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Oscillatory gamma activity in humans and its role in object representation

Catherine Tallon-Baudry and Olivier Bertrand

We experience objects as whole, complete entities irrespective of whether they are perceived by our sensory systems or are recalled from memory. However, it is also known that many of the properties of objects are encoded and processed in different areas of the brain. How then, do coherent representations emerge? One theory suggests that rhythmic synchronization of neural discharges in the gamma band (around 40 Hz) may provide the necessary spatial and temporal links that bind together the processing in different brain areas to build a coherent percept. In this article we propose that this mechanism could also be used more generally for the construction of object representations that are driven by sensory input or internal, top-down processes. The review will focus on the literature on gamma oscillatory activities in humans and will describe the different types of gamma responses and how to analyze them. Converging evidence that suggests that one particular type of gamma activity (induced gamma activity) is observed during the construction of an object representation will be discussed.

W hen one searches for a familiar person in a crowd, different cues (height, face, clothes, etc.) are retrieved from memory and combined to form a coherent representation of the desired person. Similar representations are used in many situations and can be composed of many different features and include visual, auditory, semantic, or even emotional information. Data from numerous neuropsychological and neuroimaging studies in humans[1,2], and neurophysiological studies in animals[3], indicate that the processing of these different features involves anatomically distinct

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Box 1. Three different types of gamma response

According to the nomenclature suggested by Galambos (see Ref. a) three types of gamma response can be considered:

(1) 40-Hz transient evoked response

Any evoked response, whether oscillatory or not, is characterized by precise phase-locking to the stimulus onset (Fig. I, blue boxes). It can thus be detected by averaging single-trial responses, even if the amplitude signal is small. A transient oscillatory evoked response has been observed in the first 100 ms following an auditory stimulus, after narrow-band filtering in the gamma frequency range (around 40 Hz) of either electro encephalographic (EEG) or magneto encephalographic (MEG) signals. The underlying neural sources were found in the auditory cortex (Ref. b), but did not follow a tonotopic organization, as opposed to the sources of the low-frequency evoked components in the same latency range (Ref. c). Indeed, this heavily filtered transient response may reflect the superimposed activity of several evoked-response sources each having a distinct tonotopic organization (Ref. d). An alternative view suggests that this response is initiated in the thalamus and propagates through cortico-thalamic loops from occipital to frontal areas (Ref. e). This 40-Hz evoked response disappears during deep and REM sleep (Ref. f), and is enhanced when the subject is paying attention to the acoustic input (Ref. g). It has also been suggested that the 40-Hz evoked response reflects the temporal integration of two successive brief acoustic stimuli (Ref. h). 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.

A short-latency oscillatory evoked response has also been described in the visual modality in response to brief static stimuli around 40-Hz in EEG (Refs i–k) and MEG (Ref. l), or around 100 Hz in MEG (Ref. m). A very high-frequency oscillatory response (near 600 Hz) has been found 20 ms after somatosensory stimulus onset (Refs n,o). The source of this stimulus phase-locked activity follows a somatotopic organization in the primary somatosensory cortex (Ref. o).

The functional role of the auditory and visual 40-Hz evoked responses, as well as the high-frequency somatosensory evoked response, is still unclear and their relationships with the representational hypothesis have not been studied systematically. However, in our experiments, crucial parameters such as stimulus coherency affected neither amplitude nor frequency of these responses. They are therefore not likely to be involved in the generation of object representation. Whether these early oscillatory responses should be considered as reflecting the succession of early transient evoked potentials remains a matter of discussion. Nevertheless, any early evoked component, oscillatory or not, may play a role in signaling precise temporal relationships between stimuli and thus participate in the binding of synchronously incoming events. Indeed, there is some psychophysical evidence that visual features presented simultaneously tend to be more often grouped together (Refs p,r), even though these findings remain a matter of controversy (Refs s,t).
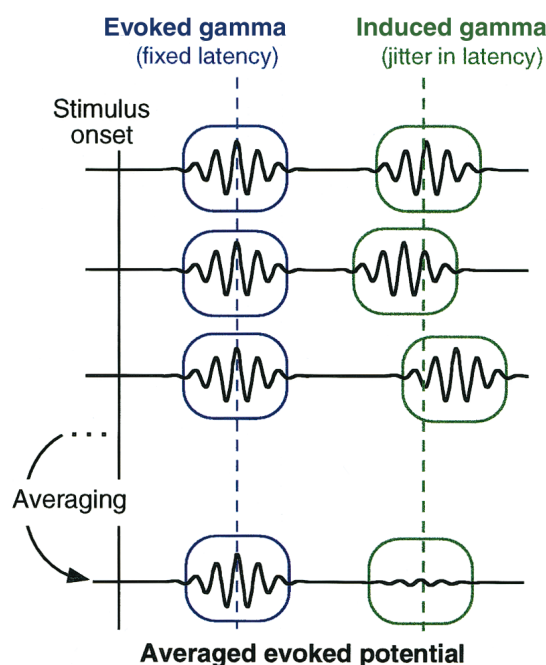

Fig. I. Schematic representation of evoked and induced gamma oscillatory responses. An *evoked* response (blue boxes) appears at the same latency and phase in each single trial and hence can be detected in the averaged evoked potential. An induced response (green boxes) appears with a jitter in latency from one trial to another, centred around a given latency (green line). It therefore tends to cancel out completely in the averaged evoked potential. Specific methods must therefore be used in order to characterize induced activities (see Box 2).

(2) 40-Hz steady-state response

A periodically modulated stimulus (auditory, visual or somatosensory) elicits a nearly sinusoidal response at the driving stimulus frequency, showing a maximum amplitude in the gamma range (usually around 40 Hz). It has been interpreted in terms of natural resonance frequencies of the brain (Ref. u), or more prosaically considered as the superposition of the early transient evoked components (Ref. v). This 40-Hz steady-state response does not seem to be related to the representational or binding hypothesis.

(3) Induced gamma (30–80 Hz) response

In contrast to the evoked 40-Hz response, the induced gamma activity consists of oscillatory bursts whose latency jitters from trial to trial (Fig. I, green boxes): its temporal relationship with stimulus (or movement) onset is fairly loose. Hence, this gamma activity is not revealed by classical averaging techniques that are used for evoked responses. For this reason, induced gamma activities have been less often reported in the literature. Specific methods based on time-varying spectral analysis of single trials (Box 2) are needed to detect them. The functional properties of these activities are described in details in the main text.

brain areas. Moreover, depending on the particular objective the same stimulus may activate different networks[4]. By what mechanism are these different brain areas dynamically linked together?

One influential proposal is that a rhythmic synchronization of neuronal discharges provides the link between and within the areas involved in a given network[5–9]. A growing body of experimental literature supports the role of oscillatory synchronization in bottom-up visual feature binding. In animals, stimulus-specific oscillatory activity in the gamma frequency range (30–80 Hz) has been observed in the visual cortex of anaesthetized cats[10–14] and awake

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monkeys[15,16]. Epochs of oscillatory spike synchronization were observed more frequently in response to visually coherent moving bars than to independently moving patterns. This temporal coding could underlie feature binding in bottom-up perceptual processes. Nevertheless, in cats or monkeys, evidence for the role of oscillatory synchronization in

grouping has been mainly obtained from low-level visual areas, under anaesthesia or during passive fixation tasks.

This mechanism could hypothetically be extended to the more general notion of object representation[17,18]. This implies the binding of spatially distinct parts of the same object through bottom-up processes, as suggested by animal studies, but also more generally the activation, retrieval or rehearsal of an internal representation through top-down processes. This 'representational hypothesis' might also apply to and across different sensory modalities. Here, we review oscillatory activity in the gamma frequency range in human electroencephalography (EEG) and magnetoencephalography (MEG), with particular emphasis on those activities that we believe relate to this representational hypothesis.

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. Three categories of 40-Hz activity can be considered (see Box 1). Firstly, the steady-state response that is elicited by a periodically modulated stimulus; secondly, the evoked response that is phase-locked to stimulus onset; and lastly, induced responses that are not phase-locked to stimulus onset. This last class of induced 40-Hz activities appear with a jitter in latency from one trial to the next and are thus partly or totally cancelled out by the averaging process classically used in evoked-potential studies. Hence, they require specific methods of detection (Box 2).

While the 40-Hz steady-state or evoked responses have been tentatively related to the binding hypothesis without clear experimental support, a growing body of evidence indicates that induced gamma activity is more likely to be relevant for 'high-level cognitive processes'[19]. In this paper, we will focus on a possible role of this induced gamma activity for the representation of objects.

When is induced-gamma activity observed?

Induced-gamma activity has been observed in response to sensory stimuli and during motor tasks in a variety of human EEG and MEG experiments. We now briefly review the somewhat disparate induced-gamma literature organized according to the type of task in which the subject is engaged. All the studies listed below point towards a modulation of induced gamma strength by the perceptive and cognitive parameters of the task; however they do not address the issue of the functional role of induced gamma in relation to the representational hypothesis.

Motor tasks
Gamma oscillations in the 40 Hz range have been observed in the EEG[20] and MEG[21,22] signal prior to, or during, voluntary finger, forearm or leg movements although they were not phase-locked to movement onset. These findings are consistent with observations of local field potential oscillations in the motor cortex of awake cats[23] and monkeys[24,25]. This movement-related oscillatory activity seems to correspond to the somatotopic organization of the primary sensorimotor

Box 2. How to identify evoked and induced gamma activities

Evoked gamma activity is strictly phase-locked to the stimulus onset and can be seen in the averaged evoked response, whereas the latency of induced gamma activity varies across trials and is therefore canceled out by averaging. Specific methods are thus necessary to detect and characterize these induced gamma responses.

One simple possibility is to estimate, on each single-trial, the time-variation of gamma power in a particular frequency band around 40 Hz (Ref. a). However, as latency and frequency of gamma activities are not known a priori, a time-frequency approach should be preferred. This can be achieved by computing the time-varying spectra of the EEG tapered by a moving window of fixed duration (Ref. b) (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 (Fig. F,G) which provides a better compromise between time and frequency resolutions (Ref. c).

When this analysis is applied to the averaged response, the phase-locked gamma activity can be clearly identified (Fig. C). When this method is applied to each single trial, followed by an averaging of the powers across trials (Fig. E), it becomes possible to identify non-phase-locked activity as long as the signal-to-noise ratio is high enough and the jitter does not exceed the wavelet duration.

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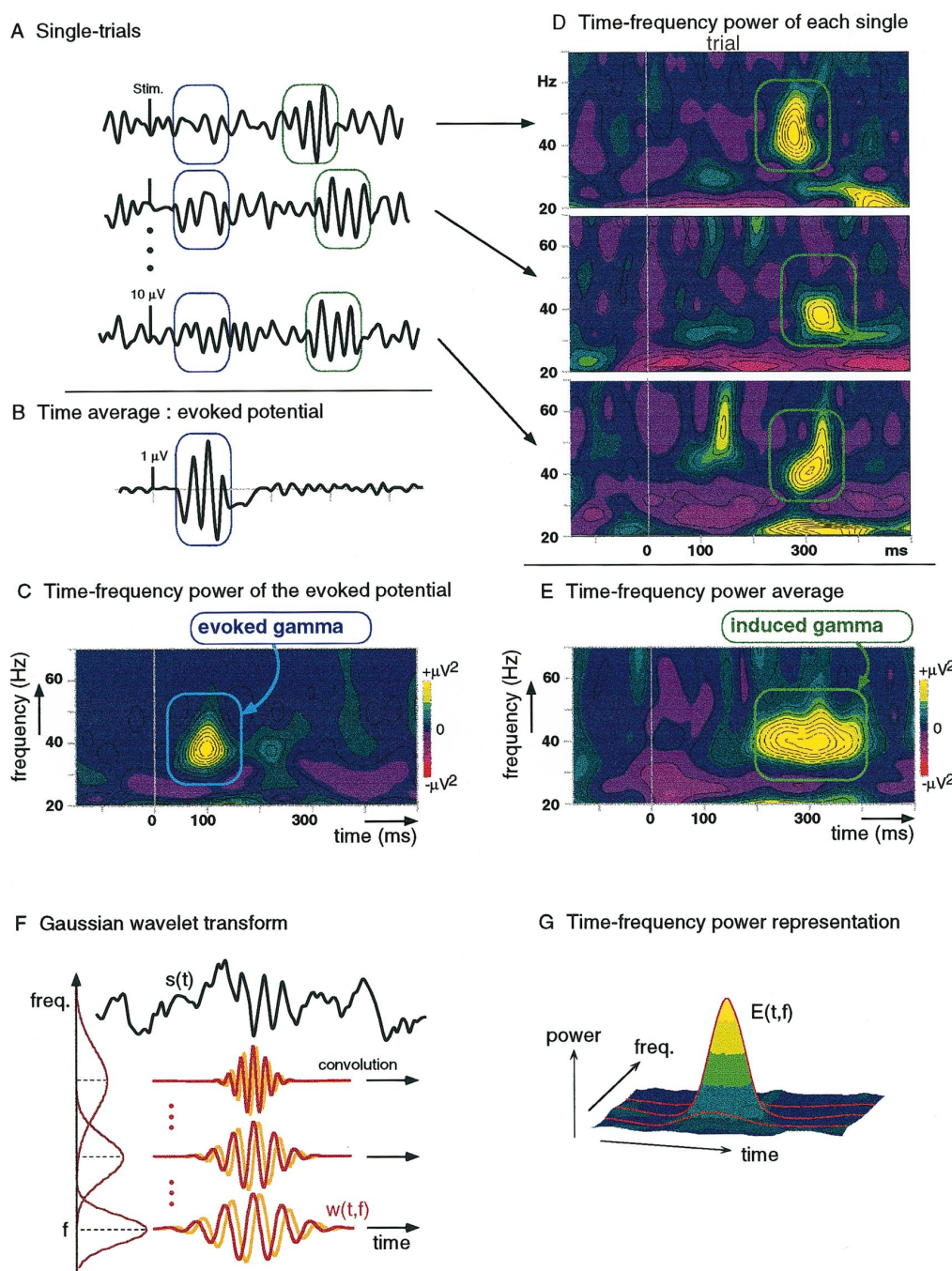
A Single-trials

B Time average : evoked potential

C Time-frequency power of the evoked potential

D Time-frequency power of each single trial

E Time-frequency power average

F Gaussian wavelet transform

G Time-frequency power representation

Fig. I. (A) Successive EEG trials (simulated data) with a small amplitude gamma response phase-locked to stimulus onset (blue boxes) and a gamma burst jittering in latency (green boxes). **(B)** Averaging across single trials leads to the conventional evoked potential. **(C)** Time–frequency power representation of the evoked gamma response. The abscissa represents time, and the ordinate, frequency. The color scale codes the variations of power (positive or negative) with respect to a pre-stimulus baseline. The non-phase-locked activity is cancelled out. When the time-frequency power is computed for each singe trial **(D)**, and then averaged across trials **(E)**, the induced gamma response is revealed. **(F, G)** Principle of the wavelet transform. **(F)** The signal to be analyzed s(t) is convoluted by complex Morlet's wavelets w(t,f) having a Gaussian shape both in the time domain (standard deviation σ_t), and in the frequency domain ($\sigma_f = 1/(2\pi\sigma_t)$) around a frequency f: $w(t,f) = A.\exp(-t^2/2\sigma_t^2).\exp(2i\pi ft)$ with A being a normalization factor: $A = 1/(\sigma_t\sqrt{\pi})^{1/2}$. As opposed to the classical moving Fourier transform, a wavelet family is defined by a constant ratio f/σ_f (greater than five in practice). The wavelets therefore have the same number of cycles for different frequency bands, resulting in different wavelet durations. The time-varying power of the signal around frequency f is the squared modulus of the convolution: $P(t,f) = |w(t,f)*s(t)|^2$. **(G)** Repeating this calculation for a family of wavelets, having different frequencies f, provides a time–frequency power representation of the signal components.
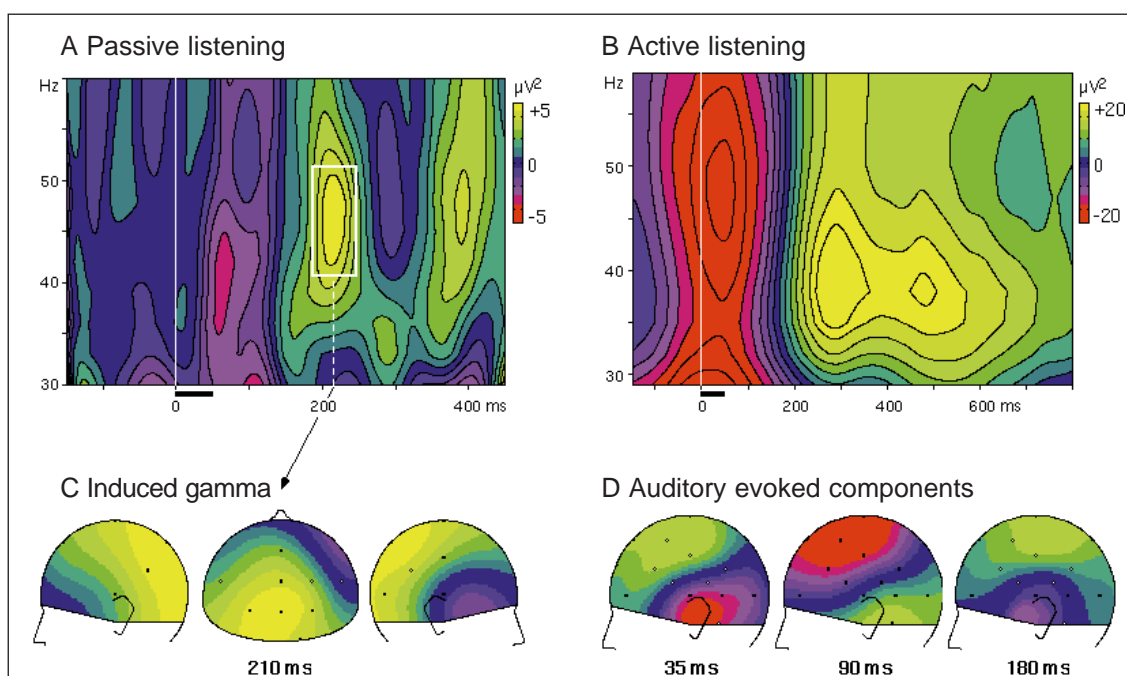
A Passive listening

B Active listening

C Induced gamma

D Auditory evoked components

210 ms

35 ms **90 ms** **180 ms**

Fig. 1. Acoustically induced gamma activity and selective attention. (A) Passive listening. Acoustic stimuli (black bar: 1000 Hz, 50 ms duration tone-bursts) were delivered binaurally to subjects who were watching a silent video movie. The average time-frequency power distribution at vertex electrode (grand average over 10 subjects) shows variations in induced gamma activity with respect to the pre-stimulus baseline: an early decrease (red) around 40 Hz and 80 ms after stimulus onset, followed by increases (yellow) around 45 Hz peaking at 210 and 400 ms. **(B)** Active listening. Average time-frequency power distribution at vertex electrode after the same acoustic stimuli (black bar: 1000 Hz, 50 ms duration tone-bursts) while the subjects are detecting 1050-Hz rare tones. This distribution shows a larger gamma power increase (yellow) compared to the passive listening situation, peaking later (300 ms) and having a longer duration. Auditory induced gamma activity is thus enhanced by selective attention. **(C)** The scalp topography of the induced gamma response at 210 ms has a maximum at parietal electrodes, whereas **(D)** the major auditory evoked components between 30 and 180 ms, known to involve both auditory cortices, show a different topography, namely, a polarity reversal pattern delineating the Sylvian fissure. (See Ref. 34.)

areas. An increase in gamma activity has also been reported prior to, or during, tasks requiring a high level of sensori-motor integration both in human[26] and monkeys[27]. This type of gamma activity has therefore been proposed to be related to the integration of sensory and motor processes during movement preparation and/or control of movement.

Detection tasks

Induced gamma activity in the 40 Hz range appeared in the scalp EEG, 200 ms after electrical stimulation of the finger during a sensory discrimination task[28]. However, in a similar task, others did not find any inter-electrode correlations in the gamma-range from intracranial recordings over the somatosensory areas[29]. This latter negative result might be because this study looked for coherence over a relatively long time window (500 ms) compared with the rather transient (around 125 ms) inter-electrode phase-locking response in the scalp EEG. During a simple auditory detection task[30], the strength of the induced 40-Hz activity 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.
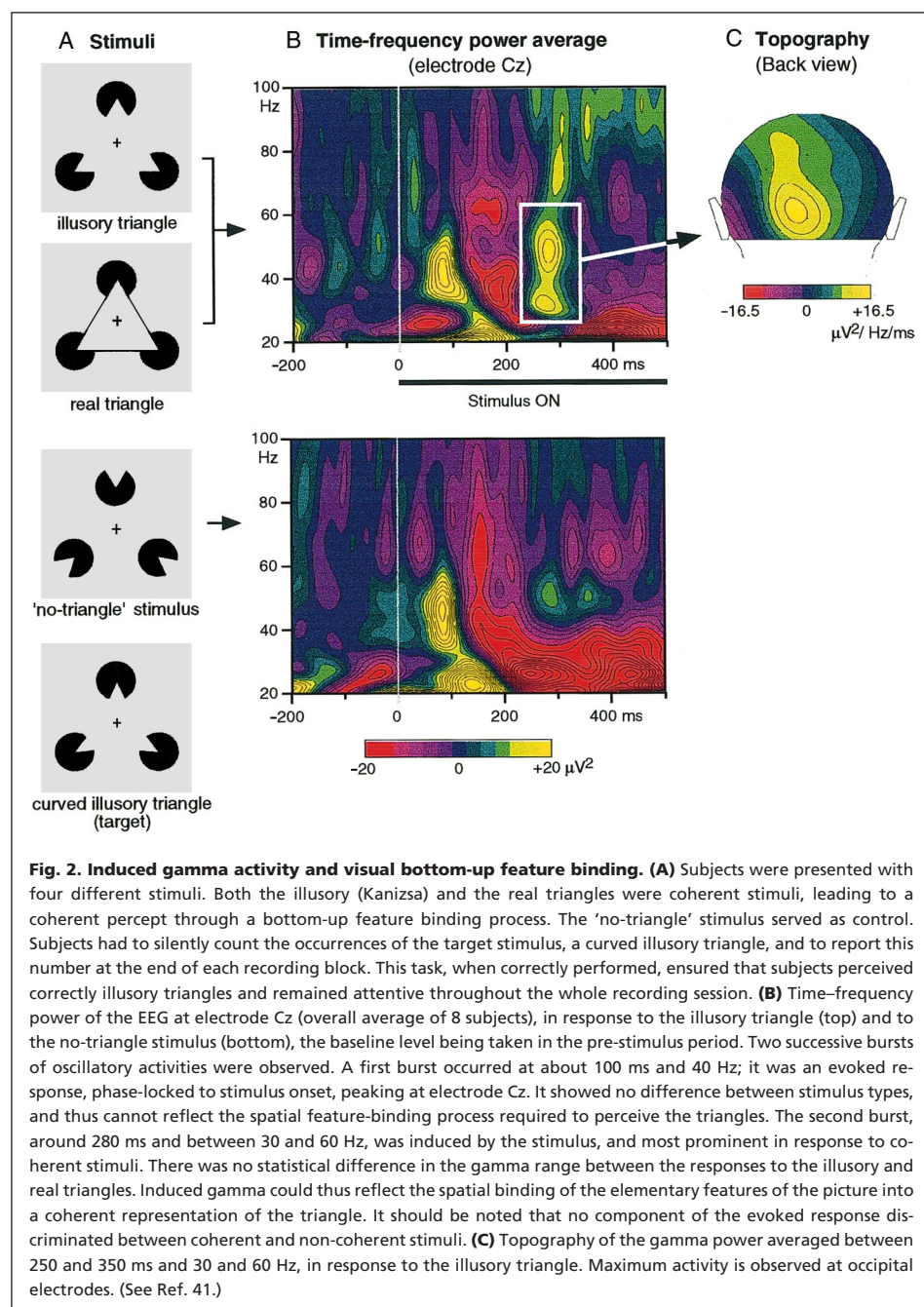
Modulation by attention

In early experiments, intracranially recorded occipital gamma responses to static visual stimuli decreased in amplitude when the subject did not pay attention to a picture that was presented[31]. Various sensory stimuli (light-flash, speech, cold,

etc.) induced a gamma oscillatory response 100–200 ms after stimulus onset in the posterior temporo-parietal lobe with a tendency for rapid habituation[32]. More recently, in passive and active auditory paradigms differences have been reported in the EEG gamma strength 200 ms and 300 ms after subjects heard standard tones compared to when they heard deviant tones[33]. In similar situations[34], we have observed that the time-course of the induced 40-Hz activity is characterized by a reduction (at around 100 ms) followed by an increase (peaking at around 250 ms) compared with pre-stimulus baseline activity (Fig. 1). This temporal pattern is similar to that found over the auditory cortex in the anaesthetized rat[35]. During attentive listening, the increase in gamma strength was enhanced and prolonged[34], and its scalp topography was different from that of the auditory evoked components known to involve an activity in both auditory cortices (Fig. 1C and 1D).

Complex tasks

In contrast to the studies mentioned above, which reported gamma activity that was induced by a sensory stimulus, several authors have reported global increases in gamma signal strength during complex tasks compared to control situations. For example, Spydell and Sheer[36] found an increased gamma signal that was left-lateralized during a verbal task, and was right-lateralized during a visual rotation task. They suggested that the gamma activity could reflect a 'focussed arousal' in the task-relevant neural circuitry. A gamma enhancement has also been observed at frontal sites[37] during

Fig. 2. Induced gamma activity and visual bottom-up feature binding. (A) Subjects were presented with four different stimuli. Both the illusory (Kanizsa) and the real triangles were coherent stimuli, leading to a coherent percept through a bottom-up feature binding process. The 'no-triangle' stimulus served as control. Subjects had to silently count the occurrences of the target stimulus, a curved illusory triangle, and to report this number at the end of each recording block. This task, when correctly performed, ensured that subjects perceived correctly illusory triangles and remained attentive throughout the whole recording session. **(B)** Time–frequency power of the EEG at electrode Cz (overall average of 8 subjects), in response to the illusory triangle (top) and to the no-triangle stimulus (bottom), the baseline level being taken in the pre-stimulus period. Two successive bursts of oscillatory activities were observed. A first burst occurred at about 100 ms and 40 Hz; it was an evoked response, phase-locked to stimulus onset, peaking at electrode Cz. It showed no difference between stimulus types, and thus cannot reflect the spatial feature-binding process required to perceive the triangles. The second burst, around 280 ms and between 30 and 60 Hz, was induced by the stimulus, and most prominent in response to coherent stimuli. There was no statistical difference in the gamma range between the responses to the illusory and real triangles. Induced gamma could thus reflect the spatial binding of the elementary features of the picture into a coherent representation of the triangle. It should be noted that no component of the evoked response discriminated between coherent and non-coherent stimuli. **(C)** Topography of the gamma power averaged between 250 and 350 ms and 30 and 60 Hz, in response to the illusory triangle. Maximum activity is observed at occipital electrodes. (See Ref. 41.)

multi-stable visual perception and was suggested to be related to phases of frequent perceptual switching, rather than phases of stable perception.

Common properties of induced gamma activity

From this brief overview it appears that stimulus-induced variations in gamma activity occur within similar time-ranges (200–400 ms) in various sensory modalities and tasks. The scalp topography of this induced gamma activity was not systematically investigated, nevertheless, it does not seem to reflect a global and unspecific activation of extended cortical structures. For example, in the motor tasks the somatotopic mapping of the movement-related gamma response suggests a rather restricted area of activation. In many of these studies, the induced gamma activity was interpreted, in very general terms, as the neural substrate of 'cognitive processes'. This interpretation is difficult to relate

to any precise functional hypothesis, although a common finding seems to be that induced gamma activity increases during complex or attention-demanding tasks. The next sections of this article will examine in more detail whether induced gamma activity could underlie the representational hypothesis. We will first present experimental results specifically related to bottom-up feature-binding processes, and then, those supporting a notion of active representation involving top-down processes.

Induced gamma and bottom-up feature-binding

If induced gamma activity reflects a binding mechanism, it should be enhanced when a coherent percept is created in response to a given stimulus. This hypothesis can be tested by evaluating the strength of the gamma signal that is induced by stimuli that share the same physical properties but do, or do not, lead to the perception of a coherent percept. Using protocols taken from animal studies[9], two different groups have reported an increase in the strength of the gamma signal in the scalp EEG while subjects were passively viewing coherent moving patterns[38–40]. The topography of this 40-Hz increase matched the retinotopic organization of areas V1 and V2 in humans[38]. These results also provide evidence for the functional specificity of gamma activity with respect to alpha activity[39,40].

Increases of gamma activity have also been reported in response to coherent versus incoherent static stimuli in active tasks. We analyzed the EEG in response to a coherent and a non-coherent visual stimulus in a discrimination task[41]. A short-lasting occipital enhancement in the 30–50 Hz band was observed around 280 ms after stimulus onset in response to coherent triangles only (Fig. 2). No such effect was observed at higher frequencies (up to 100 Hz), or in the averaged evoked potential. Only the induced gamma activity varied consistently in line with our hypothesis. Similarly, a peak of induced gamma activity was reported at 35–40 Hz, 230 ms after the presentation of human (Mooney) faces[42]. This response was much larger in response to pictures presented in the upright position than for inverted pictures (with no perceived facial content). The stereoscopic fusion of random-dot stereograms into a full 3-D percept, compared with a 2-D perception condition, also elicited an occipital gamma increase in the EEG[43], while no difference was observed in the alpha or beta bands.

These results provide evidence for a role for induced gamma activity in the construction of coherent representations

based on the integration of visual information. The signal is enhanced when spatially distinct features have to be bound together, compared with when they remain segregated as distinct percepts. No modification of evoked potentials or alpha rhythm was found to be related to this hypothesized feature-binding process. Moreover, in response to a coherent visual stimulus, the induced gamma activity was maximal at occipital and parieto-occipital locations, which suggests that it originates, at least in part, in visual areas. This view is also supported by the finding that it partially follows a retinotopic organization (upper/ lower hemifields).

The role of 40 Hz activity has also been explored in language studies in which it has been hypothesized that the activity could reflect associations between words and meanings. Indeed, a difference has been observed at long latencies (more than 400 ms) in the strength of the gamma signal between words and pseudo-words both in the visual (EEG)[44] and auditory (MEG[45] and EEG[46]) modalities. Furthermore, the topography of gamma activity induced by visually presented nouns and verbs revealed differences between 500 and 800 ms[47]. These results suggest that induced gamma could be related to the visual or motor associations prompted by verbal stimuli, although the long latencies of the effects observed seem to indicate that they do not reflect a primary differential processing of words and pseudo-words.

Induced gamma and object representation

As outlined in the introduction, an object representation can be directly built from the sensory input by bottom-up processes, but might also be expected to be activated, retrieved, or rehearsed through top-down processes. To examine the latter, we investigated the variations in gamma strength that occur when an internal representation of a picture or a tone is needed to correctly perform a task. When searching for someone in a crowd, we know in advance who we are looking for – in other words, we generate an internal representation of the particular person we are searching for. A similar process is involved when a subject must detect a hidden object in a picture. In our experiment[48], we used a modified version of the well-known Dalmatian dog picture (Fig. 3). Naive subjects did not perceive the hidden dog, and measurement revealed only a weak induced gamma response around 280 ms after stimulus
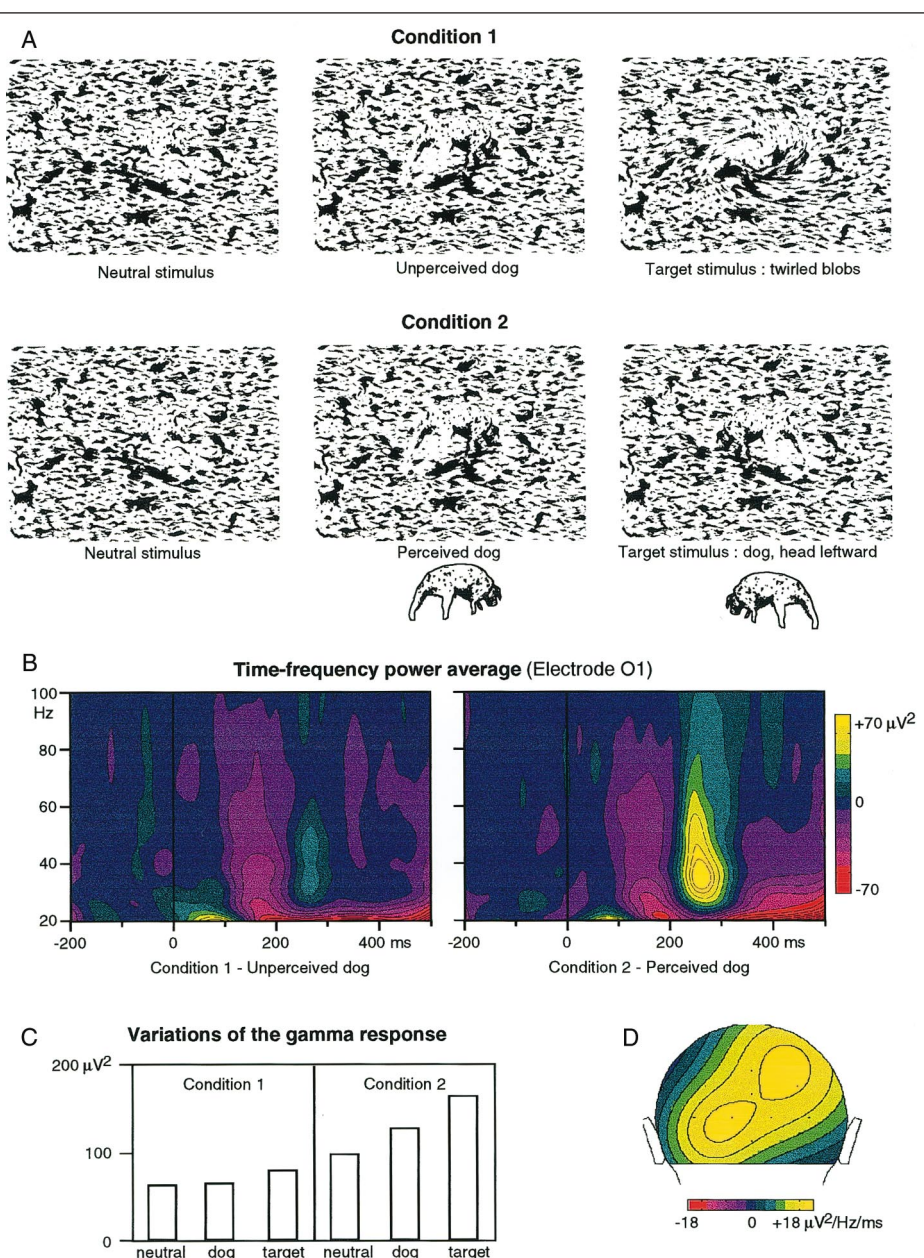
Fig. 3. Induced gamma activity and top-down activation of an internal representation. The experiment was divided in two conditions. In the first one **(A, top row)**, naive subjects were presented with three different stimuli. Two of them (neutral stimulus and unperceived dog) were perceived as meaningless black blobs on a gray background. The task of the subject was to count the occurrences of the 'twirl' target stimulus. In this condition, only a very faint induced gamma response could be observed **(B, left)**. Nevertheless, the peaking power of this gamma response was enhanced after the target stimulus **(C)**. This may reflect the bottom-up feature binding process involved in the twirl perception. Subjects were then trained to perceive the hidden Dalmatian dog, with its head oriented to the left or to the right **(A, bottom row)**; (the outlines of the dog are presented below the stimuli to help the reader to detect them in the pictures). In this second condition, their task was to count the occurrences of the Dalmatian dog with its head oriented leftward. Compared to the first condition, a large increase in the induced gamma response was observed in response to all stimuli **(B and C)**. This increase could reflect the top-down activation of the internal representation of the attended Dalmatian dog. Indeed, the subject needed this representation to perform the task, independently of the stimulus presented. An additional increase of the induced gamma response was observed in response to the target dog, and in a lesser extent to the dog with its head oriented to the right. This may reflect the bottom-up process of linking the black blobs into a coherent dog picture. The topography of the induced response in the second condition is shown in **(D)**. It peaks at occipital and right parietal locations. Differences between stimuli and/or conditions could also be found in the evoked potentials, but they all occurred at longer latencies, later than the variations of the induced gamma response. (See Ref. 48.)

onset. Once the subjects were trained to perceive and detect the hidden dog, a much larger induced gamma response was recorded, irrespective of whether the stimulus contained a Dalmatian dog or not. Our interpretation of this result is that the activity may reflect the top-down activation of a
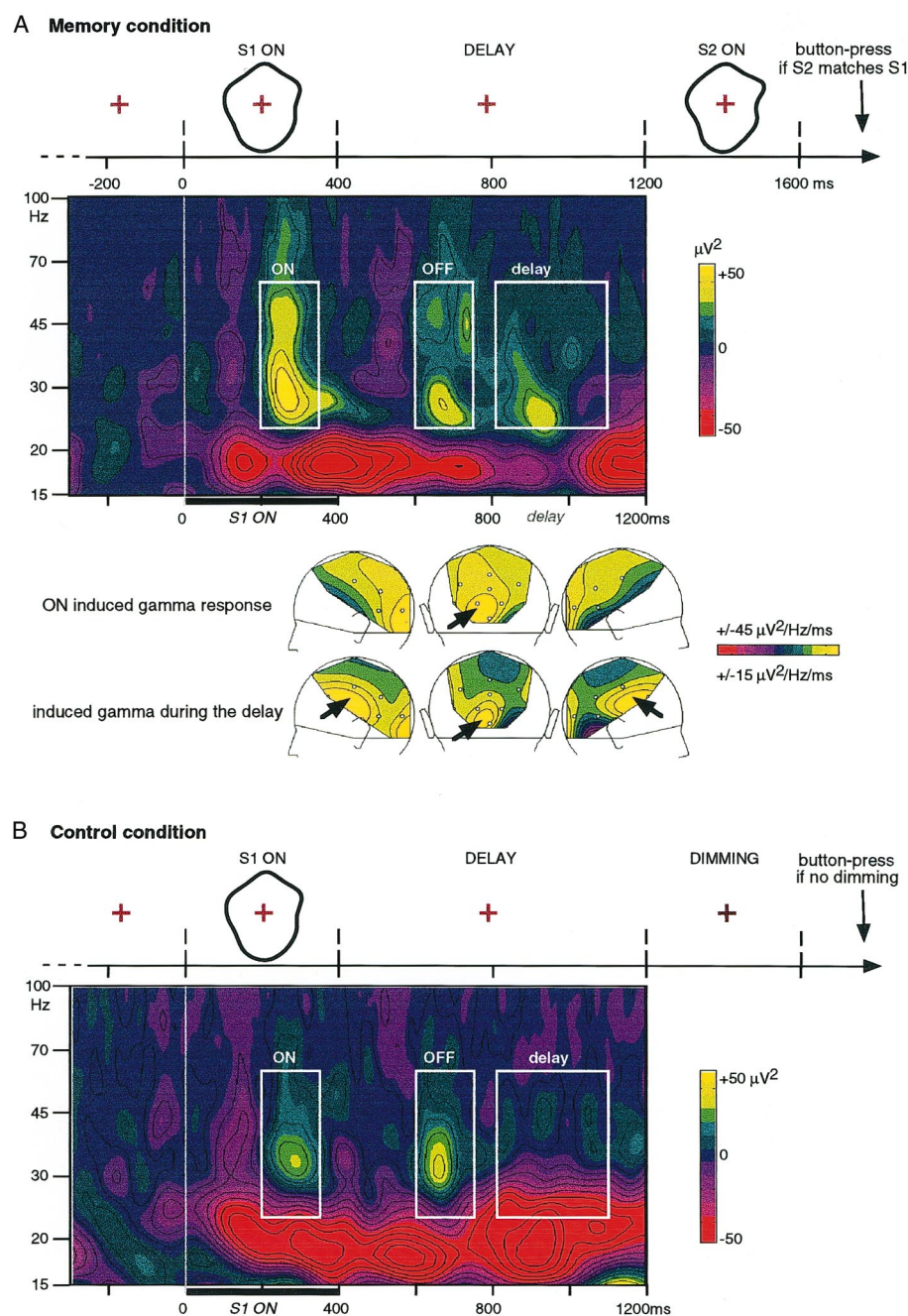
Fig. 4. Induced gamma activity and the rehearsal of a visual object representation in short-term memory. (A) In the memory condition, subjects performed a delayed-matching-to-sample task: a first stimulus (smooth shape) was presented, followed by a delay and a second stimulus. Subjects had to press a button when the two stimuli were exactly identical. To perform the task, the representation of the first stimulus had to be maintained in short-term memory. The time–frequency power at electrode O1 showed three successive bursts of activity in the gamma range: at 280 ms (ON response), 700 ms (OFF response), and later during the delay. The topography of the gamma power during the delay showed an additional bilateral frontal component as compared to the occipital topography of the ON response. **(B)** In the control condition, no memory was required: subjects had to detect a possible dimming of the fixation point at the end of the delay. The ON induced gamma response at 280 ms was reduced, and the activity during the delay completely suppressed. The gamma activity during the delay could thus reflect the rehearsal of the first stimulus in short-term memory. Furthermore, it showed specific variations and/or topography as compared to the alpha and beta band, and to the evoked potentials. (See Ref. 49.)

Internal representations may also be driven during rehearsal processes within short-term memory. In the visual modality, we studied the gamma responses elicited by a delayed-matching-to-sample task[49] (Fig. 4A). Sustained oscillatory activities in the gamma bands, and also in the beta (15–20 Hz) bands were observed during the delay period, when the target stimulus was presumably being rehearsed. These activities disappeared in a control condition, where no memory was required (Fig. 4B). We therefore suggested that the activity during the delay period could reflect the maintenance of a visual object representation in short-term memory. The topography of this activity, indicated a contribution from occipito-temporal as well as frontal areas, and is consistent with the known functional anatomy of short-term memory networks in humans[50]. No other component of the evoked potential lasted long enough to be likely to reflect the rehearsal of the stimulus representation in memory[51].

A possible role for induced gamma activity in acoustic object representation was tested in a difficult frequency discrimination paradigm[34]. Standard tones were presented, randomly intermixed with two types of deviant tones of slightly higher frequency, one of which was the target stimulus that was to be detected. An increase in induced gamma activity around 40 Hz was found, starting 250 ms after the onset of standard tones (Fig. 5). This gamma activity was clearly prolonged (up to 800 ms) when the subjects were expecting a target to occur again soon. Such sustained gamma activity after standard tones could be interpreted in terms of rehearsal of the pitch representation required to perform the discrimination task correctly. This might be related to the strategy reported by the subjects that they were internally 're-playing' the standard tone in order to be able to detect the target. However, an interpretation in terms of increased attention can not be discounted in this experiment.

Induced gamma oscillations: the signature of object representation?

In all the studies described above, the variations of induced gamma activity are predicted by the representational hypothesis. Thus, there is growing experimental evidence pointing toward a functional role for induced gamma activity in binding together the areas involved in an object representation, whether generated through bottom-up or top-down processes. Alternative explanations
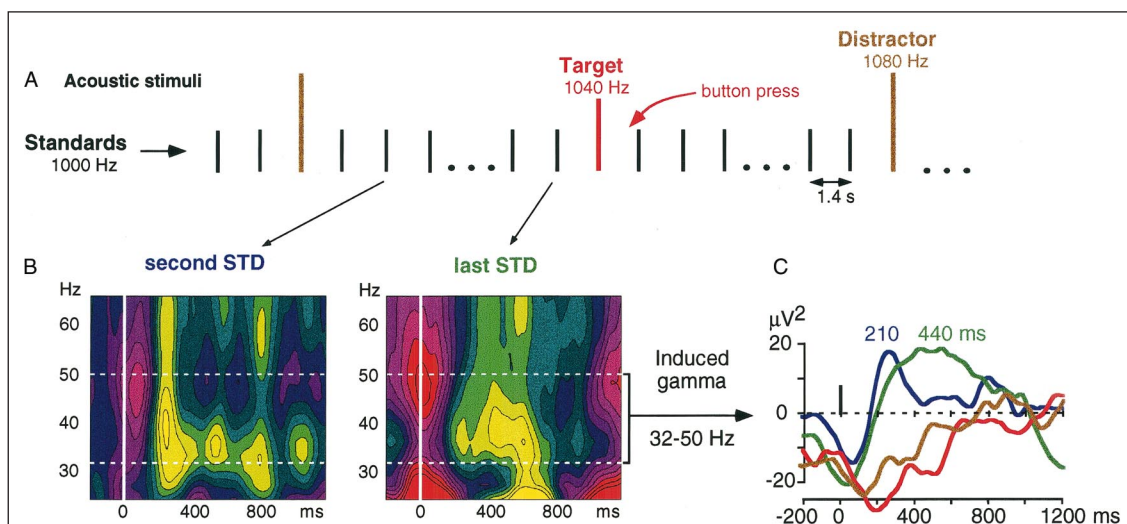
representation of the object (the dog) during the visual search. An increase in activity was also observed when the black blobs in the picture were linked together to build a coherent picture (bottom-up process). This gamma effect occurred 10 ms earlier than the first difference observed in the averaged evoked potentials.

Fig. 5. Induced gamma activity and sound representation. (A) Acoustic stimuli (pure tone-bursts, 50 ms duration) were delivered binaurally with a constant inter-stimulus interval (1.4 s): frequent standard tones at 1000 Hz (black bars) and rare deviant tones, target at 1040 Hz (red bars) or distractor at 1080 Hz (brown bars). Subjects had to press a button after each target tone, and they were aware that at least 3 standards were delivered between two deviants. The tone frequencies were chosen in order to make the task difficult enough so that it could not be performed automatically (85% of correct responses). **(B)** The average time–frequency power distributions were analyzed separately for the second standard following a deviant (second STD, in blue) and for the standard preceding a deviant (last STD, in green). **(C)** Different time courses of the gamma power were induced by the same acoustic stimulus: the gamma response peaked significantly later for the last STD (440 ms) than for the second STD (210 ms), and persisted for longer (up to 800 ms). Furthermore, following deviant tones, i.e. target (in red) or distractor (in brown), the gamma activity did not show any post-stimulus increase but rather a transient decrease followed by a return to baseline. The prolonged induced gamma activity after several standard tones could be interpreted in terms of rehearsal of the tone pitch representation required to correctly perform the task, while the absence of gamma increase after deviant tones suggests that the frequency discrimination itself is performed by faster processes and no sound rehearsal is further required. This representation is more active when the subject anticipates that a deviant is about to occur. Nevertheless, an interpretation in terms of increasing attention cannot be discounted. (See Ref. 34.)

can be found for each experiment individually (attentional selection of the stimuli looking like the target in the triangle experiment, for example), but none of the alternative accounts can explain the whole set of results.

Furthermore, induced gamma activity was the only component to vary systematically according to the representational hypothesis. Its functional specificity was demonstrated in several studies reported here, mainly in the visual modality. Induced gamma activity was topographically and temporally distinct from the alpha rhythm and from the evoked low frequency or gamma components, and thus cannot be considered as an epiphenomenon of any of these components. In particular, to answer the question raised by Jürgens *et al.*[52], it does not seem to reflect a harmonic of alpha activity[40,49]. However, its functional relationship to activities in the beta (15–20 Hz) range remains unclear[43,49,51]. Finally, the variations in induced gamma topography should be emphasized. Different areas seem to be involved in different tasks. This could indicate the existence of a flexible mechanism of dynamic recruitment of functional areas in oscillatory ensembles.

Neural substrate of induced gamma activity

Where do these oscillations recorded on the scalp originate? One could argue that muscular activity might account for these signals. However, several arguments can be put forward that rule out this interpretation. Since induced gamma activity shows task-dependent time courses and topographies, it seems unlikely that it could reflect muscle activity alone. Furthermore, the functional effects are confined to a fairly narrow frequency range (30−50 Hz), whereas muscle

activity usually has a broader spectral content[49]. Moreover, visually evoked and induced gamma bursts have been observed intracranially in human at the same latencies as those observed on the scalp surface[53].

In order to identify the underlying neural source of the induced gamma oscillations, we repeated the Kanizsa triangle experiment (Fig. 2) and recorded simultaneously EEG and MEG signals over occipital areas[54]. 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 only. Preliminary results in the auditory modality showed a similar difference between EEG and MEG in induced gamma activity during passive listening. This absence of gamma activity in the MEG signal could be explained by deep or radially oriented neural sources which gives rise to a weak magnetic field, or by an unusual source configuration.

In support of this latter interpretation, we proposed a ring-shaped distribution of current dipoles (Fig. 6) as a source model of the induced gamma oscillations[55], which creates an electric potential field but not a magnetic field (or only a weak one) on the scalp surface. Moreover, it generates a field potential that does not reverse through cortical depth, as has been observed in animal studies with spontaneous[56] or stimulus-induced gamma activities[11]. A ring-shaped source model could mimic the activity of synapses located on horizontally oriented dendrites. This geometry is consistent with the idea that interneurons might be involved in a network generating a coherent oscillatory activity[57−59]. However, a possible contribution of pyramidal neurons (basal dendrites for example) cannot be ruled out[60].
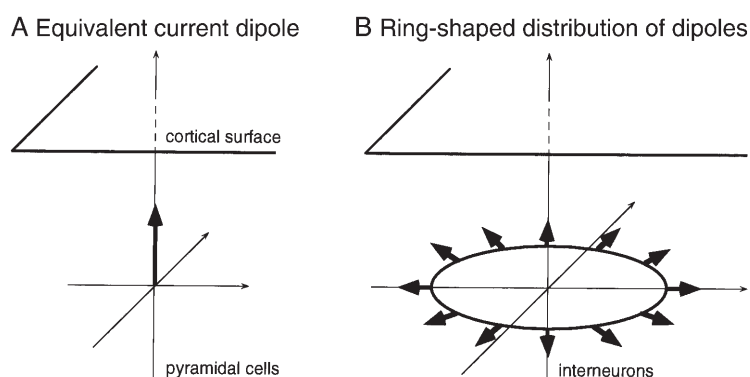
Fig. 6. Possible source model of induced gamma activity. (A) An equivalent current dipole source model, oriented perpendicular to the cortical surface, is usually proposed for the pyramidal cell synaptic activity underlying the early evoked components. This source model fits with the polarity reversal 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)** A ring-shaped distribution of dipoles is proposed as a possible source model for the induced gamma response. This configuration creates a field potential that does not reverse through cortical depth as observed in some animal studies. Moreover, it generates a potential distribution, but not a magnetic field on the scalp surface (or a weak one only), which corresponds to our observation that stimulus-induced gamma oscillations are detectable in EEG data, but not in simultaneously recorded MEG data. Such ring-shaped sources could mimic the activity of synapses located on horizontally oriented dendrites distributed all around the soma. This geometry fits with the idea that interneurons might be involved in a network generating a coherent oscillatory activity. (See Ref. 55.)

Gamma oscillations and spike synchronization

In order to better understand the neural substrate of induced gamma oscillations, we still need to fill the gap between the macroscopic approaches based on scalp EEG recordings reviewed here, and the spike-train synchronizations observed in animal studies at a microscopic scale in single or multiple-unit recordings[14,16,61,62]. At the present time the results of these two approaches are difficult to compare because of the very different spatial sampling and experimental paradigms used. Signal analysis methods are also very different. In animal studies, spike synchronizations are evaluated over quite long time periods while, in human EEG or MEG, variations in gamma strength are usually estimated over much shorter periods. The rather short-lived variations in induced gamma strength observed in humans could easily be obscured in cross-correlograms computed over several hundreds of milliseconds. Indeed, some authors have found no evidence for oscillatory synchronization in monkey cortex[63–65]

Outstanding questions

• What is the functional significance of the transient decrease of gamma strength observed after a sensory stimulus, in the time range where the major components of the evoked responses occur?
• Is multi-sensory integration also achieved through oscillatory synchronization ?
• Induced gamma activity seems to underlie the activation of fine object representations. Can more crude representations be established more quickly through other mechanisms ?
• Is it possible to bridge the gap between oscillatory synchronization observed at microscopic levels in animals and modulation of gamma strength observed at a macroscopic scale in humans?
• Could the sometimes long-lasting induced gamma responses better correlate with metabolic or haemodynamic images (PET or fMRI) than the brief components of the evoked potential ?

and this may be partly due to the use of exceedingly long time windows for computing auto- or cross-correlograms[66], systematic sampling bias toward a particular layer[67] or differences in recording techniques. In addition, part of the controversy in animal studies is due to the distinction between oscillatory patterns in the spike train of a single neuron and oscillatory synchronization between neurons[66,68]. It is worth noting that whenever an oscillatory activity emerges in the scalp EEG, a certain level of underlying neural synchronization is necessarily reached.

Nevertheless, the gamma activities observed at different recording levels share a number of properties since they are not phase-locked to stimulus onset, and they are enhanced in response to coherent stimuli. An analysis at intermediate levels (namely local-field potentials or electro-corticograms), using similar experimental paradigms could be a way to bridge this gap. Indeed, the time course of visually or acoustically induced gamma activity observed in human EEG is comparable to that found in cat local-field potentials[69] or rat electro-corticograms[35]. Finally, synchronization between EEG leads could also be evaluated on the scalp surface or in human intracranial recordings[53]. However, the contribution of a single neural source located at a distance from the two testing electrodes should first be ruled out because it could create an artificial synchronization of EEG signals by simple volume conduction effect.

Conclusion

The representational hypothesis presented here is derived from the feature-binding hypothesis from the animal literature and postulates that fast oscillatory synchronization of brain areas underlies the construction of a task-relevant object representation. When searching for experimental evidence in human EEG/MEG recordings to support this hypothesis, two types of oscillatory activity in the gamma-range should be distinguished (1) an early, transient 40-Hz evoked response and (2) a stimulus-induced response at longer latencies. Only the induced gamma activity, as opposed to the evoked activity (see Box 1), seems to be related to the generation of an object representation, both in visual and auditory modalities. In addition, the functional variations in this signal, at least in the visual modality, are different from those of the alpha rhythm and of averaged evoked low frequency or gamma components.

Induced gamma activities show a high degree of spatial and temporal flexibility that depends upon the sensory systems recruited and the experimental tasks 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 that 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. However, the transition from the emergence of such assemblies to behavior is not clearly understood at present.

While early evoked potentials could reflect the encoding of some physical attributes of the stimulus, the induced gamma oscillations that follow might play a crucial role in binding together those areas that are necessary to perform a particular task. Different types of neurons and networks might underlie each of these electrophysiological components. How these two mechanisms combine, and which one dominates in a given task, remains an open question.

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