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Review

Oscillatory synchrony as a mechanism of attentional processing

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ABSTRACT

The question of how the brain selects which stimuli in our visual field will be given priority to enter into perception, to guide our actions and to form our memories has been a matter of intense research in studies of visual attention. Work in humans and animal models has revealed an extended network of areas involved in the control and maintenance of attention. For many years, imaging studies in humans constituted the main source of a systems level approach, while electrophysiological recordings in non-human primates provided insight into the cellular mechanisms of visual attention. Recent technological advances and the development of sophisticated analytical tools have allowed us to bridge the gap between the two approaches and assess how neuronal ensembles across a distributed network of areas interact in visual attention tasks. A growing body of evidence suggests that oscillatory synchrony plays a crucial role in the selective communication of neuronal populations that encode the attended stimuli. Here, we discuss data from theoretical and electrophysiological studies, with more emphasis on findings from humans and non-human primates that point to the relevance of oscillatory activity and synchrony for attentional processing and behavior. These findings suggest that oscillatory synchrony in specific frequencies reflects the biophysical properties of specific cell types and local circuits and allows the brain to dynamically switch between different spatio-temporal patterns of activity to achieve flexible integration and selective routing of information along selected neuronal populations according to behavioral demands.

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Contents

1. Introduction

Our capacity to process the contents of a visual scene is limited to only a few objects at any given time. Thus, the ability to employ attention in order to select those stimuli or locations that are most relevant for our current goals is critical for our survival. Converging evidence from different experimental approaches has implicated a distributed network of areas in attention and has provided important insights into the role of these areas in the control and maintenance of attention (for reviews see Corbetta and Shulman, 2002; Kastner and Ungerleider, 2000). Moreover, theoretical studies as well as in vivo and in vitro electrophysiology studies have offered a wealth of evidence on the possible cellular mechanisms underlying the selective processing of attended stimuli at the expense of distracters (Desimone and Duncan, 1995; Reynolds and Heeger, 2009).

Methodological limitations, however, for several years, led to a rather restricted view of how the brain achieves a large scale coordination of activity across the extended network of areas participating in attention. On one hand, neuroimaging studies offered a holistic map of activation of the entire brain with limited insight into the temporal modulation of activity across regions. On the other hand, single unit studies in non-human primates provided an account of activity modulations at the single neuron level during attention with unprecedented temporal resolution but poor understanding of the dynamics at the systems level. As a result the question of how spatiotemporal patterns of activity at the level of neuronal ensembles change according to attentional demands remained largely unexplored for several years. In the last two decades, methodological advancements have allowed us to start examining how populations of neurons interact to give rise to behavior. Studies employing large-scale recordings from multiple sites and analytical tools that allow the examination of interactions between activities in distant brain areas have pinpointed oscillatory synchrony as a potential mechanism that boosts sensory representations and promotes effective communication among selected neuronal groups in attention.

Simultaneous multi-site recordings have produced large and complex datasets, which necessitated the development of sophisticated methods of analysis. The dynamic nature of neuronal oscillations and the detailed description of their temporal evolution required an extensive use of time–frequency analyses methods (for a review see Le Van Quyen and Bragin, 2007). Moreover, as data sets become progressively larger, there is an increasing need for the development of robust and sensitive tools that can reveal functional connectivity and directionality of interactions among the distributed nodes of the participating networks (Friston, 2011). Such tools have become freely available to the neuroscientific community and have contributed immensely to a better understanding of the role of oscillatory synchrony in neural processing (e.g. EEGLAB (Delorme and Makeig, 2004); FieldTrip (Oostenveld et al., 2011); Chronux (Mitra and Bokil, 2008); MVGC (Barnett and Seth, 2014)).

The idea that oscillatory synchrony has a functional role for large scale integration of sensory signals was initially proposed by Singer and colleagues as the "binding by synchrony" hypothesis, which aimed to explain how the different features of stimuli are bound to lead to a unified perception of an object (for reviews see Engel and Singer, 2001; Singer and Gray, 1995). This idea led to significant controversy with several studies providing evidence compatible with this hypothesis (e.g. Eckhorn et al., 1988; Engel et al., 1991; Gray et al., 1989) and other against it (Lamme and Spekreijse, 1998; Palanca and DeAngelis, 2005; Thiele and Stoner, 2003). Despite the controversy, these first studies paved the way to the idea that the precise timing of spike occurrence and the temporal structure of activity may have an important functional role in processing of incoming input and could contribute to the emergence of functional networks by gating the flow of information (Salinas and Sejnowski, 2001). Both these functions are critical for attention, which requires the selective processing of signals according to their attentional priority and the selective activation of neuronal ensembles encoding the attended stimulus or location. Although oscillatory synchrony and particularly gamma band synchronization has been associated with a variety of functions (Fries, 2009; Tallon-Baudry, 2009) and has been studied in different species including cats, monkeys, humans, rodents and invertebrates (e.g. Csicsvari et al., 2003; Fries et al., 1997; Siegel et al., 2008; Steinmetz et al., 2000; Wehr and Laurent, 1996), here, we will review findings that link neural

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synchrony with attention in humans and non-human primates, with more emphasis on studies in non-human primates. In Section 2, we review experimental and theoretical work, which suggests that neural synchrony facilitates efficient processing of selected inputs and can provide the scaffold to promote effective communication among neuronal populations. In Sections 3 and 4, we discuss results from studies that have shown how attention modulates local oscillatory activity and long-range oscillatory synchrony, respectively. In Section 5, we discuss results from studies undertaken to explore the cellular and circuit mechanisms of network oscillations. In Section 6 we summarize experimental findings that implicate acetylcholine in the modulation of oscillatory synchrony and in Section 7 we discuss the relationship of frequency-specific oscillatory synchrony and hierarchical processing in the visual system. Finally, in Section 8 we discuss findings that have established a direct link between oscillatory synchrony and behavior by highlighting how oscillatory synchrony correlates with behavioral measures that commonly benefit from attention such as response time and accuracy.

2. Synchrony as a mechanism for the effective modulation of neuronal activity

In electrophysiology studies modulations of firing rates have routinely been correlated with particular stimuli features and with changes in behavioral states. The idea that a rate code is used as an effective way of representing stimuli and mental states by the brain holds since the first attempts to record neuronal activity. Modulations in firing rate are typically measured in attention tasks (e.g. Luck et al., 1997; McAdams and Maunsell, 2000; Moran and Desimone, 1985; Motter, 1994; Reynolds et al., 1999). It is commonly assumed that these modulations in firing rate travel along the entire visual pathway from presynaptic to postsynaptic cells in order to enhance the representation of the attended stimuli at the expense of distracters in downstream areas that are responsible for object recognition. Recent experimental and theoretical studies have extended this idea by taking into account the temporal structure of presynaptic inputs and the role of activity fluctuations in neuronal populations, to explain selective communication in the brain and the formation of functional networks encoding attended objects and locations.

Postsynaptic cells are sensitive to synchronous excitatory inputs. This is reflected by the fact that spike thresholds decrease with high rates of membrane depolarization (Azouz and Gray, 2000). Several studies have shown that synchronous inputs are more effective than asynchronous ones in driving postsynaptic targets (Bernander et al., 1994; Murthy and Fetz, 1994). The importance of precise spike synchronization in postsynaptic processing is also in agreement with earlier views, which postulated that coincidence detection is the prevalent operational mode of neurons (Konig et al., 1996). Because postsynaptic potentials are short, inputs that arrive close together can be summed more effectively and can therefore be transmitted more reliably and have a greater impact on their postsynaptic targets. It has therefore been suggested that optimal communication between two groups of neurons can be achieved under two conditions. First, a group of presynaptic neurons should synchronize their activities. Second, their spikes should arrive as bursts in order to achieve the maximal possible density at the postsynaptic cell (Fries, 2005; Salinas and Sejnowski, 2001). This can be implemented through oscillatory synchrony particularly in the gamma frequency range (40–80 Hz) as this would allow spikes to be concentrated within 6–12 ms (half a gamma cycle). The critical integration window that determines whether a neuron will respond to incoming excitatory potentials is in the order of 10–30 ms, which fits the temporal structure of gamma oscillatory synchrony (Koch et al., 1996; Tallon-Baudry, 2009). It has been shown that gamma oscillations can stabilize the spike threshold leading to a reduction of response variability that could increase reliability of transmission (Rodriguez et al., 2010). Indeed, several in vivo recording studies have measured gamma frequency synchronization in the cortex during different cognitive states providing support to a functional role of gamma oscillatory synchrony. We will present some of these findings in more detail in the following sections.

It has been suggested that oscillatory activity, which reflects the rhythmic excitability fluctuations of a neuronal population, can affect signal processing by modulating the excitatory input gain. A rhythmic modulation of the input gain results in windows in time during which inputs are more effective in driving the postsynaptic neurons. Inputs that arrive when the input gain is maximal will be more likely to be processed, whereas inputs that arrive when the input gain is minimal will have a lower probability of being processed by the postsynaptic neurons. These temporally limited windows are a result of rhythmic inhibition within local networks of excitatory and inhibitory neurons. The role of rhythmic inhibition in the modulation of input gain has been supported by numerous theoretical studies (Borgers et al., 2005; Buehlmann and Deco, 2008; Salinas and Sejnowski, 2000; Tiesinga et al., 2008, 2004; Tiesinga and Sejnowski, 2009). In particular, it has been shown that when the degree of synchrony in an interneuron network changes, it affects the gain of a postsynaptic neuron receiving input from the inhibitory network (Tiesinga et al., 2004) and can lead to a multiplicative gain, mimicking the firing rate changes found in attention studies (McAdams and Maunsell, 1999). Interestingly, the largest firing rate modulations were found when the inhibitory network was oscillating in the gamma frequency range in agreement with the idea that the gamma rhythm imposes the optimal temporal pattern for effective integration of inputs (given the membrane time constants of neurons). Moreover, oscillatory synchrony in the inhibitory network acted as a gate by allowing spikes when the network was synchronous and preventing spikes when the network was asynchronous. This is simply because during synchronous inhibition windows of low inhibitory conductance allow the cell to fire, whereas with an asynchronous network there are no such temporal windows (Benchenane et al., 2011; Tiesinga et al., 2008).

The existence of windows of opportunity due to oscillatory synchrony has important implications in the selective communication between areas. According to the "communication through coherence" (CTC) theory, two rhythmically active neuronal groups can effectively communicate if the two oscillatory phases are aligned so that taking into account conduction and

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synaptic delays, spikes from the sending group arrive at the receiving group within the window of opportunity that is most likely to produce spikes (Bastos et al., 2014b; Fries, 2005, 2009; Gregoriou et al., 2009a; Tiesinga and Sejnowski, 2009; Womelsdorf and Fries, 2007). Thus, phase relations play a critical role in the effectiveness of transmission of information between neuronal populations. Inputs that are either asynchronous or arrive at the least excitable phase of the local field potential (LFP) oscillation will not be processed as effectively. In other words, the phase relation determines the gain of the input and thus the effect on the postsynaptic neuron. The dependence of neuronal communication on the phase of the LFP oscillations has been recently confirmed by experimental data in vivo. Womelsdorf et al. (2007) showed that the strength of interactions between spike trains recorded from different neuronal groups engaged in rhythmic gamma synchronization in the cat and the macaque monkey depended on the phase relations between the local oscillations. Interactions were higher during periods of particular phase relationships, a finding that supports the idea that the synchronization pattern can predict the strength of neuronal interactions. Other studies have found oscillatory coupling between distant areas at non-zero phase lags (Baldauf and Desimone, 2014; Gregoriou et al., 2009b; Jia et al., 2013; Saalmann et al., 2007), which could allow spikes from one area to reach the second area when the local excitability fluctuations are more likely to increase their effectiveness. These data provide further support to the notion that communication through oscillatory coupling is phase dependent and will be presented in more detail in Section 4. It should be noted that phase coding particularly in gamma band oscillations has been considered rather unreliable and noisy (Wang, 2010). Thus, its exact role in information processing needs to be directly addressed. To this end, manipulations of stimulus presentation time relative to light induced gamma oscillations in studies employing optogenetics have provided convincing evidence that enhanced sensory processing and improved behavioral performance depend critically on the timing of sensory input relative to the phase of the gamma rhythm (Cardin et al., 2009; Siegle et al., 2014).

So far, we have reviewed data that show how oscillatory synchrony may affect the reliability of spike transmission and processing of inputs by postsynaptic neurons. However, a critical question in attention studies is how attended stimuli gain an advantage relative to competing stimuli during visual processing. If two neuronal populations represent two different stimuli, then a selective activation of the population representing the attended stimulus could lead to selective processing of the attended object from downstream neurons at the expense of competing stimuli. This is predicted by the "biased competition model" (Desimone and Duncan, 1995) and experimental data have provided strong support to this idea (Reynolds et al., 1999). How could oscillatory synchrony contribute to the selective processing of attended stimuli over competing ones? An enhancement in gamma frequency synchronization among the neurons representing the attended stimulus could ensure that synchronous spikes from this population arrive at the postsynaptic cell downstream bundled together and at the right phase to increase the input gain for the attended stimulus (Fries, 2005, 2009). Asynchronous spikes on the other hand, corresponding to the non-attended stimulus will have a weaker effect on postsynaptic neurons downstream. This way, coherence between neuronal groups representing the attended stimulus can reinforce communication along specific routes, resulting in a selective enhancement of the representation of the behaviorally relevant stimulus (Niebur and Koch, 1994). Recent experimental studies have provided support to this hypothesis and will be presented in Section 4 (Bosman et al., 2012; Grothe et al., 2012).

Although theoretical studies have suggested that changes in firing rate with attention can occur without concomitant changes in synchrony (Ardid et al., 2010; Deco and Rolls, 2005), it has been shown that changes in synchrony can have a major effect on the degree of coherence between two areas (Ardid et al., 2010) facilitating communication along selective pathways. In the next sections, we will present physiological evidence for such selective modulation of gamma band synchronization with attention both locally and across areas.

3. Attention and local synchrony

In agreement with the proposal that precise synchronization of neuronal activity encoding the attended stimulus could have a functional role in attention, several studies have shown increased gamma synchronization with attention. In humans, increased gamma synchronization with spatial and feature attention has been reported in visual (e.g. Gruber et al., 1999; Muller and Keil, 2004; Pavlova et al., 2006; Siegel et al., 2008; Tallon-Baudry et al., 2005; Wyart and Tallon-Baudry, 2008) and somatosensory cortices (Bauer et al., 2006). Studies of selective attention in non-human primates have also found enhancements of local gamma frequency synchronization among neurons encoding an attended location or an attended feature, in extrastriate (Bichot et al., 2005; Buffalo et al., 2011; Fries et al., 2001, 2008; Gregoriou et al., 2009b, 2014; Taylor et al., 2005), frontal (Gregoriou et al., 2009b) and parietal (Saalmann et al., 2007) cortex. It is worth mentioning that initially, gamma frequency enhancements were observed in tasks that required a relatively long sustained attention period suggesting that expectation and anticipation might be crucial factors for the emergence of gamma frequency synchronization. However, gamma peaks and attention-induced enhancements in LFP power and coherence were recently reported in area V4 in a reaction time task (Gregoriou et al., 2014). Thus, an increase in gamma synchrony can be measured even when attention is transiently employed. This selective enhancement of synchronization in the gamma frequency range among neurons encoding behaviorally relevant information could contribute to a preferential processing of attended features or locations in downstream areas e.g. in inferior temporal cortex. To this end, neuronal spike trains in the lower level areas should synchronize with a relative phase close to zero. Indeed, in area V4, spike-spike and spike-LFP coherence have been shown to occur at zero phase lag (Fries et al., 2008; Gregoriou et al., 2009b). This confirms that during attention, spikes occur at the same time across the population encoding the attended location, thereby increasing the impact they may have on postsynaptic downstream targets.

To ensure that increases in gamma power reflect an increase in oscillations and not merely increases in spike counts, the use of appropriate methods is necessary (Buzsaki and Wang, 2012). Because some of the measures used to estimate oscillatory

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synchrony have often been criticized as having inherent biases for firing rate increases it is sometimes useful to demonstrate that these measures can detect increases in gamma synchrony that are not accompanied by increases in firing rates. Several studies have dissociated variations in firing rates from changes in gamma synchronization providing evidence in favor of the notion that attention changes the temporal structure of activity.

In one of the first studies measuring neuronal correlations while manipulating attention, Steinmetz et al. (2000) found significant correlations between pairs of neurons in the secondary somatosensory cortex (SII) when monkeys were asked to report whether a tactile pattern presented to their fingerprints matched a visual pattern shown on a screen. When the same tactile stimuli were rendered irrelevant in a task that required the monkeys to respond to the dimming of a visual stimulus on a screen, correlations among neurons in SII were much lower on average. Thus, attention to somatosensory stimuli synchronizes activity in SII. These changes in synchrony were not correlated with changes in firing rate.

A dissociation between variations in synchrony and variations in firing rates has been also achieved in recording data from area V4 of monkeys trained in a covert visual attention task. Here, whereas the attention-induced modulation of firing rate was evident 420 ms after stimulus onset, modulations in synchrony with attention were found much earlier (Fries et al., 2001). In other cases increases in gamma synchrony have been found among cells that decrease their firing rate or show no changes in their activity during adaptation (Brunet et al., 2014). More recently, a number of different methods have been developed to assess synchronization without the confounding factor of firing rate modulations (Lepage et al., 2013; Vinck et al., 2010, 2012). These have provided unequivocal evidence that attention leads to increased phase locking in gamma frequencies regardless of firing rate modulations.

It should be noted, however, that the increase in gamma synchronization with attention has mainly been reported in mid- and high-level visual areas. Reports on the impact of attention on neuronal synchronization in the first stages of cortical visual processing are conflicting. Whereas in one study attention induced a clear reduction in gamma band spike-LFP coherence in V1 (accompanied by an increase in firing rate) (Chalk et al., 2010), in another study the effect of attention on neuronal synchronization in V1 varied between subjects showing either a small but significant enhancement in gamma band spike-LFP coherence or no effect (Buffalo et al., 2011). A reduction in gamma band oscillatory activity with attention in the prestimulus interval has also been observed in V1/V2 in a spatially cued attention task in humans (Siegel et al., 2008). These results, which stand in striking contrast to those reported for higher-level areas, suggest that gamma band synchronization is differentially affected by attention at different levels of visual processing and in different contexts. It has been suggested that a reduction in gamma oscillations with attention in V1 could be due to a decrease in the inhibitory drive that is responsible for surround suppression (Chalk et al., 2010). Although the mechanisms of such a reduction are still unclear, the differences between studies as far as V1 is concerned and the differential effects obtained along the visual pathway, indicate that the role of gamma oscillations in attentional processing is far from well understood. The differences observed in different visual areas beg for a better understanding of how local connectivity and the distribution of specific cell types and receptors affect oscillatory activity. Although a unifying framework is still missing, some studies have provided evidence that specific neurotransmitters such as acetylcholine (ACh) can lead to diverse effects both on firing rate modulation and oscillatory synchrony across different areas and cortical layers. ACh can act on both nicotinic and muscarinic receptors, which are differentially distributed across cell types, layers and visual areas (Disney et al., 2006, 2007, 2014; Disney and Aoki, 2008) raising the interesting possibility that the observed differences may be accounted for by differences at the microscopic level. We briefly review the relevant literature on the role of ACh in attentional modulation and synchrony in Section 6.

Besides the modulation of gamma frequency synchronization, attention has been shown to also affect synchrony in lower frequencies. Local low frequency synchronization within the alpha and beta range is typically reduced with spatial attention in visual cortices and this finding has been confirmed both in monkeys (Bollimunta et al., 2011; Buffalo et al., 2011; Fries et al., 2001, 2008; Gregoriou et al., 2009b, 2014) and humans (Bauer et al., 2006; Gould et al., 2011; Kelly et al., 2006; Muller and Keil, 2004; Siegel et al., 2008; Thut et al., 2006; Worden et al., 2000; Wyart and Tallon-Baudry, 2008). Local beta band activity has been associated with a variety of functions and its role in cognition remains unclear (for a review see Engel and Fries, 2010). Alpha band activity, on the other hand, has been associated with inhibition of processing of external sensory inputs (Klimesch, 2012; Palva and Palva, 2007). Several studies have reported an enhancement in alpha band oscillatory activity for distracting stimuli and a reduction in alpha band activity for attended stimuli suggesting a role of alpha waves in the suppression of irrelevant stimuli (Dombrowe and Hilgetag, 2014; Haegens et al., 2012; Handel et al., 2011; Kelly et al., 2006). More recently, however, a closer look into the data has revealed a more elaborate picture that implicates both the amplitude and the phase of alpha oscillations as carriers of cognitive signals (Haegens et al., 2011b; Jensen et al., 2014; Klimesch et al., 2007; Klimesch, 2012). These low frequency waves have been suggested to act as carriers of higher frequency oscillations to prioritize information processing and selectively amplify relevant inputs (Jensen et al., 2014; Palva and Palva, 2007; Schroeder and Lakatos, 2009). A detailed account of these mechanisms is beyond the scope of this review.

4. Attention and long-range synchrony. Insights into interareal communication

It is conceivable that local oscillatory activity can facilitate interactions and oscillatory synchrony across brain areas and this can promote efficient communication in the brain. This proposal is in line with the CTC hypothesis (Fries, 2005) and could underlie the flexible routing of behaviorally relevant sensory information through the different stages of visual processing. In contrast to local synchronized oscillatory activity, far less is known about the way long-range synchronization is implemented in functional networks and their role in attention. The frequency of local oscillatory activity as will be discussed in Section 5 is determined by the biophysical characteristics of the local circuits. These local

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oscillators could in principle also determine the frequency of long distant interactions. Recent studies that have employed large scale recordings in distant cortical regions have demonstrated selective interactions in specific frequencies and modulations of inter-regional coherence with attention.

Invasive electrophysiological recordings in non-human primates and non-invasive MEG and EEG studies in humans have provided complementary results that highlight the specificity of interareal interactions but also a diverse pattern of synchronization across areas of the attentional network. Two patterns of synchronization across distant areas have emerged. One is related to increases in beta synchrony across a network of areas involved in integrative functions. Such interareal beta synchronization has been reported in animals during tasks that involve sensorimotor integration (Brovelli et al., 2004; Murthy and Fetz, 1992; Roelfsema et al., 1997; von Stein et al., 2000), decision making (Haegens et al., 2011a; Pesaran et al., 2008), top-down spatial attention (Buschman and Miller, 2007) and in a delayed match to sample task (Saalmann et al., 2007). It has been suggested that synchronization of activity in lower frequencies (including beta frequencies), that are more robust to conduction delays, could mediate long-range communication in the brain so that information is reliably transferred across long distances (Buschman and Miller, 2007; Kopell et al., 2000). Interestingly, synchronization in beta frequencies across areas is usually accompanied by zero phase lag between the coupled oscillations (e.g. Roelfsema et al., 1997).

However, other studies have shown a different synchronization pattern across distant areas. This second pattern highlights the importance of higher frequency (gamma band) long-range synchronization. Synchronization in the gamma band was initially suggested to reflect local computations (Kopell et al., 2000). However, recent studies have implicated gamma band synchronization in long-range communication during bottom-up attention (Buschman and Miller, 2007), top-down attention (Baldauf and Desimone, 2014; Gregoriou et al., 2009b; Grothe et al., 2012; Siegel et al., 2008), perception of ambiguous stimuli (Hipp et al., 2011) and transfer of visual information (Jia et al., 2013). These studies cast doubt on several hypotheses that have been put forward to account for the difference between long-range beta and gamma synchronization. The data suggest that gamma and beta band synchronization do not merely reflect physical distance between the synchronized groups. We further discuss the possible functional implications of synchronization in distinct frequencies in Section 7.

Interestingly, long-range gamma synchronization between neuronal groups that encode the attended location occurs at non-zero phase lags (Baldauf and Desimone, 2014; Gregoriou et al., 2009b; Grothe et al., 2012; Jia et al., 2013; Saalmann et al., 2007). A non-zero phase lag translates into a constant time difference between excitability fluctuations in the synchronized areas and could signify the time required for spikes from one area to reach the other area at its most excitable period thereby increasing the probability of spike generation in the receiving area (Bastos et al., 2014b; Fries, 2005; Gregoriou et al., 2009a; Womelsdorf and Fries, 2007). Although this proposal has been recently questioned by experimental data acquired in anesthetized animals (Jia et al., 2013), more focused studies in the future assessing directly the relative timing of spiking activity in areas synchronizing their activity in awake subjects should clarify the role of phase relationships in populations engaging in oscillatory coupling.

A non-zero phase lag can be further exploited to gain insight into the direction of information flow between areas of the attentional network. In this context a couple of different studies have found enhanced oscillatory coupling between areas traditionally implicated in top-down control (prefrontal and parietal areas) and early visual areas and have subsequently assessed which area initiates the coupled oscillations. Although a direct answer is not possible without experimental manipulations that will perturb neuronal activity, several analytical tools have been employed and have provided important insights into the direction of information flow. Using measures of directional influences and by examining the phase difference between activities in the two areas it was shown that the lateral intraparietal area (LIP) leads the middle temporal area by 5–7 ms (Saalmann et al., 2007), the frontal eye field (FEF) leads area V4 by 8–13 ms (Gregoriou et al., 2009b), whereas V1 leads V4 by 3 ms (van Kerkoerle et al., 2014), which could reflect the transmission delays between the areas under study. Moreover, by determining Granger-causal influences between FEF and V4 it was suggested that during the orientation of attention to the behaviorally relevant location, FEF initiates the coupled oscillations across FEF and V4 (Gregoriou et al., 2009b) supporting the role of FEF in providing top-down spatial attention signals to extrastriate cortex. More recently, a lesion study confirmed the critical role of prefrontal cortex (PFC) in enhancing gamma oscillatory activity in V4 with attention (Gregoriou et al., 2014). We carried out unilateral lesions of PFC together with transection of the corpus callosum and the anterior commissure in order to eliminate prefrontal inputs to area V4 in one hemisphere, while leaving intact the other hemisphere. In the absence of PFC the attention-induced effect on gamma synchrony was significantly reduced confirming that PFC input is necessary for the attentional enhancements in gamma synchrony in V4. The fact that the effect was not abolished suggests that other areas can also contribute.

Importantly, the functional coupling in gamma frequencies between FEF and V4 with attention was found to be selective (Gregoriou et al., 2009b). Only sites with overlapping RFs showed a peak in gamma coherence with attention. Specificity in synchronization was also found in the functional classes of neurons engaged in across-areas gamma coherence. Only visual, but not visuomovement or movement FEF neurons showed enhanced gamma synchronization with V4 neurons when attention was employed. This specificity provides insights into the functional anatomy of attention.

Similar results were recently obtained in humans using MEG recordings while the subjects performed an object-based attention task attending to either faces or houses (Baldauf and Desimone, 2014). Enhanced gamma synchrony was found between the inferior frontal junction (IFJ) and either the fusiform face area (FFA) or the parahippocampal place area (PPA) depending on whether a face or a house was attended, respectively. An analysis of gamma phase lags showed that IFJ led PPA and FFA by 20 ms. These data provide additional evidence for the role of oscillatory synchrony at non-zero phase lags in cortical communication.

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Besides the mechanistic consequences of a phase shifted oscillatory coupling in the gamma range, assessing the neuronal interactions at different stages of the visual hierarchy has provided important insight into the mechanisms of attentional selection. The idea that oscillatory synchronization serves as a mechanism to selectively enhance the representation of attended stimuli, postulates that synchrony acts as the bias signal in the bias competition model. Specifically, as discussed in previous sections, when a group of neurons receives converging input from two different neuronal populations (representing an attended and an unattended stimulus), the neuronal group that synchronizes its activity with the receiving group will enhance its impact at the level of the postsynaptic neuron resulting in an enhanced representation of the attended stimulus. Thus, one would expect that phase locking between the input receiving group and the input providing group that represents the attended stimulus, should be considerably higher compared to that between the same receiving group and the input providing group that represents the unattended stimulus.

This hypothesis was directly tested in two studies that provided very similar results. In the first study, Grothe et al. (2012) employed a shape-tracking task and recorded simultaneously from areas V4 and V1 of monkeys. Two stimuli were placed within the RF of a V4 neuron so as to fall within two non-overlapping RFs of different V1 neurons. This ensured that two local V1 populations provided competing inputs to a single V4 population. Monkeys were trained to attend to the location occupied by one of the stimuli and wait across a number of morph cycles until the stimulus morphed into the initially presented target at which time the monkey was required to respond by releasing a lever. Gamma band phase coherence between V4 and V1 was much higher for V4 and the V1 population that represented the attended stimulus. These results confirmed the notion that neurons can dynamically change their effective connectivity according to attentional demands so that attended stimuli are preferentially processed. Using a very similar experimental design while recording with an electrocorticogram electrode array that was implanted subdurally, Bosman et al. (2012) also found a selective enhancement in gamma coherence between V4 and the V1 population that encoded the attended location. Gamma coherence between V4 and the V1 population encoding the unattended location was significantly reduced. Thus, the existing data suggest that the selective routing of attended inputs is reflected, at least in part, on enhanced gamma band oscillatory synchrony between selected neuronal populations.

Besides beta and gamma long-range cortico-cortical synchronization, alpha frequency long-range synchronization through the thalamus, with its widespread connections to the cortex, has been implicated in the regulation of synchronized activity across cortical areas (Saalmann and Kastner, 2011; Saalmann et al., 2012). Specifically, it has been proposed that increases in alpha synchrony between the pulvinar and visual cortical areas during attention can modulate gamma synchrony across cortical areas through cross-frequency coupling (Saalmann et al., 2012). Whether increases or decreases in alpha synchronization are more relevant to information processing and coordination of cortical synchrony should be addressed in future studies in order to reconcile these findings with the suggested role of alpha synchronization in the suppression of irrelevant information.

5. Cellular and circuit mechanisms of network oscillations

Attention can modulate synchrony in different frequencies but what are the mechanisms that generate oscillatory activity in the brain? Synchronous oscillations can arise via several different mechanisms and their characteristics depend on the membrane properties of the participating cells and the intrinsic network connectivity (Wang, 2010). On the one hand, the biophysical characteristics of pacemaker cells and the resonance properties of neurons largely determine the specific frequency of the emerging oscillations. Typical examples include the hippocampus where distinct cell types show different resonance frequency i.e. in the theta range for pyramidal cells and in the gamma range for fast spiking (FS) interneurons (Pike et al., 2000). In layer V of neocortex certain pyramidal cells tend to show rhythmic bursting at low frequencies (~10 Hz) depending on their intrinsic membrane properties and calcium/sodium conductances (Silva et al., 1991). On the other hand modeling studies have highlighted that different types of synapses can give rise to oscillations in different frequencies, which are largely shaped by the specific synaptic time courses. AMPA receptors, for example, that mediate excitatory glutamatergic input have relatively long time constants, which favor low frequency synchronization. Thus, mutually excitatory interactions could potentially lead to low frequency synchronization but are less likely to lead to high frequency synchronization (Aoyagi et al., 2003; Traub et al., 1992). By contrast, networks of inhibitory neurons have long been shown to produce coherent oscillations in the gamma frequency range (Traub et al., 1996; Wang and Buzsaki, 1996; Whittington et al., 1995). A detailed discussion of the biological processes giving rise to coherent oscillations is beyond the scope of this review. Readers are encouraged to refer to classical reviews of the relevant literature (Bartos et al., 2007; Buzsaki and Wang, 2012; Cannon et al., 2014; Tiesinga and Sejnowski, 2009; Wang, 2010; Whittington et al., 2000). Here, we will only briefly discuss data from theoretical and experimental studies, which have shed light into the physiology of rhythms commonly associated with attention, i.e. gamma and alpha/beta rhythms.

5.1. *Gamma rhythms*

A large body of evidence suggests that GABA-containing interneurons play a critical role in the generation of gamma band oscillations. Of the different subtypes of GABAergic interneurons, fast-spiking basket cells that express the calcium-binding protein parvalbumin and target the perisomatic region of postsynaptic cells (Lytton and Sejnowski, 1991; Mann et al., 2005) appear to be essential for the generation of gamma band synchronization (Bartos et al., 2007; Buzsaki and Wang, 2012). The critical parameter that sets the frequency of the network oscillation in the gamma range (30–90 Hz) is the time scale of the decay of inhibition. When inhibition is mediated by $GABA_A$ receptors the decay time constant is in the order of 5–10 ms allowing synchronization in the gamma frequency range (Buhl

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et al., 1998; Kopell et al., 2000; Whittington et al., 2000). Besides FS basket cells, other types of interneurons may also contribute to the generation of gamma rhythms (Bartos et al., 2007; Freund and Buzsaki, 1996; Hajos et al., 2000; Mann et al., 2005; Somogyi and Klausberger, 2005; Whittington et al., 2011).

The two prevailing network models for the generation of gamma oscillations are the Pyramidal-Interneuron Network Gamma (PING) model (Borgers and Kopell, 2003; Borgers et al., 2005; Lytton and Sejnowski, 1991; Traub et al., 1997) and the Interneuron Network Gamma (ING) model (Chow et al., 1998; Traub et al., 2000; Wang and Rinzel, 1992; Wang and Buzsaki, 1996; White et al., 1998). Briefly, in the PING model both excitatory and inhibitory cells contribute to the generation of gamma band synchronization. Pyramidal cells excite fast-spiking, perisomatic-targeting interneurons that in turn inhibit the pyramidal cells. The frequency of the oscillations in such a network is set by the rise and decay time of the excitatory and inhibitory postsynaptic potentials. With faster excitation compared to inhibition, oscillations in the 30–80 Hz gamma frequency range can arise and the ratio between the two determines the frequency of oscillations (Brunel and Wang, 2003). The balance between excitation and inhibition also contributes to the frequency of the oscillations (Brunel and Wang, 2003). By contrast, in the ING model the generation of gamma synchronization does not depend on the activity of excitatory cells. In a network of interneurons, inhibitory cells exert inhibition onto each other and synchronous activity arises once inhibition has decayed. Thus, the period of the gamma cycle depends on the recovery of interneurons from inhibition. In this case, although synchronous firing of excitatory cells is not necessary for the generation of gamma synchronization, excitatory cells are entrained to the inhibitory rhythm and in turn synchronize their activity.

The role of excitatory and inhibitory cells in the generation of gamma rhythms has been examined both in vitro (e.g. Fisahn et al., 1998; Sohal et al., 2009; Whittington et al., 1995) and in vivo (Cardin et al., 2009; Siegle et al., 2014; Sohal et al., 2009). Recently, the use of optogenetics has facilitated a direct test of the causal role of FS neurons in the generation of the gamma rhythm in vivo. In one study, Cardin et al. showed that selective activation of fast-spiking interneurons by periodic light pulses is more effective at eliciting gamma oscillations than activation of excitatory cells. The latter induced increases in lower frequency oscillations when stimulated (Cardin et al., 2009). Moreover, as predicted by the relevant theoretical models, sensory transmission depended on the timing of the sensory input relative to the phase of the gamma rhythm. These findings demonstrate a causal role of gamma oscillations in effective signal transmission. Using a similar approach, Sohal et al. (2009) illustrated that inhibition of parvalbumin positive interneurons suppresses gamma oscillations, whereas excitation of these interneurons is sufficient to generate gamma synchronization in the neocortex. The results provide strong support to the causal role of inhibitory cells in the generation of gamma synchrony. However, the experimental data so far cannot conclusively demonstrate the exact mechanism (PING or ING) through which gamma synchrony comes about (see Tiesinga and Sejnowski, 2009; Whittington et al., 2011; Womelsdorf et al., 2014 for a relevant discussion).

How these different classes of neurons contribute to modulations of gamma synchrony during sensory processing has been further explored using extracellular recordings in awake behaving monkeys. Extracellular recordings cannot differentiate between distinct neuronal types on the basis of morphology and protein expression patterns. However, intracellular recording studies have demonstrated that the action potential duration can be a strong predictor of cell type (Krimer et al., 2005). In most cases, fast-spiking GABAergic interneurons have shorter-duration action potentials, whereas excitatory pyramidal neurons exhibit longer-duration action potentials (McCormick et al., 1985; Nowak et al., 2003, 2008). The waveform durations of extracellularly recorded action potentials has been shown to follow a bimodal distribution, with broad spiking and narrow spiking cells labeled as putative pyramidal neurons and putative inhibitory interneurons, respectively (e.g. Mitchell et al., 2007).

Using this approach two recent studies examined the contribution of putative pyramidal cells and putative interneurons in gamma synchronization during visual stimulation and attention (Brunet et al., 2014; Vinck et al., 2013). In the first study, Vinck et al. (2013) showed a cell-type specific effect of attention on gamma phase locking. Specifically, during an attentional cue period (in the absence of visual stimulation) activity of putative interneurons in the macaque V4 was strongly gamma phase-locked indicating a strong top-down effect of attention on gamma synchrony among inhibitory neurons. By contrast, pyramidal cells showed only weak gamma synchronization. In this cognitive state, interneuron synchronization is dissociated from the synchronization of pyramidal cells as predicted by the ING model. During visual stimulation both narrow and broad spiking cells were gamma synchronized, with activity of narrow spiking cells being twice as strongly gamma locked. Notably, in this epoch narrow spiking cells were, on average, phase locked at later phases than broad spiking cells (~60 deg) in agreement with the predictions of the PING model, which postulates that interneurons receive excitation from pyramidal cells and feedback inhibition onto them. Moreover, the cell-type specific pattern of synchronization observed during the cue and stimulation period raises the interesting possibility that the PING and ING mechanisms may be employed during bottom-up and top-down processing, respectively.

In the second study, Brunet et al. (2014) demonstrated that repeated presentations of a visual stimulus increased gamma band activity of putative interneurons, although their firing rate decreased. Interestingly, putative pyramidal cells showed no repetition related changes in firing rate, but changes in gamma synchronization depended on the degree of their stimulus-driven activation. Weakly stimulus-driven cells showed a decrease in gamma synchronization, whereas strongly driven cells showed no changes in gamma synchronization. Thus, a cell-type specific effect of stimulus repetition on gamma synchronization was demonstrated that was dissociated from firing rate modulation. Moreover, the data suggest that inputs from strongly driven excitatory neurons contribute substantially more to the gamma synchronization thereby enhancing the representation of the relevant stimulus.

The data reviewed so far indicate that specific cell types and network structures are associated with the generation of

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gamma rhythms underscoring the critical role of the local circuits in the emergence of network oscillations. In this context it is worth emphasizing that gamma frequency oscillations have been reported to be stronger in layer 4 and in the superficial layers of visual cortex (Maier et al., 2010; van Kerkoerle et al., 2014; Xing et al., 2012), in contrast to lower frequency oscillations, which are stronger in infragranular layers and will be discussed below. This difference could be due to differences in the density of synapses, specific receptors or interneurons as previously suggested (Maier et al., 2010). Nevertheless, the laminar differences in oscillatory activity corroborate the prominent role of distinct local microcircuits in the generation of different rhythms. We will further discuss the potential functional implications of this diversity in Section 7.

5.2. *Alpha and beta rhythms*

The mechanisms that give rise to lower frequency oscillations are less clear. Numerous studies have provided evidence that alpha rhythms originate in the deep cortical layers (Silva et al., 1991; Sun and Dan, 2009), with many pyramidal cells in layer 5 showing rhythmic firing at ~10 Hz (Flint and Connors, 1996; Lopes da Silva, 1991; Silva et al., 1991). In visual areas V2 and V4 of behaving macaques, although alpha current generators can be found in all layers, the infragranular alpha current generator is the primary pacemaker (Bollimunta et al., 2008). Interestingly, in the same study, a supragranular origin of the alpha rhythm was found in the inferior temporal cortex suggesting differences across areas that may reflect the functional, anatomical and morphological differences encountered at different stages of the visual hierarchy. A subsequent study showed that in V1, layer 4, the main thalamorecipient layer, acts as a primary pacemaker together with the infragranular layers (Bollimunta et al., 2011). This suggests that the V1 alpha is generated by thalamocortical interactions. A thalamic origin of the alpha rhythm and a role of the thalamocortical circuit in the establishment of the alpha rhythm has also been suggested in other studies (Lorincz et al., 2009).

Insight into the cell types involved in a network capable of oscillating in alpha frequencies was also obtained by a modeling study (Vierling-Claassen et al., 2010) undertaken to explore the network structures that could explain the results of Cardin et al. (2009) described above. The low frequency enhancements obtained following the administration of light pulses to the pyramidal cells were replicated by including a population of inhibitory low threshold spiking (LTS) cells. These cells synapse on distal dendrites of pyramidal cells (Markram et al., 2004) and can induce longer lasting inhibition compared to FS cells (Silberberg and Markram, 2007). When regular spiking (RS) pyramidal cells are strongly synchronized they can drive LTS neurons, which will subsequently induce long lasting inhibition of pyramidal and FS cells, leading to the low frequency power enhancement seen with RS neurons activation. Thus, this study suggests that the interaction of RS with LTS cells can lead to alpha power enhancement following RS drive, whereas the interaction between RS and FS cells can lead to gamma enhancements providing a possible network structure for the alpha rhythm.

The mechanisms giving rise to the beta rhythm are also less clear. Theoretical and in vitro studies have suggested that the beta frequency range could be divided into a lower band characterized as beta1 and a higher band—beta2 (Kramer et al., 2008; Roopun et al., 2006, 2008a, 2010). Whereas beta2 oscillations arise from the infragranular layers (Roopun et al., 2006, 2010), beta1 rhythms are suggested to result from the interaction (concatenation) of beta2 and gamma oscillations in deep and superficial layers (Kramer et al., 2008; Roopun et al., 2008a). Interestingly, here too, the inclusion of LTS cells together with intrinsically bursting layer 5 excitatory cells has been modelled to explain the generation of the beta1 rhythm (Roopun et al., 2008b).

In conclusion, in vitro, in vivo and theoretical studies have provided important insights into the anatomy and the physiology of different rhythms. Accumulating evidence suggests that parvalbumin-expressing, FS interneurons play a prominent role in the generation of gamma oscillations which are more pronounced in the supragranular cortical areas, whereas interactions between LTS neurons and excitatory layer 5 neurons may underlie the generation of lower frequency rhythms, which are more prominent in the infragranular layers. These differences have functional implications, which will be discussed in Section 7. In the next section we discuss how these rhythms may be modulated by specific neurotransmitters in attention.

6. A microscopic account of modulation of synchrony with attention

The role of different neurotransmitters and specific receptors in the modulation of oscillatory synchrony with attention has been examined in modeling, in vivo and in vitro studies. Both glutamatergic and cholinergic systems have been suggested to contribute to enhanced processing in sensory areas during top-down attention (for a review see Deco and Thiele, 2009) For glutamatergic neurotransmission it was shown that the ratio of conductances of AMPA and NMDA receptors is critical for modulation of gamma synchrony; although modulation of firing rate was observed in a broad range of gAMPA:gNMDA ratios, attentional modulation of activity in the gamma band was possible only for a limited range of gAMPA:gNMDA ratios (Buehlmann and Deco, 2008).

The cholinergic system has also been implicated in the attentional modulation of visual processing. Although the role of ACh in selective attention has been questioned due to the diffuse cholinergic projections in the brain, experimental evidence suggests that activation of the cholinergic system facilitates the selective processing of attended stimuli (for reviews see Hasselmo and Sarter, 2011; Sarter et al., 2005; Thiele, 2013). The cholinergic system can be driven bottom-up but also by top-down signals through projections of the prefrontal cortical areas to the basal forebrain (BF, the main source of cholinergic projections to the cortex) (Sarter et al., 2005). Several lines of evidence suggest a tight link between ACh and attentional mechanisms. Local application of ACh or stimulation of BF mimic the effects of attention on neuronal responses in visual cortical areas including sharper spatial tuning, increased response reliability, reduced noise

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correlations, enhanced gain of thalamic input and enhanced attentional modulation of firing rates in visual cortex (Disney et al., 2007; Goard and Dan, 2009; Herrero et al., 2008; Roberts et al., 2005; Rodriguez et al., 2010).

Importantly, besides its effects on neuronal responses the cholinergic system also modulates oscillatory network activity. In vitro experiments have shown that cholinergic agonists induce gamma frequency oscillations (Buhl et al., 1998; Fisahn et al., 1998; Traub et al., 2000) and this effect is mediated by muscarinic receptors. In the macaque V1, m1 muscarinic receptors are expressed in the vast majority of parvalbumin positive cells and much less in excitatory neurons suggesting that the induction of gamma oscillations by ACh entails the excitation of FS cells, in agreement with their role in the generation of gamma rhythms (Disney and Aoki, 2008). In vivo studies have confirmed a facilitatory effect of ACh on gamma oscillations. Stimulation of the mesencephalic reticular formation (MRF), which increases ACh levels in the cortex through its projections to the nucleus basalis, increased gamma synchrony induced by visual stimuli in the visual cortex of anesthetized cats (Munk et al., 1996). In a similar experiment, application of a muscarinic antagonist abolished the facilitatory effect of MRF stimulation on gamma oscillation indicating that these effects are mainly mediated via muscarinic receptors (Rodriguez et al., 2004). Application, however, of cholinergic agonists did not have an immediate effect on light evoked gamma synchronization, a result inconsistent with the idea that ACh is sufficient to increase gamma band oscillations. An increase of LFP power at high frequencies (10–100 Hz) and a decrease at low frequencies (similar to the effect of attention) has also been found in V1 of anesthetized rats after electrical stimulation of the nucleus basalis (Goard and Dan, 2009) and in awake mice after optogenetic activation of cholinergic neurons or their V1 axon terminals (Pinto et al., 2013). In the latter study, activation of basal forebrain cholinergic neurons improved visual discrimination, whereas optogenetic inactivation of basal forebrain cholinergic neurons decreased behavioral performance, increased low frequency power and impaired visual responses without, however, affecting power at gamma frequencies. These results demonstrate a causal role of ACh in low frequency desynchronization and enhancement of visual performance and a facilitatory effect of ACh on gamma oscillatory activity in V1, casting doubt, however, on the necessity of ACh for the induction of gamma rhythms.

In a recent human MEG study, administration of a cholinergic agonist enhanced the effect of attention on low (alpha/beta) frequency oscillations in visual cortex in a spatial visual attention task but had no effect on gamma frequency oscillations in the same areas (Bauer et al., 2012). The enhanced low frequency effect correlated with an improvement in performance. An enhancement in gamma oscillatory activity with the drug was found only in frontal areas but this effect did not correlate with performance. The differential cholinergic effects on oscillatory activity in frontal and visual areas may reflect a differential distribution of cholinergic receptors (Disney et al., 2006, 2014) as well as differences in the local circuits.

The results of Bauer et al. and Pinto and Dan suggest that the prominent role of cholinergic neuromodulation on attentional selection and visual discrimination is mainly reflected on its impact on low frequency oscillatory synchrony in visual cortex. Low frequency oscillatory activity is stronger in infragranular layers of visual cortex, whereas gamma frequency oscillatory synchrony prevails in supragranular layers as discussed in Section 5 (Buffalo et al., 2011; Maier et al., 2010; van Kerkoerle et al., 2014). Based on this, Bauer et al. suggested that the stronger desynchronization effect with cholinergic agonists may be due to a stronger cholinergic impact on deep cortical layers, which are the source and main recipient of top-down signals. A preferential role of cholinergic signals in top-down attention was also suggested by a human study in which administration of a cholinesterase inhibitor improved voluntary but not involuntary attention (Rokem et al., 2010). Moreover, a recent modeling study suggested that high levels of ACh enhance feedback-mediated attentional modulation through a decrease in excitatory recurrent interactions and an increase in inhibitory drive bringing the network in a less activated state whereby top-down signals can exert stronger effects (Deco and Thiele, 2011). Although such an interpretation is plausible, a complete dissociation of top-down and bottom up signaling is almost impossible considering that top-down signals ultimately enhance bottom-up signaling. Interestingly, however, an in vitro study showed that in rat visual cortex, layer 5 LTS cells, which have been implicated in networks generating low frequency rhythms (discussed in Section 5) are excited by ACh through nicotinic receptors, whereas FS cells are inhibited via muscarinic receptors (Xiang et al., 1998). Based on the existing models the excitation of LTS cells would be expected to lead to an increase in low frequency oscillatory activity rather than the decrease observed by Bauer et al. although differences among species should not be ruled out. Interestingly, a different effect of cholinergic modulation on parvalbumin positive cells in superficial layers (compared to the layer 5 effects reported in Xiang et al.) was recently reported in an *in vivo* study (Alitto and Dan, 2012). This result raises the possibility that cholinergic modulation may have different effects on parvalbumin cells in superficial and deep layers. *In vivo* techniques with higher spatial resolution and sensitivity would need to be employed to reconcile all findings and elucidate the specific circuits involved.

7. Relationship of oscillatory synchrony to hierarchical processing and information flow

In non-human primates, recording studies that can afford a high enough spatial resolution to examine the laminar profiles of synchrony, have shown a frequency-specific distribution of oscillatory activity across layers as discussed in previous sections. Specifically, low frequency, mainly alpha band oscillations originate in deeper layers where they are usually stronger, with gamma oscillatory activity originating and being stronger in layer 4 and in the superficial layers (Bollimunta et al., 2011; Buffalo et al., 2011; Maier et al., 2010; van Kerkoerle et al., 2014; Xing et al., 2012). Anatomically, distinct roles have traditionally been assigned to superficial and deep cortical layers with regard to the transmission of signals along the visual hierarchy. Specifically, supragranular layers are the main source of feedforward projections, whereas infragranular layers are the main source of feedback projections (Felleman and Van Essen, 1991; Markov et al., 2014).

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These functional and anatomical laminar differences have led to the suggestion that oscillations of different frequencies could be tags of feedforward or feedback communication, with gamma band oscillations playing a prominent role in bottom-up, feedforward signaling and alpha/beta band oscillations underlying top-down, feedback signaling (Bressler and Richter, 2014; Engel et al., 2001; Siegel et al., 2012; Wang, 2010). Direct experimental support of this proposal was limited (von Stein et al., 2000), whereas indirect support came from studies showing long range beta band oscillatory synchrony in tasks requiring top-down control (Buschman and Miller, 2007; Donner et al., 2007; Saalmann et al., 2007; Tallon-Baudry et al., 2001). However, prominent long range gamma synchrony has been found in tasks employing top-down attention (Gregoriou et al., 2009b; Siegel et al., 2008) indicating that a distinction based on cognitive requirements is not supported by the available data.

Recent studies have directly addressed this hypothesis. The use of translaminar recordings and current source density analysis in behaving macaques, showed that in V1 the alpha rhythm starts in layers 1/2 and 5 (main recipients of feedback inputs), whereas the gamma rhythm starts in layer 4 (main recipient of feedforward projections from the thalamus) (van Kerkoerle et al., 2014). Visual context and task demands changed only the amplitude of oscillations, the laminar pattern remained the same, indicating that the mechanisms that give rise to these rhythms are independent of cognitive state. More importantly, the authors convincingly showed that alpha oscillations propagate from V4 to V1 i.e. in the feedback direction, whereas gamma oscillations propagate from V1 to V4 i.e. in the feedforward direction in agreement with the notion that the frequency range of oscillatory synchrony is a marker of the direction of information transfer. Other studies using measures of directional influences have also suggested a feedforward routing of information in the gamma band along the visual hierarchy (Bosman et al., 2012; Roberts et al., 2013). Additional evidence that supports the use of distinct frequencies for feedforward and feedback signaling in the visual system has been provided by a correlation of frequency-specific directed influences with metrics that quantify the feedforward or feedback character of projections between pairs of visual areas (Bastos et al., 2014a). The results suggested that theta and gamma band synchronization mediate feedforward influences, whereas beta band synchronization mediates feedback influences. It should be kept in mind, however, that this distinction is likely to hold for areas that occupy positions at clearly distinct levels of the hierarchal ranking in which case patterns of connections can be clearly identified as feedforward or feedback. Nevertheless, the results so far clearly suggest that alpha/beta and gamma frequency oscillatory synchrony reflect the laminar origin of interareal anatomical projections.

Two questions arise: First, how does attention fit into that scheme? Cognitive factors including attention could modulate the amplitude of synchrony via the action of neuromodulators such as ACh. Such a modulation could enhance reliability of firing, filtering of distracting stimuli and the selective routing of information along specific neuronal populations. Second, if bottom-up and top-down signaling are subserved by oscillatory synchrony in distinct frequency bands, how could we account for the data that show enhanced gamma-band oscillations during top-down attention tasks? In a bidirectional communication scheme, top-down and bottom-up signals have to interact at some point. Ideally, one would expect that top-down signals would reach the superficial layers and modulate the locally generated gamma oscillations in order to enhance perception and bottom-up processing. Modeling studies have described how a beta band feedback signal can influence gamma power in the superficial layers and have made specific predictions on the cell types involved (Lee et al., 2013).

8. Oscillatory synchrony and attentional benefit. Correlation with behavioral measures

Although attention related modulations of oscillatory synchrony have been established a key question related to the functional role of oscillatory synchrony is whether neuronal synchronization is causally related to behavior. To prove that oscillatory synchrony is relevant for behavior, one would need to establish that disruptions of synchrony lead to impaired behavior, whereas enhancements in synchrony improve behavioral performance. However, the commonly used methodologies to date do not allow for selective manipulations of synchrony without concomitant changes in firing rates. Thus, a direct proof for the causal role of neuronal synchronization in behavior has long been missing and remains a challenge.

The use of optogenetics has more recently allowed for the selective manipulation of activity patterns of specific cell types. Such approaches can directly test the causal role of oscillatory activity in behavior. One study in behaving mice has provided evidence for a causal role of FS induced gamma oscillatory activity in enhanced processing and improved detection ability of less salient stimuli, similar to the behavioral benefit of employing attention (Siegle et al., 2014). Importantly, the behavioral benefit associated with gamma synchronization was obtained only when the stimulus driven excitation arrived in the window of opportunity created by the FS synchronization and did not appear to be caused by a generic increase in firing rate.

Although additional causal links between oscillatory synchrony and attention are missing, a number of studies have demonstrated that the strength of synchronization is predictive of behavioral performance. Attention typically results in shorter response times and in improved performance as reflected in accuracy and discrimination thresholds (Carrasco, 2011). Should oscillatory synchrony play any role in behavior, one would expect that changes in synchrony during attention tasks should correlate with accuracy and reaction times (RTs). Here, we will review evidence for correlations between attention-related behavioral benefits and aspects of oscillatory synchrony.

8.1. *Correlation of oscillatory synchrony with response speed*

Several studies in both humans and non-human primates have demonstrated that the strength of synchrony is predictive of response speed in attention tasks. The most compelling evidence was provided by Womelsdorf et al. (2006) who trained monkeys to covertly attend a drifting grating at a pre-cued location and respond by releasing a bar when the stimulus

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changed color. Color changes of a distracter grating at a non-cued location had to be ignored. The authors recorded multi-unit activity and LFPs in area V4 while the monkeys were performing the task. They found that faster RTs were associated with stronger gamma band synchronization in V4 among neurons encoding the attended location. This was reflected both in LFP gamma power and the gamma spike-LFP coherence. Importantly, this enhancement in synchronization was spatially selective and was not a result of general arousal. Distracters inside the RF of the recorded neurons induced the lowest synchronization in trials that elicited fast responses, whereas they induced higher gamma band synchronization in trials in which the monkeys' RTs were slower. These results indicate that the degree of gamma synchrony can predict response/change detection speeds. Interestingly, the correlation between RTs and firing rates was less prominent. Besides changes in gamma power, alpha and beta frequency power also differed in fast and slow trials. However, contrary to gamma power, faster RTs were associated with decreased power in alpha and beta band before the color change, in agreement with the notion that these frequencies reflect inhibitory processes. Similar results were obtained in an EEG study in humans (Gonzalez Andino et al., 2005). The authors used a visuomotor task in which subjects had to report the presence of a stimulus by a finger movement. They found that prestimulus LFP gamma power (30–100 Hz) in a frontoparietal network was negatively correlated with RTs for more than 85% of the subjects. Interestingly, significant positive correlations in the alpha band were found for more than half of the subjects.

Besides the relationship between RT and strength of synchronization, the relative phase of oscillatory activity has also been associated with behavior and response speed. Recently it was shown that a decrease in RT can be directly linked to the phase of low frequency oscillations entrained to the rhythm of presentation of attended stimuli in a visual–auditory attention task (Lakatos et al., 2008). This finding stresses the notion that rhythmic behavior shifts the excitability fluctuations within local networks so that high excitability phases are optimally aligned to external events in order to facilitate perception and action.

Shifts of attention have also been correlated with the phase of beta frequency oscillations in the FEF in a covert visual search task (Buschman and Miller, 2009). Monkeys had to make a single saccade to a previously memorized target in a search array comprising of the target and three distracters. During covert search, strong correlations were found between the peak frequency of LFP oscillations and the saccadic RT. Within the frequency range of 20–32 Hz, fast RTs, indicating faster shifts of attention, were correlated with oscillations at higher frequencies, whereas slower RTs, indicative of slower shifts of attention, were correlated with lower frequency oscillations. Based on these results the authors suggested that differences in oscillatory frequency could be task specific e.g. faster shifts of attention and eventually higher oscillatory frequencies could accompany search tasks that prohibit saccades, whereas lower frequency oscillations are expected to accompany the slower process of moving the eyes to shift attention. Thus, important insights into the computations inherent in different behavioral responses can be gained from a complete account of the synchrony profiles. These include not only the strength and the relative phase of oscillations but also their exact frequencies.

Human studies have provided evidence that alpha oscillatory synchronization correlates with RT. In one study, which employed Posner's attentional paradigm, faster reaction times were correlated with enhanced alpha oscillations in parieto-occipital areas, ipsilateral to the direction of attention (Thut et al., 2006). Similarly, in a second study, a reduction in alpha oscillatory activity over occipitoparietal areas contralateral to the attended location led to decreased reaction times during an attention task (Gould et al., 2011). These findings are in agreement with a role of alpha waves in suppressing processing of contralateral distracters.

It is worth mentioning that correlation of RT with high (gamma) and low (alpha, beta) frequency power has also been reported in studies examining the role of oscillatory synchrony in motor readiness (Schoffelen et al., 2005), planning and execution of saccades (Chan et al., 2014) and near-threshold detection of weak stimuli (Linkenkaer-Hansen et al., 2004).

8.2. *Correlation of oscillatory synchrony with response accuracy*

It is well established that besides a decrease in RT, attention to a location or stimulus greatly improves behavioral accuracy. It is therefore reasonable to test whether features of oscillatory synchrony are reflected in behavioral performance and consequently whether the degree of synchrony can predict accuracy. Two studies employing recordings from monkey's V4 during a covert attention task have provided evidence that links modulations of oscillatory activity to the allocation of attention. The first study, which employed epidural recordings of LFPs during a shape tracking task, showed that attentional modulation of oscillatory synchrony reflected the locus of attention in correct and error trials (Taylor et al., 2005). As expected, enhanced gamma oscillatory synchrony was found among V4 neurons representing the target when attention was correctly directed toward the hemifield opposite to the recording side, with gamma power being significantly lower when attention was directed in the ipsilateral hemifield in correct trials. Interestingly, erroneous responses to the distracter were accompanied by the reverse pattern of modulation. Specifically, in false alarm trials, in which attention was most likely shifted to the distracter, the authors found reduced gamma power for the target and enhanced gamma power for the distracter when these appeared in the hemifield opposite to the recording site. Other errors did not evoke a similar pattern of modulation.

Additional evidence comes from a second study in which monkeys had to report the presence of a vertical grating of a pre-cued color by releasing a bar (Gregoriou et al., 2014). We found that the gamma synchrony enhancement and the alpha synchrony reduction typically found in V4 when attention is directed inside the receptive field of the recorded neurons were absent in error trials. Moreover, in agreement with the findings of Taylor et al. (2005) when monkeys responded to vertical distracters inside the RF, gamma power among the neurons representing the distracter was enhanced as if the target was inside the RF, whereas when the monkey

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responded to vertical distracters outside the RF, gamma power was reduced as if the target was outside the RF. This latter effect was more pronounced when PFC was ablated in which case the influence of distracters was stronger. The data from the two studies confirm that gamma synchrony modulations reflect the locus of attention and are spatially selective. Enhancements in LFP power for correct compared to error trials have also been found in the superior colliculus in a prosaccade task (Chan et al., 2014) providing further support to the idea that the strength of oscillatory synchrony can be a predictor of behavioral performance.

An association between oscillatory synchrony and behavioral outcome has also been established in human studies. In the majority of these studies increases in beta and gamma band synchronization are associated with improved behavioral performance. In one MEG study long-range beta band synchronization across frontal, parietal and temporal areas was associated with the detection of a target in an attentional blink paradigm (Gross et al., 2004). Stronger beta band synchronization was observed when the second target was detected compared to the condition that it was not detected. Similarly, enhanced beta band activity for correct trials relative to error trials in visual, posterior parietal and prefrontal areas has been measured in a visual motion detection task (Donner et al., 2007). Moreover, the amplitude of low frequency (10 and 20 Hz) prestimulus oscillations over the parietal cortex increases linearly with the probability of detection of a weak tactile stimulus (Linkenkaer-Hansen et al., 2004). Alpha and gamma band synchronization have also been found to correlate with behavioral outcome. The strength of alpha band suppression over visual areas contralateral to the locus of attention in the prestimulus period, as well as the strength of gamma band enhancements (60–100 Hz) during stimulus presentation correlated with the correctness of the behavioral response (Siegel et al., 2008). Finally, in a task where subjects were asked to detect auditory or visual deviants, gamma band synchronization in visual and auditory cortices correlated positively and linearly with behavioral accuracy (hit rate) (Kaiser et al., 2006).

Taking all data into account, increases in high frequency (gamma) and decreases in low frequency (mainly alpha) synchrony correlate with higher detection speeds, improved perception and faster responses. These results provide additional support to a functional role of oscillatory synchronization in the selective processing of attended stimuli. However, correlations do not provide causal links; hence solid conclusions about the role of synchrony in behavior cannot be extracted until methodological advances allow us to selectively perturb synchrony without affecting the average rate of firing. Moreover, given that behavioral measures are correlated with modulations of synchrony in diverse frequencies, high spatial resolution translaminar recordings are required to help elucidate how alpha, beta and gamma band oscillations originating in different layers relate to behavioral measures.

9. Conclusion

A wealth of evidence has shown that attention modulates oscillatory activity and synchrony locally as well as across different brain areas. Several theories have been formulated to account for how an increase in oscillatory synchrony could facilitate attentional filtering and selective processing in the brain. Electrophysiological studies have provided supporting evidence that implicates a diverse range of frequencies in oscillatory synchronization during sensory and cognitive processing. A clear mapping between these frequency-specific neuronal oscillations and function is still missing. However, the available evidence suggests that the frequency of local oscillations is determined by the biophysical properties of the local circuits and that the origin of such oscillations determines the frequency of inter-areal coupling. This view holds that the frequency of oscillatory activity reflects patterns of network interactions rather than specific functions. Although the detailed mechanisms of frequency-specific oscillatory synchrony have not been elucidated, theoretical and experimental studies have provided valuable insights into the local and long-range interactions that can give rise to oscillatory activity and how network activity can be modulated by bottom-up and top-down inputs during attention.

The accumulating evidence highlights the need to optimize current approaches and develop innovative methodologies that will allow us to dissect the role of specific neuronal types in the circuit mechanisms that give rise to modulations of oscillatory synchronization in attention. Moreover, it is essential that future studies assess how manipulations of synchrony affect processing in the brain and behavior in attention tasks. These research aims are the focus of ongoing work, which can contribute to a better understanding of the mechanisms that underlie attentional processing and dynamic communication in the brain in different contexts.

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