Alpha Oscillations in Resisting Distraction

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Highlights

- We review the studies for and against alpha oscillations reflecting suppression of anticipated distractors
- We have identified some of the methodological differences in experimental designs explaining the diverging results on alpha oscillations and distractor inhibition.
- Beyond gain reduction in early visual regions, parietal alpha oscillations may implement gating or stabilization of attentional focus.

- Alpha oscillations generated in the ventral attention network may reflect the resistance to attentional capture by salient events.
- We propose new directions for research to identify the specific task contexts required for explaining necessary to clarify the mechanistic role of alpha oscillations.

Abstract

The role of alpha oscillations (8-13Hz) in suppressing distractors has been extensively debated. Some studies suggest that alpha oscillations support distractor suppression by increasing in regions processing anticipated distractors. However, other studies did not reproduce this effect. We identify the methodological differences in experimental designs that may explain these discrepancies. Another debate centers on the mechanistic role of alpha oscillations. While we and others have proposed alpha oscillations implementing a gain reduction in early visual regions when e.g. target load or distractor interference are high, we suggest that parietal alpha oscillations support gating or stabilization of the attentional focus and alpha in ventral attention network implement resistance to distraction. We will outline future studies needed to identify the task contexts required to uncover the precise mechanistic role of alpha oscillations.

Alpha oscillations: from idling to functional inhibition

Alpha oscillations (8-13 Hz; see box 1) were discovered in 1924 by Hans Berger and were for decades thought to reflect a state of rest. However, in the 2000s, it was established that alpha oscillations can remain strong during working memory maintenance and even increase with memory load [1,2]. These findings prompted a paradigm shift in our understanding of alpha oscillations as the power increase was interpreted to reflect functional inhibition of brain areas processing distractors that could interfere with working memory maintenance. The inhibition hypothesis prompted a lot of excitement in the field as it suggested that alpha oscillations played an active role in cognitive tasks. The inhibitory role of alpha oscillations was further investigated in spatial attention tasks in which targets and distractors were manipulated. More recently, the specific role of alpha oscillations in functional inhibition has been intensively discussed [3–9]. One core issue of debate is whether alpha oscillations under top-down control can increase in order to suppress anticipated visual distractors. A second core issue is whether the increase occurs in early visual regions thereby reducing the gain of the visual input.

These debates have prompted us to identify (1) the task context determining when and how alpha oscillations serve to suppress distractors and (2) alternatives to gain control mechanisms in early visual regions by which alpha can reduce interferences from distractors. The role of alpha activity in distractor suppression might be more complex than initially proposed but we believe that it remains a strong candidate for controlling the information flow in complex environments through direct distractor suppression in early brain regions, gating mechanism or stabilization of the attentional focus in parietal cortex or through resistance to attention capture by salient events in the ventral attention network.

Can alpha oscillations serve to suppress anticipated distractors?

A large body of literature shows that the magnitude (and phase) of spontaneous prestimulus alpha oscillations influence visual processing as revealed by stimulus detection measures and event-related potentials (e.g. [10–14]). It has therefore been suggested that alpha power decreases would be associated with increases in sensory excitability and that alpha power increases would result in decreases of sensory excitability [15]. These results are in line with the alpha-inhibition hypothesis [16–19]; more specifically, an increase in alpha amplitude would be associated with stronger pulses of inhibition. These findings are also consistent with the idea that the magnitude of alpha oscillations is inversely related to gain in early sensory regions.

A related question is the mechanism controlling the magnitude of the alpha oscillations. Are they under direct top-down control to optimize the processing of task-relevant information while diminishing the interference from distractors in attention or working memory tasks? Attention studies in different sensory modalities, have reported an anticipatory decrease of alpha amplitude in areas associated with the processing of attended locations and/or features (e.g. [20–40]) which often predict performances (e.g. [20]). It is the relationship between top-down controlled alpha power increases in relation to the suppression of distractors that remains debated (see Table).

Support for alpha oscillations promoting distractor suppression through gain modulation

If alpha oscillations are related to distractor suppression through gain modulation, several predictions can be made. First, an increase of alpha power should be observed in anticipation of distractors. Second, this increase should be observed over regions associated with distractor processing, i.e. early sensory or feature-specific areas, and predictive of performances. Finally, if alpha oscillations support distractors suppression through gain modulation, the effect should be observed as a decrease in neuronal excitability in sensory regions, e.g. by a reduction in neuronal firing, the BOLD signal, event-related and frequency-tagged responses.

Several studies have observed alpha power increases relative to preceding baseline interval in areas related to unattended locations and features in visual attention tasks ([3,5,20,24,27,28,33,41–51]; see Figure 1 for examples of paradigms used). In spatial somatosensory and auditory tasks, some studies have also reported an alpha power increase (compared to baseline) over somatosensory and higher-order areas contralateral to the distractors (i.e. in the hemisphere processing the distractor; e.g. [39,52–55]). Finally, alpha power increases have also been reported in task-irrelevant areas in both feature and cross-modal attention tasks [40,56–60] as well as during working memory maintenance (see Figure 1A) [46,61–63]. In line with a role for alpha power increases in relation to efficient distractor suppression, several of these studies showed that stronger alpha power was related to better performances, e.g. faster reaction times reflecting a weaker interference of the distractor on behavior (e.g. [45] in a retro-cue task;

[39,43,46,53,56,58,61,62]). As we will discuss later, in some of these studies the alpha increase might have been driven by the perceptual load of the target or task difficulty (see Figure 1B), rather than by distractor anticipation per se.

In line with alpha oscillations implementing gain modulation, several studies have reported modulation of alpha oscillations specifically in sensory areas. For instance, a depression in alpha power contralateral to the attended hemifield was observed in V1/V2 in the cue-target interval in an attention task ([48]; see Figure 1B) and it was accompanied by a relative increase in ipsi-lateral alpha power in V1/V2. The source of the alpha power increase contralateral to distracting faces in a covert attention task was found just outside the calcarine sulcus extending into the fusiform face area during stimulus presentation [43]. Simultaneous fMRI and electroencephalography (EEG) recordings[42] showed that increases in occipital alpha power contralateral to the distractor were negatively correlated with the BOLD signal in V1 using an attention discrimination task. Alpha increases have also been found in somatosensory areas. For example, the alpha power increase observed contralateral to the somatosensory distractor was located around the primary somatosensory cortex [39]. Some studies have also reported potential gain modulation in regions beyond the sensory areas, particularly when the processing of the target and distractor share neural substrates in early sensory regions. In a feature-attention task involving coloured moving dots, an increase in alpha power was reported in feature-specific areas associated with motion and colour in the respective dorsal and ventral areas ([59] see also [64]). In a Sternberg-like task using letters as distractors, a distractor-related alpha power increase was observed in the occipital and the left temporal cortex around the visual word form area [61,65].

The last prediction is that alpha power increases should be associated with a decrease in neuronal excitability. A few studies found an inverse relationship between alpha power and indexes of excitability such as spiking, high gamma (80-120Hz) or stimulus-induced gamma (60-80Hz) during rest, attention and working memory tasks in early sensory regions and beyond [66–71]. In addition, pre-stimulus alpha power negatively relates to the C1 evoked component in the visual cortex which is thought to be generated by the thalamus input to V1 [10,11]. Alpha oscillations have also been shown to be negatively correlated with BOLD signals over sensory regions in working memory and attention fMRI studies (e.g. [42,72–74]).

Null results relating alpha oscillations to distractor suppression

Some groups have questioned the role of alpha oscillations in suppressing distracting information [4]. These concerns were based on studies that did not find an alpha power increase in the presence or anticipation of distractors [21,21–23,26,30–35,75]. When cuing the distractor position, an EEG study did not observe a clear alpha increase contralateral to the anticipated distractor [6]. In addition, several studies did not find a modulation with increasing distractor strengths in several attention and working memory tasks [39,45,76,77].

Furthermore, four studies tested the link between alpha oscillations and neuronal excitability measured by frequency tagging using EEG or MEG ([3,5,43,50]; see Figure 1B). Challenging the idea that alpha oscillations implement gain modulation to suppress distractors in early sensory areas, they reported that the alpha power contralateral to the distractors did not correlate negatively with the frequency-tagged neuronal response when considering single-trial correlations.

In sum, we have reported on the findings for and against alpha oscillations reflecting distractor suppression (summarized in Table 1). Next, we will examine the experimental parameters that might explain the discrepancies in the literature.

Experimental conditions determining when alpha oscillations operate to suppress distraction

We will here examine the tasks and experimental parameters that may determine when alpha oscillations serve to suppress distractors or not.

Paradigms necessitating distractor suppression

When investigating distractor suppression and alpha oscillations, one has to make sure that the experimental design promotes distractor suppression. Indeed, in some of the experiments used, there was not a need for distractor suppression per se. Recent reviews have discussed the experimental details being important for the study of distractors suppression [7,78–80]. According to these reviews and our analysis of the literature, a key parameter promoting the need for anticipatory distractor suppression is related to the target rather than the distractor. Importantly, the perceptual load of the target needs to be high. This is aligned with the perceptual load theory [81] which holds that suppression of unattended distractors is a consequence of an increased perceptual load. A model has been associated with this indirect inhibition or “secondary inhibition” [7] in which neurons representing the distractors are not inhibited directly but via a competitive mechanism following the top-down controlled facilitation of target processing. Consistent with this perspective, the need for distractor suppression is promoted if its location is predictable by knowing the cued target’s position [7,82], e.g. when the target is expected in the left lower hemifield, this may implicitly predict the distractor in the right lower hemifield. However, two recent studies which directly cue the distractor’s position, do report an alpha increase related to anticipated distractors ([49,51]; see below). From these considerations, we conclude that alpha oscillations, if related to functional inhibition, should be observed when the location of the distractor, as well as the target, is predictable and the perceptual target load is high. Indeed, higher anticipatory alpha power contralateral to the distractor was observed in the high target load condition ([43] note there was also a more modest increase in alpha power associated with the distractor load). The study also reported a behavioral benefit of the alpha power increase in terms of distractor suppression when the target load was low (see [83] for full discussion). In sum, perceptual load could be an important precondition for distractor-related alpha power increases observed over parieto-occipital areas (see Figure 2). Some of the reported discrepancies in regard to distractor related alpha power are therefore likely explained by differences in demands associated with the target.

Alpha power increases have, however, been shown to be modulated solely by the presence of distractors compared to conditions without distractors [39,45,76,77]. The sole presence of distractors can lead to an increase in alpha power compared to an experiment without distractors ([39,40]).

Distractor suppression has also been investigated in statistical learning paradigms which specifically hinge on altering environmental statistics, such as modifying the frequency of distractors at similar locations or their features (e.g. [6,84–87]). It has been proposed that the distractor suppression observed in these statistical learning paradigms would be related to implicitly or explicitly learned expectations (see figure 2), i.e. inhibition of stimuli representing the predictable distractors via hierarchical feedback processes to sensory regions [7,79]. This is partly related to predictive coding models in which statistical regularities of the environment are used to limit the processing of the less informative stimuli [88–90]. One study using a statistical learning paradigm specifically studied the effect of repeated distractor positions in visual search tasks and reported an robust alpha power increase [87]. However, other studies did not report alpha increases in statistical learning paradigms [9,86,91]. It has been suggested that suppression mechanisms associated with statistical learning may occur via synaptic changes rather changes in oscillatory dynamics (e.g. [79]). However, the absence of alpha power increases in some of the statistical learning paradigms could also be explained by the load of the target being low (see above), a low level of competition between targets and distractors or other methodological aspects detailed below. In short, it remains to be further investigated which factors result in a robust distractor-related alpha power increase in statistical learning paradigms.

One aspect that has not been thoroughly explored is the effect of the distractors competing with the targets (see also [80]). Such competition might result in decision interference, i.e. the target features to process might compete with salient but irrelevant distractor features (e.g. as in the Stroop tasks). The competition could also occur at the perceptual level when targets and distractors have a high degree of similarity and/or spatial proximity. As we know that the receptive fields increase in size along the visual hierarchy, it is possible that a distractor and target are processed by different populations of neurons in early regions but by partially overlapping populations in higher-order regions [92,93]. Without competition, anticipatory inhibition of distractor processing may be of less importance. For instance, in two studies mentioned above [6,91], the absence of a distractor-related alpha power increase, might be explained by low interference from the distractors. On the contrary, in a study which did show a distractor-related alpha power increase [43], faces were used as stimuli and they might compete in the fusiform face area. Another study [49], which reported an alpha power increase in a distractor-cue design, also used tasks with high perceptual/decision competition (oriented lines at multiple locations; [51]). We suggest that one important factor that may increase the need for alpha oscillations to suppress distractors is the degree of competition between target and distractors.

Optimizing the detection of target and distractor related alpha modulations

We will here discuss which other parameters may facilitate the detection of alpha modulation. Due to the relatively low spatial resolution of EEG and MEG, it is important to ensure spatially separate neuronal sources processing distractors and targets (see [48]). For instance, in two studies mentioned above [6,9], one of the possible target positions was in the same hemifield as the distractor possibly making it difficult to isolate the alpha power associated with the distractor (but see [91]). Another study which reported a distractor-related alpha increase in a statistical learning paradigm, separated distractors and target positions as they could appear on the vertical center line or in the left or right hemifield [87] (see also [53]). We advise using designs, where the dissociation between the neuronal sources processing the targets and the distractors can be isolated and thereby related to the alpha power modulation for instance by presenting the stimuli in different hemifields (see [47]). Another study [49] applied an analysis based on the use of an inverted encoding model.

The studies that did not report a link between alpha power increases and gain modulation were based on the use of frequency tagging for measuring neuronal excitability while the studies relating alpha oscillations and gain modulation used spike rates, gamma power, early event-related potentials (e.g. C1) or BOLD signal. It is possible that when using frequency tagging, even at high frequency, this could alter the detection of alpha oscillations in early regions as discussed by [15]. For instance, each flicker from the tagging might produce an unintended decrease in alpha power. This effect might explain the absence of correlation between alpha power modulations and frequency tagging in early visual cortex increase [3,5,43,50]. This could also explain the absence of alpha power decreases contralateral to the attended side in some of these studies while it has been observed in many more classical studies (see above). Even in [43], the alpha increase contralateral to distractors was observed in occipital and temporal areas (including the fusiform) but not in the early visual regions in which frequency tagging modulation was observed. The hypothesis of the effect of frequency-tagging could be tested by localizing the alpha sources in the presence and absence of frequency tagging. However, the optimal way to determine whether alpha oscillations in sensory regions are associated with gain modulation is to use animal recordings [94] which allow to investigate more precisely the link between alpha power and simultaneous excitability or distractor-related response. As such, it might be wise to complement the studies on frequency tagging with other approaches for assessing neuronal excitability. This could involve quantifying the gamma band activity or the BOLD signal in early visual regions.

Another potential issue is that oscillations at different alpha frequencies are involved and they might interfere (e.g. [95,96]). In a working memory study [96], slow alpha oscillations in the 8-10Hz range were associated with distractor suppression while faster 10-12Hz alpha oscillations were associated with working-memory and feature-related processing. It might therefore be important to study alpha oscillations in different frequency bands using tools which allow for optimizing the frequency resolution [97].

Another factor pertains to using jittered versus constant interstimulus intervals (ISIs). When the ISI is constant, alpha phase adjustment has been observed, i.e. the alpha phase was adjusted differently to the onset of anticipated targets or distractors [38,61,98]. Possibly, when the timing is predictable, inhibition can rely on alpha phase adjustments and less so on power modulations. However, the existence of phase adjustment in anticipation of distractors is debated with three studies reporting an effect [38,61,98] (see also [99]) and one which did not [100]. The use of alpha phase adjustment as an optimal brain mechanism for distractor suppression in designs with predictive timing remains to be further explored. Nevertheless, we note that the timing of the distractor was predictable in several experiments which did not report distractor-related alpha power modulations [e.g. 6,72] and we speculate that it could have been associated with an alpha phase adjustment. Experiments comparing jittered versus constant ISI could be used to test this hypothesis. Meanwhile, the use of jittered ISIs would be recommended when investigating alpha oscillations in relation to distractor inhibition.

A critical methodological and theoretical aspect involves oculomotor activity. Recent studies have demonstrated a complex relationship between microsaccades and alpha modulation [101,102]. It was shown that high microsaccadic activity was associated with low alpha power, while low activity was related to high alpha power. Furthermore, it has been demonstrated that the phase of alpha oscillations can predict saccade onset [103,104]. Given these links, it is essential to record eye-tracking data during EEG and MEG experiments to disentangle cognitive and oculomotor influences on alpha oscillations.

Yet an important issue to consider is the relationship between alpha oscillations and aperiodic activity which is also thought to reflect the ratio between excitatory and inhibitory currents [105]. However, most of the studies cited in this review have not considered the aperiodic activity in their analyses. In future work, it would be of great interest to consider how an increase in alpha oscillations relates to the changes in aperiodic activity as reflected in the 1/f slope of the power spectra [106].

It is also crucial to take into account the effect sizes might be lower for distractors as compared to targets (see [80] for a thorough discussion of this issue). Detecting alpha modulations related to distractor suppression might result in longer paradigms to ensure sufficient distractor trials

Extrastriate mechanisms supporting resistance to distractor interference

In this section, we discuss the alternative mechanisms to gain control in sensory areas that may be involved in implementing resistance to distractor interference.

First, gain control may be implemented in the thalamus. An alpha increase could possibly occur there but may not be detected using EEG/MEG [107]. Several fMRI studies have indeed shown that attention modulations can be observed in the lateral geniculate (LGN) using fMRI [108]). Animal recordings could uncover the possibility of alpha oscillations implementing gain control at the thalamic level.

In addition, many studies have shown attention-related modulations in the parietal cortex. This parietal origin might explain the lack of correlation between alpha power and frequency tagging in some studies [3,5,50]. In addition, an EEG study found that parietal alpha power decreased when attention was divided across modalities or hemifields [41]. This may reflect a gating mechanism beyond early visual regions [50], or it could indicate that alpha power increase during sustained attention paradigms are associated with the stabilization of attentional focus via inhibition of the ipsilateral parietal cortex (refer to [20] for a brief post-cue increase that may also suggest a role for alpha oscillations in shifting attention). In line with this idea, tACS studies have shown that 10 Hz stimulation over the left parietal cortex induces a leftward bias in reaction times, i.e. a decrease of RT to targets presented in the left-hemifield[109]. In addition, alpha oscillations, likely of parietal origin, often increase ipsilaterally to the target in the absence of distractors (e.g. [23]), suggesting it could play a role in stabilizing attention.

As an alternative action of alpha oscillations, resistance to distractors could be implemented via changes in the inter-regional phase difference in the alpha-band leading to decreased communication between higher-order and lower-order regions associated with the processing of the distractor [110–114] . The local interactions between alpha and gamma oscillations could further promote of block the information flow [113,114]. Therefore, not only alpha power but also inter-region connectivity reflected by alpha phase-synchronization should be studied. In line with this idea, recent studies suggested that the direction of *travelling alpha waves* could reflect the feed-forward and feedback flow of information [115–117]. In a recent attention study [116], propagation from frontal to occipital areas increased contralateral to the unattended hemifield (where distractors could occur) and was correlated with frontal and occipital alpha power in line with a role in distractor suppression. However, the functional role of the forward-travelling alpha waves during visual stimulation needs to be further investigated [118] (see *Outstanding Questions*).

Finally, it has been suggested that the inhibition of the so-called ventral attention network (VAN) would prevent the capture of attention by competitive distractors ([119]; see Figure 2) and may be supported by an increase in the alpha/beta band power [120]. A study has reported that alpha/beta power increases in the VAN results in lower distractor interference [120]. The involvement of this mostly right lateralized network, independently of distractor position, cannot be captured by contrasting between left versus right attention conditions. We suggest further investigations of alpha-beta oscillations in the VAN and how they relate to performances. Such a mechanism may be sufficient to prevent interference from distractors in some attention tasks.

Concluding remarks

The link between alpha oscillations and distractor suppression has been challenged which then has prompted a revision of the general framework. Given the diverging findings on the role of alpha oscillations for distractor suppression, we have reviewed the literature to identify the key experimental parameters that may explain the discrepancies. We discussed that it is crucial to develop designs in which distractor suppression is observed behaviorally, e.g. block design with high frequency of distractor or designs using targets with high load. Recent studies suggest that alpha modulation is driven by the properties of the target, more so than the saliency of the distractor. Finally, we propose that the degree of interference and competition between the target and distractor are important factors. When there is little interference between targets and distractors, modulations of alpha power in parietal or ventral attention networks may be sufficient to prevent distraction. Analysis of both occipital as well as dorsal and ventral parietal alpha activity will be important for uncovering how the brain deals with distractors in different contexts (Figure 2). We believe that the debate regarding the role of alpha oscillations in distractor suppression presents a remarkable opportunity to better define which neuronal mechanisms supported by alpha oscillations are at play to control the flow of information when operating in complex environments (see box 2 and Outstanding Questions).

Outstanding questions

How are alpha oscillations top-down controlled? One possibility is that the frontal-eye field exercises the control via the superior longitudinal fasciculus but a subcortical pathway including the pulvinar might also be a play. A few studies have reported a role of the frontal eye field, the dorsolateral prefrontal cortex and the pulvinar in controlling alpha oscillations. Still, their specific roles need to be further elucidated.

What are the specific roles of occipital versus parietal alpha oscillations? Understanding the specific functions of alpha oscillations in these regions could clarify their relationship to different signal detection theory parameters, such as criterion and sensitivity.

Does the brain rely on alpha oscillations for distractor inhibition in more ecological settings requiring fast distractor suppression? In the cases of natural viewing, in which people typically saccade 3-4 time per second, inhibitory mechanisms working on fast time scales must be considered as for instance beta (12-25Hz) bursts (see box 2) or fast synaptic actions. Another possibility is that saccades are locked to the phase of ongoing alpha oscillations to deliver pulses on inhibition aligned with saccades.

Are alpha oscillations involved in reactive suppression? While a lot of work has focused on anticipatory or retro-cue-induced alpha activity, we need to understand the role of alpha oscillations during reactive suppression, i.e. in response to, rather than in anticipation of, distractors. This is in line with the idea that in ecological settings, it is not necessarily possible to proactively inhibit the processing of distracting information.

Box1: The physiological origin of the alpha oscillations

While the functional role of alpha oscillations has been extensively investigated, the underlying neuronal mechanisms remain elusive. Many studies suggest that beyond cortico-cortical interaction, also cortico-thalamic interactions are important for the generation of alpha. A neocortical generator was first reported using intracranial laminar recordings in the visual cortex of dogs [121] where a phase-reversal of the alpha oscillations was observed in deep cortical layers. This suggests the involvement of layers 5 and 6 pyramidal neurons in generating the alpha rhythm. Later, laminar recordings in macaques have revealed alpha generators across all layers of the cortex ([122]), albeit some would claim that the dominant generators are in the deep layers [67,71]. In addition, some studies have reported distinct roles of the different thalamic nuclei in controlling the neocortical alpha rhythms. For example, damage to the LGN has been linked to a reduction of the amplitude of alpha oscillations [123]. Some neurons, the high threshold neurons bursting cells, in the LGN can produce spiking activity at alpha frequency [107,124]. Interestingly, interneurons play a crucial role in generating this phasic activity in the thalamus. Importantly, the phase of alpha oscillations in the visual cortex has been associated with neuronal spiking in the LGN [125], a finding complemented by reports on strong coherence between the LGN and neocortex [125,126] . Beyond the role of the LGN, several studies have highlighted the involvement of the thalamic pulvinar nucleus in controlling cortical alpha rhythms [127]). Recent recordings in ferrets have revealed that parietal cortex was controlling the alpha rhythm in the occipital cortex and the pulvinar. This study further showed that fast-spiking interneurons were crucial for generating the alpha rhythm in parietal cortex [128]. Unravelling the mechanism behind alpha generation is crucial, in particular as a recent study has shown that this rhythm is widely distributed across the cortex [129]. In summary, while further work is needed, it is clear that alpha oscillations do not have a single origin but are the result of complex interactions involving various brain regions including different subcortical areas and neocortical lamina.

Box2: The functional relationship between alpha and beta oscillations

This review focuses on alpha oscillations which are considered a leading candidate for functional inhibition in attention tasks. However, beta activity also warrants a thorough investigation, especially given its occurrence in short bursts). Traditionally associated with motor inhibition, beta activity has recently been implicated in other inhibitory roles, such as executive control of working memory or in visual discrimination involving crowding (see [131] for a comprehensive review). As noted in the *Outstanding Questions*, the timing and duration of inhibition may be critical in determining whether alpha or beta activity predominates. These two reflections of functional inhibition may also be linked to distinct cognitive processes. For example, a recent working memory study involving distractors [63] demonstrated that the rate of posterior alpha bursts increased during distractor presentation. In contrast, beta bursts increased following distractor presentation, and this effect was interpreted to regulate the transition from sensory processing to working memory retention. Interestingly, the activity observed in the ventral attention network (VAN) encompassed both alpha and beta frequencies [120]. Trial-by-trial analyses and specific designs could shed light on whether these frequencies co-occur or fluctuate over time, offering further insights into their distinct or complementary roles in cognitive processes.

Figure Legends

Figure 1 Examples of paradigms used for testing the link between alpha power and distractor suppression.

A. Working memory tasks involve presenting a set of items that are later compared to a probe. During the retention phase, a distractor may be introduced. These tasks were among the first to challenge the notion of the alpha rhythm as an idling rhythm, as they demonstrated that alpha power increases with the number of items held in working memory during retention[1]. Importantly, the alpha power during the retention interval was found to predict the ability to suppress distractors [61,65].

B. A typical paradigm used to explore the functional role of alpha oscillations in spatial attention tasks involves participants being cued to detect targets in either the left or right hemifield. Items in the unattended hemifield are considered distractors. Related paradigms have been applied in the somatosensory and auditory domains[39,49,62]. However, this class of paradigms has yielded mixed results regarding whether alpha oscillations serve to inhibit distractors Several adaptions of this paradigm have since been implemented. For example, frequency tagging of both the target and distractor has been used to test the link between alpha power and neuronal excitability [3,44]. These studies did not find a correlation between the frequency tagging signal and alpha power, raising questions about whether alpha oscillations function by modulating gain control in the early visual cortex. This null finding has led to the hypothesis that alpha oscillations may instead regulate gating or stabilization of the attentional focus in the posterior parietal cortex. Another significant recent development involves manipulating both the perceptual load of the target and the saliency of the distractors [43]. MEG findings suggest that the perceptual load of the cued target is a strong predictor of distractor-related alpha power.

Figure 2. **The functional role and control of alpha oscillations.** Various tasks have converged on the notion that the feed-forward sensory flow is modulated by alpha inhibition in early visual regions by gain control. Alpha oscillations often measured in the posterior parietal cortex might reflect gating mechanisms [50] or stabilization of the attention focus. The possibility of the implementation of gain control by alpha oscillations in thalamus LGN needs to be explored further. Alpha oscillations in the ventral attention network might further reflect the resistance to attention capture by salient events and include the ventral parietal cortex, the right temporo-parietal junction and the ventral prefrontal cortex [120]. Top-down control of alpha oscillations is likely implemented in the dorsal attention network with the frontal eye-field playing a prominent role; however, the pulvinar has also been shown to partake in the control [70,127].

Table. **Key hypotheses and lists of references in favor or against each of them**

* Studies in which only a subgroup of participants exhibited alpha increase during the task (e.g. participants with high baseline alpha in Rhis et al. 2009)

** alpha power during, not in anticipation of, distractor processing was related to performances in this study.

*** These studies did show an increase of alpha with the presence of distractors, but this increase was not further modulated by distractor strength.

**** In this study, a link between alpha oscillations and the evoked potentials Pd has been shown. This result is relevant even though the Pd is thought to be a marker of distractor suppression rather than to directly excitability

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Declaration of interests

The authors declare no competing interests.

References

1. Jensen, O. *et al.* (2002) Oscillations in the alpha band (9-12 Hz) increase with memory load during retention in a short-term memory task. *Cereb Cortex* 12, 877–82
2. Klimesch, W. *et al.* (1999) “Paradoxical” alpha synchronization in a memory task. *Brain Res. Cogn. Brain Res.* 7, 493–501
3. Antonov, P.A. *et al.* (2020) Too little, too late, and in the wrong place: Alpha band activity does not reflect an active mechanism of selective attention. *NeuroImage* 219, 117006
4. Foster, J.J. and Awh, E. (2019) The role of alpha oscillations in spatial attention: limited evidence for a suppression account. *Curr. Opin. Psychol.* 29, 34–40
5. Gundlach, C. *et al.* (2020) Spatial Attentional Selection Modulates Early Visual Stimulus Processing Independently of Visual Alpha Modulations. *Cereb. Cortex* 30, 3686–3703
6. Noonan, M.P. *et al.* (2016) Distinct Mechanisms for Distractor Suppression and Target Facilitation. *J. Neurosci. Off. J. Soc. Neurosci.* 36, 1797–1807
7. Noonan, M.P. *et al.* (2018) Selective inhibition of distracting input. *Behav. Brain Res.* 355, 36–47
8. Slagter, H.A. *et al.* (2015) Facilitation and inhibition in attention: Functional dissociation of pre-stimulus alpha activity, P1, and N1 components. *Neuroimage* DOI: 10.1016/j.neuroimage.2015.09.058
9. van Moorselaar, D. *et al.* (2021) Neural mechanisms underlying distractor inhibition on the basis of feature and/or spatial expectations. *Cortex* 137, 232–250
10. Iemi, L. *et al.* (2019) Multiple mechanisms link prestimulus neural oscillations to sensory responses. *eLife* 8, e43620
11. Dou, W. *et al.* (2021) Prestimulus Alpha Phase Gates Afferent Visual Cortex Responses. *J. Vis.* 21, 2075
12. VanRullen, R. (2016) Perceptual Cycles. *Trends Cogn Sci* 20, 723–35
13. Zazio, A. *et al.* (2022) Pre-stimulus alpha-band power and phase fluctuations originate from different neural sources and exert distinct impact on stimulus-evoked responses. *Eur. J. Neurosci.* 55, 3178–3190
14. Fakche, C. *et al.* (2022) α Phase-Amplitude Tradeoffs Predict Visual Perception. *eNeuro* 9
15. Samaha, J. *et al.* (2020) Spontaneous Brain Oscillations and Perceptual Decision-Making. *Trends Cogn. Sci.* 24, 639–653

16. Foxe, J.J. and Snyder, A.C. (2011) The Role of Alpha-Band Brain Oscillations as a Sensory Suppression Mechanism during Selective Attention. *Front Psychol* 2, 154
17. Jensen, O. and Mazaheri, A. (2010) Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front Hum Neurosci* 4, 186
18. Klimesch, W. *et al.* (2007) EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res Rev* 53, 63–88
19. Mathewson, K.E. *et al.* (2011) Pulsed out of awareness: EEG alpha oscillations represent a pulsed-inhibition of ongoing cortical processing. *Front Psychol* 2, 99
20. Capilla, A. *et al.* (2014) Dissociated α-Band Modulations in the Dorsal and Ventral Visual Pathways in Visuospatial Attention and Perception. *Cereb. Cortex* 24, 550–561
21. Dombrowe, I. and Hilgetag, C.C. (2014) Occipitoparietal alpha-band responses to the graded allocation of top-down spatial attention. *J. Neurophysiol.* 112, 1307–1316
22. Gould, I.C. *et al.* (2011) Indexing the graded allocation of visuospatial attention using anticipatory alpha oscillations. *J. Neurophysiol.* 105, 1318–1326
23. Grent-'t-Jong, T. *et al.* (2011) Differential functional roles of slow-wave and oscillatory-α activity in visual sensory cortex during anticipatory visual-spatial attention. *Cereb. Cortex N. Y. N 1991* 21, 2204–2216
24. Ikkai, A. *et al.* (2016) Lateralization in Alpha-Band Oscillations Predicts the Locus and Spatial Distribution of Attention. *PLoS ONE* 11
25. Jongen, E.M.M. *et al.* (2006) Varieties of attention in neutral trials: linking RT to ERPs and EEG frequencies. *Psychophysiology* 43, 113–125
26. Kelly, S.P. *et al.* (2009) The strength of anticipatory spatial biasing predicts target discrimination at attended locations: a high-density EEG study. *Eur. J. Neurosci.* 30, 2224–2234
27. Rihs, T.A. *et al.* (2007) Mechanisms of selective inhibition in visual spatial attention are indexed by alpha-band EEG synchronization. *Eur J Neurosci* 25, 603–10
28. Rihs, T.A. *et al.* (2009) A bias for posterior α-band power suppression versus enhancement during shifting versus maintenance of spatial attention. *NeuroImage* 44, 190–199
29. Sauseng, P. *et al.* (2005) A shift of visual spatial attention is selectively associated with human EEG alpha activity. *Eur J Neurosci* 22, 2917–26
30. Thut, G. *et al.* (2006) α-Band Electroencephalographic Activity over Occipital Cortex Indexes Visuospatial Attention Bias and Predicts Visual Target Detection. *J. Neurosci.* 26, 9494–9502
31. Trenner, M.U. *et al.* (2008) What happens in between? Human oscillatory brain activity related to crossmodal spatial cueing. *PloS One* 3, e1467
32. Voytek, B. *et al.* (2017) Preparatory Encoding of the Fine Scale of Human Spatial Attention. *J. Cogn. Neurosci.* 29, 1302–1310
33. Wildegger, T. *et al.* (2017) Preparatory α-band oscillations reflect spatial gating independently of predictions regarding target identity. *J. Neurophysiol.* 117, 1385–1394
34. Worden, M.S. *et al.* (2000) Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *J Neurosci* 20, RC63
35. Wyart, V. and Tallon-Baudry, C. (2008) Neural Dissociation between Visual Awareness and Spatial Attention. *J. Neurosci.* 28, 2667–2679
36. Yamagishi, N. *et al.* (2005) Attentional shifts towards an expected visual target alter the level of alpha-band oscillatory activity in the human calcarine cortex. *Cogn. Brain Res.* 25, 799–809
37. Yamagishi, N. *et al.* (2008) Attentional changes in pre-stimulus oscillatory activity within early visual cortex are predictive of human visual performance. *Brain Res.* 1197, 115–122
38. Solis-Vivanco, R. *et al.* (2018) Top-Down Control of Alpha Phase Adjustment in Anticipation of Temporally Predictable Visual Stimuli. *J Cogn Neurosci* 30, 1157–1169

39. Haegens, S. *et al.* (2012) Somatosensory anticipatory alpha activity increases to suppress distracting input. *J Cogn Neurosci* 24, 677–85
40. Diepen, R.M. van and Mazaheri, A. (2017) Cross-sensory modulation of alpha oscillatory activity: suppression, idling, and default resource allocation. *Eur. J. Neurosci.* 45, 1431–1438
41. Frey, H.-P. *et al.* (2014) Modulation of early cortical processing during divided attention to non-contiguous locations. *Eur. J. Neurosci.* 39, 1499–1507
42. Green, J.J. *et al.* (2017) Cortical and Subcortical Coordination of Visual Spatial Attention Revealed by Simultaneous EEG–fMRI Recording. *J. Neurosci.* 37, 7803–7810
43. Gutteling, T.P. *et al.* (2022) Alpha oscillations reflect suppression of distractors with increased perceptual load. *Prog. Neurobiol.* 214, 102285
44. Kelly, S.P. *et al.* (2006) Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *J Neurophysiol* 95, 3844–51
45. Rösner, M. *et al.* (2020) The spatial orienting of the focus of attention in working memory makes use of inhibition: Evidence by hemispheric asymmetries in posterior alpha oscillations. *Neuropsychologia* 142, 107442
46. Sauseng, P. *et al.* (2009) Brain oscillatory substrates of visual short-term memory capacity. *Curr Biol* 19, 1846–52
47. Schneider, D. *et al.* (2022) Target enhancement or distractor suppression? Functionally distinct alpha oscillations form the basis of attention. *Eur. J. Neurosci.* 55, 3256–3265
48. Siegel, M. *et al.* (2008) Neuronal Synchronization along the Dorsal Visual Pathway Reflects the Focus of Spatial Attention. *Neuron* 60, 709–719
49. Zhao, C. *et al.* (2023) Suppression of distracting inputs by visual-spatial cues is driven by anticipatory alpha activity. *PLOS Biol.* 21, e3002014
50. Zhigalov, A. and Jensen, O. (2020) Alpha oscillations do not implement gain control in early visual cortex but rather gating in parieto-occipital regions. *Hum. Brain Mapp.* 41, 5176–5186
51. Zoest, W. van *et al.* (2021) Strategic Distractor Suppression Improves Selective Control in Human Vision. *J. Neurosci.* 41, 7120–7135
52. Haegens, S. *et al.* (2011) Top-down controlled alpha band activity in somatosensory areas determines behavioral performance in a discrimination task. *J Neurosci* 31, 5197–204
53. Wöstmann, M. *et al.* (2019) Alpha Oscillations in the Human Brain Implement Distractor Suppression Independent of Target Selection. *J. Neurosci.* 39, 9797–9805
54. Klatt, L.-I. *et al.* (2020) A dual mechanism underlying retroactive shifts of auditory spatial attention: dissociating target- and distractor-related modulations of alpha lateralization. *Sci. Rep.* 10, 13860
55. Wöstmann, M. *et al.* (2017) The Human Neural Alpha Response to Speech is a Proxy of Attentional Control. *Cereb. Cortex* 27, 3307–3317
56. Bollimunta, A. *et al.* (2008) Neuronal mechanisms of cortical alpha oscillations in awake-behaving macaques. *J. Neurosci. Off. J. Soc. Neurosci.* 28, 9976–88
57. Gomez-Ramirez, M. *et al.* (2011) Oscillatory Sensory Selection Mechanisms during Intersensory Attention to Rhythmic Auditory and Visual Inputs: A Human Electrocorticographic Investigation. *J. Neurosci.* 31, 18556–18567
58. Mazaheri, A. *et al.* (2014) Region-specific modulations in oscillatory alpha activity serve to facilitate processing in the visual and auditory modalities. *Neuroimage* 87, 356–62
59. Snyder, A.C. and Foxe, J.J. (2010) Anticipatory attentional suppression of visual features indexed by oscillatory alpha-band power increases: a high-density electrical mapping study. *J Neurosci* 30, 4024–32
60. Bollimunta, A. *et al.* (2011) Neuronal Mechanisms and Attentional Modulation of Corticothalamic Alpha Oscillations. *J. Neurosci.* 31, 4935–4943
61. Bonnefond, M. and Jensen, O. (2012) Alpha oscillations serve to protect working memory maintenance against anticipated distracters. *Curr Biol* 22, 1969–74

62. Payne, L. *et al.* (2013) Attention-modulated alpha-band oscillations protect against intrusion of irrelevant information. *J. Cogn. Neurosci.* 25, 1463–76

63. Liljefors, J. *et al.* (2023) Distinct Functions for Beta and Alpha Bursts in Gating of Human Working MemorybioRxiv, 2023.11.17.566386

64. Jokisch, D. and Jensen, O. (2007) Modulation of gamma and alpha activity during a working memory task engaging the dorsal or ventral stream. *J Neurosci* 27, 3244–51

65. Magosso, E. and Borra, D. (2024) The strength of anticipated distractors shapes EEG alpha and theta oscillations in a Working Memory task. *NeuroImage* DOI: 10.1016/j.neuroimage.2024.120835

66. Bonnefond, M. and Jensen, O. (2015) Gamma Activity Coupled to Alpha Phase as a Mechanism for Top-Down Controlled Gating. *PLOS ONE* 10, e0128667

67. Buffalo, E.A. *et al.* (2011) Laminar differences in gamma and alpha coherence in the ventral stream. *Proc Natl Acad Sci U A* 108, 11262–7

68. Dougherty, K. *et al.* (2015) Ongoing Alpha Activity in V1 Regulates Visually Driven Spiking Responses. *Cereb. Cortex* DOI: 10.1093/cercor/bhv304

69. Haegens, S. *et al.* (2011) α-Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proc. Natl. Acad. Sci.* 108, 19377–19382

70. Popov, T. *et al.* (2017) FEF-Controlled Alpha Delay Activity Precedes Stimulus-Induced Gamma-Band Activity in Visual Cortex. *J Neurosci* 37, 4117–4127

71. Spaak, E. *et al.* (2012) Layer-Specific Entrainment of Gamma-Band Neural Activity by the Alpha Rhythm in Monkey Visual Cortex. *Curr. Biol.* 22, 2313–2318

72. Scheeringa, R. *et al.* (2011) Modulation of visually evoked cortical FMRI responses by phase of ongoing occipital alpha oscillations. *J Neurosci* 31, 3813–20

73. Scheeringa, R. *et al.* (2009) Trial-by-trial coupling between EEG and BOLD identifies networks related to alpha and theta EEG power increases during working memory maintenance. *Neuroimage* 44, 1224–38

74. Zumer, J.M. *et al.* (2014) Occipital alpha activity during stimulus processing gates the information flow to object-selective cortex. *PLoS Biol* 12, e1001965

75. van Moorselaar, D. *et al.* (2020) Neural mechanisms underlying expectation-dependent inhibition of distracting information. *eLife* 9, e61048

76. Poch, C. *et al.* (2018) Suppression of no-longer relevant information in Working Memory: An alpha-power related mechanism? *Biol. Psychol.* 135, 112–116

77. Sghirripa, S. *et al.* (2021) The Role of Alpha Power in the Suppression of Anticipated Distractors During Verbal Working Memory. *Brain Topogr.* 34, 102–109

78. Luck, S.J. *et al.* (2021) Progress toward resolving the attentional capture debate. *Vis. Cogn.* 29, 1–21

79. van Moorselaar, D. and Slagter, H.A. (2020) Inhibition in selective attention. *Ann. N. Y. Acad. Sci.* 1464, 204–221

80. Wöstmann, M. *et al.* (2022) Ten simple rules to study distractor suppression. *Prog. Neurobiol.* 213, 102269

81. Lavie, N. (2005) Distracted and confused?: selective attention under load. *Trends Cogn Sci* 9, 75–82

82. Leber, A.B. *et al.* (2016) Implicitly learned suppression of irrelevant spatial locations. *Psychon. Bull. Rev.* 23, 1873–1881

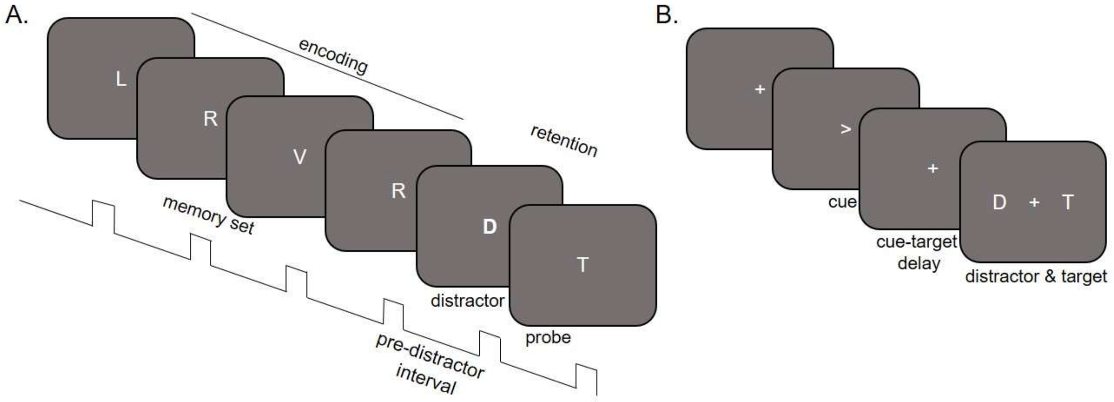
83. Jensen, O. (2024) Distractor inhibition by alpha oscillations is controlled by an indirect mechanism governed by goal-relevant information. *Commun. Psychol.* 2, 1–11

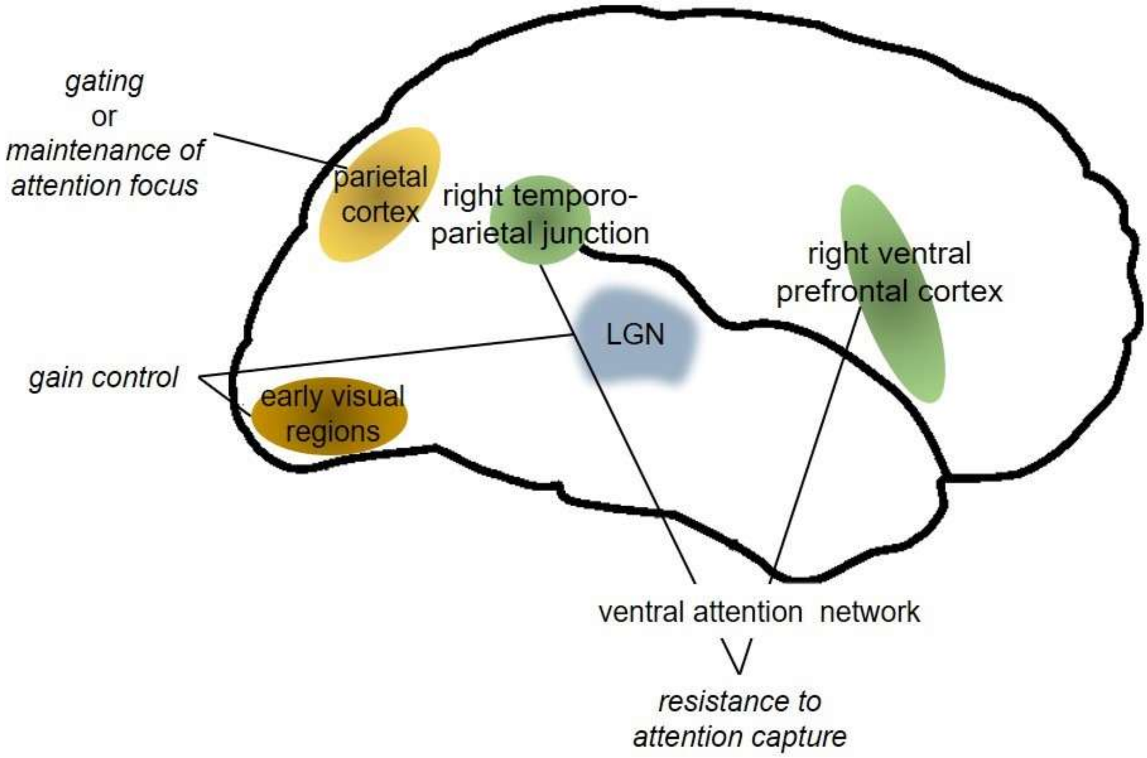
84. Vatterott, D.B. and Vecera, S.P. (2012) Experience-dependent attentional tuning of distractor rejection. *Psychon. Bull. Rev.* 19, 871–878

85. Bogaerts, L. *et al.* (2022) Does it help to expect distraction? Attentional capture is attenuated by high distractor frequency but not by trial-to-trial predictability. *J. Exp. Psychol. Hum. Percept. Perform.* 48, 246–261
86. Ferrante, O. *et al.* (2023) Statistical Learning of Distractor Suppression Downregulates Prestimulus Neural Excitability in Early Visual Cortex. *J. Neurosci.* 43, 2190–2198
87. Wang, B. *et al.* (2019) Anticipatory Distractor Suppression Elicited by Statistical Regularities in Visual Search. *J. Cogn. Neurosci.* 31, 1535–1548
88. Friston, K. (2005) A theory of cortical responses. *Philos. Trans. R. Soc. B Biol. Sci.* 360, 815–836
89. Friston, K.J. (2019) Waves of prediction. *PLoS Biol.* 17, e3000426
90. Rao, R.P.N. and Ballard, D.H. (1999) Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nat. Neurosci.* 2, 79–87
91. van Moorselaar, D. and Slagter, H.A. (2019) Learning what is irrelevant or relevant: Expectations facilitate distractor inhibition and target facilitation through distinct neural mechanisms. *J. Neurosci.* 39, 6953–6967
92. Desimone, R. and Duncan, J. (1995) Neural Mechanisms of Selective Visual Attention. *Annu. Rev. Neurosci.* 18, 193–222
93. Luck, S.J. *et al.* (1997) Bridging the Gap between Monkey Neurophysiology and Human Perception: An Ambiguity Resolution Theory of Visual Selective Attention. *Cognit. Psychol.* 33, 64–87
94. Sellers, K.K. *et al.* (2015) Frequency-band signatures of visual responses to naturalistic input in ferret primary visual cortex during free viewing. *Brain Res.* 1598, 31–45
95. ElShafei, H.A. *et al.* (2018) Two Sides of the Same Coin: Distinct Sub-Bands in the α Rhythm Reflect Facilitation and Suppression Mechanisms during Auditory Anticipatory Attention. *eNeuro* 5
96. Rodriguez-Larios, J. *et al.* (2022) Visual working memory recruits two functionally distinct alpha rhythms in posterior cortex. *eNeuro* 9, ENEURO.0159-22.2022
97. Moca, V.V. *et al.* (2021) Time-frequency super-resolution with superlets. *Nat. Commun.* 12, 337
98. Samaha, J. *et al.* (2015) Top-down control of the phase of alpha-band oscillations as a mechanism for temporal prediction. *Proc Natl Acad Sci U A* 112, 8439–44
99. Harris, A.M. *et al.* (2018) Detecting Unattended Stimuli Depends on the Phase of Prestimulus Neural Oscillations. *J Neurosci* 38, 3092–3101
100. van Diepen, R.M. *et al.* (2015) Attention and temporal expectations modulate power, not phase, of ongoing alpha oscillations. *J Cogn Neurosci* 27, 1573–86
101. Liu, B. *et al.* (2023) Microsaccades transiently lateralise EEG alpha activity. *Prog. Neurobiol.* 224, 102433
102. Liu, B. *et al.* (2022) Functional but not obligatory link between microsaccades and neural modulation by covert spatial attention. *Nat. Commun.* 13, 3503
103. Pan, Y. *et al.* (2023) Saccades are locked to the phase of alpha oscillations during natural reading. *PLOS Biol.* 21, e3001968
104. Popov, T. *et al.* (2021) Alpha oscillations link action to cognition: An oculomotor account of the brain's dominant rhythmbioRxiv, 2021.09.24.461634
105. Gao, R. *et al.* (2017) Inferring synaptic excitation/inhibition balance from field potentials. *NeuroImage* 158, 70–78
106. Donoghue, T. *et al.* (2020) Parameterizing neural power spectra into periodic and aperiodic components. *Nat. Neurosci.* 23, 1655–1665
107. Hughes, S.W. *et al.* (2004) Synchronized oscillations at alpha and theta frequencies in the lateral geniculate nucleus. *Neuron* 42, 253–68
108. Schneider, K.A. and Kastner, S. (2009) Effects of Sustained Spatial Attention in the Human Lateral Geniculate Nucleus and Superior Colliculus. *J. Neurosci.* 29, 1784–1795

109. Schuhmann, T. *et al.* (2019) Left parietal tACS at alpha frequency induces a shift of visuospatial attention. *PLOS ONE* 14, e0217729
110. Bonnefond, M. *et al.* (2017) Communication between Brain Areas Based on Nested Oscillations. *eNeuro* 4
111. Bosman, C.A. *et al.* (2012) Attentional Stimulus Selection through Selective Synchronization between Monkey Visual Areas. *Neuron* 75, 875–888
112. Chapeton, J.I. *et al.* (2019) Large-Scale Communication in the Human Brain Is Rhythmically Modulated through Alpha Coherence. *Curr. Biol.* 29, 2801-2811.e5
113. Pascucci, D. *et al.* (2018) Gating by induced Α–Γ asynchrony in selective attention. *Hum. Brain Mapp.* 39, 3854–3870
114. Yang, X. *et al.* (2023) Differential neural mechanisms underlie cortical gating of visual spatial attention mediated by alpha-band oscillationsbioRxiv, 2023.08.21.553303
115. Lozano-Soldevilla, D. and VanRullen, R. (2019) The Hidden Spatial Dimension of Alpha: 10-Hz Perceptual Echoes Propagate as Periodic Traveling Waves in the Human Brain. *Cell Rep.* 26, 374-380.e4
116. Alamia, A. *et al.* (2023) Distinct roles of forward and backward alpha-band waves in spatial visual attention. *eLife* 12, e85035
117. VanRullen, R. and Macdonald, J.S.P. (2012) Perceptual Echoes at 10 Hz in the Human Brain. *Curr. Biol.* 22, 995–999
118. Zhigalov, A. and Jensen, O. (2023) Perceptual echoes as travelling waves may arise from two discrete neuronal sources. *NeuroImage* 272, 120047
119. Corbetta, M. and Shulman, G.L. (2002) Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3, 201–15
120. Solís-Vivanco, R. *et al.* (2021) New insights on the ventral attention network: Active suppression and involuntary recruitment during a bimodal task. *Hum. Brain Mapp.* 42, 1699–1713
121. Lopes Da Silva, F.H. and Storm Van Leeuwen, W. (1977) The cortical source of the alpha rhythm. *Neurosci. Lett.* 6, 237–241
122. Haegens, S. *et al.* (2015) Laminar Profile and Physiology of the alpha Rhythm in Primary Visual, Auditory, and Somatosensory Regions of Neocortex. *J Neurosci* 35, 14341–52
123. Lukashevich, I.P. and Sazonova, O.B. (1996) [The effect of lesions of different parts of the optic thalamus on the nature of the bioelectrical activity of the human brain]. *Zh. Vyssh. Nerv. Deiat. Im. I. P. Pavlova* 46, 866–874
124. Hughes, S.W. and Crunelli, V. (2005) Thalamic mechanisms of EEG alpha rhythms and their pathological implications. *Neurosci. Rev. J. Bringing Neurobiol. Neurol. Psychiatry* 11, 357–372
125. Lorincz, M.L. *et al.* (2009) Temporal framing of thalamic relay-mode firing by phasic inhibition during the alpha rhythm. *Neuron* 63, 683–96
126. Hughes, S. *et al.* (2011) Thalamic Gap Junctions Control Local Neuronal Synchrony and Influence Macroscopic Oscillation Amplitude during EEG Alpha Rhythms. *Front. Psychol.* 2
127. Saalmann, Y.B. *et al.* (2012) The Pulvinar Regulates Information Transmission Between Cortical Areas Based on Attention Demands. *Science* 337, 753–756
128. Huang, W.A. *et al.* (2021) Transcranial alternating current stimulation entrains alpha oscillations by preferential phase synchronization of fast-spiking cortical neurons to stimulation waveform. *Nat. Commun.* 12, 3151
129. Hoffman, S.J. *et al.* (2024) The primate cortical LFP exhibits multiple spectral and temporal gradients and widespread task dependence during visual short-term memory. *J. Neurophysiol.* 132, 206–225
130. Ronconi, L. and Bellacosa Marotti, R. (2017) Awareness in the crowd: Beta power and alpha phase of prestimulus oscillations predict object discrimination in visual crowding. *Conscious. Cogn.* 54, 36–46

131. Lundqvist, M. *et al.* (2024) Beta: bursts of cognition. *Trends Cogn. Sci.* 0




gating
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early visual regions
ventral attention network
resistance to attention capture