

# The functional role of alpha-band activity in attentional processing: the current zeitgeist and future outlook

Rosanne M Van Diepen<sup>1</sup>, John J Foxe<sup>2</sup> and Ali Mazaheri<sup>3</sup>

Electrophysiological activity measured at the scalp surface using electroencephalography or magnetoencephalography (EEG or MEG) contains prominent ongoing rhythmic activity across a mixture of different frequency bands. This rhythmic oscillatory activity is present during both rest and task performance. The most visible rhythm in the adult human brain is in the band between approximately 8–12 Hz, and is referred to as alpha activity. While sometimes dismissed by neurophysiologists as a nuisance biological artefact, since it often interferes with the recording of event-related potentials (ERPs), there has been an explosion of research linking it to specific functional roles in cognition and behavior over the past two decades. Here, we review some of the research into the functional significance of alpha oscillations with respect to attention and expectation. We focus our discussion on how the amplitude and phase of alpha activity might be involved in the prioritization of relevant sensory input. In addition to summarizing the literature, we also endeavor to provide a critical appraisal as well as highlight limitations and conceptual gaps in the field.

## Addresses

<sup>1</sup>Academic Medical Center Amsterdam, Department of Psychiatry, Meibergdreef, The Netherlands

<sup>2</sup>Department of Neuroscience, The Ernest J. Del Monte Institute for Neuroscience, University of Rochester School of Medicine and Dentistry, Rochester, NY, USA

<sup>3</sup>Centre for Human Brain Health, School of Psychology, University of Birmingham, Birmingham, United Kingdom

Corresponding author: Mazaheri, Ali ([a.mazaheri@bham.ac.uk](mailto:a.mazaheri@bham.ac.uk))

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Old joke: Once upon a time a disciple went to his guru and said: ‘Guru, what is life?’ To which the Guru replies, after much thinking, ‘My Son, life is like a fountain.’ The disciple is outraged. ‘Is that the best that you can do? Is that what you call wisdom?’ ‘All right,’ says the guru; ‘don’t get excited. So maybe it’s not like a fountain.’

Jerry Fodor (from *Concepts: Where Cognitive Science Went Wrong*, 1998)

The most visible rhythm in the adult human brain is in the band between 8–12 Hz, and is referred to as alpha activity. Although almost a century has passed since it was first observed by Hans Berger, a recent groundswell of new research activity on brain oscillations is providing powerful new insights into the functional significance of this oscillation in humans [1]. In the current review we, much like the guru above, will do our best to detail what appears to be an emerging consensus regarding the functional roles that the power and phase of alpha activity might play in selective attention and stimulus expectation.

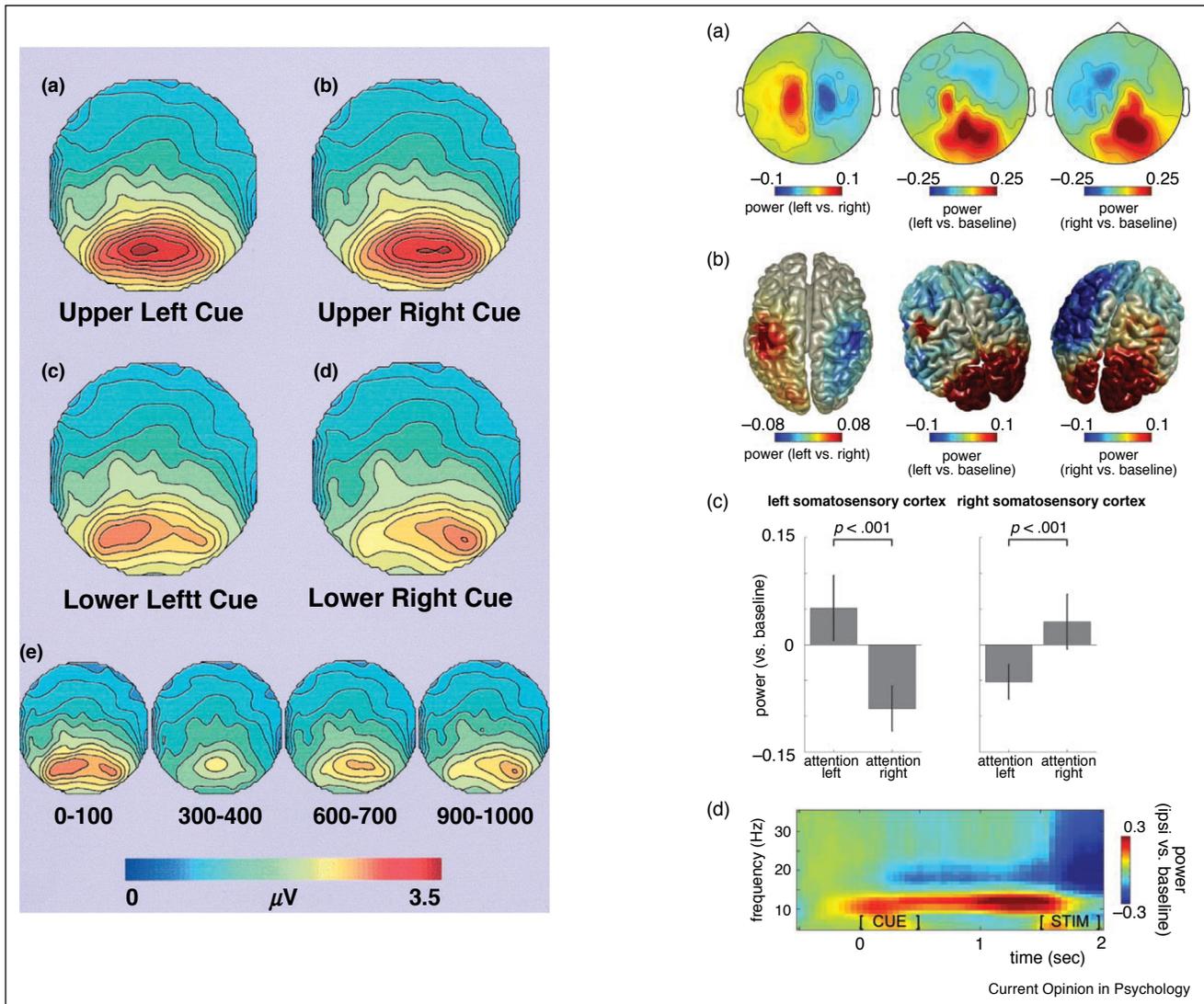
The prominent view in the current literature is that top-down mediated modulation of the power of alpha activity in sensory cortices, can facilitate the processing of a specific input stream, through functional inhibition of irrelevant input, and an increase in the excitability of task-relevant regions dedicated to the processing of an anticipated input. While there is certainly a lot of evidence supporting this view, the field still has some ways to go in determining precisely how alpha exerts inhibition, and the role this inhibition plays in attention which we operationalize as the prioritization of processing for task-relevant sensory input at the expense of task-irrelevant input. For expectation, we refer to the modulation in the processing of sensory input by its probabilistic context.

## Top-down modulation of alpha power and its link to inhibition

Attentional cuing paradigms have shown that fluctuations in the amplitude of alpha oscillations are not random, but can be controlled by top-down factors. Attentionally driven changes in local alpha power have now widely been embraced as a mechanism to direct attention: irrelevant information is filtered out by increasing alpha power in regions associated with processing this information [2–6]. As illustrated in [Figure 1](#), it has been commonly reported that after presentation of a directional cue that is informative as to whether a target will be presented in the left or right visual field, alpha activity is increased over the occipital hemisphere contralateral to distractor presentation compared to alpha activity contralateral to target presentation [7–9].

Similarly, when a cue indicates whether the upcoming target will be presented in the auditory or visual modality,

Figure 1



The power of alpha activity has often been observed to be greater over task-relevant sensory regions ipsilateral to the cued side of attention. The current figure illustrates this in both the visual (left panel) and somatosensory modalities (right panel). Reproduced from Worden *et al.* [9] and Haegens *et al.* [10].

alpha activity before stimulus presentation shows a relative increase or decrease in the occipital cortex, respectively [2,11,12], while an equi-opposite effect is observed in auditory cortex [12,13].

While the top-down increase in alpha activity has been hypothesized to be involved in suppressing distracting input, it should be noted that the relative nature of the results (the alpha activity is often compared between conditions) makes it difficult to separate processes related to active suppression of distractors from processes that increase excitability to enhance target processing. Relatively few studies have tried to separate inhibitory processes and found evidence supporting benefits of both

increases to suppress distraction and decreases to enhance targets in a spatial attention task [14,15] as well as for a somatosensory attention task [11]. For example Kelly *et al.* [16] found a trial-by-trial relationship between alpha-lateralization and target discriminability ( $d'$ ) and reaction times [16]. It is also worth noting that another study only found a relation between behavior and alpha power contralateral to target presentation [17].

The relationship between alpha increases during distraction and task performance in inter-sensory attention has also been studied, although considerably less often than visuo-spatial attention. To the best of our knowledge an increase from baseline has been observed only in a few

studies [2,10]. However, these studies have not shown any behavioral consequence of the alpha increase, making its role in suppressing distracting input under intersensory conditions equivocal at this stage.

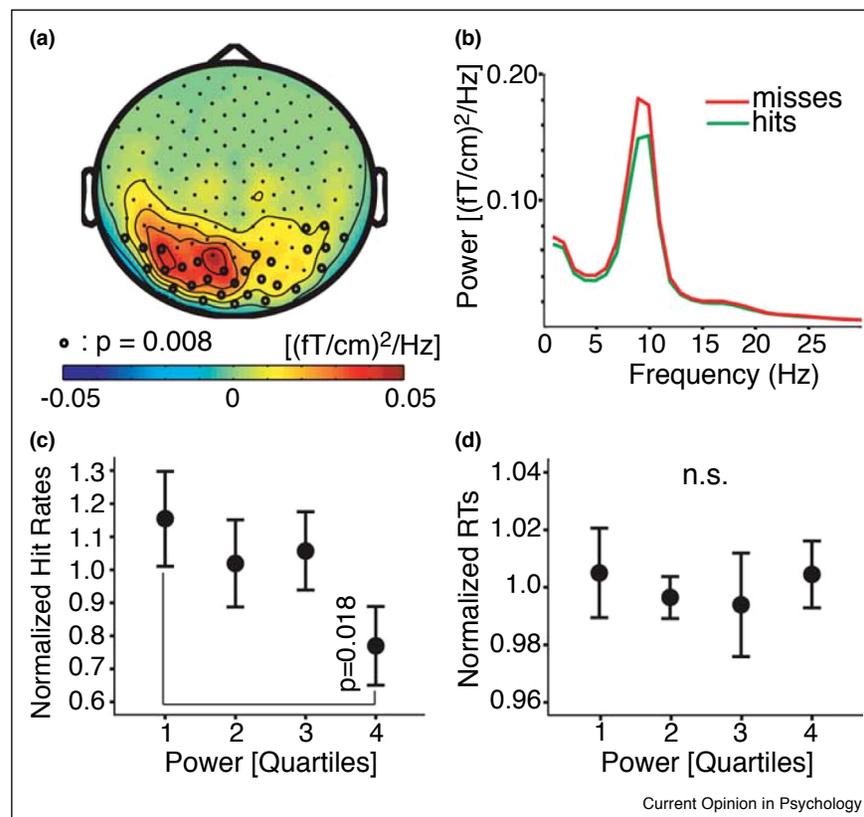
### The influence of pre-stimulus alpha on perception

Going beyond explicitly cued attention-driven modulations of alpha power, there is also accumulating evidence that ongoing ‘spontaneous fluctuations’ in alpha power in sensory regions relates to excitability within those regions, which in turn impacts perception. For example, some studies have observed an inverse relationship between visual discrimination/detection abilities and the power of prestimulus alpha over occipital cortex (see Figure 2) [18\*\*,19\*\*,20]. Consistent with this observation is the finding that visual percepts (i.e. phosphenes) that can be evoked using *trans*-cranial magnetic stimulation (TMS) over visual cortex in blindfolded participants, is more likely to be observed when alpha power is low

before stimulation, rather than when it is high [21,22], suggesting that higher spontaneous alpha-power in visual cortex serves to reduce excitability.

However, it should be noted that these aforementioned studies compared prestimulus alpha activity before ‘hit’ trials (visual stimuli were detected), against ‘miss’ trials (visual stimuli were not detected). Interestingly, more recent studies have observed that lower-alpha power is associated with false-alarms (i.e. when a visual stimulus is reported when none actually exists) [23,24\*\*]. Moreover, a study looking at both discrimination accuracy and its confidence in a two-choice discrimination task, found that pre-stimulus alpha activity was not a significant factor in discrimination accuracy, but rather, appeared to play a role in participants subjective confidence in their judgements [25]. These authors interpreted this to suggest that the increase in excitability of the visual cortex (reflected by low alpha activity) is ‘non-specific’, in that the representations of both targets are enhanced, which does not

Figure 2



The relationship between visual discrimination ability and prestimulus alpha activity recorded via MEG data (adapted from Ref. [19\*\*]). There was significantly greater pre-stimulus alpha power for misses than hits (highlighted with dots,  $p = 0.008$ ; corrected for multiple comparisons). (b) Grand averages of the spectra calculated for the 1 s prestimulus time window preceding misses (red) and hits (green), over sensors that showed a significant difference between misses and hits in the 8–12 Hz band. (c) The trials of the detection session were sorted according to prestimulus alpha power and binned into quartiles. The hit rates (hits divided by misses) were normalized and then averaged over subjects. The hit rates in the first quartile (low alpha power) were significantly higher than those in the fourth quartile ( $p = 0.018$ ). (d) The reaction times for each quartile normalized and averaged over subjects. The reaction times did not show a statistically significant correlation with alpha power. Error bars represent SEM. Reproduced, with modification from Ref. [19\*\*].

influence the discriminability between them. Here, confidence will be systematically higher when cortical excitability is higher (e.g. when alpha is low), despite no change in accuracy. However, the increase in excitability has biased perception (i.e. evidence) toward the decision (i.e. choice made), and as such bears a relationship to confidence in the decision. The relationship between alpha power and confidence has also been recently shown for auditory processing [26].

These studies raise the question of whether spontaneous fluctuations in alpha amplitude result in a perceptual bias *per-se*, or perhaps instead represent a change in decision strategies [27] or response criteria [28]. A study using a two-interval forced-choice paradigm involving target detection and discrimination found evidence for the latter [29]. Specifically, the authors found that performance in the two-interval forced-choice detection task was most accurate when pre-stimulus alpha was low (facilitating the processing of a stimulus if it was present) in the target present interval, but high in the target absent interval. Critically, this pattern was not observed in the two-interval choice paradigm involving target discrimination, suggesting that spontaneous fluctuations of alpha power do not significantly influence discrimination accuracy or decision strategies.

### Post-stimulus modulation of alpha activity

As mentioned at the beginning of this discussion, functional inhibition on a stimulus could be mediated by processes after the onset of a stimulus. Indeed, in addition to prestimulus alpha modulations in expectancy of target or distracting information, alpha modulations *following* stimulus presentation have also been observed [30,31]. Vanni *et al.* observed that when participant had to discriminate pictures of coherent and meaningful objects (e.g. a drawing of guitar) from non-objects (random line patterns), the former induced greater suppression of alpha activity. Interestingly, this alpha difference (occurring ~400 ms post-stimulus) was only observed when the participants were required to perform a discrimination, and disappeared when stimuli were presented without a discriminatory task. Simply put, active attentional engagement was necessary to induce the alpha-band modulations observed. In a similar vein, the study by Van Diepen *et al.* investigated whether the hemispheric modulations of alpha power were also present *after* the onset of a bilaterally presented target and distractor. Here, feature-based attention was manipulated through adjusting the color-similarity of distractors to the target while spatial attention was manipulated through spatial cues. It was observed that informative spatial cues induced a relatively late (300–750 ms after stimulus onset) decrease of pretarget alpha power at occipital electrodes contralateral to the target location. Behaviorally, this alpha lateralization was inversely related to the slowing down of reaction times induced by the target–distractor

similarity manipulation (i.e. a distraction cost). Taken together, these results suggest poststimulus alpha lateralization might serve to facilitate the processing of sensory input, well after its presentation

### Top-down modulation of alpha phase . . . . It's complicated

In the last decade, an intriguing thesis regarding the mechanisms by which alpha-band activity exerts its effect has been forwarded — that visual perception is rhythmic, and that the phase of alpha-band oscillations (~10 Hz) can, at least in part, determine whether briefly presented images are consciously perceived. Evidence for this view (see Figure 3) has come from studies showing that the phase angle at time of stimulus presentation is different for detected versus undetected stimuli [32–34]

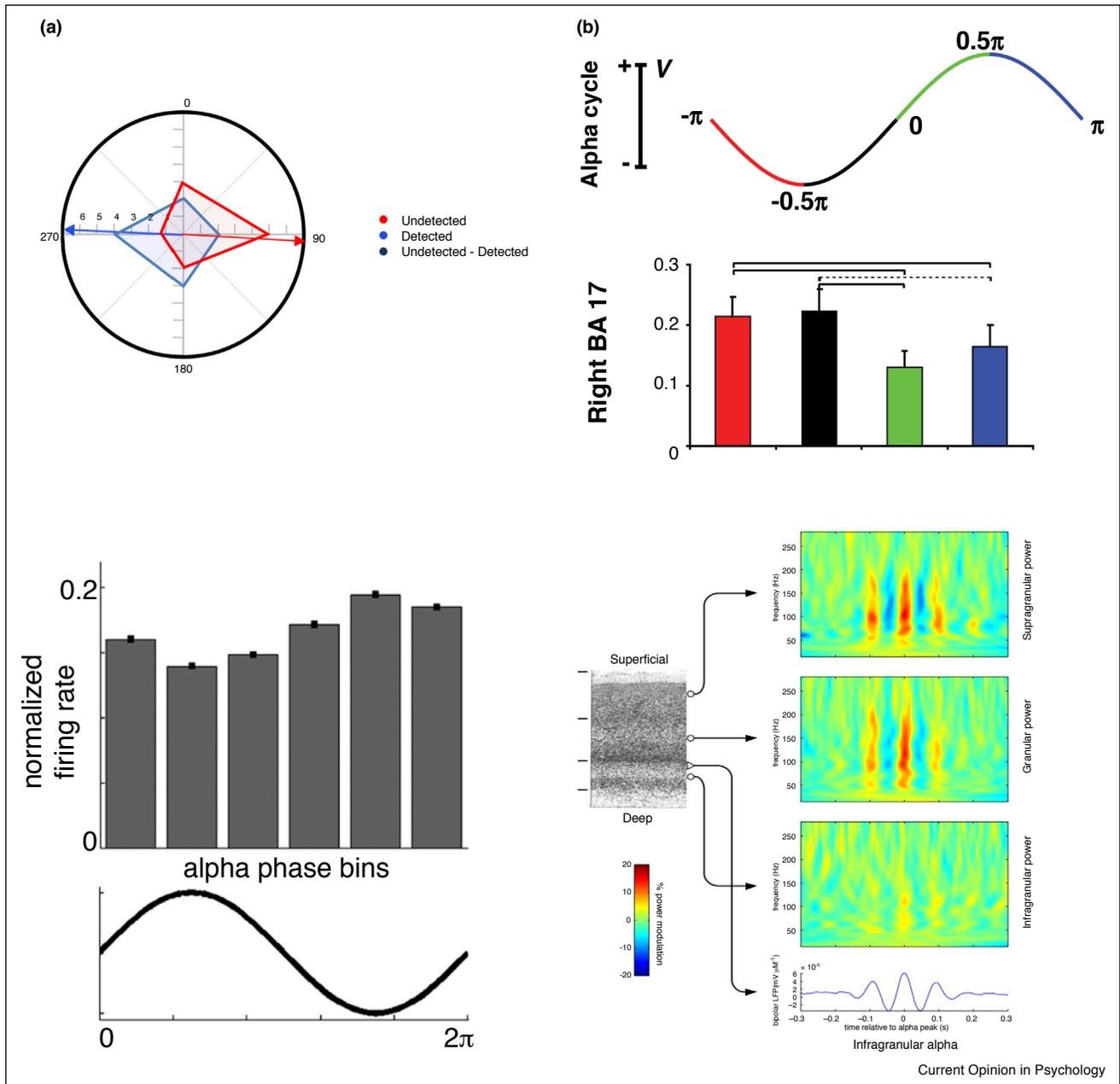
Furthermore, it has also been shown (see Figure 3b) that stimuli arriving during different phases in the alpha cycle illicit different BOLD (blood oxygenation level dependent) responses, measured using functional magnetic resonance imaging (fMRI: [35]). Taken together, these findings suggest that the inhibitory influence of high power alpha oscillations on ongoing neural activity is in specific segments of the alpha cycle, (i.e. discrete pulses) than over the entire cycle [36,37].

The dependency of visual perception on alpha phase would mean that any top-down control of the phase of an oscillation could ensure that targets are presented at times of high neuronal excitability instead of functional inhibition. This could also serve as a mechanism by which the brain can suppress distracting information through adjusting the phase of alpha activity to be at the inhibitory cycle during the arrival of an expected distractor, a mechanism that would afford a high degree of temporal precision in the deployment of attentional resources.

However, it still remains an open question whether the phase of alpha activity can be controlled by top-down factors such as attention and expectation. Evidence supporting an attention/expectation driven modulation of alpha phase angle was reported in a temporal cuing paradigm [38\*\*]. In the Samaha study, visual cues signaled the imminent arrival of visual gratings at a predictable and unpredictable time. The central idea here was that if the phase of alpha oscillations can be adjusted by expectation then there should be more phase consistency at the time of expected stimuli than unexpected. The authors found evidence that there was indeed more phase-consistency of alpha oscillations during expected versus unexpected visual stimuli, suggesting temporal predictions modulate alpha phase.

A phase modulation was, however, not found in a series of experiments (conducted by two of the current authors) in which the adjustment was beneficial for inhibitory

Figure 3



The influence of phase on perception and the visual response. **(a)** Two overlaid circular histograms of the mean phase of  $\alpha$  activity preceding both detected (blue) and undetected (red) visual stimuli. **(b)** The evoked cortical blood oxygenation level-dependent (BOLD) response in the early visual areas was modulated depending on the phase of ongoing alpha activity at the onset of a brief visual stimulus. Adapted from Refs. [32] and [35], respectively. **(c)** The spiking of neurons in the sensorimotor cortex of monkeys performing a discrimination task had a relationship with the phase of alpha activity measured in local-field potentials suggesting the alpha cycle reflects phasic silencing of neurons neural activity. Adapted from Ref. [44]. **(d)** In the V1 cortex of monkeys robust modulation of gamma activity (50–200 Hz) phase locked to the alpha oscillations was observed in the supragranular and granular layers but not in the infragranular layers. Adapted from Ref. [46].

purposes [39\*\*]. In a task similar to Samaha *et al.*, cues signaled the imminent arrival of stimuli either in the visual (gratings) or auditory (simple tones) modalities. However, here the paradigm was set up such that the targets in one modality (e.g. visual) were presented with

distractors in another modality (e.g. auditory). Under these circumstances, one would certainly have predicted that adjusting the phase angle of the alpha oscillation should have been beneficial in achieving optimal suppression of the distracting sensory stimuli. The important

distinction here though was that we looked for evidence of phase adjustments in anticipation of targets and distractors in less-frequent ‘catch’ trials containing no sensory stimuli (i.e. stimulus-absent trials) at the expected time of the target or distractor. We took this precaution due to the fact that stimulus evoked responses add a waveform with a specific phase to the ongoing alpha activity and can subsequently confound its phase estimation [40,41]. We here did not find, across three separate experiments, any evidence for a preferred phase during expected presentation of either distractors or targets.

Is it possible to reconcile these divergent findings? It first needs to be recognized that accurate measurement of phase perturbation in ongoing oscillatory activity is complicated business. Modulations in the phase-angle of alpha oscillations are examined in various ways. For instance, the instantaneous phase angle can be assessed and compared between conditions with different attentional requirements. However, a large number of trials are needed to make a reliable estimation of the preferred phase angle for a certain condition. Also, here both conditions must show a preferred phase-angle to reliably assess whether a significant difference is present. Alternatively, when a phase modulation is only expected in one condition, and phases are expected to be random in the other condition, a measure called inter-trial-phase locking (ITPC, sometimes also referred to as Phase-Locking-Factor, PLF) is often employed [42]. ITPC is essentially the complex average of the phase-angles normalized to be between 0 and 1.

A significant limitation of the ITPC is that it can be influenced by the power of oscillatory activity. While phase and amplitude are independent measures, signal to noise differences between conditions (which are dependent on the amplitude of an oscillation relative to noise) could lead to differences in ITPC and thereby cause false discoveries [41,43]. In addition, evoked responses are highly phase-locked to stimulus presentation, which means that inter-trial phase-locking can be overestimated due to temporal leakage of the ERP when ITPC is estimated at a time point close to stimulus presentation. Thus, any top-down modulation of the ERP in terms of its peak amplitude/latency by attention and expectation can lead to modulation in the ITPC, irrespective of any perturbation of the phase of ongoing rhythms (see [Figure 4](#)).

### How is alpha activity proposed to inhibit processing?

The majority of the work we have reviewed suggests that the attentional modulation of alpha power likely serves to gate the flow of relevant and irrelevant information. But how does this inhibition come about at the level of neurons? There are some suggestions that alpha pulses could be inhibiting the firing rate of neurons [44]. The

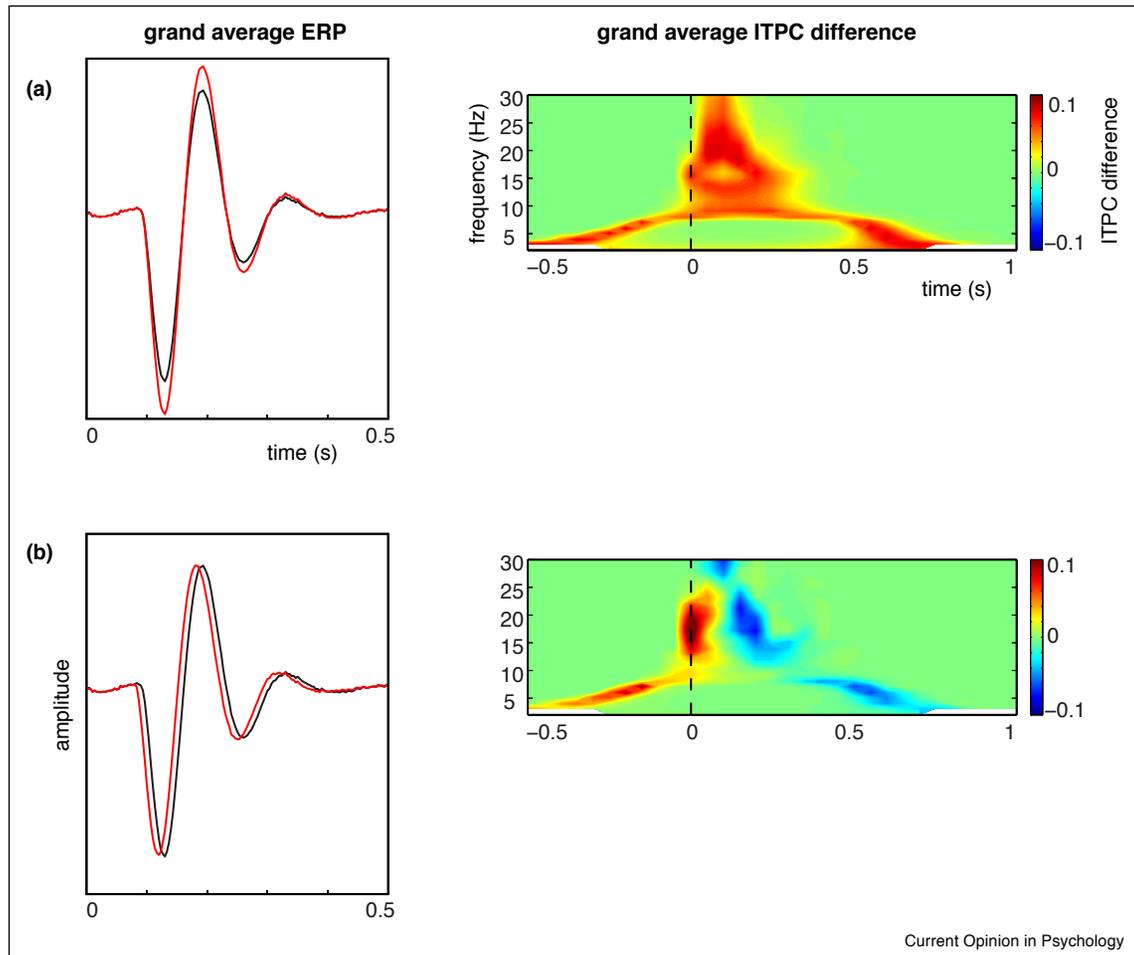
phase of alpha activity appears to be coupled to the amplitude of high-frequency activity in the gamma range (30–200 Hz), detected both at the scalp [45] but also rather intriguingly across laminar layers in V1 [46]. The latter study used laminar electrophysiological recordings in simians to find gamma activity in the granular layer (the layer directly receiving visual input from the lateral geniculate nucleus of the thalamus), and showed that it was coupled to the phase of alpha activity in infragranular layers. The authors speculated that the phase of alpha activity could serve as ‘gain-control’ by limiting the duty-cycle of visual processing.

In another study, also using laminar recordings in V1, high-frequency activity in the gamma range appeared to originate in the granular layer before feeding forward into both the deep and superficial layers [47]. In contrast, alpha activity travelled from deep layers toward the granular layer, suggesting that alpha might reflect a feedback signal from higher-up nodes that phasically modulates neural excitability in the thalamo-recipient layer. However, it should be noted that another study observed alpha activity across all cortical layers, suggesting that it could function in both a feedforward and feedback manner [48].

It is also important to recognize that research examining alpha activity outside the scope of attention suggests a more expansive view on the role of alpha modulation in cognitive processes such as memory (see very informative reviews by Refs. [49,50]) and language processing [51,52]. Here, it would appear that alpha modulation serves a more computational role by holding and transferring information rather than simply inhibiting task irrelevant regions.

We ourselves, initially favored an account whereby cortical alpha activity primarily served an inhibitory role, but emerging evidence has necessitated a modification of this view. We now favor a more expansive view whereby alpha activity can be conceived of as rhythmic pulses that produce bouts of both inhibition that cycles on and off approximately every 100 ms [53]. A key issue is the spatial scale at which alpha oscillatory activity occurs within a given functional cortical region. An increase in alpha power (or any oscillation for that matter) at the scalp, or in local field potentials, reflects the spatial summation of synchronized post-synaptic potentials across ensembles of neurons (illustrated in [Figure 5](#)). But, it is important to bear in mind that an increase in power does not necessarily reflect increased neural activity in a given band (i.e. more neurons engaged), but rather, can also simply reflect greater phase synchronization across a population of neurons (i.e. higher phase synchrony). Conversely, desynchronization of the neuronal population firing results in the cancellation (through destructive interference) of post-synaptic potentials, and as such, a

Figure 4



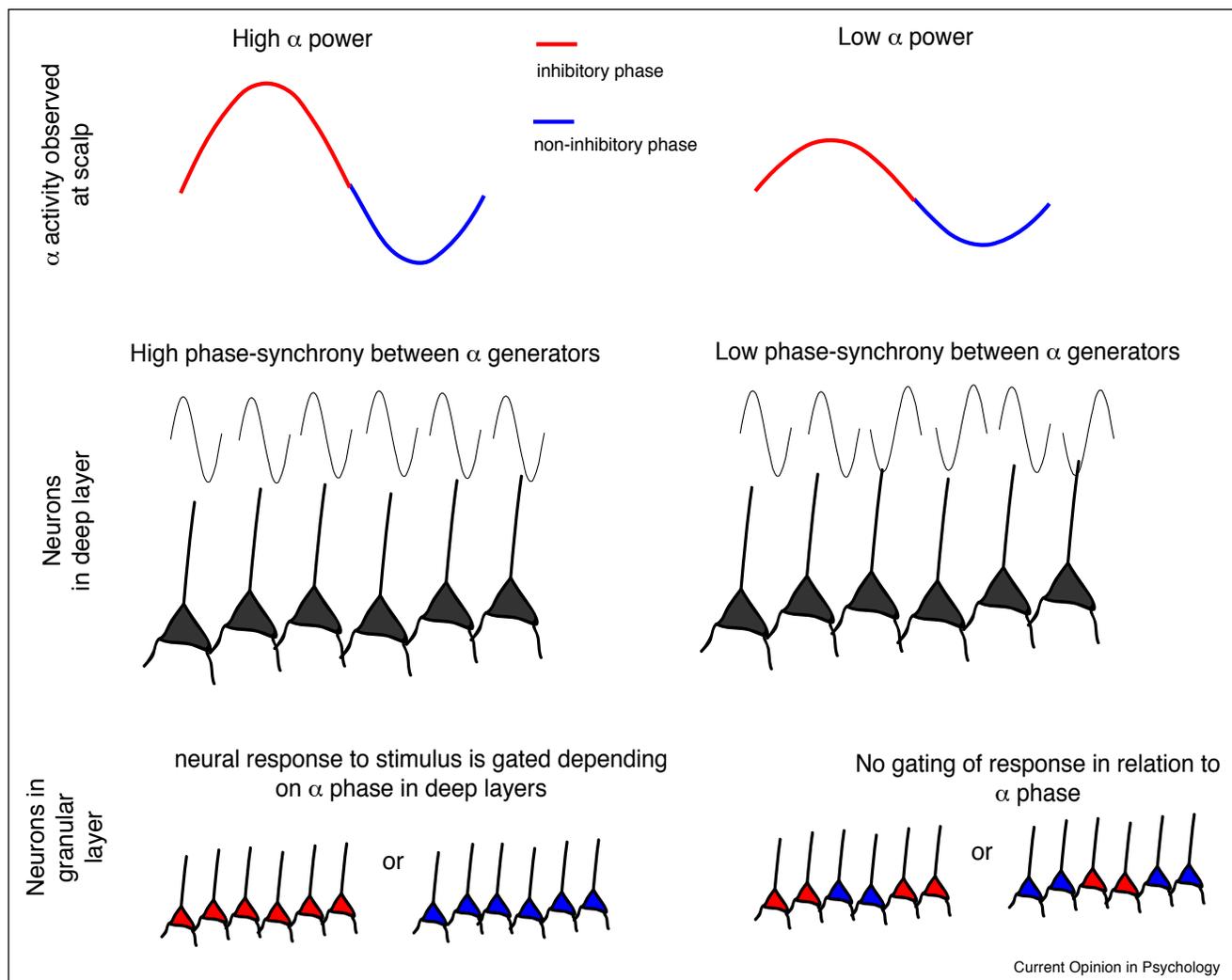
A small increase in amplitude **(a)** or reduction in latency **(b)** of an ERP caused an increase in ITPC around target presentation. The left panels show the grand average ERP of 20 simulated subjects. The right panels show the accompanying grand average of the difference in ITPC between the two ERP conditions (reproduced from Ref. [41]).

drop in oscillatory amplitude within a frequency band, sometimes referred to as an event-related desynchronization (ERD). We speculate that in cases where alpha power is low at the scalp, neurons in deep and superficial layers may still be producing alpha pulses, but these are not synchronized across large ensembles of neurons, which means that at any given time, there may be neurons in the granular layer that are in an 'inhibited state' while others will be in a 'disinhibited state'. Here, suppression of processing cannot take place since the inhibitory state is not uniform or complete across the neuronal population. In contrast, high alpha power at the scalp reflects greater synchronization in the activity of alpha generating neurons in the deep and superficial layers. This would have the effect of inhibiting granular layer neurons in a cyclical manner, limiting the duty cycle of processing, but allowing for rudimentary sequencing and parcellation of the incoming sensory input.

Furthermore, we propose that the absolute baseline level of alpha power in a given sensory region reflects the default allocation of neural resources earmarked to that region for processing. Any changes in alpha power in that region due to task demands reflect not necessarily inhibition, but the redistribution of resources to optimize task performance [54]. This redistribution of resources could mean recruitment of more neurons for processing, functional inhibition of task-irrelevant neurons, or an increase in the excitability threshold of task-relevant neurons.

One caveat to this overly simplified framework, a matter left open in the literature, is how the neurons generating alpha activity exert inhibition. It could be that the alpha oscillations are a consequence of a GABAergic inhibitory feedback paced by neocortical or thalamic rhythm generators [55,56]. But how precisely this would fit with the

Figure 5



A simple model accounting for the relationship between both alpha power and phase (detected at the scalp) to stimulus processing. Alpha activity detected at the scalp is likely due to the summation of synchronized post-synaptic potentials in deep and superficial layers. It should be noted that the number of neurons generating alpha activity is not a factor in the power of alpha activity at the scalp, but rather their synchronization is. The activity of neurons in the granular layer is silenced in a phasic manner at the time of the 'inhibitory alpha phase'. High alpha power at the scalp would mean feedback from the deep or superficial layers would be homogenous in its modulation of excitability in the granular layer, allowing for the sequencing, parsing, or gating of stimulus processing in this layer. In contrast, low alpha power at the scalp would mean the alpha-generating neurons are not synchronized in their phasic silencing of stimulus processing in the granular layer. Here, a sufficient gating of processing cannot take place since the inhibition is not unanimous.

observation that alpha activity has been observed across layers in laminar recordings [48] remains to be elucidated.

Returning to the quote that opened this review: What is alpha activity? Well, simply put, it is the predominant rhythm over visual cortex, visible to the naked eye with no preprocessing steps. But what is alpha activity? We speculate it to be phasic bouts of inhibition which serve to silence parts of the cortex, allowing for the parcellation of information processing, as well as reallocation of neuronal resources.

How is it generated, and what are the mechanisms by which it carries out the functions we have discussed? These questions remain to be answered. For now, all we can really say is that alpha activity can be likened to a fountain . . . and not.

#### Conflict of interest statement

Nothing declared.

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

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This study used MEG to not only investigate the influence of alpha activity on absolute threshold stimuli, but also localized the source of this alpha to be in the parieto-occipital sulcus. Interestingly they also looked at the relationship between reaction times and alpha power, and found no such relationship, which they interpreted to mean the observed effect was not due to changes in vigilance, but rather the inhibition of the visual stream.
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These studies looking at the pre-stimulus influence of alpha on visual perception are a conceptual leap to the previous studies on the topic, since rather than look at hits (i.e. the detection of the stimulus, when it was actually presented) versus misses (i.e. the failure to perceive a stimulus when it was actually presented) they focused on "false alarms" (i.e. reporting the presence of a visual stimulus, when one was not actually presented).
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