Review

Is synchronized neuronal gamma activity relevant for selective attention?

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Abstract

Today, much evidence exists that sensory feature binding is accomplished by phase synchronization of induced neuronal gamma activity (30–80 Hz). Recent studies furthermore suggest that phase synchronization of induced gamma activity may represent a general mechanism enabling transient associations of neural assemblies and thus may play a central role in cortical information processing. Here, we describe findings indicating that synchronized gamma activity is moreover specifically involved in selective attention. While feature binding appears to depend primarily on induced gamma synchronization, attentional processes seem to involve both induced and evoked gamma oscillations. Yet it is still an open question, as to which top-down and bottom-up processes are associated with attentional modulation of gamma activity. A possible mechanism to project influences from attentional control structures to areas concerned with stimulus representation and vice versa, may be neuronal synchronization and the resulting firing rate changes of coincidence-detecting neurons in target areas.
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Contents

1. Introduction

According to William James [44], attention is ''the taking possession by the mind in clear and vivid form, of one out of what seem several simultaneously possibly objects or trains of thought.'' Focused or selective attention allows selection of certain items from the stream of information processing. In general, brain processes which are at the focus of attention, enter awareness [66,92]. In a strict sense, one does not become immediately aware of a stimulus or one's own response, but only slightly after one has selected it [52,74]. Studies on selective attention are

mainly concerned with perceptual selection, i.e. selection of sensory information [16,57]. Several mechanisms underlying perceptual selection have been proposed. The most obvious mechanism is selection based on firing rates and several experimental studies support this hypothesis [85]. A principal drawback of this mechanism is that it interferes with the rate coding of stimulus properties, which is the prime modulatory influence on firing rates. Another possible candidate, however not yet supported by much experimental evidence, is the implementation of so-called shifter-circuits that gate bottom-up processing streams [4]. Recently, it has been proposed that synchronization of neural firing may accomplish attentional selection in an effective manner, in particular perceptual selection [68]. This mechanism could provide an additional coding dimension independent of rate coding. Precise synchronization of neural firing within the millisecond range is associated with phase synchronization of gamma activity, i.e. high frequency EEG activity above 30 Hz [22]. As described in the following, there is already significant evidence in support of the idea that gamma synchronization may represent a general mechanism enabling transient association of neural assemblies. However, recent findings reported below indicate that, in addition, synchronized gamma activity may indeed play a specific role in selective attention.

2. Synchronization of gamma activity: a neural coupling mechanism

Phase synchronization of neuronal gamma activity is regarded as the most probable mechanism underlying so-called feature binding. It is well known that different features of a visual object are processed in different submodules of the visual system, for example color in V4 and motion in MT (V5) [26]. Each sensory submodule contains a complete map of the respective feature. A central neuroscientific problem has been how these different aspects are bound together to become one coherent representation of the perceived object (feature integration). This has been called the binding problem. A more specialized aspect of the binding problem is the question of how visual scenes are spatially segmented into different objects (perceptual segmentation). Complementary to the binding problem is the superposition problem. How are different perceptual entities prevented from interference, i.e. how are the different features belonging to different objects grouped together and how are false conjunctions avoided?

Historically, the first hypothesis about the brain's solution to the binding problem was the model of cardinal neurons. In this model, complex information is represented in the brain by convergence of the processing stream to highly specified assemblies or even single neurons [7]. This model, however, could not explain why objects that are perceived for the first time, are obviously processed instantaneously by the brain. Furthermore, this kind of representation would be very costly and there would not be enough neurons in the brain to account for the astronomical number of possible feature combinations. Nevertheless, it has been experimentally demonstrated that there are cells that enhance their firing rate selectively upon presentation of highly complex stimuli like faces [100]. However, even those neurons are not true cardinal cells and do not encode all attributes of a given face, since their responses show a great deal of invariance, i.e. they are unaffected by changes in the size of the face stimulus or in the lighting conditions [36].

Because of the shortcomings of the cardinal cell hypothesis, another binding mechanism was proposed at the beginning of the 1980s by von der Malsburg and colleagues [94,95]. This model assumes a coding mechanism that relies on time-based coding. The idea is that neurons belonging to one functional neural assembly are bound together by synchronization of their action potentials. Even neurons exhibiting the same firing rate but belonging to different assemblies, could be distinguished on the basis of the relative timing of their discharges. Since neurons could participate in different transient assemblies via slight changes in their action potential timing, this mechanism would be fast and flexible and would enable the representation of a very large number of feature combinations. The simultaneous action potential firing of associated neurons or assemblies would correspond to phase synchronous oscillations in the domain of field potentials and EEG.

Experimental evidence supporting the feature binding hypothesis was first reported at the end of the 1980s. Synchronization of intracranially recorded gamma activity (30–80 Hz) was observed in the visual cortex of anesthetized cats, when they were presented with coherently moving bars as compared to independently moving patterns [19,37]. This effect could not be attributed to static structural connectivity patterns, because synchronization changed dynamically according to visual stimulation conditions. Later, analogous findings were reported for intracranial recordings from awake monkeys [31,48]. With similar experimental paradigms, an amplitude enhancement of occipital gamma power was observed in human scalp EEG recordings [54,62]. From scalp recorded EEG, it is not possible to separate changes in local synchronization from changes in the number of activated neurons or the strength of their activation. Thus, the observed enhancement in EEG gamma power may have been caused by either increased precision of synchronization or increased neuronal activation with no changes in synchronization precision. Correlated firing and synchronized gamma activity have moreover been shown to be extended across the border of a single visual area. In animal experiments, stimulus-specific synchronization of gamma activity was for example reported between V1 and V2 [31], between V1 and area PLMS (posterio-medial lateral sup-

rasylvian), an extrastriate motion area [24] and between the V1 areas belonging to different hemispheres [25].

In principle, two types of gamma band activity occurring in response to sensory stimuli can be differentiated. Firstly, the evoked response, which is observed up to 150 ms after stimulus presentation. Since the evoked response is precisely time locked to the stimulus, it can be analyzed by simple averaging in the time domain. The evoked response is followed by induced gamma activity, which occurs in a non time-locked fashion. In simple visual detection tasks for example, induced gamma activity can be observed in a time range of up to 400 ms after stimulus onset [82]. The nonphase-locked, jittering induced response cancels out in the time-domain average and therefore has to be analyzed by frequency-domain approaches based on evaluation of single trials. The findings of stimulus-specific synchronization described above are related to induced gamma activity.

Stimulus-specific phase synchronization of induced gamma oscillations has not only been observed in the visual domain, but also within the somatosensory [17,50], the olfactory [12,30] and the auditory system [13]. In addition, it has been shown that odor discrimination deteriorates in insects when synchronization is pharmacologically blocked in neurons of the olfactory bulb, thus yielding a direct proof for the functional role of synchronization [81]. Recently, gamma synchronization was reported to be involved in learning visuotactile associations [61], in the cognitive integration of visual face perception and task related motor responses [72], in visual working memory [71] and in the coupling of hippocampus and rhinal cortex during declarative memory formation [28]. Subsequent phase desynchronization on the other hand was suggested to dissolve the connection between two structures and hereby to terminate perceptual or cognitive operations [28,72].

To summarize, the above findings point to the view that gamma synchronization is neither confined to the visual cortex, nor is its function restricted to object representation and feature binding. Phase synchronization of gamma activity rather appears to represent a general mechanism enabling a transient association of cortical assemblies [22,91]. This mechanism seems to provide effective coupling and decoupling within, as well as between different subsystems of the brain. Thus, synchronized gamma activity probably plays a general role in cortical information processing.

3. Synchronized gamma oscillations: role in selective attention

But is there any evidence that synchronized gamma activity is also specifically involved in selective attention, i.e. the ability to focus on a subset of items during information processing? Several recent studies support this view. With respect to visual selective attention, an enhancement of scalp recorded induced gamma activity was reported when subjects attended to a certain stimulus or when they perceived a Gestalt [38,63]. In intracranial recordings from area V4 in monkeys, increased gamma range synchronization and reduced low-frequency synchronization was found among neurons activated by the attended stimulus as compared to neurons activated by an identical but non-attended stimulus [34]. For many recording sites reported in this study, the enhancement of gamma synchronization was not accompanied by simultaneous increases of firing rates. Therefore, synchronization of spike discharges in the gamma range seems to be a mechanism supporting selective attention that is independent of firing rate modulation. Increased phase synchronization as well as increased event-related gamma power has also been reported under selective somatosensory attention [17,40]. Shifts in attention between a visual and a tactile task have moreover been shown to result in changes in the degree of synchronization of neural firing within somatosensory cortex of monkeys [80].

Apart from induced gamma activity, evoked gamma activity was also found to be modulated by selective attention. An enhancement of the scalp recorded auditory evoked gamma response has for example been detected, when attention was directed to tones presented to one ear while ignoring tones being presented to the other ear [83,84]. It has been pointed out that the auditory gamma band response shows some functional similarities with the middle-latency response [9,56,65]. Today, it is not yet clear whether the evoked gamma band response and the auditory middle-latency response represent two functionally distinct phenomena [70], or whether they are just two appearances of the same cortical response [14]. More recently, it has been reported that the visually evoked gamma response is affected by the target-like properties of a stimulus and the need to discriminate between the features of a stimulus [41,42]. Thus, the early evoked gamma response may represent an important processing step related to the selection and identification of target stimuli. With respect to scalp EEG recordings, these findings have not been replicated yet by other studies. However, a recent study using intracortical microelectrode recordings in awake monkeys also found evoked gamma-frequency synchronization to be modulated by attention [34]. In this study, gamma-frequency synchronization was stimulus-locked (evoked) from 50 to 150 ms after stimulus onset and it was non stimulus-locked (induced) for the remainder of the stimulus presentation, that lasted up to 5 s. Attention enhanced both the early evoked and the later induced gamma-frequency synchronization. Interestingly, gamma-frequency synchronization was already enhanced before stimulus onset, after the monkey had been cued where to attend, thus clearly indicating a top-down mechanism. It is conceivable that the enhanced evoked gamma is

due to phase resetting of the already enhanced pre-stimulus gamma [29,55].

A modulation of gamma band responses due to attention and target detection has also been observed in event-related potential (ERP) studies. In the ERP domain, processing of target stimuli towards which attention is directed, among others, is accompanied by a larger P3 component compared to non-target stimuli. This component has been interpreted as a correlate of the updating or closure of a context within working memory [18,93]. The P3 was moreover reported to represent a decreased excitability of cortical networks [78,98]. In several studies implementing auditory oddball paradigms, a reduction of cortical gamma activity in the time range corresponding to the P3 component has been observed [10,29,59]. In the somatosensory modality a suppression of prefrontal-parietal 40 Hz phase-synchronization starting at P3 onset has been found [86]. These studies may suggest a P3 related inhibition of the amplitude and synchronization of cortical gamma activity in the sense of a decreased excitability of cortical networks supporting gamma oscillations, which may be caused by cortical threshold regulation associated with slow ERP components [20,78]. However, a hippocampal gamma response accompanying auditory P3 in cats has also been reported [8]. Moreover, results for visual oddball paradigms are not in line with the findings from the auditory and somatosensory modality. Here, for target responses, a reduction of stimulus-related phase-locking of gamma activity in the time range following P3 maximum [76], an amplitude increase of gamma activity in the P3 range [39] and an MTL gamma band response in the post-P3 range [97] were reported. Since neuronal mechanisms of attention differ for different sensory modalities [66], one anyhow might not expect complete concordance. Taken together, all these oddball studies demonstrate the modulation of several aspects of gamma activity in the P3 or post-P3 time range. In this context, it has been proposed that the attentional blink phenomenon might be caused by P3 related disturbance of the early gamma response to the consecutive target stimulus [27].

Perceptual selection as accomplished by selective attention is triggered by the salience of external stimuli (bottom-up), as well as modulated by task relevant features of those stimuli (top-down) [43]. However, there are a few cases where perceptual selection occurs completely intrinsically, for example in the case of binocular rivalry or multistable perceptions. Here, perceptual selection is not completely under attentional control, but can be modulated by selective attention [69,77]. In the case of binocular rivalry, the images presented to the two eyes are incoherent and cannot be fused to one percept [11]. Under these conditions, only information corresponding to one of the two eyes is selected and perceived, whereas information from the other eye is suppressed. The perceived image alternates between both eyes. Since these perceptual shifts occur without changes in stimulus presentation, experiments of binocular rivalry are particularly revealing for the study of intrinsically induced perceptual selection. Several studies in monkeys investigated whether response selection in binocular rivalry is achieved by changes in neural firing rates. It was found that firing rate changes, which are correlated with the dominant percept, mainly occur in higher areas of visual processing, whereas the correlations between perceptual stimulus selection and discharge rates in lower visual processing areas are weak and can be both positive or negative [51,79].

However, it was shown that an increase in phase synchronization of gamma-oscillations in lower visual areas (V1 and V2) of cats strongly correlates with the dominant percept under interocular rivalry in strabismic cats [32,35]. In these studies, no or even inverse correlations of firing rates with the dominant stimulus condition were observed. In addition, phase synchronization corresponding to the dominant percept was found to be stronger when two competitive patterns were presented than for the case when the dominant pattern was presented together with a blank field. Together with the findings on firing rates, this could mean that synchronized gamma activity may emerge in lower visual areas in a first step. Afterwards, these synchronized assemblies may trigger target neurons in higher visual areas and cause changes in firing rates in these areas.

4. Critical viewpoints

Contrary to the data described above, some groups investigating monkey visual cortex have either failed to find functional modulations of synchronized gamma oscillations or have failed to find gamma synchronization at all [49,87,99]. Other authors have attributed these discrepancies in experimental findings to the fact that recordings were from different cortical sites or layers [53], that diverse techniques to analyse synchronization were used, in particular different time windows for the calculation of correlograms [23], and that the spiking behaviour of single neurons must be distinguished from the oscillatory synchronization between neurons and groups of neurons [82]. On the other hand, it has been reported that with the same visual grating stimuli, synchronized gamma oscillations in local field potentials and scalp EEG could only be recorded from monkeys, but not from humans [45]. However, it has been pointed out that this result may be due to the fact that humans only showed a low level of attention to the stimuli, since they were not trained for the task with the same reinforcement schedules as monkeys are [46].

Related to human electrocorticogram data, another group reported that under a somatosensory discrimination task, only local synchronization effects could be detected for electrode distances of up to 1.4 cm, but not for larger distances [60]. This may be different for the visual system

because of its larger spatial extension. But indeed, data indicating functionally relevant long distance synchronization within the gamma band or synchronization between neural areas belonging to different sensory modalities are yet very rare [72]. With respect to computational modelling, it has been argued that the functional significance of spike timing, in contrast to neural firing rate, is still an unresolved issue [6]. From a modelling point of view, it is still an open question whether spike timing really reveals a neural code, or whether this mechanism may only contribute to the understanding of neural circuitry.

5. Discussion and outlook

In conclusion, the majority of experimental data point to the view that phase synchronization of gamma activity not only seems to be a general mechanism underlying cortical information processing, but also appears to be particularly involved in attentional processes. As described above, in several studies, increased synchronization within the gamma range was reported during conditions of focused attention compared to control conditions, i.e. the degree of gamma synchronization seems to be correlated with selective attention. But, more data are needed addressing the interaction of attention related gamma synchronization with synchronization effects within lower frequency bands [34]. Moreover, the exact role of synchronized gamma activity with respect to different aspects of attentional processing like top-down versus bottom-up processing, early versus late selection, spatial versus object-based attention is yet unclear.

According to the feature integration theory, different features of visual stimuli are extracted preattentively and attention is then needed to integrate these features into one coherent percept [88]. But, there are some conditions in which feature binding seems to occur without attention, as has for example been demonstrated in experiments investigating unattentive negative priming of complex shapes [15]. However, in these experiments, evidence for unattentive priming was found only for one unattended object and disappeared when more objects were added [67]. Thus, it seems that attention is necessary only for the representation of several competing objects, but not of single objects. Additional studies are needed to clarify whether this hypothesis is generally valid. In this context, it is an important issue for future research whether synchronization of gamma activity is a mechanism underlying attentive, as well as unattentive feature binding, or whether unattentive binding of features of isolated objects is accomplished without gamma synchronization. By studying oscillatory neural dynamics in case of attentive versus unattentive feature binding, the question may be addressed, as to whether the function of synchronized gamma activity is more closely related to object representation or to selective attention.

Most data on feature binding relate to induced gamma activity which is typically recorded within 100 to 500 ms after stimulus presentation. This time course may suggest an involvement of gamma synchronization in object-based and late selection mechanisms. However, one should be aware that these data only indicate that synchronized gamma activity may accomplish feature binding, whereas the initialization of this binding may occur at an earlier stage [89]. As described above, attentional modulation of gamma oscillations was not only found for induced gamma activity, but also for the earlier occurring evoked activity. But, it is an open question whether the initialization of feature binding is associated with attentional modulation of gamma synchronization at earlier processing stages. Taken together, the position of the gamma synchronization hypothesis is still rather neutral with respect to theories of early versus late selection or spatial versus object-based attention.

Synchronized gamma activity has been reported to be involved in bottom-up, as well as top-down processes [21,46,82]. How can bottom-up and top-down mechanisms be explained within the framework of the gamma synchronization hypothesis? It has been suggested that synchronized neural assemblies can reliably trigger activity of coincidence-sensitive target neurons [1,47]. Members of phase synchronized neural assemblies fire action potentials in a highly time locked manner. When these action potentials are propagated to common target neurons they can cooperate in elevating the membrane potential above firing threshold [96]. Such rapid depolarizations depending on synchronous excitatory synaptic inputs were shown to result from voltage-gated Na^+ and K^+ conductances [5]. This cooperation does not occur for incoming action potentials, which are not time locked, since the membrane potential meanwhile decays depending on membrane time constants. Experimental evidence for this kind of activity propagation has been reported for neurons in the visual and the somatosensory cortex, which were triggered by synchronized thalamic afferents [3,73]. In the cat geniculocortical pathway, the maximal delay times for which spikes from two different presynaptic neurons can cooperatively enhance postsynaptic firing probabilities, were observed to be around 7 ms [90]. Synchronized oscillations in the gamma range were found to be associated with such precise spike timing [22,33]. Thus, synchronized gamma activity might provide a mechanism to enhance the impact of neurons in lower-order sensory areas onto higher-order areas. On the other hand, influences from higher-order areas responsible for attentional control might be conveyed to lower-order sensory areas via the same mechanism [21,46,64].

Synchronized firing in the gamma range may cause Hebbian modification of synaptic efficacy, which could provide the basis for the attentional influence on neuronal plasticity and learning. Hebbian synaptic plasticity was described to depend on the interaction between postsynap-

tic potentials and action potentials back-propagating into the dendrite of the postsynaptic neuron [58]. The required delay times for effective Hebbian synaptic modifications by correlated firing of the pre- and postsynaptic neurons are in the order of less than ±10 ms [2]. Since synchronization of gamma oscillations has been shown to enable such exact timing of neural action potentials, synchronized gamma activity provides an optimal condition for the establishment of Hebbian assemblies. In this sense, synchronized gamma activity may also play an important role in the attentionally modulated segregation of different paths of neural processing [75]. However, experimental evidence directly relating synchronized gamma oscillations to Hebbian assembly formation and neural segregation is still needed.

Acknowledgements

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