.*

Altogether, these intracranial results in humans and in monkeys, first, confirm the neural origin of gamma oscillations, and, second, are consistent with the idea that gamma oscillations observed on the scalp might be due to the activation of multiple oscillatory foci. One should note that, to emerge and to be detectable in the scalp EEG, an induced oscillation should correspond to a large and highly synchronized cell ensemble. This cell assembly could be located in one particular area, or distributed over neighboring or distant areas in the brain.

5 Conclusions

The representational hypothesis presented in the introduction is derived from the basic feature-binding hypothesis tested in animal studies and postulates that fast oscillatory synchronization of brain areas underlies the construction of a task-relevant object representation.

The results presented here thus suggest that early evoked ERP components, including 40-Hz transient responses, and stimulus induced gamma oscillatory activities might reflect different brain processes with distinct types of neural sources. Although all those electrophysiological components have been found to play a role in visual or auditory information processing, it seems that induced gamma oscillations might more specifically reflect the neural mechanism underlying the activation of coherent object representation, triggered either by a sensory input or by top-down internal processes.

Induced gamma activities recorded on the human scalp may take different spatial and temporal forms, thus showing a high degree of flexibility that depends upon the sensory system recruited and the behavioral task involved. They should not be considered as a unique or stereotyped brain response derived from the same set of neural sources. On the contrary, they seem to reflect interactions within networks organized both in space and time. This accords with an interpretation in terms of dynamic cooperative mechanisms that link together various brain areas to encode the different features of an object and have their own specific function in relation to the task to be performed.

Fast oscillatory synchronization of distributed cell assemblies may thus be proposed as a very general neural mechanism underlying sensory integration and object representation in different behavioral situation (stimulus detection or discrimination, stimulus recognition, and memory processes). While early evoked potentials could reflect the encoding of some physical attributes of the stimulus, possibly modulated by attentional processes, the induced gamma oscillations that follow might play a crucial role in binding together those areas that are necessary to perform a particular task. They should thus not be attributed to a particular psychological process, but could rather be considered as a general neural mechanism that binds together the sensory and cognitive properties of any perceived or recalled object into an experienced entity, and could also play a role in linking together an integrated sensory percept to an adapted motor behavior.

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