Oscillatory gamma activity in humans: a possible role for object representation

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Abstract

The coherent representation of an object has been suggested to be established by the synchronization in the gamma range (20–100 Hz) of a distributed neural network. So-called ‘40-Hz’ activity in humans could reflect such a mechanism. We have presented here experimental evidence supporting this hypothesis, both in the visual and auditory modalities. However, different types of gamma activity should be distinguished, mainly the evoked 40-Hz response and the induced gamma activities. Only induced gamma activities seem to be related to coherent object representations. In addition, their topography depends on sensory modality and task, which is in line with the idea that they reflect the oscillatory synchronization of task-dependent networks. They can also be functionally and topographically distinguished from the classical evoked potentials and from the alpha rhythm. It was also proposed that the functional role of gamma oscillations is not restricted to object representation established through bottom-up mechanisms of feature binding, but also extends to the cases of internally driven representations and to the maintenance of information in memory. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Synchronized oscillatory activity in the gamma range (30–100 Hz) could play a major role in linking the different areas involved in the same object representation into a unified, coherent percept. Indeed, the distributed nature of the network coding for a given object in a particular task is now well documented, in particular by many neuroimaging studies (for review see Courtney et al., 1997). Following the theoretical proposal from Milner (1974), von der Malsburg and Schneider (1986), the neural structures participating in this...
network might be dynamically linked by oscillatory synchronous firing. Over the last decade, this hypothesis has been supported by a growing body of experimental findings in anesthetized and awake animals (Gray et al., 1989; Kreiter and Singer, 1996; for review see Singer and Gray, 1995).

The inspection of the human EEG/MEG literature since the 1950s reveals numerous reports of gamma oscillatory activities in various sensory modalities and tasks (Galambos et al., 1981; Pantev et al., 1991; Pfurtscheller et al., 1994, among many others: Sem-Jacobsen et al., 1956; Sheer, 1989; for review see Tallon-Baudry and Bertrand, 1999). 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 term ‘40-Hz activity’ in an undifferentiated manner; and (2) a common framework for interpretation is somehow lacking.

The three different types of 40-Hz activities observed in humans (namely, evoked, induced and steady-state responses) (Galambos, 1992) will be presented. Experimental evidence showing that induced gamma activity can be related to the generation of unified object representation will be given. The functional specificity of induced gamma oscillations, as compared to the evoked gamma response or classical evoked potential, will be assessed.

2. The three different types of ‘40-Hz’ activities

2.1. Steady-state response

Steady-state evoked potentials are obtained in response to periodically modulated stimuli (auditory, visual or somatosensory). They have a sinusoidal-like waveform at the driving stimulus frequency, and show amplitude maxima in different frequency bands, particularly at approximately 40 Hz. They could reflect the superposition of transient early evoked components (Galambos et al., 1981; Morgan et al., 1996).

2.2. Evoked gamma

A transient oscillatory evoked response has been observed in the first 100 ms following auditory, visual or somatosensory stimuli. It has the general property of evoked responses to be quite strictly phase-locked to stimulus onset. It could thus be easily detected in the narrow-band filtered average evoked potential. It has first been described in the auditory modality (Pantev et al., 1991; Ribary et al., 1991), and later in the visual modality (Sannita et al., 1995; Tallon et al., 1995) at approximately 40 Hz.

This evoked gamma response, mainly studied in the auditory modality, has never been systematically compared to the classical evoked components occurring in the same latency range. An alternative interpretation is that this 40-Hz evoked response could be part of a large-band complex response. Indeed, narrow-band filtering could artificially create an oscillatory phenomenon. In addition, no specific functional role of this gamma response has been demonstrated so far in the framework of the object representation hypothesis.

2.3. Induced gamma

The third type of gamma response that has been observed in the human EEG, namely induced gamma activity, could be related to the object representation hypothesis. It appears as bursts of oscillatory activity with a latency jitter from trial to trial (Fig. 1a, dashed box). Such an induced gamma response cancels out by classical stimulus-locked potential averaging (Fig. 1b). It thus requires specific detection methods based on spectral analysis, yielding to positive power values that could sum up in the average across trials (Fig. 1c).

Since both the latency and frequency of oscillatory bursts are a priori not known, a time-frequency representation of the signal is more appropriate (Makeig, 1993; Tallon-Baudry and Bertrand, 1999). The approach we propose is based on a wavelet transform which provides a better compromise between time and frequency resolution than the more classical moving short-
Fig. 1. (a). Successive simulated EEG trials with an early gamma response phase-locked to stimulus onset (full line boxes) and a late gamma burst jittering in latency (dashed line boxes). (b). Averaging in the time domain across trials leads to the conventional evoked potential. (c). Time-frequency power representation (wavelet transform) of the evoked gamma response. The x-axis is time, and the y-axis is frequency. The gray scale codes the variations of power positive or negative with respect to a prestimulus baseline. The non-phase-locked activity cancels out. (d). Time-frequency power computed for each single trial. (e). Average of time-frequency powers across trials. The induced gamma response is clearly visible.

To detect stimulus-induced activities, a wavelet-based analysis (complex Gaussian wavelet, fully detailed in Tallon-Baudry and Bertrand 1999) is applied on each single trial (Fig. 1d), and time-frequency powers are then averaged across trials (Fig. 1e). It is thus possible to identify non-phase-locked activity as long as its signal-to-noise ratio is high enough and its latency jitter does not exceed the wavelet duration. What is usually considered are the variations of gamma power with respect to a particular baseline level that is usually taken in the pre-stimulus period.

Evidence will be given that such induced activities could reflect the activation of an object representation, both in the visual and auditory modality.

3. Functional importance of visually induced gamma activity

If synchronized oscillatory activity indeed plays a role in linking together the different neural regions involved in the same object processing, it should be enhanced whenever a coherent percept is being built. So far, we have tested three different experimental paradigms involving the activation of an object representation.

In the first case (Tallon-Baudry et al., 1996), subjects were presented with coherent triangles or an incoherent control (Fig. 2a). Both coherent stimuli (illusory and real triangles) elicit a significantly increased induced gamma response compared to the no-triangle stimulus, at approximately 280 ms (Fig. 2b,c). In this experiment, all stimuli share the same type of physical properties; however, only the perception of the illusory and real triangles involves some binding between the different parts of the image to build a coherent representation. The increased induced gamma response could thus correspond to the synchronized oscillatory cell assembly reflecting the activation of this representation. These results are in keeping with those of Lutzenberger et al. (1995),
Müller et al. (1996, 1997); see also this issue (Müller et al., 2000) who observed an increase in gamma power on response to coherently moving bars or with ambiguous rotating figures.

On the other hand, the evoked potentials do not vary according to stimulus coherency: two successive effects are observed, the illusory triangle eliciting a more prominent temporo-occipital negativity at approximately 250 ms and the real triangle a parietal positivity at 320 ms (Fig. 2d). In addition, in a similar experiment, Herrmann and Mecklinger (2000) observed an increase of the early evoked gamma response to the target stimulus.

However, the general hypothesis on the functional role of oscillatory synchronization does not
only predict an increase in gamma power when an object representation is being built from the stimulus presented, as in the experiences above, but also whenever an internal representation is being activated through top-down processes or retrieved from memory.

Fig. 2 (a). Stimuli. Subjects were presented with two coherent stimuli (illusory and real triangles) and a not coherent stimulus ('no-triangle' stimulus). They had to count the occurrences of a curved illusory triangle. Correct performance of this task indicates that subjects perceive correctly illusory contours throughout the whole experiment. (b). Time–frequency plots (grand average across eight subjects, 150 trials per subject and stimulus condition) at electrode Cz, in response to the illusory triangle (left) and to the no-triangle stimulus (right). At this electrode, both evoked and induced gamma responses could be observed. An evoked gamma response could be seen at 100 ms and 40 Hz, in response to all stimuli. It did not vary with stimulus coherency, and peaked at Cz. Later, an induced gamma response appears at approximately 280 ms, extending from 30 to 60 Hz. This induced gamma activity was much more pronounced in response to coherent stimuli than in response to the no-triangle stimulus, and peaked at more occipital electrodes. (c). Topographical maps of the mean 250–350-ms, 30–70-Hz energy in response to the three stimulus types (back view of the head). Both the illusory and real triangles elicit a prominent occipital induced gamma activity (arrows). Differences between the two triangles are not significant. This induced gamma activity could thus reflect the spatial binding between the different parts of the picture into a coherent triangle representation. (d). Topographical maps (back views) of the classical evoked potentials, at the two latencies where significant differences can be observed. At 250 ms, the illusory triangle elicits a more pronounced occipital and bilateral negativity (arrows) than the two other stimuli. At 320 ms, the parietal positivity is extended over the right hemisphere in response to the real triangle. The effects observed in the evoked potentials are thus different from those in the gamma range.

Fig. 3. (a). Example of the stimuli used. A naive subject perceives such a stimulus as meaningless blobs. However, subjects can be trained to detect the Dalmatian dog that is hidden in the picture. The outlines of the Dalmatian dog have been extracted (rightmost column) to provide the reader with the object searched for. (b). Time–frequency plots (grand average across 13 subjects) at electrode O1, in response to the Dalmatian dog picture in naive (left) or trained (right) subjects. The induced gamma activity at 280 ms after stimulus onset is massively increased in trained subjects. This could indicate that it reflects the activation of the internal representation of the Dalmatian dog that is needed to perform the task. An evoked gamma response peaking at 100 ms at Cz was also present in these data, but not visible at electrode O1. This evoked gamma response did not vary with stimulus conditions. (c). Topographical map of the induced gamma response (back view of the head).
In a second experiment (Tallon-Baudry et al., 1997), we tested whether the activation of an internal object representation also elicits a strong gamma activity. We used a modified version of the well-known Dalmatian dog picture (Fig. 3). Naive subjects perceive this kind of pictures as meaningless black blobs on a gray background. However, once trained, subjects can detect the Dalmatian dog that is hidden in the picture, provided that they know what they are looking for. In other words, they need to activate an internal representation of the dog to be able to dissociate it from the background. To ensure the perception of the Dalmatian dog, the subjects had to discriminate between two dogs (head rightward or leftward). When subjects actively search for the
dog, the induced gamma response is massively enhanced, suggesting that the activation of a mental representation through top-down mechanisms also involves the oscillatory synchronization of a distributed cell assembly. It should be noted that, in this experiment, the increase of gamma activity occurs earlier than any change in the evoked potentials.

A third prediction was that gamma activity should be present during the rehearsal of an object representation in short-term memory (Tallon-Baudry et al., 1998, 1999). To test this prediction, subjects had to perform a delayed-matching-to-sample task, with rounded shapes as stimuli (Fig. 4a). An induced gamma appears in response to the first stimulus, at occipital electrodes. During the delay, a sustained gamma activity is observed. It disappears in a control condition in which sustained attention, but no stimulus memorization is required (Fig. 4b).

The topography of the sustained gamma activity appearing during rehearsal in memory (Fig. 4c) shows both an occipito-temporal and a frontal maximum, which is in line with the hypothesis of the synchronization of an occipito-frontal network in visual short-term memory tasks (Fuster, 1997). In addition, the topographies of gamma activity in the delayed-matching-to-sample task, in the Dalmatian dog (Fig. 3c) and in the triangles (Fig. 2c) experiments are different, suggesting that different gamma networks can be activated depending on the task to be performed.

Another component of the response, in the beta range (15–20 Hz), was also enhanced during the delay in the memory condition compared to the control condition. Its topographical distribution suggests the existence of a second memory-related occipito-frontal network, not overlapping the one in the gamma range (Fig. 4c,d). No effect was observed in the alpha (8–12 Hz) range during the delay (Fig. 4e). In addition, the manipulation of the delay duration (Tallon-Baudry et al., 1999) revealed that no component of the evoked potential was likely to reflect the rehearsal of the first stimulus in short-term memory. Indeed, only the oscillatory activities in the gamma and beta range showed a sustained time-course during the delay compatible with an active maintenance of information in visual short-term memory. However, we did not investigate oscillations in the theta band which may play a role in memory processes (von Stein and Sarnthein, 2000; Klimesch et al., 1997).

4. Auditory evoked and induced gamma responses

4.1. Evoked 40-Hz response

A transient 40-Hz oscillatory component has been observed in the first 100 ms following a transient acoustic stimulus in the averaged evoked response from either electrical or magnetic signals. It consists of a small amplitude response,
phase-locked to the stimulus onset and occurring in the same time range as the middle-latency auditory components (Fig. 5a). Pantev et al. (1991) revealed from magnetic recordings that this 40-Hz response is generated at least partially in the auditory cortex. Similarly, we have shown (Bertrand and Pantev, 1994) that the scalp distribution of the electrical 40-Hz response presents a topographical pattern characterized by a polarity reversal across the Sylvian fissure of both scalp potential and scalp current density. This suggests neural generators of alternating orientation in a rather focal area, in or near the auditory cortex (Fig. 5b), as observed for middle-latency (Pa) or N100 components. However, from MEG signals, these neural sources were found 5 mm more anterior and more medial than the sources of the slow auditory component peaking at 100 ms (N100) (Pantev et al., 1993). Furthermore, the sources of the 40-Hz components do not follow a tonotopic organization, as opposed to the sources of the low-frequency evoked components in the

Fig. 5. Stimuli: 50 ms tone burst (1000 Hz) presented binaurally (random ISI, mean = 700 ms) to subjects watching a silent video movie. (a). Averaged evoked response at electrode Cz (1000 stimuli, grand average across 10 subjects), wide-band (0–50 Hz) and narrow-band (35–50 Hz) digitally filtered. Oscillations appearing in the first 70 ms could be related to the successive middle-latency components. (b). Scalp topography of two successive peaks (38 and 50 ms) of the filtered gamma response. Potential and scalp current density (surface Laplacian) distributions show a polarity reversal across a line delineating the Sylvian fissure. These patterns are very similar to those classically observed for Pa (30 ms) and N100 components. (c). Time-frequency representation at electrode Cz of the average evoked response, with the time-course of the mean power between 35 and 50 Hz, and its topography at the latency of the maximum (30 ms). (d). Average across trials of the time-frequency representations with a baseline power level in the pre-stimulus (−200 to −50 ms). The time-course of the mean power between 35 and 50 Hz shows a decrease followed by a decrease. The topography at the latency of the maximum (210 ms) clearly differs from that of the evoked gamma power. Note the difference in amplitude between the induced and the evoked gamma responses.
same latency range (components Pa approx. 30 ms and N100 approx. 90 ms) (Bertrand and Pantev, 1994). This may then suggest the contribution of functionally distinct neural populations. However, due to the narrow filters used (30–50 Hz), this 40-Hz response may also correspond to the superimposition of successive evoked components having sources following distinct tonotopic organization.

An alternative interpretation suggested that oscillatory 40-Hz spontaneous activity may be reset and enhanced by sensory stimuli, thus leading to a response phase-locked to the stimulus (Ribary et al., 1991). These authors also claimed that it is initiated in the thalamus and propagates through cortico-thalamic loops with rostro-caudal sweeps. 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.

The amplitude characteristics with stimulus rate of the magnetic 40-Hz response and the N100 component were found to be different, thus suggesting the contribution of neural generators having distinct habituation pattern (Pantev et al., 1993). This response disappears during deep and REM sleep (Llinas and Ribary, 1993), and is enhanced by selective attention to the acoustic input (Tiitinen et al., 1993). The 40-Hz response seems also to be related to the temporal integration of two successive click stimuli (Joliot et al., 1994). Finally, in a passive odd-ball paradigm, no difference was found in the 40-Hz response between standard and deviant tones (Tiitinen et al., 1994).

However, in none of these experiments was the 40-Hz response compared to the multiple components of the wide-band response occurring in the very same latency range, namely the middle-lateney components (30–70 ms). When comparisons were made in these studies, they concerned only the 40-Hz maximum peak and N100 component occurring in successive time-periods. The functional specificity of this response as a unitary event thus remains to be established.

4.2. Induced gamma activity

Induced gamma activity, not phase-locked to the stimulus, was observed on the human scalp during a simple acoustic detection task (Jokeit and Makeig, 1994). The strength of the induced response increased between 200 and 400 ms after stimulus onset in subjects who reacted rapidly, whereas it increased before stimulus onset for subjects who reacted more slowly. Another study based on passive and active auditory paradigms has reported differences in the EEG gamma power, 200–300 ms after subjects heard standard tones compared to when they heard deviant tones (Marshall et al., 1996).

In an experiment where subjects were passively listening 1000 Hz tone-bursts of 50 ms duration (Bertrand et al., 1999), we detected in the EEG an induced oscillatory response characterized by a reduction (before 150 ms) followed by an increase (peaking between 150 and 300 ms) of gamma power with respect to the pre-stimulus level (Fig. 5d). This temporal pattern of activation is similar to that reported from epipial electrode array placed over the auditory cortex of anaesthetized rats after acoustic click presentation (Franowicz and Barth, 1995). Furthermore, the scalp topography of the induced gamma response, with a maximum spreading over parietal electrodes (Fig. 5d), clearly differs from that of the evoked 40-Hz response as well as later auditory evoked components (N100 and P200), suggesting different neural sources.

A frequency discrimination paradigm was used to test for a possible role of induced gamma activity in acoustic object representation (Bertrand et al., 1998; Tallon-Baudry and Bertrand, 1999). Frequent standard tones (1000 Hz) and rare deviant tones, targets (1040 Hz) and distractors (1080 Hz), were presented to the subjects who had to detect targets by a button press. The tone frequencies 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 three standard tones were delivered between two deviants. As in the passive listening situation, although with five times higher ampli-
tude, the induced gamma response to standard tones was characterized by a power decrease (approx. 100 ms) followed by an increase (approx. 250 ms).

The gamma response to the second standard tone (second 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. 6a) that the induced gamma response peaks significantly later for the last STD (approx. 500 ms) than for the second STD (approx. 250 ms) and remains longer (up to 1000 ms). Furthermore, following deviant tones (target or distractor) the gamma activity does not show any increased power but rather a transient decrease followed by a return to baseline.

The time averaged evoked potentials after the second and last STD showed a very clear difference characterized by a large parieto-central positive component between 200 and 400 ms (Fig. 6b). These evoked responses start to differ in the same time period as the induced gamma responses, which present 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 (200–1000 ms). These different time-courses suggest that induced gamma oscillations and ERP components reflect distinct neural processes.

The prolonged induced gamma activity after several standard tones could be interpreted in terms of increased attention oriented towards an

![Fig. 6. Stimuli: 50 ms pure tone burst were delivered binaurally with a constant ISI (1.4 s): frequent standard tones (1000 Hz) and rare deviant tones (target at 1040 Hz or distractor at 1080 Hz). Subjects had to press a button after each target tone, and they were aware that at least three standards were delivered between two deviants. Induced and evoked responses were computed separately for the second standard (second STD in full thin line) following a deviant and the last standard (last STD in full thick line) preceding a deviant. (a). Time-course of the mean power between 35 and 50 Hz (induced gamma response) is presented for second STD, last STD and target tones. The baseline level is the same for the three curves: pre-stimulus period (−250 to −50 ms) of the second STD tone. The last STD elicits a more prolonged gamma activity that may be related to increased attention or pitch rehearsal in memory. Bottom: topography of the prolonged gamma response at 450 ms. (b). Evoked responses of the same tones showing clear differences between the second and the last STD tones between 200 and 400 ms. The response to the target shows a P300 component at approximately 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 second and the last STD are significantly different (400–800 ms), the corresponding evoked responses are identical.]
expected target. The subjects reported that, because of the difficulty of the task, they had to actively maintain in memory each of the short-duration standard tones to detect small stimulus frequency differences. The sustained gamma could thus be also interpreted in terms of rehearsal of the pitch representation required to correctly perform the task. Furthermore, after the presentation of a deviant tone, the gamma activity is no longer increased, suggesting that the frequency discrimination is performed by faster different 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.

5. Conclusions

Do induced gamma activities and evoked potentials reflect distinct processes? Several arguments stand in favor of a clear distinction between these two phenomena. Indeed, the topographies of induced gamma and evoked potentials can be very different, as for example during the delay in the visual short-term memory experiment (Fig. 4), or fairly close, as in the acoustic frequency discrimination task (Fig. 6). The effects observed on induced gamma activity can occur at shorter latencies than those observed in the evoked potentials (as in the Dalmatian dog experiment), or at longer latencies (as in the acoustic frequency discrimination task). Therefore, the precedence of evoked potentials effects on induced gamma modulations cannot be considered to be a general rule. Finally, the effect of stimulus features or task is different on the evoked potential and on the induced gamma activity.

Could gamma oscillations be harmonics of lower-frequency rhythms (Jurgens et al., 1995)? The visual short-term memory experiment provides evidence that induced gamma and alpha rhythms are functionally and topographically distinct. However, in the same experiment, the relationships between gamma and beta activities are less clear-cut, since they both show the same type of variation with the task, although with different topographies.

With the only restriction concerning beta activities, the induced gamma activity was the only component of the response to vary in accordance with the predictions of the object representation hypothesis. In addition, the task-dependency of gamma activity suggests that it reflects the activation of a task-oriented network. These results thus give strong support to the idea that the establishment of a coherent and unified percept is achieved through the oscillatory synchronization in the gamma range of a distributed neural network.

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References


