Effects of Pre-stimulus Alpha Oscillations on Visual Perception

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Abstract

Human perception of visual stimuli near sensory thresholds is not always consistent. To investigate this phenomenon of perceptual inconsistency and its underlying neural mechanisms, some researchers have focused on the influence of prestimulus spontaneous alpha neural oscillations (8-13 Hz) on visual perception. Recent studies have found that decreased prestimulus alpha oscillation power can enhance participants' detection hit rates, but not perceptual accuracy; whereas the phase of prestimulus alpha oscillations can predict whether participants successfully detect a stimulus. Prestimulus alpha power is believed to regulate the baseline activity level of the visual cortex; decreased alpha power reflects enhanced cortical baseline activity, thereby improving detection rates for weaker stimuli. Prestimulus alpha phase, in contrast, is believed to regulate the timing of cortical excitation and inhibition; the brain' s state (excitation/inhibition) at the moment of stimulus presentation determines the final perceptual outcome.

Full Text

The Influences of Prestimulus Alpha Oscillation on Visual Perception

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Abstract: Human perception of visual stimuli near the sensory threshold is not always consistent. To investigate this phenomenon of inconsistent visual perception and its neural mechanisms, researchers have focused on how spontaneous alpha neural oscillations (8-13 Hz) prior to stimulus presentation affect subsequent visual perception. Recent studies have found that decreased prestimulus alpha oscillation power can improve observers’ detection hit rates, but does not enhance perceptual accuracy. In contrast, the phase of prestimulus alpha oscillations can predict whether a stimulus will be successfully detected. Prestimulus alpha power is thought to regulate the baseline activity level of visual cortex; reduced alpha power reflects enhanced cortical baseline activity, thereby improving detection rates for weak stimuli. Prestimulus alpha phase, however, is believed to regulate the timing of cortical excitation and inhibition, with the brain’ s state (excited or inhibited) at stimulus onset determining the final perceptual outcome.

Keywords: prestimulus; neural oscillation; alpha power; alpha phase; visual perception

1. Introduction

Our perception of the external world relies heavily on visual information. Light signals received by the retina undergo a series of neural processes to form visual perception—what we see. However, our perception does not always faithfully reflect external reality; identical visual stimuli can produce different percepts at different times. For instance, when a visual stimulus is presented very briefly or at very low intensity, we may sometimes perceive it and sometimes not. When the difference between two stimuli is minimal, we may sometimes discriminate them and sometimes fail. In psychophysics, the weakest stimulus intensity at which an individual can detect a stimulus with a certain probability (typically 50%, as in Busch, Dubois, & VanRullen, 2009; Ergenogle et al., 2004; van Dijk, Schoffelen, Oostenveld, & Jensen, 2008; though some studies use probabilities greater than 50%, such as Iemi & Busch, 2018; Iemi, Chaumon, Crouzet, & Busch, 2017) or the minimum difference needed to discriminate between two stimuli is defined as that individual’ s sensory threshold. By this definition, perception of visual stimuli near the sensory threshold is not always consistent.

Why do people produce different percepts for the same near-threshold stimulus? Some researchers argue that because transforming visual input into perception involves multiple processing stages, variations in these stages may lead to different perceptual outcomes. Consequently, these researchers have used methods such as event-related potentials (ERPs) to investigate relationships between post-stimulus neural activity and different perceptual results (e.g., Bernat, Shevrin, & Snodgrass, 2001; Devrim, Demiralp, & Kurt, 1997; Koivisto, Grassini, Salminen-Vaparanta, & Revonsuo, 2017; Rutiku, Aru & Bachmann, 2016; Wilenius & Revonsuo, 2007). While these studies can explain from a neural mechanism perspective why identical stimuli produce different percepts, they raise a new question: Why do identical stimuli evoke different neural activities?

With deepening research into spontaneous human electroencephalographic (EEG) activity, a new perspective has emerged. This view suggests that we produce different percepts for identical stimuli because the brain resides in different states at different moments, which in turn generates different neural responses to the same stimulus. Spontaneous EEG is not evoked by external stimuli but rather represents ongoing, self-generated neural activity that is often considered to reflect the brain' s state (Ruhnau, Hauswald, & Weisz, 2014; Steriade, McCormick, & Sejnowski, 1993; Ward, 2003). From spontaneous EEG, different frequencies of neural oscillations can be extracted—rhythmic neural activity that continuously waxes and wanes. Among these, spontaneous neural oscillations around 10 Hz (8-13 Hz) are called alpha oscillations, which constitute the predominant neural oscillation in awake humans (Dalal et al., 2011; Jensen, Bonnefond, & VanRullen, 2012). Alpha oscillations have been implicated in various cognitive processes including spatial attention (e.g., Foster, Sutterer, Serences, Vogel, & Awh, 2017; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden, Foxe, Wang, & Simpson, 2000) and working memory (e.g., Bae, & Luck, 2018; Foster, Bsales, Jaffe, & Awh, 2017; Tran, Hoffner, LaHue, Tseng, & Voytek, 2016). In recent years, researchers have begun investigating whether alpha oscillations prior to visual stimulus presentation influence the processing of upcoming visual stimuli and the formation of perception, gradually developing an understanding of the relationship between alpha oscillations and visual perception and its neural mechanisms.

This paper will first briefly introduce the neural mechanisms of alpha oscillations, then chronologically review previous research findings, theoretical interpretations, and main points of debate regarding the relationship between prestimulus alpha oscillations and visual perception, and finally propose our perspectives on future research directions in this field.

2. Neural Mechanisms of Alpha Oscillations

Neural oscillations extracted from human EEG signals are generally believed to originate from periodically firing neuronal populations (Wang, 2010; Cohen, 2017). When the periodic firing activity of neurons within a population becomes synchronized, the resulting postsynaptic potentials in target neurons also become synchronized, generating stronger periodic local field potentials (LFPs) and enhancing the neural oscillations at specific frequencies (or frequency bands) recorded by scalp electrodes (Klimesch, Sauseng, & Hanslmayr, 2007; Pfurtscheller, Stancak Jr, & Neuper, 1996; Varela, Lachaux, Rodriguez, & Martinerie, 2001). The strength of neural oscillations extracted from EEG is typically measured using power, which is thought to reflect the synchrony of periodically firing neuronal populations and serves as an index of the intensity of neural activity or cognitive processing.

Extensive evidence from EEG/MEG (magnetoencephalography) (e.g., Bonnefond & Jensen, 2012; Samaha & Postle, 2015; Sauseng, Klimesch, Doppelmayr, Pecherstorfer, Freunberger, & Hanslmayr, 2005), LFP (e.g., Bahramisharif et al., 2013; de Pesters et al., 2016; Dougherty, Cox, Ninomiya, Leopold, & Maier, 2017; Haegens, Nácher, Luna, Romo, & Jensen, 2011), and single-neuron (e.g., Dougherty et al., 2017; Haegens et al., 2011; Watson, Ding, & Buzsáki, 2018) levels has linked alpha oscillations to inhibitory functions. Alpha oscillations are thought to originate from neuronal populations that fire at approximately 10 Hz and release inhibitory neurotransmitters. The most direct evidence comes from Haegens et al. (2011), who found that alpha oscillation activity in LFPs could reduce neuronal firing rates. Consequently, researchers believe that alpha oscillation power is related to the strength of inhibitory function: higher alpha power indicates greater synchrony of inhibitory neuronal populations and stronger inhibition (e.g., Kelly, Lalor, Reilly, & Foxe, 2006; Sauseng, et al., 2005; Thut et al., 2006).

Because the neuronal populations generating neural oscillations engage in periodic firing activity, their activity states differ at specific time points: at some moments, most neurons are firing, while at others, most are at rest. This periodic variation in population activity states produces the rhythmic oscillatory signals we record from the scalp. The state of an oscillation at a given moment is called its phase (Klimesch, 2012; VanRullen, 2016). Neural oscillations extracted from EEG signals are typically represented as cosine curves of different frequencies, and phase can be understood as the position along this cosine curve at a particular time point. A standard cosine curve can also be viewed as the projection onto the x-axis of the trajectory of a point moving along a circle centered at the origin (Figure 1 [Figure 1: see original paper]), so oscillatory phase can be represented by the angle of the central angle. In terms of neuronal population activity, phase reflects the state of the population at a given moment: when the neural oscillation is at its peak phase, the number of firing neurons reaches its maximum; when at its trough phase, the number of quiescent neurons reaches its maximum (Hanslmayr, Gross, Klimesch, & Shapiro, 2011). For alpha oscillations, phase is thought to reflect the activity state of inhibitory neurons at different times and the strength of inhibitory function at a given moment (Klimesch et al., 2007).

Although there is broad consensus on the function of alpha oscillations, their origin in the brain remains debated (Cohen, 2017; Klimesch, 2012), with some researchers suggesting multiple origins (Haegens et al., 2015).

3. Prestimulus Alpha Oscillation Power and Visual Perception

Ergenogle et al. (2004) first reported that prestimulus alpha oscillation power could predict whether participants would successfully detect visual stimuli near perceptual threshold. In their study, participants were required to detect a briefly presented light spot while their EEG was recorded. Results showed that, compared to trials in which the spot was not detected, trials with successful detection exhibited lower alpha oscillation power in occipital and parietal electrodes during the 1-second period preceding stimulus presentation. Van Dijk et al. (2008) found consistent results in a task requiring participants to judge subtle grayscale differences between two concentric disks, observing that detection rates were higher in trials with low prestimulus alpha power than in those with high prestimulus alpha power.

Since then, similar within-subject effects have been replicated across different studies using various types of near-threshold stimuli (Achim, Bouchard, & Braun, 2013; Chaumon & Busch, 2014; Mathewson, Grattion, Fabiani, Beck, & Ro, 2009; Roberts, Fedota, Buzzell, Parasuraman, & McDonald, 2014; Romei, Gross, & Thut, 2010; though see Babiloni, Vecchio, Bultrini, Luca Romani, & Rossini, 2005 for different results). Given that low prestimulus alpha power is associated with higher detection rates, researchers initially hypothesized that prestimulus alpha power influences perceptual accuracy. Some interpreted lower prestimulus alpha power as indicating a more alert or vigilant state with higher cortical excitability or arousal, enabling better processing of upcoming stimuli and improved perceptual performance (e.g., Ergenogle et al., 2004; Roberts et al., 2014). Others argued that changes in alpha power reflect variations in inhibition (e.g., Romei et al., 2010; van Dijk et al., 2008). In spatial attention tasks, alpha power is lower in the hemisphere contralateral to the attended visual field than in the ipsilateral hemisphere, leading to the view that high alpha power is associated with inhibition of unattended stimuli (e.g., Thut et al., 2006; Worden et al., 2000). These researchers proposed that even in non-spatial attention tasks, alpha oscillations may be related to inhibition, with high alpha power suppressing bottom-up visual information transmission and impairing perceptual performance.

Notably, all these findings were based on detection tasks requiring "yes/no" forced-choice responses, where researchers either compared prestimulus alpha power between hit and miss trials or compared detection rates between high and low prestimulus alpha power trials. According to signal detection theory (Macmillan & Creelman, 2005), "decreased prestimulus alpha power improves perceptual accuracy" is not the only possible interpretation. An alternative explanation involves response bias: decreased prestimulus alpha power might make participants more likely to respond "yes" (i.e., report stimulus presence or difference), which would increase hit rates in low-alpha trials and produce the observed pattern of lower prestimulus alpha power in hit trials compared to false alarm trials.

[Figure 2: see original paper] Signal detection theory interpretation of neural mechanisms in detection tasks. A: Probability distributions of neural activity intensity evoked by signal (target stimulus present) and noise (target absent or random noise stimulus). *c* represents the response criterion; when neural activity exceeds *c*, the individual makes a "yes" judgment regardless of whether the activity was evoked by signal or noise. *d'* represents discriminability—the ability to distinguish signal from noise—modeled as the separation between the two probability distributions. Hit and miss rates correspond to areas under the signal distribution curve to the right and left of *c*, respectively; false alarm and correct rejection rates correspond to areas under the noise distribution curve to the right and left of *c*, respectively. B: Two possible mechanisms for increased hit rate. The perceptual accuracy improvement mechanism involves increased separation between signal and noise distributions (from d' to d'), expanding the area under the signal curve to the right of c and increasing hit rate. The response bias mechanism involves a change in the position of c relative to the distributions (i.e., the x in the figure), increasing areas under both signal and noise curves to the right of c—raising both hit and false alarm rates without changing d' . Gray lines represent baseline states; black lines represent changed states.

Two methods can distinguish between “perceptual accuracy improvement” and “response bias change” explanations. The first involves considering both hit and false alarm rates in detection tasks, for example using discriminability (d') as an index (Figure 2A). If decreased prestimulus alpha power improves perceptual accuracy, hit rates should increase while false alarm rates decrease or remain unchanged, resulting in higher discriminability (Figure 2B, top). If decreased prestimulus alpha power biases participants toward “yes” responses, false alarm rates should increase alongside hit rates, leaving discriminability unchanged (Figure 2B, bottom). The second method uses discrimination tasks requiring participants to report which specific stimulus was presented. If prestimulus alpha power relates to perceptual accuracy, discrimination accuracy should be higher when prestimulus alpha power is low. If alpha power influences response bias, overall discrimination accuracy should remain stable regardless of prestimulus alpha power variations. The relationship between prestimulus alpha power and discrimination task performance can thus provide evidence supporting or challenging the “perceptual accuracy improvement” account.

Recent evidence largely does not support the interpretation that prestimulus alpha power relates to visual perceptual accuracy. For example, Limbach and Corballis (2016) had participants report whether they saw a briefly presented diamond pattern using different response keys. Examining relationships among hit rates, false alarm rates, discriminability, and prestimulus alpha power, they found that lower prestimulus alpha power was associated with higher hit rates but also higher false alarm rates, with no significant difference in discriminability between high and low prestimulus alpha power trials. Iemi, Chaumon, Crouzet, and Busch (2017) investigated these relationships across three perceptual tasks: grating detection (reporting presence of a faint grating via key press), grating position discrimination, and grating orientation discrimination. They found that while prestimulus alpha power variations related to detection task hit rates, they were unrelated to detection task discriminability or discrimination task accuracy. Other discrimination task studies have reported similar results, showing no effect of prestimulus alpha power on discrimination accuracy (e.g., Benwell et al., 2017; Samaha, Iemi, & Postle, 2017). Furthermore, by fitting psychometric curves at different prestimulus alpha power levels, Chaumon and Busch (2014) found that the effects of prestimulus alpha power changes on psychometric functions were more consistent with predictions from a response bias model than a discriminability change model.

[Figure 3: see original paper] Two hypotheses—decision bias and perceptual bias—explaining effects of decreased prestimulus alpha power in detection tasks. A: The decision bias hypothesis posits that decreased prestimulus alpha power leads participants to adopt a more liberal response criterion (i.e., lower c, from c to c), requiring less neural activity to exceed the threshold for a "yes" judgment. B: The perceptual bias hypothesis suggests that decreased prestimulus alpha power enhances baseline activity in visual cortex, equally boosting neural activity evoked by both signal and noise (from gray to black curves) without changing the separation between distributions (i.e., d'). Both hypotheses increase the frequency of "yes" responses, manifested as simultaneous increases in hit and false alarm rates.

These findings not only challenge the notion that prestimulus alpha power relates to perceptual ability but also raise a new question: What physiological and psychological changes do variations in prestimulus alpha power actually reflect? The aforementioned studies suggest that in detection tasks, decreased alpha power is associated with a greater tendency to report stimulus detection. Witt, Taylor, Sugovic, and Wixted (2015) proposed that such response bias changes in detection tasks could arise through two possible mechanisms: decision bias and perceptual bias. Decision bias posits that response bias changes stem from criterion shifts; if the response criterion c is lowered, less neural activity is required to exceed the threshold for a "yes" judgment, increasing the frequency of "yes" responses (Figure 3A). Perceptual bias suggests that response bias changes result from equal enhancement of neural activity evoked by both noise and signal; if both are equally strengthened, the probability of neural activity exceeding the response criterion increases, leading to more "yes" judgments (Figure 3B). Witt et al. noted that conventional detection and discrimination tasks cannot distinguish between these mechanisms. Although Limbach and Corballis (2016) favored the decision bias hypothesis, they acknowledged that their detection task could not effectively differentiate the two explanations. Similarly, while Iemi et al. (2017) suggested that perceptual bias could explain their results across both detection and discrimination tasks, their study also could not distinguish between perceptual and decision bias accounts.

In a recent study, Iemi and Busch (2018) attempted to differentiate between perceptual and decision bias explanations using a novel "two-interval forced-choice" detection paradigm. In each trial, two temporal intervals were presented sequentially, with the target stimulus appearing in only one interval and no stimulus in the other. Participants judged which interval contained the target. In this paradigm, the brain must compare neural activity between the two intervals to determine target location. The logic was: if prestimulus alpha power relates to baseline visual cortex activity, performance should be affected by the relationship between alpha power preceding the two intervals; if prestimulus alpha power relates to response criterion, performance should be unaffected by this relationship (Figure 4 [Figure 4: see original paper]). Results showed that in correct-response trials, alpha power was lower before the interval containing the target than before the empty interval, while the opposite pattern occurred in error trials. Thus, the relative magnitude of alpha power preceding the target-present versus target-absent intervals predicted response accuracy. These findings support the perceptual bias hypothesis, suggesting that alpha power changes influence baseline activity levels in visual cortex.

[Figure 4: see original paper] Logic of the two-interval forced-choice detection task. The most effective strategy is to compare neural activity between the two intervals and report the interval with stronger activity. Accuracy correlates positively with the probability that activity in the target-present interval exceeds that in the target-absent interval, which in signal detection theory corresponds to the separation between the probability distributions of neural activity in the two intervals (i.e., x in the figure). A, B: Probability distributions of neural activity intensity when prestimulus alpha power is equal before both intervals, serving as a baseline for comparison. C: If alpha power is lower before the target-present interval, the perceptual bias hypothesis predicts enhanced evoked activity (shifting the target-present distribution from gray to black), increasing x and improving accuracy. D: If alpha power is lower before the target-present interval, the decision bias hypothesis predicts only a change in response criterion (shifting from c to c), leaving x unchanged and producing no accuracy improvement. E: If alpha power is lower before the target-absent interval, the perceptual bias hypothesis predicts enhanced activity in the target-absent interval (shifting its distribution from gray dashed to black dashed line), decreasing x and reducing accuracy. F: If alpha power is lower before the target-absent interval, the decision bias hypothesis again predicts only criterion change, leaving x unchanged.

In summary, research on prestimulus alpha power and visual perception indicates that prestimulus alpha power does not affect perceptual accuracy. Its influence on detection rates for weak, near-threshold stimuli likely arises from changes in baseline visual cortex activity. Higher alpha power corresponds to lower baseline cortical activity, impeding processing of subsequent visual stimuli and making weak stimuli harder to detect. When alpha power is lower, visual cortex activity is higher, enhancing neural responses to weak stimuli and making them more detectable. However, this also enhances activity when no stimulus is present, increasing the likelihood of "stimulus present" illusions and leaving perceptual accuracy unaffected.

Although within-subject comparisons have not found evidence that prestimulus alpha power affects perceptual accuracy, between-subject comparisons have revealed negative correlations between average prestimulus alpha power levels and overall task performance. Limbach and Corballis (2016) found that participants with lower mean prestimulus alpha power showed higher discriminability in detection tasks. Hanslmayr et al. (2005) reported that participants with better discrimination task performance had significantly lower mean prestimulus alpha power than poorer performers, and that participants' task performance rank correlated negatively with their mean prestimulus alpha power rank (Hanslmayr et al., 2007). Hanslmayr et al. (2007) termed this mean prestimulus alpha power "tonic alpha" and suggested that tonic alpha strength may reflect individual perceptual ability levels. Klimesch (2012) proposed that mean prestimulus alpha power reflects anticipatory attention ability—the capacity to maintain target-relevant information to facilitate post-stimulus processing—with lower levels indicating stronger anticipatory attention. Currently, there is no consensus on what neural mechanisms mean prestimulus alpha power reflects, nor whether it shares the same origins and functions as trial-by-trial prestimulus alpha power, requiring further investigation.

4. Prestimulus Alpha Oscillation Phase and Visual Perception

While prestimulus neural oscillation power reflects relatively stable neural activity over a period, neural oscillations are periodic activities that change over time. Could more fine-grained investigation of prestimulus alpha phase further illuminate the relationship between prestimulus alpha oscillations and visual perception?

Research on prestimulus alpha phase and visual perception dates back to the 1960s, when researchers found that suprathreshold visual stimuli presented during the peak of occipital EEG alpha oscillations produced longer reaction times, while stimuli presented during the trough produced shorter reaction times (Callaway & Yeager, 1960; Dustman & Beck, 1965; see Drewes & VanRullen, 2011; Hamm, Dyckman, McDowell, & Clementz, 2012 for recent replications). These studies suggested that alpha phase might influence visual information processing.

Recent studies have used near-threshold visual stimuli to investigate the relationship between prestimulus alpha phase and visual perception. Mathewson et al. (2009) required participants to detect a brief light spot and found that detected stimuli were predominantly presented near the trough of occipital EEG alpha oscillations, while undetected stimuli mostly occurred near the peak. In another study, Busch, Dubois, and VanRullen (2009) also had participants detect a brief light spot. Using inter-trial coherence (also called phase-locking index; Wuxia et al., 2018) to index phase consistency across trials during the brief period before stimulus presentation, they found strong occipital alpha phase consistency in both detected and undetected trials, with opposite phases (differing by radians) between conditions—consistent with Mathewson et al. (2009).

Subsequent studies have employed multiple methods to further explore the relationship between prestimulus alpha phase and visual perception task performance. Some researchers have investigated whether the covariation between prestimulus alpha phase and perception reflects a causal relationship—whether different prestimulus phases cause different percepts. In Mathewson, Fabiani, Gratton, Beck, and Lleras (2010), participants viewed a 12 Hz flickering annulus before target onset. Since flickering visual stimuli evoke steady-state visual evoked potentials at the same frequency (Herrmann, 2001), the researchers attempted to manipulate prestimulus alpha phase by varying the interval between target presentation and the final flicker, investigating whether detection performance was affected. They found that both hit rate and discriminability peaked when the target appeared 83 ms after the final flicker—exactly equal to the interval between flickers. The authors proposed that the prestimulus flicker altered the periodic cycle of visual sensitivity, with the target’ s position in this cycle determining its processing and perception. However, Mathewson et al. (2010) did not record EEG, lacking direct evidence for a causal relationship between prestimulus EEG alpha phase and perception. In subsequent work, Mathewson and colleagues demonstrated that 12 Hz flicker could indeed alter the phase of spontaneous 12 Hz EEG oscillations and that detection of post-flicker targets related to 12 Hz EEG phase, providing more direct evidence for causality (Mathewson et al., 2012).

Dugué, Marque, and VanRullen (2011) used direct cortical stimulation to investigate causality. They applied single-pulse transcranial magnetic stimulation (TMS) at intensity sufficient to induce phosphenes to participants’ right occipital cortex while participants reported phosphene perception. EEG analysis revealed significant differences in occipital and midfrontal alpha phase during the 400 ms preceding TMS pulses that produced versus failed to produce phosphenes, linking alpha phase to phosphene generation. The authors argued that alpha phase reflects visual cortex excitability, making phosphene induction probability phase-dependent.

Other researchers have examined whether prestimulus alpha phase influences perception in different task contexts. Busch and VanRullen (2010) found in a spatial cueing task that detection of faint visual stimuli at cued locations related to the phase of ~7 Hz oscillations (sometimes termed low alpha or theta) in central frontal regions during the 400–100 ms before stimulus onset. Harris, Dux, and Mattingley (2018) further showed that in spatial cueing tasks, detection of both cued and uncued stimuli related to prestimulus alpha phase. Additionally, alpha phase has been implicated in tasks involving integration of visual information across spatial locations (Hanslmayr, Volberg, Wimber, Dalal, & Greenlee, 2013). In that study, participants detected contour patterns in grating arrays, with successfully detected arrays showing significantly different ~7 Hz phase 250 ms before stimulus presentation compared to undetected arrays. Some studies have found that prestimulus alpha phase does not affect discrimination task performance (Benwell et al., 2017), suggesting that, like alpha power, alpha phase may only modulate baseline cortical excitability without altering perceptual accuracy.

The most widely accepted mechanism for prestimulus alpha phase effects on visual perception is that alpha phase reflects the temporal dynamics of inhibitory function. Klimesch’ s “inhibition-timing” hypothesis proposes that alpha oscillations serve not only an inhibitory function but also a “timing” function (Klimesch et al., 2007; Klimesch, 2012). This hypothesis suggests that whether a neuron fires depends on its excitability and the inhibition it receives. When inhibition exceeds excitability, the neuron cannot fire; when inhibition does not exceed excitability, the neuron can fire at a certain frequency. Alpha oscillations provide the source of this inhibition. Because alpha oscillations are neural activities with continuously changing intensity, the inhibition exerted on neurons fluctuates over time, altering the balance between inhibition and excitability and causing neurons to cycle periodically between excitatory and inhibitory states (Figure 5 [Figure 5: see original paper]). The "timing" function of alpha oscillations is manifested in this control over neuronal activity cycles, with alpha phase determining when neurons can or cannot fire.

[Figure 5: see original paper] Inhibition-timing theory. Top: Relationship between inhibitory function and neuronal excitability. Alpha oscillations reflect temporal changes in inhibition strength (cosine curve), with inhibition exceeding neuronal excitability during certain periods (two horizontal lines represent excitability levels of two neurons). Bottom: The balance between inhibition and excitability causes neurons to alternate periodically between excitatory and inhibitory states. When inhibition is weaker than excitability, neurons can fire; when inhibition is stronger, they cannot. Vertical lines represent individual action potentials. [Figure adapted from Klimesch et al. (2007)]

According to the inhibition-timing hypothesis, prestimulus alpha oscillations influence perception by affecting brain state at stimulus onset. When alpha-mediated inhibition exceeds neuronal excitability at a given moment, neurons struggle to fire, making external visual input difficult to process effectively. This manifests as lower detection probability for near-threshold stimuli at certain phases (Busch et al., 2009, 2010; Mathewson et al., 2009, 2012; Harris et al., 2018) and increased reaction times to suprathreshold stimuli (Callaway & Yeager, 1960; Drewes & VanRullen, 2011; Dustman & Beck, 1965; Hamm et al., 2012). Conversely, at other alpha phases where inhibition is weaker, visual stimuli can more easily activate neurons, allowing unimpeded processing and increasing detection probability. In essence, alpha phase "times" when brain neurons can fire, determining whether a weak stimulus is detected based on its alignment with particular neuronal states.

However, the inhibition-timing theory does not specify which brain regions' neuronal activity is inhibited by alpha oscillations. Among existing findings, alpha phases influencing visual perception have primarily originated from occipital and parietal regions (e.g., Mathewson et al., 2010; Mathewson et al., 2012; Dugué et al., 2011; Harris et al., 2018), but substantial evidence also points to frontal sources (Busch, Dubois, & VanRullen, 2009; Busch & VanRullen, 2010; Hanslmayr et al., 2013). This raises the question: At which processing stage does alpha phase exert its influence? In other words, does alpha phase affect visual information processing or response processes?

Recent studies provide clues. Brüers and VanRullen (2018) argued that the most influential alpha phase for perception should be that during stimulus processing, not before or at stimulus onset. They constructed EEG signals from participants' impulse response functions while viewing brightness-varying stimulus sequences, inserted brief targets into these sequences, and recorded EEG during viewing. By comparing constructed no-target EEG with actual target-present EEG, they found the most influential phase occurred approximately 75 ms after target presentation. Other work shows that occipital alpha phase 125 ms before stimulus onset can affect peak latency of ERPs within 100 ms post-stimulus (Hülsdünker, Strüder, & Mierau, 2018). Additionally, Hanslmayr et al. (2013) found that prestimulus alpha phase could predict functional connectivity between lateral occipital cortex and intraparietal sulcus. These results suggest that alpha inhibition may act during early visual processing stages rather than late response stages.

In summary, current research demonstrates that prestimulus alpha phase can predict performance in perceptual detection tasks, supporting the inhibition-timing hypothesis. However, further in-depth research is needed to determine exactly which perceptual processing stages are modulated by alpha phase.

5. Summary and Outlook

Current research suggests that prestimulus alpha oscillation power may reflect baseline activity levels in visual cortex. Higher alpha power corresponds to lower cortical activation, potentially obstructing processing of subsequent visual stimuli and preventing detection of weak stimuli. Lower alpha power corresponds to higher cortical activity, enabling detection of weak stimuli but also increasing illusion rates. Thus, while prestimulus alpha power influences visual information processing, it does not improve perceptual accuracy. Alpha oscillation phase, in contrast, reflects periodic changes in neuronal excitability: during some periods, neurons are inhibited and less easily activated by external stimuli, while during others, reduced inhibition makes neurons more responsive to external input. Consequently, our perception of stimuli differs depending on the brain state at stimulus onset.

We believe several issues regarding alpha oscillation function and its mechanisms of influence on visual perception warrant further investigation. First, what brain regions generate prestimulus alpha oscillations and where do they exert their effects? Although research has focused on occipital and parietal alpha oscillations, significant prestimulus alpha effects have also been observed in frontal regions. Notably, significant frontal alpha effects typically occur earlier than occipital and parietal effects. Previous studies have reported stronger prestimulus alpha phase synchronization between frontal and occipitoparietal regions when targets were undetected (Hanslmayr et al., 2007), and that frontal alpha can predict occipital and parietal activity (Hanslmayr et al., 2013). Recent animal and human studies have also linked alpha oscillations to top-down feedback signals (Michalareas et al., 2016; van Kerkoerle et al., 2014; Bonaiuto et al., 2018). These findings suggest a possibility that frontal cortex generates alpha oscillations while occipital and parietal cortices are target regions. Investigating this issue could clarify the origins and scope of alpha-mediated inhibition and identify which neural activities and cognitive processes are suppressed.

Second, do alpha oscillations influencing different cognitive tasks share the same origins and functions? As mentioned in the introduction, alpha oscillations affect not only visual perception but also spatial attention and working memory. In working memory tasks, for instance, alpha power increases in occipital and parietal regions during the retention period before test stimulus presentation (Bastiaansen, Posthuma, Groot, & De Geus, 2002; Jensen, Gelfand, Kounios, & Lisman, 2002), and this retention-period alpha activity relates to working memory capacity (Leenders, Lozano-Soldevilla, Roberts, Jensen, & De Weerd, 2016; Tran et al., 2016; Wang, Tseng, Liu, & Tsai, 2017), leading to the view that it suppresses interference from irrelevant information. Some researchers propose that representations of different objects in the visual field occur at different alpha phases, with alpha power determining how many stimuli can be represented within one alpha cycle, thus potentially influencing working memory encoding (Jensen, Gips, Bergmann, & Bonnefond, 2014). Others have decoded attended spatial locations (Foster et al., 2017) and spatial information maintained in working memory (Bae, & Luck, 2018; Foster et al., 2017) from alpha power topographies, suggesting alpha function may extend beyond inhibition (Foster & Awh, 2018). Additionally, as noted earlier, trial-by-trial and mean prestimulus alpha power have different effects on visual perception. It remains uncertain whether these alpha oscillations have distinct sources and functions. If they differ, what are their respective brain regions and functions, and how does the brain prevent interference among them? If they share sources and functions, what are these common origins and functions? For example, if the inhibitory functions observed in spatial attention and visual perception tasks are identical, what neuropsychological processes are being inhibited? Addressing this question would deepen our understanding of the physiological and psychological processes reflected by alpha oscillations and may provide a medium for investigating interactions among different cognitive functions.

Finally, how do prestimulus alpha oscillations influence post-stimulus neural activity? Research on prestimulus alpha oscillations rests on the assumption that different power and phase values reflect different brain states, which in turn affect visually evoked neural activity. Most previous studies have focused on behavioral effects, with only a few examining influences on early ERP components (Gruber et al., 2014; Hülsdünker et al., 2018; Jansen & Brandt, 1991; Risner, Aura, Black, & Gawne, 2009). Some controversy remains, with reports that prestimulus alpha phase does not affect visual evoked potentials (Risner et al., 2009). Recent studies have found that periodic external stimulation—including rhythmic transcranial magnetic stimulation (rTMS), transcranial alternating current stimulation (tACS), and flickering visual stimuli—can influence spontaneous neural oscillations, producing entrainment: synchronization of spontaneous oscillations to external stimulation rhythms (reviewed in Thut, Schyns, & Gross, 2011; Vosskuhl, Strüber, & Herrmann, 2018). These techniques can help manipulate prestimulus alpha oscillations to better investigate relationships between pre- and post-stimulus neural activity and their behavioral consequences, advancing our understanding of visual processing time courses and the complete cognitive pathway from stimulus processing to behavioral response.

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