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The role of neuronal synchronization in selective attention

Thilo Womelsdorf and Pascal Fries

Attention selectively enhances the influence of neuronal responses conveying information about relevant sensory attributes. Accumulating evidence suggests that this selective neuronal modulation relies on rhythmic synchronization at local and long-range spatial scales: attention selectively synchronizes the rhythmic responses of those neurons that are tuned to the spatial and featural attributes of the attended sensory input. The strength of synchronization is thereby functionally related to perceptual accuracy and behavioural efficiency. Complementing this synchronization at a local level, attention has recently been demonstrated to regulate which locally synchronized neuronal groups phase-synchronize their rhythmic activity across long-range connections. These results point to a general computational role for selective synchronization in dynamically controlling which neurons communicate information about sensory inputs effectively.

Addresses

FC Donders Centre for Cognitive Neuroimaging, Radboud University Nijmegen, Kapittelweg 29, 6525 EN Nijmegen, The Netherlands

Corresponding author: Womelsdorf, Thilo
(t.womelsdorf@fcdonders.ru.nl)

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Introduction

Voluntary ‘top-down’ attention is a key mechanism to select relevant subsets of sensory information for detailed and effective processing and to actively suppress distracting irrelevant sensory information. The behavioural consequences of attentional selection are manifold and include faster processing and reaction times, higher accuracy levels, enhanced sensitivity for fine changes and increased apparent contrast. These behavioural consequences of attention are accomplished by highly selective modulation of neuronal responses at two spatial scales of processing: within and across cortical regions. First, attention enhances the neuronal representation of attended sensory input within the local neuronal populations that are tuned to the attended spatial [1] or featural [2] dimensions. Second, selective attention regulates the communication among neuronal groups in spatially

distant areas, ultimately enhancing effective interactions among those neuronal groups that convey the behaviourally relevant information [3].

Growing evidence suggests that both of these neuronal characteristics of selective attention depend on selective neuronal synchronization. Attention selectively modulates which neurons synchronize their responses with the rhythmic fluctuation of a local functional group of neurons that represents the attended stimulus feature or position. Likewise, the influence of selective attention to shape neuronal interactions among distant neuronal populations is likely to recruit selective synchronization. Such long-range synchronization of locally enhanced neuronal representations has long been implicated in attention, but only recent studies demonstrate that neuronal representations that pertain to attended, relevant information are mutually phase-synchronized across long distances.

In this article we review evidence, gathered over the past two years from animal and human studies, that suggests a functional role for local and long-range selective synchronization of rhythmic neuronal activity. The view emerging from these studies is that synchronization might reflect a basic computational principle that underlies the dynamic control of effective interactions along selective subsets of the anatomically possible neuronal connections [4].

Selective synchronization and spatial attention

Investigating the influence of selective attention on neuronal synchronization depends on tasks in which there is identical sensory stimulation across conditions but covert attention is directed to different aspects of this sensory input. Based on such tasks, visual cortical neurons that have receptive fields overlapping with an attended stimulus synchronize their spiking responses more strongly with the local field potential (LFP) than do neurons that are activated by a non-attended stimulus [5]. This early finding from monkey visual area V4 has recently been extended by showing a rather continuous relationship between the strength of selective synchronization and behavioural performance [6••]. In this study, attention was spatially cued to select one of two stimuli to detect a colour change of the attended stimulus. The speed of detecting the behaviourally relevant colour change in an attended stimulus varied across trials and could be partially predicted by the degree of synchronization in response to that stimulus. Notably, synchronization in the gamma-frequency band (40–100 Hz) predicted the speed of change detection shortly before the colour

2 Cognitive neuroscience

change had occurred. This finding suggests that the processing or the signalling of a sensory change is more efficient when it is handled by an area that is engaged in enhanced gamma-band synchronization [6**].

Importantly, the influence of local synchronization of behavioural responses was spatially selective: neurons activated by an unattended stimulus showed the lowest synchronization when the monkeys were particularly fast in detecting changes of the attended stimulus that were outside their neuronal receptive fields [6**]. Thus, the strength of synchronization is modulated at a fine spatial scale in the visual cortex, being upregulated and down-regulated for neuronal groups that process relevant and distracting information, respectively. This finding rules out a possible influence of globally increased synchronization during states of enhanced alertness and arousal (compare with [7–9]).

In addition to using reaction time as a measure of behavioural performance, a recent study [10**] successfully used an error analysis based on gamma-band synchronization to predict the spatial focus of attention in macaque visual cortex. Taylor *et al.* cued attention to one of two visual shapes, both of which changed continuously throughout the trial. Monkeys had to track the cued shape to detect the reoccurrence of its first outline. Epidurally-recorded field potentials revealed a strong attentional effect, with enhanced gamma-band synchronization in response to the attended shape within visual area V4. This effect was stronger for correct trials than for miss trials, and the degree of synchronization also predicted whether the monkey was paying attention to the distractor, ultimately demonstrating that the strength of synchronization indexes which stimulus the monkey attended.

Attention and gamma-frequency synchronization in humans

The aforementioned studies from macaque cortex demonstrate that the degree of synchronization indexes whether a spatially confined, local neuronal group is processing an attended stimulus effectively. This conclusion is also consistent with recent results from electroencephalography (EEG), magnetoencephalography (MEG) and intracortical EEG in humans demonstrating enhanced gamma-band oscillatory activity for attended versus non-attended stimuli in the visual cortex [11*], the auditory cortex [12–16] and the somatosensory cortex [17*–19] (see also [20]). For example, tactile selective attention to a spatially cued versus non-cued Braille pattern has been found to enhance induced gamma-frequency power in primary somatosensory cortex [17*]. This finding extends an earlier report of attentional modulation of synchronization in secondary somatosensory cortex in monkeys during a non-spatial Go–No-Go task [21].

Recent EEG and MEG recordings in humans also complement the results from monkey cortex about the functional relevance of gamma-band oscillations, by demonstrating a relationship to response times [22] and accuracy [16]. Although macroscopic EEG and MEG recordings in humans are limited in how precisely they can locate the cortical sources of the observed attentional effects, they have the advantage of enabling the functional coupling to be analyzed across distant cortical areas. With regard to attentional processing, this is demonstrated in a recent human EEG study [23**], which cued attention to either global or local letter stimuli and reports phase synchronization selectively among bilateral parietal sites during global attention suggestive of selective interhemispheric integration.

Feature-based attention and selective synchronization

Attention does more than synchronize the responses of neurons based on the spatial proximity of their receptive fields to the focus of attention. Recent evidence demonstrates that attention to a particular feature selectively synchronizes the responses of those sensory neurons that are tuned to the attended feature. Bichot *et al.* [24**] recorded neuronal spiking responses and LFPs in macaque visual area V4 while monkeys searched in multi-stimulus displays for a target stimulus defined by colour, shape or both. When monkeys searched, for example for a red stimulus, by shifting their gaze across stimuli on the display, the receptive fields of the recorded neurons could encompass either non-target stimuli (e.g. of blue colour) or the target stimulus (red) before the time when the monkey detected the target. The authors found that neurons synchronized to the LFP more strongly in response to their preferred stimulus feature when it was the attended target feature of the search rather than a distractor feature.

Thus, attention enhanced synchronization of the responses of neurons that shared a preference for the attended target feature — and did so irrespective of the spatial location of attention [24**]. This feature-based modulation was also evident during a conjunction search task involving targets that were defined by two features: when monkeys searched for a target stimulus that had a particular orientation and colour (e.g. a red horizontal bar), neurons with a preference for one of these features enhanced their neuronal synchronization [24**]. This enhancement was observed not only in response to the target that had the defined colour and shape in conjunction but also in response to distractors that shared one feature with the target (e.g. red colour). This finding corresponds well with the behavioural consequences of increased difficulty and search time needed for conjunction-defined targets.

This study [24**] strongly suggests that feature salience is indexed not only by changes in firing rates (e.g. [25]) but also by selectively synchronizing neuronal responses as a

function of the similarity between their feature preferences and the attended stimulus feature. This idea of feature-similarity to determine the selective attentional gain pattern has been outlined before for modulation of neuronal spiking responses in parietal area MT [25,26]. It should be noted that information about feature salience needs to be combined with spatial information to guide the actual visual search ultimately to the correct target location. It will therefore be interesting to see in future studies how neuronal groups that represent the salient feature communicate with neuronal groups that index spatial salience and guide eye movements.

Notably, results in human MEG subjects are beginning to complement the reported feature-based selective effects on gamma-frequency synchronization and extend them to attentional selection of coherent objects [27–29]. For example, Müller and Keil [28] found spatially confined enhanced synchronization in response to an attended versus a non-attended colour that was presented in a sequence of coloured checkerboard stimuli, and Pavlova *et al.* [29] showed that object-based attention to coherent versus scrambled biological motion stimuli enhanced gamma-frequency synchronization in right parietal and frontotemporal cortex.

Selective long-range neuronal interactions during attentional processing

The aforementioned evidence is largely restricted to local gamma-band synchronization, indicating that neuronal representations of behaviourally relevant sensory information are enhanced relative to those of other sensory information. However, recent studies are beginning to demonstrate that cortical circuits also recruit synchronization to render the interactions of neuronal groups from distant cortical areas effective.

One set of studies shows selective phase synchronization and desynchronization in frontoparietal and frontotemporal cortical regions during target selection in attentional blink paradigms [30,31]. Attentional blink describes the failure to detect the second of two targets in rapid serial streams of sensory input when both targets are separated by less than ~ 500 ms. This failure to detect the second target has been associated with reduced phase synchronization in the beta-frequency band [30], whereas a separate study reported enhanced gamma-band synchronization preceding correct detection of second targets [31]. These results suggest that beta- and/or gamma-frequency synchronization during target processing could subserves effective integration within a broad and distributed attention network (see also [32]).

The suggestion that beta-frequency phase synchronization subserves long-range functional coupling is supported by further lines of evidence. The failure of attentional target selection in the attentional blink paradigm [33] and

attentional lapses in general [34] are typically attributed to restrictions of functional interactions in a frontoparietal attention network rather than to processing limitations at sensory processing stages. Consequently, the observed relationship between long-range beta-band synchronization and target selection could reflect changes in effective neuronal communication within this network. This suggested role of beta-frequency synchronization has also been derived from earlier studies reporting inter-areal beta synchronization during Go–No-Go tasks in cats [35,36], during sensorimotor integration in monkeys [37], and in humans during task intervals that require selective spatial attention [20] and perceptual integration [38,39].

It should be noted that synchronization at beta frequencies is not the sole candidate for mediating long-range interactions between cortical areas, and it might also have more specific functional roles within local neuronal groups. For example, recent reports link beta synchronization in primary visual cortex, but not in extrastriate visual area V4, to the maintenance of a visual percept [40] (see also [41]). Furthermore, in a working-memory context, beta synchronization in area V4 has been linked to successful maintenance of a remembered shape [42].

Theta- and gamma-frequency synchronization: an interface of attentional and mnemonic processing?

The previous sections surveyed evidence suggesting that gamma-band synchronization indexes whether a sensory stimulus is processed effectively. A similar conclusion follows from recent studies suggesting that gamma-band synchronization indexes whether a sensory stimulus is successfully encoded in short-term and long-term memory. In various memory paradigms, the strength of stimulus-induced gamma-band synchronization could predict later memory of that stimulus [43–49]. This capability to predict successful encoding is not restricted to synchronization in the gamma-frequency band: it is frequently accompanied by modulation of oscillatory activity in the theta-frequency band (4–8 Hz) [46,48] or is exclusively present at the theta rhythm [50].

Although the comodulation of gamma-frequency and theta-frequency oscillation could be coincidental, it is more likely to be a relevant functional signature of inter-areal coupling of attentional and memory processes. The strength of gamma-band synchronization has been shown to be modulated by the theta rhythm [51,52]. Interestingly, theta-frequency oscillations have been shown to carry stimulus-specific information in the visual cortex and are related to successful working-memory performance in monkeys [53], rats [54,55] and humans [56]. Particularly noteworthy in this regard is the finding that hippocampal theta activity is likely to exert directed influences on distant cortical sites [54,57]. The functional significance of this intriguing finding and its relationship

4 Cognitive neuroscience

to attentional processes in the frontal cortex is strongly suggested by a carefully controlled study in rats trained on a spatial working-memory task. Jones and Wilson [54] analyzed task epochs with a spatial working-memory load requiring the rat to utilize learned spatial associations to decide whether a leftward or rightward turn would lead to reward, and they compared such 'free-choice' epochs with 'forced-choice' epochs, which were void of the memory and decision demand. Their results not only showed stronger cross-correlations of prefrontal to hippocampal spiking responses during correct free-choice epochs but also revealed significant phase synchronization of prefrontal spiking responses to the theta rhythm of the hippocampal LFP. Moreover, phase-locked spiking responses in prefrontal cortex distinguished which choice (i.e. leftwards versus rightwards) was made [54]. Thus, in addition to being selective to task epochs that resulted in successful integration of memorized spatial information into current movement plans, inter-areal phase synchronization also conveyed information about the actual choice that was made.

Active functional role of alpha-frequency desynchronization

So far in this review, we have associated selective attention with gamma-, beta- and theta-band synchronization, which all seem to be involved in establishing and sustaining effective neuronal communication. Interestingly, an active functional role for efficient attentional processing is also emerging for the alpha-frequency band (8–12 Hz) in the form of spatially selective desynchronization.

Alpha-band synchronization is typically reduced during attentional processing [5,17^{*},28,58–60]. Recent human EEG studies [61,62^{*},63] extend this observation by reporting that the degree of alpha-frequency desynchronization during pre-target intervals of visuospatial attention tasks indicates how fast a subsequent target stimulus is processed. For example, reaction times to a peripherally cued target stimulus are partially predicted by the lateralization of alpha-frequency activity in the second before target appearance [62^{*}]. Although this predictive effect was based predominantly on reduced alpha-band responses over the hemisphere that was processing the attended position, recent studies suggest that alpha-band oscillations are selectively enhanced within local neuronal groups that are processing distracting information (i.e. relating to a stimulus at an unattended location) [64,65]. According to these findings, rhythmic alpha-band synchronization might have an active role in preventing effective local neuronal processing. Although this suggestion might be attractive and pave the way for new empirical tests on the function of the alpha band, it should be noted that alpha-band modulation might also have more specific roles in the functional integration of neuronal activity that are not easily reconciled with the suggested view (e.g. [35,40,66]).

Conclusion

Recent years have witnessed a wealth of evidence showing that selective neuronal synchronization has functional consequences for perceptual performance and behavioural efficiency during selective attentional processing. Spatial and feature-based attention selectively shapes which neurons synchronize their responses within local neuronal groups. The strength of synchronization can be used to predict behavioural response speed [6^{**},16,22], perceptual accuracy [10^{**},18,30,31,41,42] and which conditions confer selective advantages for memory formation [46–48,59]. This evidence suggests that synchronization is instrumental for establishing a selective neuronal representation of behavioural relevance. However, it should be noted that these functional implications of enhanced synchronization are still mostly correlational in nature. Few studies have yet attempted to go beyond correlational evidence by investigating the functional consequences of experimentally enhancing or reducing the level of synchronization (e.g. [67,68]).

An intriguing insight from recent research pertains to the functional role of the selective inter-areal synchronization that underlies selective attention and working memory. Responses of neuronal groups in separate areas synchronize dynamically during task epochs that require selective functional integration [23^{**},30,37,52,54,55,69]. This evidence strongly suggests that long-range oscillatory coupling is crucial for promoting selective neuronal communication and that selective attention could be the key mechanism underlying such dynamic control of effective neuronal interactions [4]. However, it is apparent that this evidence is still sparse and is derived from studies that used highly heterogeneous task contexts and implicated different frequency bands as the substrate for long-range oscillatory coupling. It will therefore be particularly important in future studies to clarify the functional role of oscillatory coupling at different frequencies.

Notably, the aforementioned accumulation of evidence that rhythmic synchronization has a crucial functional role in selective attention has been paralleled by increasingly detailed insights about the physiological origin of rhythmic neuronal synchronization. For example, at the network level, synchronization seems to emerge from inhibitory interneuron networks that can control the gain of spiking responses [32,70–75]. At the level of single neurons, recent studies illustrate how precise timing information is conveyed and sustained even at high oscillation frequencies [76,77], and how oscillatory coupling of interneurons is actively made robust against external influences [78–80].

These studies suggest that basic physiological characteristics render rhythmic synchronization particularly suited to establish and sustain the functional coupling of selective groups of neurons [4,73,81]. These mechanisms seem

to be recruited by attention to render selective subsets of neuronal interactions effective. The basic physiological processes that underlie neuronal synchronization also provide a promising new perspective on the possible ways in which attention might exert its selective influence within neuronal circuits.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Reynolds JH, Chelazzi L: **Attentional modulation of visual processing.** *Annu Rev Neurosci* 2004, **27**:611-647.
2. Maunsell JH, Treue S: **Feature-based attention in visual cortex.** *Trends Neurosci* 2006, **29**:317-322.
3. Miller BT, D'Esposito M: **Searching for 'the top' in top-down control.** *Neuron* 2005, **48**:535-538.
4. Fries P: **A mechanism for cognitive dynamics: neuronal communication through neuronal coherence.** *Trends Cogn Sci* 2005, **9**:474-480.
5. Fries P, Reynolds JH, Rorie AE, Desimone R: **Modulation of oscillatory neuronal synchronization by selective visual attention.** *Science* 2001, **291**:1560-1563.
6. Womelsdorf T, Fries P, Mitra PP, Desimone R: **Gamma-band •• synchronization in visual cortex predicts speed of change detection.** *Nature* 2006, **439**:733-736.
This study demonstrates that trial-by-trial fluctuations of spike-LFP coherence in the gamma-frequency band in visual cortex predict trial-by-trial fluctuations in behavioural performance. The observed predictive synchronization was spatially selective and emerged before the behavioural relevant stimulus change, indicating that synchronization could be instrumental for efficient processing and transmission of the sensory change to postsynaptic target areas. Importantly, enhanced synchronization preceded more rapid onset latencies of neuronal spiking (in addition to enhanced gamma-band synchronization) in response to the sensory change.
7. Herculano-Houzel S, Munk MH, Neuenschwander S, Singer W: **Precisely synchronized oscillatory firing patterns require electroencephalographic activation.** *J Neurosci* 1999, **19**:3992-4010.
8. Rodriguez R, Kallenbach U, Singer W, Munk MH: **Short- and long-term effects of cholinergic modulation on gamma oscillations and response synchronization in the visual cortex.** *J Neurosci* 2004, **24**:10369-10378.
9. Mann EO, Suckling JM, Hajos N, Greenfield SA, Paulsen O: **Perisomatic feedback inhibition underlies cholinergically induced fast network oscillations in the rat hippocampus in vitro.** *Neuron* 2005, **45**:105-117.
10. Taylor K, Mandon S, Freiwald WA, Kreiter AK: **Coherent •• oscillatory activity in monkey area v4 predicts successful allocation of attention.** *Cereb Cortex* 2005, **15**:1424-1437.
This report used a novel shape-tracking task to study the effects of spatial attention on the power of signals recorded from electrodes implanted epidurally over area V4 in the macaque monkey. Monkeys had to detect the re-occurrence of an initial shape, which was morphed through 2-6 sequences of different shapes at a spatially cued location. The strength of induced gamma-band power gave a clear indication of whether the monkey was performing correctly, attended incorrectly to the uncued shape, or missed a target shape. The outcome from this detailed error analysis strongly supports the functional relevance of gamma-frequency synchronization.
11. Tallon-Baudry C, Bertrand O, Henaff MA, Isnard J, Fischer C: **Attention modulates gamma-band oscillations differently in the human lateral occipital cortex and fusiform gyrus.** *Cereb Cortex* 2005, **15**:654-662.
In this study, LFPs were recorded intracortically in response to either an attended or an unattended shape stimulus in human epileptic subjects during pre-surgical screening. Importantly, the study demonstrates that, across all 14 subjects, two regions consistently showed gamma-frequency synchronization (the fusiform gyrus and lateral occipital sulcus), whereas only one of them displayed significant enhanced gamma-frequency synchronization in response to the attended stimulus.
12. Debener S, Herrmann CS, Kranczioch C, Gembris D, Engel AK: **Top-down attentional processing enhances auditory evoked gamma band activity.** *Neuroreport* 2003, **14**:683-686.
13. Tiitinen H, Sinkkonen J, Reinikainen K, Alho K, Lavikainen J, Naatanen R: **Selective attention enhances the auditory 40-Hz transient response in humans.** *Nature* 1993, **364**:59-60.
14. Lenz D, Schadow J, Thaeig S, Busch NA, Herrmann CS: **What's that sound? Matches with auditory long-term memory induce gamma activity in human EEG.** *Int J Psychophysiol* 2006, doi: 10.1016/j.ijpsycho.2006.07.008. (<http://www.sciencedirect.com/science/journal/01678760>).
15. Sokolov A, Pavlova M, Lutzenberger W, Birbaumer N: **Reciprocal modulation of neuromagnetic induced gamma activity by attention in the human visual and auditory cortex.** *Neuroimage* 2004, **22**:521-529.
16. Kaiser J, Hertrich I, Ackermann H, Lutzenberger W: **Gamma-band activity over early sensory areas predicts detection of changes in audiovisual speech stimuli.** *Neuroimage* 2006, **30**:1376-1382.
17. Bauer M, Oostenveld R, Peeters M, Fries P: **Tactile spatial • attention enhances gamma band activity in somatosensory cortex and reduces low-frequency activity in parieto occipital areas.** *J Neurosci* 2006, **26**:490-501.
In this study of spatial tactile attention, subjects had to detect a cued Braille pattern in either a right or a left visuospatially cued sequence of brief Braille stimuli. For attended tactile stimuli, somatosensory cortex showed stronger stimulus-induced gamma-frequency synchronization in the hemisphere that was processing the attended tactile location. Interestingly, attentional processing also affected visual occipital and parietal areas with a marked decrease in alpha- and beta-frequency power compared with unattended tactile stimuli.
18. Linkenkaer-Hansen K, Nikulin VV, Palva S, Ilmoniemi RJ, Palva JM: **Prestimulus oscillations enhance psychophysical performance in humans.** *J Neurosci* 2004, **24**:10186-10190.
19. Palva S, Linkenkaer-Hansen K, Naatanen R, Palva JM: **Early neural correlates of conscious somatosensory perception.** *J Neurosci* 2005, **25**:5248-5258.
20. Brovelli A, Lachaux JP, Kahane P, Boussaoud D: **High gamma frequency oscillatory activity dissociates attention from intention in the human premotor cortex.** *Neuroimage* 2005, **28**:154-164.
21. Steinmetz PN, Roy A, Fitzgerald PJ, Hsiao SS, Johnson KO, Niebur E: **Attention modulates synchronized neuronal firing in primate somatosensory cortex.** *Nature* 2000, **404**:187-190.
22. Gonzalez Andino SL, Michel CM, Thut G, Landis T, Grave de Peralta R: **Prediction of response speed by anticipatory high-frequency (gamma band) oscillations in the human brain.** *Hum Brain Mapp* 2005, **24**:50-58.
23. Rose M, Sommer T, Büchel C: **Integration of local features to a •• global percept by neural coupling.** *Cereb Cortex* 2006, **16**:1522-1528.
This study reports enhanced inter-hemispheric phase synchronization and coherence during attentional processing. Human subjects were cued to indicate the global or local identity of target letters. When the task difficulty was controlled, the authors reported enhanced phase synchronization at low gamma frequencies (30-40 Hz) at parietal and occipital electrodes.
24. Bichot NP, Rossi AF, Desimone R: **Parallel and serial neural •• mechanisms for visual search in macaque area V4.** *Science* 2005, **308**:529-534.
This study is the first demonstration of feature-based modulation of spike-LFP coherence in macaque extrastriate visual cortex (area V4).

6 Cognitive neuroscience

Using a visual search task, the authors analyzed responses of neurons that shared a feature (a particular colour or shape) with the search target. Activity was measured in response to stimuli in the receptive fields of the neurons before the stimulus had actually been found and selected by an eye movement. Throughout attentive search, spike-LFP coherence and firing rates were enhanced in response to a search target when it matched the feature preference of the recorded neuron. This shows that attention selectively synchronizes neuronal responses based on neuronal feature preference.

25. Treue S, Martinez Trujillo JC: **Feature-based attention influences motion processing gain in macaque visual cortex.** *Nature* 1999, **399**:575-579.
26. Martinez-Trujillo JC, Treue S: **Feature-based attention increases the selectivity of population responses in primate visual cortex.** *Curr Biol* 2004, **14**:744-751.
27. Tallon-Baudry C, Bertrand O, Delpuech C, Permier J: **Oscillatory gamma-band (30–70 Hz) activity induced by a visual search task in humans.** *J Neurosci* 1997, **17**:722-734.
28. Müller MM, Keil A: **Neuronal synchronization and selective color processing in the human brain.** *J Cogn Neurosci* 2004, **16**:503-522.
29. Pavlova M, Birbaumer N, Sokolov A: **Attentional modulation of cortical neuromagnetic gamma response to biological movement.** *Cereb Cortex* 2006, **16**:321-327.
30. Gross J, Schmitz F, Schnitzler I, Kessler K, Shapiro K, Hommel B, Schnitzler A: **Modulation of long-range neural synchrony reflects temporal limitations of visual attention in humans.** *Proc Natl Acad Sci USA* 2004, **101**:13050-13055.
31. Nakatani C, Ito J, Nikolaev AR, Gong P, van Leeuwen C: **Phase synchronization analysis of EEG during attentional blink.** *J Cogn Neurosci* 2005, **17**:1969-1979.
32. Kopell N, Ermentrout GB, Whittington MA, Traub RD: **Gamma rhythms and beta rhythms have different synchronization properties.** *Proc Natl Acad Sci USA* 2000, **97**:1867-1872.
33. Marois R, Yi DJ, Chun MM: **The neural fate of consciously perceived and missed events in the attentional blink.** *Neuron* 2004, **41**:465-472.
34. Weissman DH, Roberts KC, Visscher KM, Woldorff MG: **The neural bases of momentary lapses in attention.** *Nat Neurosci* 2006, **9**:971-978.
35. von Stein A, Chiang C, König P: **Top-down processing mediated by interareal synchronization.** *Proc Natl Acad Sci USA* 2000, **97**:14748-14753.
36. Roelfsema PR, Engel AK, König P, Singer W: **Visuomotor integration is associated with zero time-lag synchronization among cortical areas.** *Nature* 1997, **385**:157-161.
37. Brovelli A, Ding M, Ledberg A, Chen Y, Nakamura R, Bressler SL: **Beta oscillations in a large-scale sensorimotor cortical network: directional influences revealed by Granger causality.** *Proc Natl Acad Sci USA* 2004, **101**:9849-9854.
38. Liang H, Bressler SL, Ding M, Truccolo WA, Nakamura R: **Synchronized activity in prefrontal cortex during anticipation of visuomotor processing.** *Neuroreport* 2002, **13**:2011-2015.
39. Rodriguez E, George N, Lachaux JP, Martinerie J, Renault B, Varela FJ: **Perception's shadow: long-distance synchronization of human brain activity.** *Nature* 1999, **397**:430-433.
40. Wilke M, Logothetis NK, Leopold DA: **Local field potential reflects perceptual suppression in monkey visual cortex.** *Proc Natl Acad Sci USA* 2006, **103**:17507-17512.
41. Gail A, Brinksmeier HJ, Eckhorn R: **Perception-related modulations of local field potential power and coherence in primary visual cortex of awake monkey during binocular rivalry.** *Cereb Cortex* 2004, **14**:300-313.
42. Tallon-Baudry C, Mandon S, Freiwald WA, Kreiter AK: **Oscillatory synchrony in the monkey temporal lobe correlates with performance in a visual short-term memory task.** *Cereb Cortex* 2004, **14**:713-720.
43. Fell J, Klaver P, Lehnertz K, Grunwald T, Schaller C, Elger CE, Fernandez G: **Human memory formation is accompanied by rhinal-hippocampal coupling and decoupling.** *Nat Neurosci* 2001, **4**:1259-1264.
44. Fell J, Klaver P, Elfidil H, Schaller C, Elger CE, Fernandez G: **Rhinal-hippocampal theta coherence during declarative memory formation: interaction with gamma synchronization?** *Eur J Neurosci* 2003, **17**:1082-1088.
45. Sederberg PB, Kahana MJ, Howard MW, Donner EJ, Madsen JR: **Theta and gamma oscillations during encoding predict subsequent recall.** *J Neurosci* 2003, **23**:10809-10814.
46. Osipova D, Takashima A, Oostenveld R, Fernandez G, Maris E, Jensen O: **Theta and gamma oscillations predict encoding and retrieval of declarative memory.** *J Neurosci* 2006, **26**:7523-7531.
47. Summerfield C, Mangels JA: **Dissociable neural mechanisms for encoding predictable and unpredictable events.** *J Cogn Neurosci* 2006, **18**:1120-1132.
48. Sederberg PB, Schulze-Bonhage A, Madsen JR, Bromfield EB, McCarthy DC, Brandt A, Tully MS, Kahana MJ: **Hippocampal and neocortical gamma oscillations predict memory formation in humans.** *Cereb Cortex* 2006, doi: 10.1093/cercor/bhl030. (<http://cercor.oxfordjournals.org/>).
49. Sederberg PB, Gauthier LV, Terushkin V, Miller JF, Barnathan JA, Kahana MJ: **Oscillatory correlates of the primacy effect in episodic memory.** *Neuroimage* 2006, **32**:1422-1431.
50. Summerfield C, Mangels JA: **Coherent theta-band EEG activity predicts item-context binding during encoding.** *Neuroimage* 2005, **24**:692-703.
51. Csicsvari J, Jamieson B, Wise KD, Buzsáki G: **Mechanisms of gamma oscillations in the hippocampus of the behaving rat.** *Neuron* 2003, **37**:311-322.
52. Canolty RT, Edwards E, Dalal SS, Soltani M, Nagarajan SS, Kirsch HE, Berger MS, Barbaro NM, Knight RT: **High gamma power is phase-locked to theta oscillations in human neocortex.** *Science* 2006, **313**:1626-1628.
53. Lee H, Simpson GV, Logothetis NK, Rainer G: **Phase locking of single neuron activity to theta oscillations during working memory in monkey extrastriate visual cortex.** *Neuron* 2005, **45**:147-156.
54. Jones MW, Wilson MA: **Theta rhythms coordinate hippocampal-prefrontal interactions in a spatial memory task.** *PLoS Biol* 2005, **3**:e402.
55. Hyman JM, Zilli EA, Paley AM, Hasselmo ME: **Medial prefrontal cortex cells show dynamic modulation with the hippocampal theta rhythm dependent on behavior.** *Hippocampus* 2005, **15**:739-749.
56. Ekstrom AD, Caplan JB, Ho E, Shattuck K, Fried I, Kahana MJ: **Human hippocampal theta activity during virtual navigation.** *Hippocampus* 2005, **15**:881-889.
57. Siapas AG, Lubenov EV, Wilson MA: **Prefrontal phase locking to hippocampal theta oscillations.** *Neuron* 2005, **46**:141-151.
58. Yamagishi N, Goda N, Callan DE, Anderson SJ, Kawato M: **Attentional shifts towards an expected visual target alter the level of alpha-band oscillatory activity in the human calcarine cortex.** *Brain Res Cogn Brain Res* 2005, **25**:799-809.
59. Pesaran B, Pezaris JS, Sahani M, Mitra PP, Andersen RA: **Temporal structure in neuronal activity during working memory in macaque parietal cortex.** *Nat Neurosci* 2002, **5**:805-811.
60. Palva JM, Palva S, Kaila K: **Phase synchrony among neuronal oscillations in the human cortex.** *J Neurosci* 2005, **25**:3962-3972.
61. Sauseng P, Klimesch W, Freunberger R, Pecherstorfer T, Hanslmayr S, Doppelmayr M: **Relevance of EEG alpha and theta oscillations during task switching.** *Exp Brain Res* 2006, **170**:295-301.
62. Thut G, Nietzel A, Brandt SA, Pascual-Leone A: **Alpha-band electroencephalographic activity over occipital cortex**

- indexes visuospatial attention bias and predicts visual target detection. *J Neurosci* 2006, **26**:9494-9502.**
- These authors relate lateralized alpha-band desynchronization that precedes the onset of a visual target to the speed of target detection. Importantly, detection accuracy could not be predicted based on alpha-band synchronization. Lateralized alpha-band effects over parieto-occipital sites were dominated by suppressed alpha-frequency oscillations over the hemisphere contralateral to the attended position.
63. Jin Y, O'Halloran JP, Plon L, Sandman CA, Potkin SG: **Alpha EEG predicts visual reaction time.** *Int J Neurosci* 2006, **116**:1035-1044.
 64. Yamagishi N, Callan DE, Goda N, Anderson SJ, Yoshida Y, Kawato M: **Attentional modulation of oscillatory activity in human visual cortex.** *Neuroimage* 2003, **20**:98-113.
 65. Kelly SP, Lalor EC, Reilly RB, Foxe JJ: **Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention.** *J Neurophysiol* 2006, **95**:3844-3851.
 66. Hummel F, Gerloff C: **Larger interregional synchrony is associated with greater behavioral success in a complex sensory integration task in humans.** *Cereb Cortex* 2005, **15**:670-678.
 67. Stopfer M, Bhagavan S, Smith BH, Laurent G: **Impaired odour discrimination on desynchronization of odour-encoding neural assemblies.** *Nature* 1997, **390**:70-74.
 68. Ishikane H, Gangi M, Honda S, Tachibana M: **Synchronized retinal oscillations encode essential information for escape behavior in frogs.** *Nat Neurosci* 2005, **8**:1087-1095.
 69. Schoffelen JM, Oostenveld R, Fries P: **Neuronal coherence as a mechanism of effective corticospinal interaction.** *Science* 2005, **308**:111-113.
 70. Salinas E, Sejnowski TJ: **Impact of correlated synaptic input on output firing rate and variability in simple neuronal models.** *J Neurosci* 2000, **20**:6193-6209.
 71. Whittington MA, Traub RD: **Interneuron diversity series: inhibitory interneurons and network oscillations *in vitro*.** *Trends Neurosci* 2003, **26**:676-682.
 72. Azouz R, Gray CM: **Adaptive coincidence detection and dynamic gain control in visual cortical neurons *in vivo*.** *Neuron* 2003, **37**:513-523.
 73. Buzsaki G, Draguhn A: **Neuronal oscillations in cortical networks.** *Science* 2004, **304**:1926-1929.
 74. Börgers C, Epstein S, Kopell NJ: **Background gamma rhythmicity and attention in cortical local circuits: A computational study.** *Proc Natl Acad Sci USA* 2005, **102**:7002-7007.
 75. Tiesinga PH, Fellous JM, Salinas E, Jose JV, Sejnowski TJ: **Inhibitory synchrony as a mechanism for attentional gain modulation.** *J Physiol Paris* 2005, **98**:296-314.
 76. Hasenstaub A, Shu Y, Haider B, Kraushaar U, Duque A, McCormick DA: **Inhibitory postsynaptic potentials carry synchronized frequency information in active cortical networks.** *Neuron* 2005, **47**:423-435.
 77. Bacci A, Huguenard JR: **Enhancement of spike-timing precision by autaptic transmission in neocortical inhibitory interneurons.** *Neuron* 2006, **49**:119-130.
 78. Galarreta M, Hestrin S: **Spike transmission and synchrony detection in networks of GABAergic interneurons.** *Science* 2001, **292**:2295-2299.
 79. Vida I, Bartos M, Jonas P: **Shunting inhibition improves robustness of gamma oscillations in hippocampal interneuron networks by homogenizing firing rates.** *Neuron* 2006, **49**:107-117.
 80. Mann EO, Radcliffe CA, Paulsen O: **Hippocampal gamma-frequency oscillations: from interneurons to pyramidal cells, and back.** *J Physiol* 2005, **562**:55-63.
 81. Sejnowski TJ, Paulsen O: **Network oscillations: emerging computational principles.** *J Neurosci* 2006, **26**:1673-1676.