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Cognitive functions of gamma-band activity: memory match and utilization

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Oscillatory neural activity in the gamma frequency range (>30 Hz) has been shown to accompany a wide variety of cognitive processes. So far, there has been limited success in assigning a unitary basic function to these oscillations, and critics have raised the argument that they could just be an epiphenomenon of neural processing. We propose a new framework that relates gamma oscillations observed in human, as well as in animal, experiments to two underlying processes: the comparison of memory contents with stimulus-related information and the utilization of signals derived from this comparison. This model attempts to explain early gamma-band responses in terms of the match between bottom-up and top-down information. Furthermore, it assumes that late gamma-band activity reflects the readout and utilization of the information resulting from this match.

Neural signals in the gamma frequency range (roughly 30–100 Hz) have received considerable attention in neuroscience for the past 15 years. Although the phenomenon of fast neuronal oscillations had been described as early as 1942 in animals [1] and 1960 in humans [2] it started to attract major interest only in the late nineteen-eighties when it was shown to correlate with perceptual binding [3]. In addition to perceptual processing, gamma-band activity accompanies also many other cognitive functions like attention [4,5], arousal [6], object recognition [7,8], and language perception [9,10]. However, it is not unique to any of these and one might conclude that it is not a specific indicator of these processes. In the following, we attempt a new interpretation of the available data. A mechanism which underlies many of the abovementioned cognitive functions is the match of sensory information with memory contents. We will argue here that so-called 'early' gamma-band activity occurring in EEG or MEG measurements before 150 ms after stimulus presentation (Box 1) reflects such a match with memory and is therefore observed in many experimental conditions. In addition, we will argue that 'late' gamma activity which typically emerges with a latency of more than 200 ms (Box 1) is a temporal signature of utilization processes such as response selection or context updating. If valid, this

'match-and-utilization model' (MUM) could unify a large number of experimental findings in the field of oscillatory electrophysiology. We suggest that it can offer a framework to understand and predict the generation of gamma-band oscillations. In the following, we will first review evidence for the modulation of gamma activity by bottom-up, stimulus-related information. Subsequently, we discuss gamma oscillations in the context of attention and memory paradigms as examples for top-down modulation of this phenomenon. Finally, we describe our model attempting to integrate these two perspectives and discuss some of its implications.

Low-level influences on gamma activity
Stimulus features
A wide variety of stimulus features have been shown to modulate gamma-band responses in animals and humans. This is to be expected because, in early sensory cortices, neuronal responses are largely determined by physical stimulus properties. Recently, it has been demonstrated that the size, eccentricity and duration of visual stimuli influence the strength of evoked and induced gamma responses in humans [11] (for a comparison of evoked and induced responses, see Box 1). Visual stimuli evoke largest early gamma responses if they are of sufficient size (Figure 1a) or presented in the central visual field (Figure 1b). This might also be one of the reasons why some authors failed to find gamma responses in human EEG [12,13]. Because stimuli evoke an ON response as well as an OFF response these two superimpose in case stimuli are presented for short durations. Only if durations of stimuli exceed the latency of evoked responses they will result in two clearly separable peaks; that is, for a peak latency of 100 ms the stimulus duration needs to be longer than 100 ms [11]. Animal studies, mainly from the cat, have also revealed low-level modulations of the gamma response by stimulus features like size, velocity, contrast or spatial frequency [14,15].

Feature binding
Another important function of sensory systems that strongly relies on bottom-up influences is to bind together the activity of those neurons which represent features of the same object (for review, see [16,17]). In the cat visual

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Box 1. 'Early' evoked versus 'late' induced gamma oscillations

To analyze oscillations in neuronal activity one needs to use appropriate mathematical tools. To extract amplitude or power of oscillations in particular frequency bands, the so-called wavelet transform is particularly well suited, because it allows us to describe task-dependent variations of these parameters at convenient temporal resolution. If there is a burst of oscillatory activity after stimulus onset (Figure Ia) the wavelet transform (Figure Ib) does not show the oscillatory behaviour of the data. Instead, it represents the absolute values of the oscillations which can be thought of as the envelope of the oscillation. This representation is better suited to compare different conditions and does not cancel out as easily when averaging across subjects.

Oscillations in the brain can either occur spontaneously, that is, without relation to external stimuli, or they can be related to the processing of stimuli. In the latter case, a distinction is usually made between 'evoked' and 'induced' oscillations [55]. If an oscillation appears with the same latency and phase after each stimulus, it is considered evoked activity (Figure Ic) which is usually the case for early gamma activity before 150 ms after stimulus presentation (peak latencies are typically around 50 ms for auditory and around 100 ms for visual stimuli). If, however, the oscillation varies in either latency or phase from trial to trial it is called induced activity (Figure Ic). This is typically the case for the late gamma activity which occurs 200–300 ms after stimulus presentation and later. Gamma activity appears in a wide frequency band between about 30 and 80 Hz. Evoked responses often oscillate around 40 Hz whereas induced responses might also reveal higher frequencies. When computing the average potentials across many experimental trials, as it is usually done in electrophysiology to yield the event-related potential (Figure Id), evoked oscillations are summed because they are phase-locked to stimulation (Figure Ie). Induced activity, on the other hand, almost cancels out completely in the averaged event-related potential.
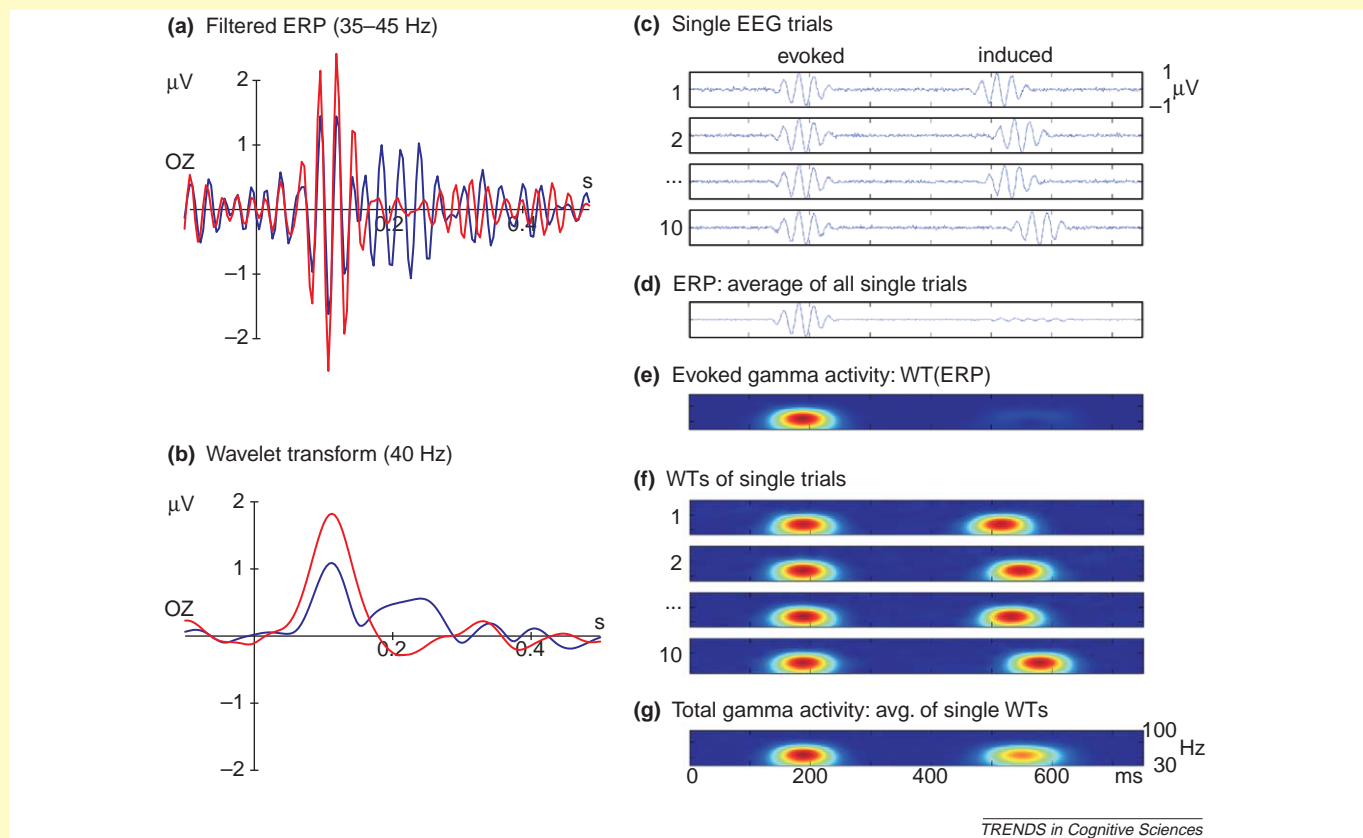

Figure I. Analysis of evoked and induced gamma-band oscillations. **(a)** In classical approaches a narrow band-pass filter, for example 35–45 Hz as here, is applied to the event-related potential (ERP) displaying the oscillatory character of the data. The two lines exemplify evoked gamma responses recorded under different stimulus conditions. **(b)** Alternatively, the so-called wavelet transform can be applied, which returns only the amplitude of the oscillation and does not show oscillatory signal fluctuations. The two lines show the time course of evoked 40 Hz activity for the same experimental conditions as in (a). **(c–g)** To differentiate between evoked and induced oscillations, averaging and frequency transforms need to be applied in different order. **(c)** To illustrate the two approaches, 10 simulated single trials are used which contain early bursts of evoked as well as late induced gamma bursts. **(d)** Averaging all single trials yields the ERP. **(e)** Applying the wavelet transformation (WT) to the ERP yields only evoked gamma activity. **(f)** The total activity comprising both evoked and induced components is obtained if each single trial is first transformed into the frequency domain. **(g)** The average of the absolute values of each single trials WT represents the total activity. Whereas induced oscillations appear only in the average of the single-trial WTs (g), evoked activity will show up in both measures.

cortex, it has been demonstrated that synchronous firing of neurons at frequencies in the gamma range is associated with feature binding. When two neurons are driven by one visual stimulus which extends across both their receptive fields they fire in synchrony. If, however, the two neurons are activated by different objects they fire asynchronously [3]. Very similar data have been obtained in awake macaque monkeys [18]. The same paradigm was also applied to human subjects and enhanced gamma activity was found for one coherently moving object [19]. Similar effects have been obtained with illusory figures where the inducing parts need to be bound together to coherent figures [20,21]. Earlier models of the human data therefore concluded that gamma-band activity primarily reflects binding processes for the construction of object representations [22].
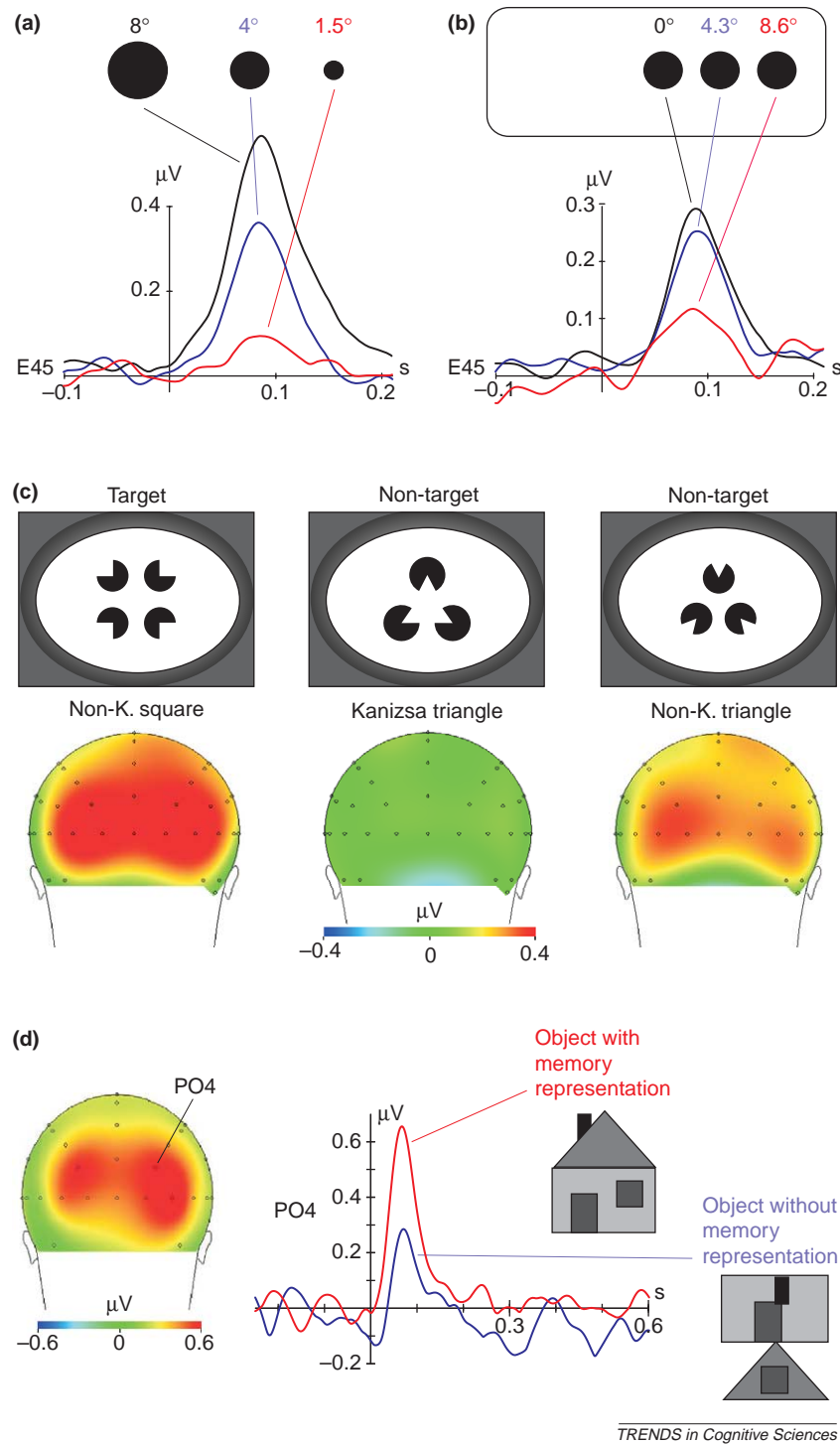
Figure 1. Influence of stimulus features, attention and memory on human gamma-band responses. **(a)** Gamma-band activity in the human EEG is influenced by stimulus features such as size or eccentricity. Larger stimuli (8° visual angle) evoke significantly larger gamma responses than smaller stimuli (4° or 1.5°). (Data redrawn from [11].) **(b)** Moreover, central stimuli evoke significantly larger gamma responses than stimuli at 4.3° or 8.6° eccentricity. (Data redrawn from [11].) **(c)** Illusory Kanizsa figures (e.g. Kanizsa triangle, middle) which are bound together by the subjects from their constituent parts are physically very similar to non-Kanizsa figures (e.g. non-Kanizsa triangle, right). When subjects were instructed to detect the non-Kanizsa square (left) as a target, attention to the target evoked the largest early gamma responses even though the features of the target could not be bound together. (Data redrawn from [31].) **(d)** Objects for which human subjects already have a memory representation (house) evoke significantly larger early gamma-band responses over occipital cortex (red trace) than physically similar objects for which subjects do not have such a memory representation (blue trace). (Data redrawn from [34].)

High-level modulation
Attention
Several recent studies show that, in addition to bottom-up factors like the ones described above, top-down influences can also strongly modulate activity in the gamma-band.

Most notably, the influence of attention has been demonstrated both in animal and in human experiments. These data show that coherent activity in the gamma-band is enhanced during attentional selection of sensory information. In cats, gamma activity has been found to

accompany the attention-related P3 component in the event-related potential [23]. A strong attentional effect on gamma-band responses has been observed in cortical area V4 in awake behaving monkeys [24]. In this study, two visual stimuli were presented simultaneously on a screen, one inside the receptive fields of the recorded neurons and the other nearby. The animals had to detect subtle changes in one or the other stimulus. If attention was shifted towards the stimulus processed by the recorded cells, there was a marked increase in local coherence in the gamma-band [24]. A large number of EEG and MEG studies in humans have provided related evidence. Thus, when directing spatial attention to a specific location, auditory stimuli presented at the attended location result in enhanced gamma activity [4] and the same is true for visual stimuli [25]. In accordance with this evidence, it has been suggested that the attentional blink, which corresponds to a temporary deficit of attention, should be accompanied by a transient suppression of gamma activity [26]. Based on computer simulations, cellular mechanisms have been suggested for how oscillatory synchronization of neurons could be used for attentional selection [27].

Several studies have also compared the relative influence of attention with that of stimulus coherence, or binding. Stimuli which can be bound together to coherent pictures usually capture more attention than stimuli which cannot be bound. Therefore, bound objects usually pop out of visual search displays by drawing the subject's spatial attention to their location [28]. Conversely, classical feature integration models have predicted that attention could also be a prerequisite for achieving appropriate feature binding [29]. Therefore, it seems important to differentiate the processes of attention and binding when investigating their influence on gamma responses [30]. When testing which of the two modulations, binding or attention, is more relevant for gamma activity the latter seems to dominate over the former. If directly compared, attention towards targets leads to larger evoked gamma-band responses in human EEG than binding together illusory figures (Figure 1c) [31]. However, when only the influence of binding mechanisms is investigated, experiments demonstrate larger gamma responses for bound objects as compared with unbound stimuli. This has been shown explicitly for the 'late', induced gamma-band activity [21,32], but remains to be tested for the 'early' gamma.

Memory

A second top-down factor of interest in the present context is memory. Obviously, there is a close relation between memory and attention, because shifting of spatial or object-based attention towards a target will usually occur with reference to memory contents. Typically, an attended target stimulus has to be matched against information stored in working memory pertaining to target features or location. Thus, attentional selection is closely related to memory, and it seems plausible to assume that stimuli which match memory contents evoke more gamma activity than others. This has been investigated in the human EEG for auditory target (sine tones) and novel stimuli (computer generated sounds) which were presented among standard stimuli (other sine tones) [33]. To perform target detection, subjects have to activate a template of the target in working memory and, subsequently, every stimulus needs to be compared with this template. Novel stimuli, however, have never been perceived before and thus do not match with memory contents. The target stimuli which matched with working memory contents lead to significantly more 'early' evoked gamma activity than both the novel and standard stimuli [33]. These data suggest that the above-mentioned attentional modulation of gamma activity actually reflects the matching of attended objects with working memory contents.

Memory effects on 'early' evoked gamma-band activity are also demonstrated by other recent EEG experiments, showing that stimuli for which subjects have a long-term memory representation lead to significantly larger gamma responses over occipital cortex than physically similar stimuli which subjects had never seen before [34] (Figure 1d). In addition to the prominent occipital peak in the topography of the evoked gamma activity some authors find an additional more anterior peak [6,20]. This might indicate that processes which modulate the occipital gamma activity reside in frontal cortex. A relation between gamma-band activity and memory processing is also suggested by EEG and MEG studies that have focussed on changes of 'late' induced gamma activity during visual short-term memory tasks and perceptual learning [35–37]. Moreover, the coherence of human gamma activity has been found to correlate with associative learning mechanisms [38]. Finally, invasive recordings in the medial temporal lobe of patients have revealed coupling in the gamma frequency range between hippocampus and entorhinal cortex during declarative memory formation [39].

In comparison with the available evidence in humans, animal data supporting the notion that synchronized gamma activity is correlated with memory processes is still rather sparse. Evidence from in-vitro studies in slices shows that synaptic gain changes during the induction of long-term potentiation (LTP) or long-term depression (LTD) are strongly dependent on the timing of neural signals. Thus, the precise temporal relationship of pre- and postsynaptic activation determines whether a synapse is strengthened or weakened [40–42]. Synapses potentiate when a presynaptic spike occurs just before a postsynaptic signal, which means that the presynaptic spike could have been causally related to the postsynaptic response. By contrast, presynaptic spikes that arrive shortly after a postsynaptic activation which is driven by other inputs to the postsynaptic cell, will lead to weakening of the involved synapse.

Evidence from animal experiments also suggests a relevance of oscillatory neural processes for memory. Changing the content of memory by learning requires the presence of substances such as noradrenaline or acetylcholine that modulate cortical plasticity (for review, see e.g. [43]). It has been shown several years ago that the reticular formation, which is one of the most important sources of modulatory factors in this context, can facilitate neuronal gamma oscillations in the visual cortex [44].
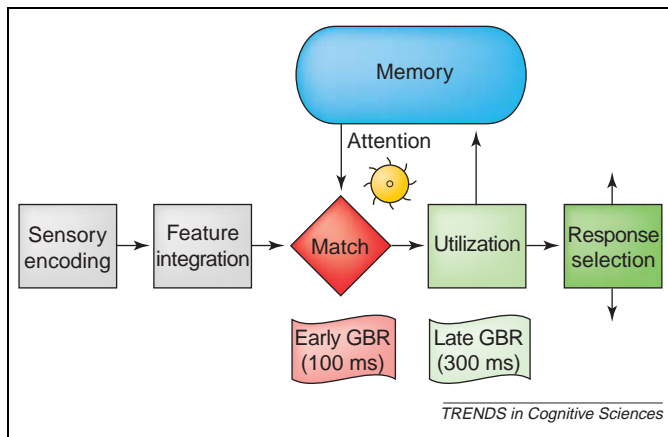
Figure 2. Schematic illustration of the 'match-and-utilization model' (MUM). The crucial step in this model is the match between stimulus-related information and memory contents that has been activated and loaded into short-term memory. The result of this comparison, which can be either *match* or *mismatch*, is then 'read out' by another set of processes which we jointly refer to as 'utilization'. Utilization can lead to updating of memory contents, selection of different behavioural responses, reallocating attention, or any combination of these. In MUM, memory is conceived similar to the model of Cowan [54] where working memory is implemented by the same neuronal architecture as long-term memory. Working memory, thus, corresponds to the dynamics of neuronal activation in the same network which implements long-term memory in the patterns of synaptic weights. Attention, in MUM, has the role of regulating the speed and capacity of the interactions between the three component processes 'memory', 'match' and 'utilization'. It should be noted that attention has an ambiguous nature: on the one hand, it enables and facilitates the match but, on the other hand, it is itself also influenced by the outcome of the match. Note that feature integration might also be subject to memory influences because 'binding rules' are mostly learned postnatally and results of the matching operation could influence perceptual feature integration.

More recently, these changes could be assigned to the activation of cholinergic receptors in the cortex [45]. The oscillations found to be modulated in the context of plasticity and memory formation could have a profound impact on synaptic plasticity because they convey a highly repetitive and precise temporal structure to the postsynaptic cells [46]. Recent in-vitro studies have shown that synaptic plasticity of cortical neurons is sensitive to the phase of the oscillations during which inputs arrive [47]. In these experiments, sinusoidal current at 20 or 40 Hz was injected into the recorded cells, and input signals were given at different phases of the oscillation. If the peak of the oscillation coincides with the peak of the afferent input, the synaptic response was found to be strengthened. The reverse happened if the incoming signal coincided with the trough of the membrane potential oscillation [47]. Taken together, these data clearly demonstrate that precise timing of neuronal activity is an important factor determining the mechanisms of memory formation.

Recent evidence from in-vivo recordings in monkeys establishes a direct relation between gamma-band activity and working memory, suggesting that gamma oscillations carry information about stimuli that have to be memorized. In these experiments, field potentials were recorded from ventral prefrontal cortex in awake macaques while the animals performed a short-term memory task. Interestingly, fast oscillations recorded during the delay phase of the task showed coherence patterns that were specific to certain object classes [48]. Thus, synchrony in the gamma band could differentiate between the stimuli whereas gamma power was almost identical for all stimuli. These

data support the idea that working memory processes directly use gamma oscillations – perhaps to encode templates for matching with subsequently perceived stimuli.

The match-and-utilization model
Integrating bottom-up with top-down processing
As discussed in the preceding sections, bottom-up and top-down factors both have an influence on synchronization of neural activity in the gamma band. We suggest that they do not just relate to these influences *per se* but, more prominently, to the interaction between these influences. On closer inspection, all of the tasks mentioned above contain as a crucial element the comparison of stimulus-related information with memory contents. Although also possible in modes of more automatic processing, in many cases this comparative operation is speeded up and focussed by attention. Following comparison, the resulting information can then be used to generate a behavioural response, to update memory, or to reallocate attention. In agreement with the data reviewed above, we suggest that gamma band activity might be related to each of these computational steps.

Our model, which we term the 'match-and-utilization-model' (MUM) is schematically illustrated in Figure 2. We assume that the 'early' gamma-band response reflects the matching of bottom-up signals with memory contents that occurs rapidly (before 150 ms) after stimulus onset. Typically, the early gamma response is rather well localized and is mainly observed over the region computing the match (Figure 1c,d). Our model predicts that, whenever the matching process yields a positive result for comparing incoming stimuli with memory contents, this should lead to enhanced early gamma responses. Although these memory matches could explain the early evoked gamma response, we suggest that a different mechanism is reponsible for the 'late', induced response (after 200 ms) – argued to occur too late to correlate with perceptual processes [49].

Once a stimulus has been identified and classified by comparing it with data in memory, this information can be used for coordinating behavioural performance, for redirecting attention or for storage in memory. According to MUM, the 'late' gamma response might be a signature of such utilization processes. We assume that the information resulting from the match is implemented by synchronized neural signals [17] and, thus, 'utilization' could involve, in principle, any neural process that 'reads' or uses temporally structured information. Because read-out processes like action planning, behavioural control or memory storage involve highly distributed brain regions, MUM predicts that the 'late' gamma response should be associated with large-scale coherence [32,50] reflecting the 'broadcasting' of a synchronized neural message to other centers. Our model could also explain why late gamma is not always seen – it is observed only when utilization involves regions whose activity can be detected in the EEG (i.e. cortex), but does not occur with rather automated responses like button-presses, which may rely mainly on subcortical structures.

An important prediction of MUM is that temporal patterning of activity could be ideally suited to achieve

matching of top-down predictions with bottom-up inputs (cf. Box 2). If top-down effects induce a particular pattern of subthreshold fluctuations in dendrites of the target population, these could be compared with temporal patterns arising from peripheral input by virtue of the fact that phase-shifted fluctuations will cancel each other, whereas in-phase signals will summate and amplify in a highly non-linear way, leading to a salient postsynaptic signal. Thus, temporal patterning could provide a straightforward implementation of the mechanisms of 'quenching' and amplification predicted by Grossberg's ART model [51]. It should be noted that MUM does not imply that particular 'interface' areas would be dedicated to the matching process. Depending on the sensory modality involved, different thalamo-cortical circuits will come into play. Most probably, such matching operations are carried out in primary cortices, specifically in their thalamic input layers. However, it is conceivable that, in principle, any cortical or thalamic nucleus can be involved in such functions because signals sent along such pathways can be compared by any node in a network, owing to the ubiquity of feedforward and feedback connections.

Relation to other models

As outlined here, the MUM bears similarities to several previous models. Previous computational models of attention like the one suggested by Itti and Koch [52] have explicitly addressed the interaction of bottom-up and top-down factors. The match between bottom-up and top-down processes and its relation to memory are the central topic of Grossberg's Adaptive Resonance Theory (ART) [51]. However, at least in its classical version, ART does not relate these processes to oscillatory brain dynamics. Tallon-Baudry and Bertrand [22] have formulated a 'representational hypothesis' to account for the 'late' induced gamma activity in human EEG. According to their view, the 'late' gamma specifically relates to the match between stimulus-related information and top-down factors and the emergence of an object representation. Given the evidence on modulation of the 'early' gamma by both stimulus features and top-down processes, we consider this unlikely. According to our view, integration of the sensory signals and comparison with memory can occur much faster. This seems possible because, even before stimulus appearance, top-down processes can lead to the 'priming' of neural assemblies, allowing for rapid computation of the match once the stimulus appears [17,51].

An important question concerns the relation of the MUM to earlier models on gamma-band synchrony and perceptual binding [3,16–18]. We wish to emphasize that, actually, perceptual binding closely relates to the mechanism we address with our present model: First, binding is not a purely low-level process, but also the result of an interplay between bottom-up and top-down mechanisms. Binding operations are fundamentally constrained by knowledge (e.g. Gestalt laws) that has been stored in the system architecture during developmental learning. Perceptual integration therefore requires a match between information about object features and stored rules. Second, binding requires selection of the information,
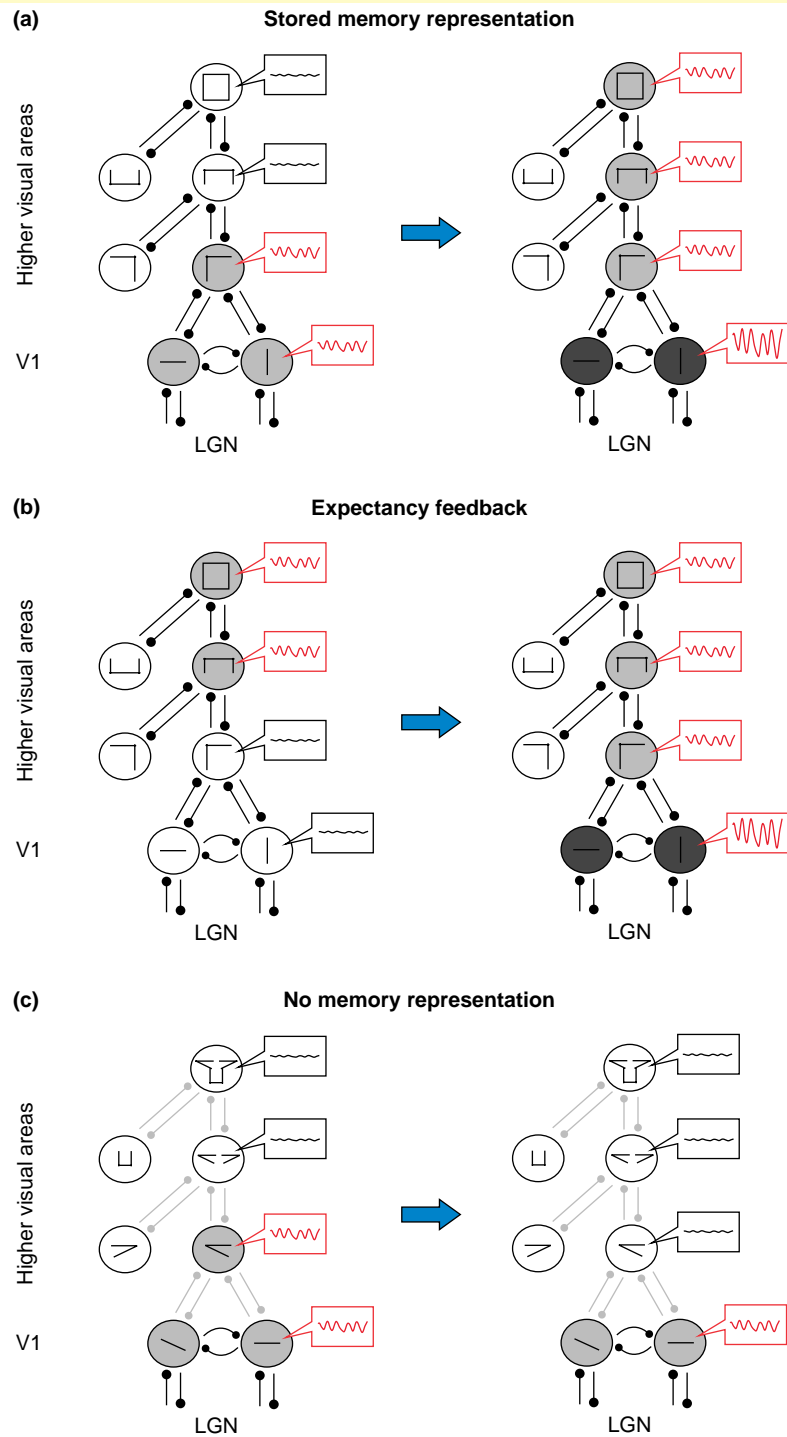
because it not only involves coordination of low-level feature detectors, but also the readout of the coherent population signal by downstream cells [53]. Whereas the first exemplifies the match operation, the second provides an example for the utilization processes mentioned above. In this sense, perceptual binding appears to be a special case of the match-and-utilization scheme suggested here.

Conclusions

The data summarized here demonstrate how low-level (bottom-up) as well as high-level (top-down) brain factors modulate gamma-band activity. The model we have suggested explains these effects by assuming that match and utilization processes are directly related to comparison, readout and storage of synchronized neural signals. Several predictions can be derived from this model that could be tested to validate MUM and to further elucidate the relation between oscillatory activity and memory-based cognitive functions (see also Box 3). First, it should be possible to test differentially the two aspects of MUM by separately varying the match and utilization aspects of a given task. Systematic variation of the former should primarily influence the 'early' gamma, whereas manipulations of the latter should have an impact on the 'late' gamma response. Second, at least in principle, 'late' gamma-band activity should not occur without preceding 'early' gamma, because utilization presupposes the matching operations. In EEG and MEG recordings, however, this is, to a substantial degree, a matter of signal-to-noise ratios, dipole localization and recording approaches. Third, future investigations applying coherence measures in source space should reveal differences between early and late processes, because utilization is likely to involve much more distributed brain regions than the matching

Figure I. (Box 2). Schematic neuronal model accounting for enhanced gamma oscillations in case of matches with memory. Memory is represented by enhanced synaptic connections between neurons (black lines). A lack of memory representation is represented by grey connections. Red oscillatory traces (insets) symbolize the presumed strength of gamma-band activity. V1, primary visual cortex; LGN, lateral geniculate nucleus. **(a)** If neurons in V1 are stimulated by appropriate input from LGN (left), they will activate neurons in higher visual areas (right). In case of a match with memory contents, reentrant interactions with higher-order areas will occur and feedback into V1 will lead to enhanced gamma oscillations and 'resonance' in the cortical network. **(b)** Alternatively, top-down influences propagated from higher-order areas through the cortical network could produce subthreshold oscillations in a given area before stimulation (left), expressing a 'prediction' about expected spatiotemporal input patterns. If the thalamus then sends oscillatory input to V1, the cortical subthreshold pattern will be augmented if prediction and bottom-up input match in terms of phase information (right). In both cases, (a) and (b), the local resonance resulting from the match could explain the augmentation of early gamma-band responses during attentive stimulus processing. **(c)** If there is no memory representation in the form of strengthened synaptic connections (grey lines instead of black), reentrant interactions do not occur in the cortical network. This leads to weaker gamma oscillations at the neural site where the matching operation has been carried out and prevents signal propagation through the network.

operations which might be confined to areas that specifically process the respective sensory contents. Fourth, clear evidence for 'match-related synchrony' as opposed to 'utilization-related synchrony' should also be obtained in intracortical recordings. It would be desirable to relate, in awake behaving animals, synchronization processes observed with microelectrodes more clearly to evoked and induced gamma observed by coregistration of the surface EEG. Testing these predictions remains a challenge for the field of oscillatory electrophysiology.

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