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Review

The role of alpha oscillations in temporal attention

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ABSTRACT

Our brain does not process incoming sensory stimuli mechanistically. Instead the current brain state modulates our reaction to a stimulus. This modulation can be investigated by cognitive paradigms such as the attentional blink, which reveal that identical visual target stimuli are correctly reported only on about half the trials. Support for the notion that the fluctuating state of the brain determines stimulus detection comes from electrophysiological investigations of brain oscillations, which have shown that different parameters of ongoing oscillatory alpha activity (~10 Hz) can predict whether a visual stimulus will be perceived or not. The present article reviews recent findings on the role of prestimulus alpha oscillatory activity for visual perception and incorporates these results into a neurocognitive model that is able to account for various findings in temporal attention paradigms, specifically the attentional blink.

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1. Introduction

1.1. Externally and internally oriented brain states

From time to time we all fail to perceive a salient sensory stimulus because the brain was occupied with some other cognitive process. For instance, we may not recognize an old friend passing by on our way to work, because we are thinking about a new friend who passed by just moments before. Such incidents show that our brain does not process incoming stimuli mechanistically; instead, whether or not a certain stimulus will be perceived partly depends on the brain's current state. Presumably, these brain states differ by whether the brain is biased towards processing stimuli from the external world (*the old friend*), or towards processing of internal representations (*first friend passed*). Identifying the neurophysiological signatures of such brain states, and predicting whether or not a sensory stimulus will be perceived, are two of the key goals in modern cognitive neuroscience. Brain oscillations have for a long time been recognized as indexing brain states. Several EEG/MEG studies point toward a fundamental role of ongoing oscillations for shaping perception and cognition. More specifically, a number of recent studies have revealed a significant correlation between the perception of a visual stimulus and different parameters of ongoing alpha activity prior to stimulus presentation¹ (Ergenoglu et al., 2004; Hanslmayr et al., 2007; van Dijk et al., 2008; Busch et al., 2009; Busch and VanRullen, 2010; Mathewson et al., 2009). These findings suggest that brain oscillations indicate fluctuations between externally and internally oriented brain states, thus determining whether a visual stimulus will be perceived or not.

One of the key paradigms to study the effects of temporal attention is the attentional blink (AB) paradigm (Raymond et

al., 1992). The basic finding of the AB is that the processing of a briefly presented stimulus (T1) leads to a significant decrease in the ability to correctly report a subsequent stimulus (T2) if it is presented ~250 ms after T1. Among others, a prominent hypothesis is that the AB arises because processing the first (external) stimulus (T1) forces the brain into an internal processing mode which renders the system unable to process the second stimulus (T2) to the level of conscious awareness (Shapiro et al., 1997; see Section 2.2 for details). The attentional blink paradigm is thus well suited for studying fluctuations between externally or internally oriented brain states. The goal of the current review is to integrate the findings of the aforementioned EEG/MEG studies into a neurocognitive framework that is able to explain temporal (i.e., sequentially occurring) attentional outcomes, such as revealed by the attentional blink paradigm.

We begin by providing a basic introduction into brain oscillations, with a specific focus on what different parameters of oscillatory activity tell us about the underlying neural processes. In section two, the attentional blink paradigm and its outcomes will be described, focussing on how current cognitive theories explain the AB. In section three, studies which examined the role of prestimulus alpha oscillatory activity for the perception of visual stimuli are reviewed. In the fourth section, the neurophysiological underpinnings of the different parameters of alpha oscillatory activity are considered. Finally, in section five a neurocognitive framework is presented that aims to integrate these findings into a coherent account of the AB and other phenomena of temporal attention.

1.2. Brain oscillations: frequency, amplitude, and phase

Brain oscillations reflect rhythmic fluctuations of local field potentials between excitatory and inhibitory states of neural populations. Oscillations are generated by summated excitatory post-synaptic potentials (EPSPs) of several thousands of neurons (Lopes da Silva, 1991). The raw EEG/MEG signal contains various different brain oscillations, which can be analyzed by applying spectral analysis (e.g. Wavelet analysis; Fig. 1A). Oscillations are unambiguously characterized by three parameters: (i) frequency (Fig. 1B); (ii) amplitude (Fig. 1C); and (iii) phase (Fig. 1D).

¹ To date, the role of prestimulus alpha oscillations on the perception of a sensory stimulus has mostly been explored in the visual domain. Although, similar findings emerged in the somatosensory domain (Linkenkaer-Hansen et al., 2004; Schubert et al., 2009), we are not yet aware of any studies in the auditory domain. As most AB studies were also carried out in the visual domain, the current review is focussed on the visual system.

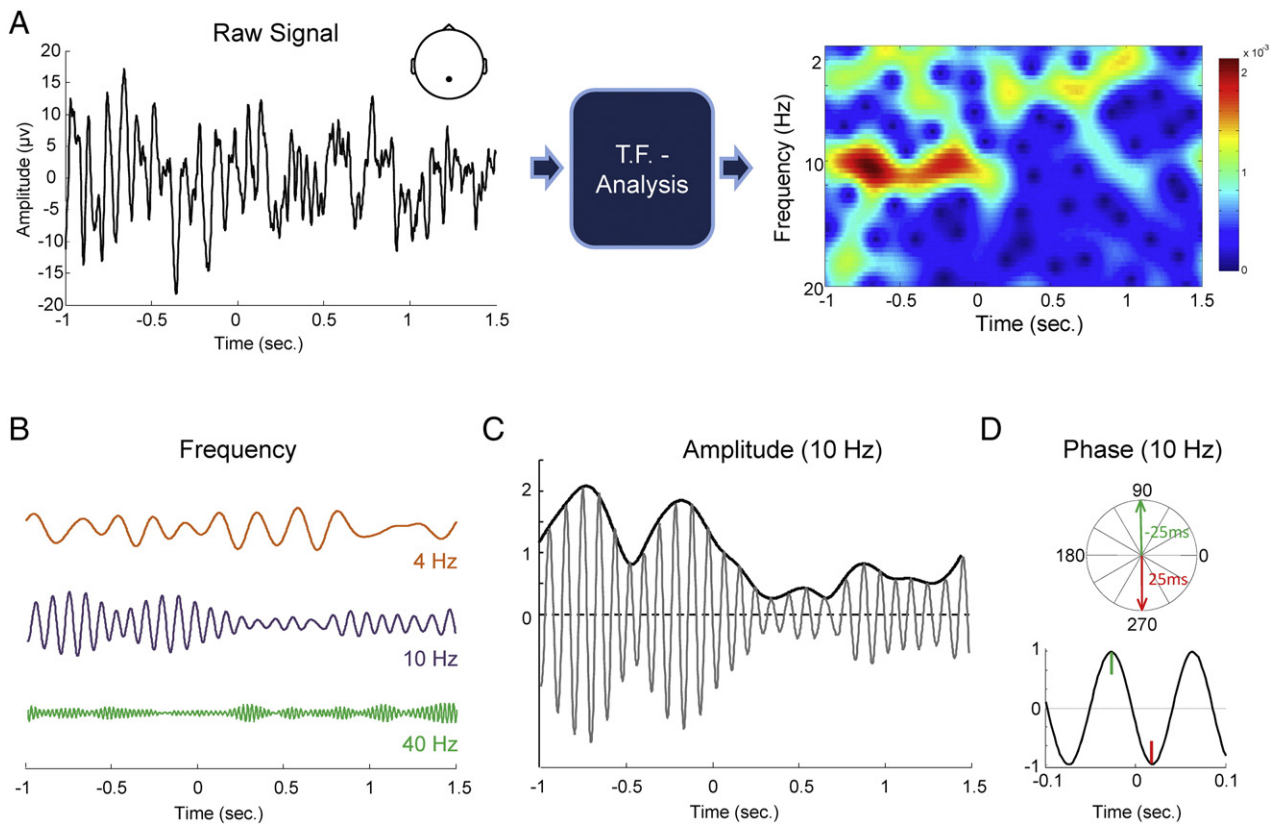


Fig. 1 – Brain oscillations and their parameters. (A) An example of a raw signal as recorded with a parietal EEG electrode is shown on the left. A stimulus was presented at time 0. The plot on the right shows the results of a time-frequency analysis in which the amplitude is depicted for each time-point (x-axis) and frequency band (y-axis). **(B)** Theta (4 Hz), alpha (10 Hz), and gamma (40 Hz) oscillations as extracted from the above raw signal by means of band-pass filtering. **(C)** The time-course of alpha (10 Hz) amplitude is shown. Amplitude can be computed from the Hilbert transform of the band-pass filtered signal. **(D)** Alpha phase at two different time points, (25 ms prior, and 25 after stimulus presentation) is illustrated.

1.2.1. Frequency (Fig. 1B)

Different brain networks are hypothesized to oscillate in different frequencies, with small networks oscillating in fast frequencies (>40 Hz) and large networks oscillating in slower frequencies (<20 Hz) (von Stein and Sarnthein, 2000; Buzsáki and Draguhn, 2004). Thereby, slower oscillations may represent brain networks of a higher hierarchy, encompassing multiple lower level networks, and thereby gating faster oscillations in a top-down manner (Lakatos et al., 2005; Lakatos et al., 2008). It is important to note that small and large networks do not refer to the Euclidian space covered by the neural network, but rather refer to the number of connections involved in a network. Thus, a fronto-parietal network with monosynaptic connections could be a small network, despite covering a distance of several centimeters.

1.2.2. Amplitude (Fig. 1C)

The amplitude of MEG/EEG oscillations is determined by the total number of active neurons and their synchrony, and gives an estimate of how many EPSPs arrive in a given neural assembly at a certain time point (Varela et al., 2001). Therefore, stimulus-induced increases and decreases in oscillatory amplitude have been termed event-related synchronization

and de-synchronization, respectively (Pfurtscheller and Aranibar, 1977; but see Hughes and Crunelli, 2007). Different frequencies, however, behave rather differently in response to sensory stimulation: alpha and beta (~15 Hz) oscillations typically decrease, whereas theta (~5 Hz) and gamma (~40 Hz) oscillations typically increase their amplitudes.

1.2.3. Phase (Fig. 1D)

The phase of an oscillation specifies the current position in a given cycle and triggers the timing of neural signals by providing fine grained windows of excitation and inhibition. Evidence for this assumption comes from studies using intracranial recordings in primates and humans which show that the probability of a single neuron to fire is not random with regard to the local field potential, but is triggered by its phase (Lee et al., 2005; Jacobs et al., 2007). Using phase information, two different measures of neural activity can be calculated: (i) phase consistency across single trials, and (ii) phase-coupling between EEG/MEG sensors or brain regions. Although these two measures are mathematically closely related, they reflect totally different neural processes and should not be confused. Phase-consistency across single trials measures the variability in phase at a certain time point at one

2.2. Theoretical accounts of the AB

Since the first report of the attentional blink in 1992 there have been a number of theories advanced as to its cause. All theories have in common the basic idea that attending to T1 for subsequent report causes T2 to fail to be encoded and/or retrieved. These accounts all place the attentional blink at a post-perceptual level, quite late in the information processing continuum, as evidenced by an early report (Luck et al., 1996) revealing that T2 is processed to the level of meaning in spite of its inability to be reported correctly on a significant percentage of trials. To briefly present a summary of these accounts, we group them into three categories.

The first category, ‘filter’ theories, is based on the notion that searching the RSVP stream for a match to the T1 target template (i.e., a white letter in the example above), causes the information processing system to suspend operation for a brief period of time when the match occurs. The suspended processing is argued to prevent interference arising from processing stimuli in the stream subsequent to the T1 target. This account was advanced in the original report by Raymond et al. (1992) and served as the basis for a recent model advanced by Olivers and Meeter (2008), where these investigators suggest the basis of the AB is a suppression of information processing following the inadvertent processing of the T1 mask. A different variation on filtering was proposed by Di Lollo et al. (2005) and Kawahara et al. (2006) who argued that the AB occurs when the filter invoked for processing T1 must be reconfigured to process T2. It is important to note that this first category of filtering models has in common the notion that the AB arises from a process encountered when the first target is detected with inherently less reliance on processes arising from the occurrence of T2.

The second category of theories has as their basis the notion that the AB arises from capacity limitations during the transfer of information to a durable form of memory (i.e., working memory), as required for later retrieval at the end of the trial (cf. Chun and Potter, 1995). Jolicoeur (1998, 1999) and Jolicoeur and Dell’Acqua (1998) embellished this notion by connecting it to the psychological refractory period (PRP; Pashler, 1994) phenomenon, arguing that T2 encoding must wait for the completion of critical stages involved in the processing of T1. A recent formal model of the Chun and Potter account has been advanced by Bowman and Wyble (2007) where they proposed that a representation (‘type’) of T1 and T2 can be accomplished under conditions producing an AB but that the episodic (‘token’) information required to segregate one target from the other cannot occur to T2 while T1 is still being processed. This second category of models is different from the first in that the focus is shifted to an interaction of processes between T1 and T2, though we note that Di Lollo’s theory does place a role on the reconfiguration of the filter in response to the occurrence of T2.

The third category of AB account contends the AB results from a failure to retrieve T2 from working memory, implying that it has successfully been encoded. This account was originally advanced by Shapiro et al. (1994) and later extended by Duncan et al. (1994) and Ward et al. (1996), arguing the two targets and their respective masks compete for retrieval to a stage where they become conscious, i.e., reportable. A related

idea has been advanced by Dehaene et al. (2003) who proposed a ‘global workspace’ model where a target must activate multiple brain areas in a reverberating manner for it to become consciously accessible. This third category of models is differentiated from the previous two by virtue of the emphasis on retrieval, rather than encoding, failure as the basis of the AB.

2.3. Brain oscillatory correlates of the AB

Although much has been learned about the processing of rapidly presented visual information from behavioral investigations using the AB paradigm, only relatively recently have there been serious attempts to use neuroscience approaches to understand the brain mechanisms underlying this phenomenon. To date there have been important findings revealed by the use of fMRI (cf., Marois et al., 2000, 2004; Shapiro et al., 2007) but the slow hemodynamic-dependent recovery associated with this approach presents formidable obstacles to real-time analysis. Indeed the rapid changes in brain function associated with the rapid information processing requirements of the AB paradigm necessitate a different approach. The use of EEG/ERP (e.g., Luck et al., 1996) and, more recently, of MEG (Gross et al., 2004) has stepped in to fill this void. Indeed, to return now to the principle theme of this review as regards the role of ongoing oscillations in the AB phenomenon, we conclude this section with a brief description of an MEG investigation into oscillatory mechanisms associated with the AB outcome.³

Gross et al. (2004; see also Gross et al., 2006) used a variant of the standard AB paradigm, requiring subjects to search for two specified black letters in a stream of black distractor letters. These investigators examined long-range synchronization between sources of brain activity (cf. Gross et al., 2001). As shown in Fig. 3A, brain oscillations in the lower beta range (15 Hz) were most responding to successful identification of a target (T1 or T2). Source analysis showed that this activity predominantly originated in bilateral frontal, bilateral posterior parietal, bilateral temporal, and the anterior cingulate and occipital cortical regions (Fig. 3B). As shown in Fig. 3C, the synchronization analysis revealed two different networks, a distractor related and a target related network. Of central interest was to examine the modulation of the target-related network with regard to the stimulus elements known to be involved in production of the AB, i.e., T1, T2, and their respective masks. As shown in Fig. 3D, trials were divided into the four possible types that could arise in the paradigm: distractor only, single target, dual target where T1 but not T2 was identified correctly (i.e., an AB occurred), and dual target where both targets were identified correctly (i.e., no AB occurred). These four trial types were examined for the degree of synchronization modulation (0–1 on the synchronization index, or SI) and de-synchronization (–1–0 SI) to the four

³ Note that several previous EEG studies also investigated brain oscillatory correlates of the AB (e.g. Keil and Heim, 2009; Keil et al., 2006; Slagter et al., 2009). However, these studies analyzed evoked (i.e. phase-locked) activity, and not measures of ongoing brain oscillatory activity (i.e. phase coupling, power) which is the primary focus of this review.

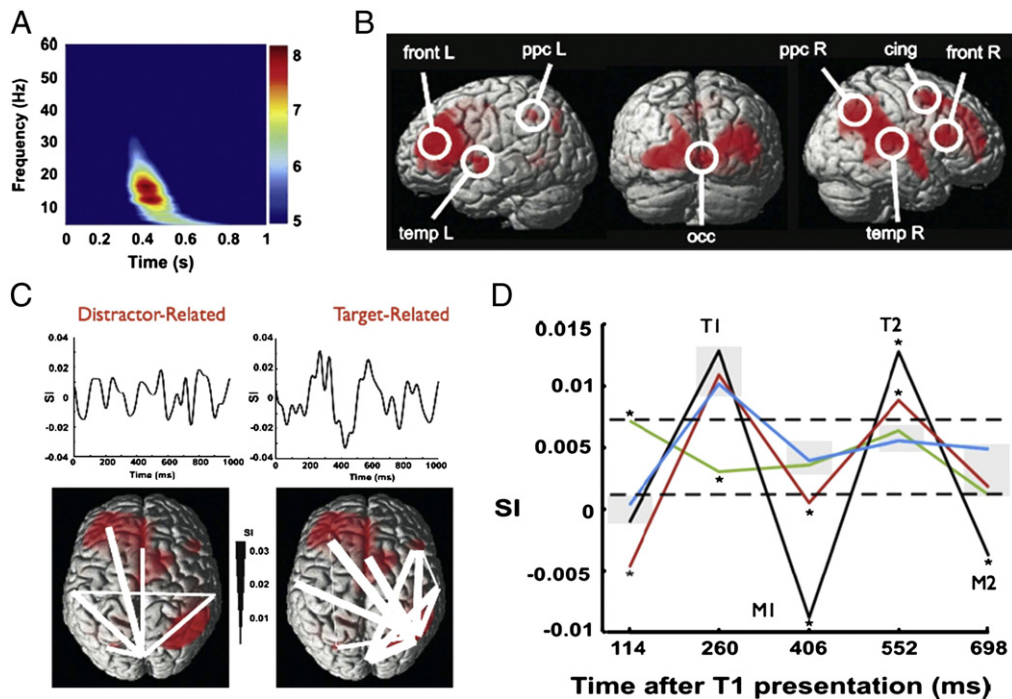


Fig. 3 – (A) Time-frequency representation (TFR) of target-related activity. TFRs timelocked to distractor presentation (at 0 ms) are subtracted from TFRs timelocked to target presentation and averaged across all MEG channels. Power is color-coded and expressed in standard deviations of power at baseline. The TFRs reveal a prominent power increase at around 15 Hz and 300–500 ms induced by targets. **(B)** Generators of this component can be identified in occipital and bilateral parietal, temporal and frontal areas (for details of source localization see Gross et al., 2004). **(C)** Phase synchronization (SI) at 15 Hz between all combinations of areas allows identification of two networks. One network shows similar modulation of synchronization to each stimulus (distractor and target, left panel) whereas the other network shows a pronounced modulation of synchronization to targets only (right panel). **(D)** Mean phase synchronization (SI) in the target-related network is shown for four conditions (black: both targets perceived, red: second target not perceived (AB), blue: only T1 was presented, green: no target was presented) in response to 5 stimuli around the first and second targets (T1: first target, M1: first mask, T2: second target, M2: second mask). Note the significant differences between the black line and the red line at the time of the first mask (M1), prior to the second target (T2).

Figure modified from Gross et al., 2004; copyright 2004 National Academy of Sciences, USA.

stimulus elements defined above, i.e., T1, T2, and the T1/T2 masks.

The results (Fig. 3D) reveal an equal amount of synchronization occurring whenever a target (T1 or T2) was identified correctly, suggesting synchronization reflects a brain-behavior correspondence to correctly identified targets. Unexpectedly, and of considerable interest, was the de-synchronization revealed on no-AB trials prior to the second target processing, presumably reflecting inhibition of the mask following T1. This was interpreted by Gross et al. to suggest that only when the deleterious effect of the mask is uncoupled from the target preceding it (i.e., via de-synchronization), can accurate target identification occur. As outlined below, this finding complements results from recent EEG studies (Hanslmayr et al., 2007; Kranczioch et al., 2007) showing that reduced long-range synchrony in the prestimulus interval predicts successful stimulus identification. In summary, rapidly changing patterns of synchronization and de-synchronization were revealed to index the behavioral outcomes found in the attentional blink paradigm. Specifically relevant for this

review is the finding that the synchronization pattern before T2 processing predicted whether or not an AB occurred.

An open question, however, is how these effects, which were found in the lower beta band, relate to alpha oscillations. One possibility would be that the frequency in which the AB effects are found, is related to the rate at which the RSVP stream is presented. In the study by Gross et al. (2004) the stimuli were presented at a rate of ~7 Hz, of which 15 Hz is very close to the first harmonic (14 Hz). A recent AB study by Kranczioch et al. (2007) presented their stimuli at a rate of 10 Hz and replicated the basic finding of Gross et al., in showing that decreased synchronization prior to the second target correlated with its perception. Interestingly, these effects emerged in the alpha frequency band (at 10 Hz), which might suggest that stimulation frequency partly determines the frequency band in which the AB effects occur. Moreover, in EEG/MEG data alpha and beta oscillations very often go hand-in-hand and it is hard to draw a clear line between upper alpha and lower beta. Likely these questions will be resolved by future studies.

3. Prestimulus alpha activity predicts visual perception

As mentioned above, three different parameters of prestimulus alpha oscillatory activity have been used successfully in several prior studies to predict the perception of a visual stimulus, (i) amplitude, (ii) phase at stimulus onset, and (iii) phase-coupling. The results of these studies are reviewed below.

3.1. Alpha amplitude

Alpha amplitudes are most evident in a resting condition prior to the presentation of a stimulus and typically decrease when a sensory stimulus is presented. Ongoing alpha amplitudes, however, do not stay at a consistently high level, but show a significant amount of variation. In continuous EEG/MEG recordings alpha oscillations typically exhibit a pattern of waxing and waning (Fig. 4A; Lopes da Silva, 1991). These characteristics led researchers to conclude that fluctuations in

alpha amplitude point to different behaviorally relevant brain states (Linkenkaer-Hansen et al., 2001). In line with this assumption recent studies reported that whether or not a visual stimulus will be perceived can be predicted on a trial-by-trial basis by prestimulus alpha amplitudes (Ergenoglu et al., 2004; van Dijk et al., 2008). In both studies visual stimuli were presented for a very short duration (3.3 ms and 16 ms, respectively), close to the sensory threshold, and not masked. Both studies revealed highly similar results in showing a negative correlation between alpha amplitude and perception performance. In both studies periods of high prestimulus alpha amplitude predicted a miss, whereas low alpha amplitude predicted a hit. This effect was most evident over parieto-occipital regions, and van Dijk et al. (2008) were able to localize these effects to the precuneus (~BA 7). Using transcranial magnetic stimulation (TMS) similar findings emerged. When TMS is applied over the visual cortex, subjects usually perceive an unstructured flash of light, termed phosphene. Romei et al. (2008) demonstrated that whether or not a phosphene is perceived depends on alpha amplitudes, with low amplitudes predicting phosphene perception. On a

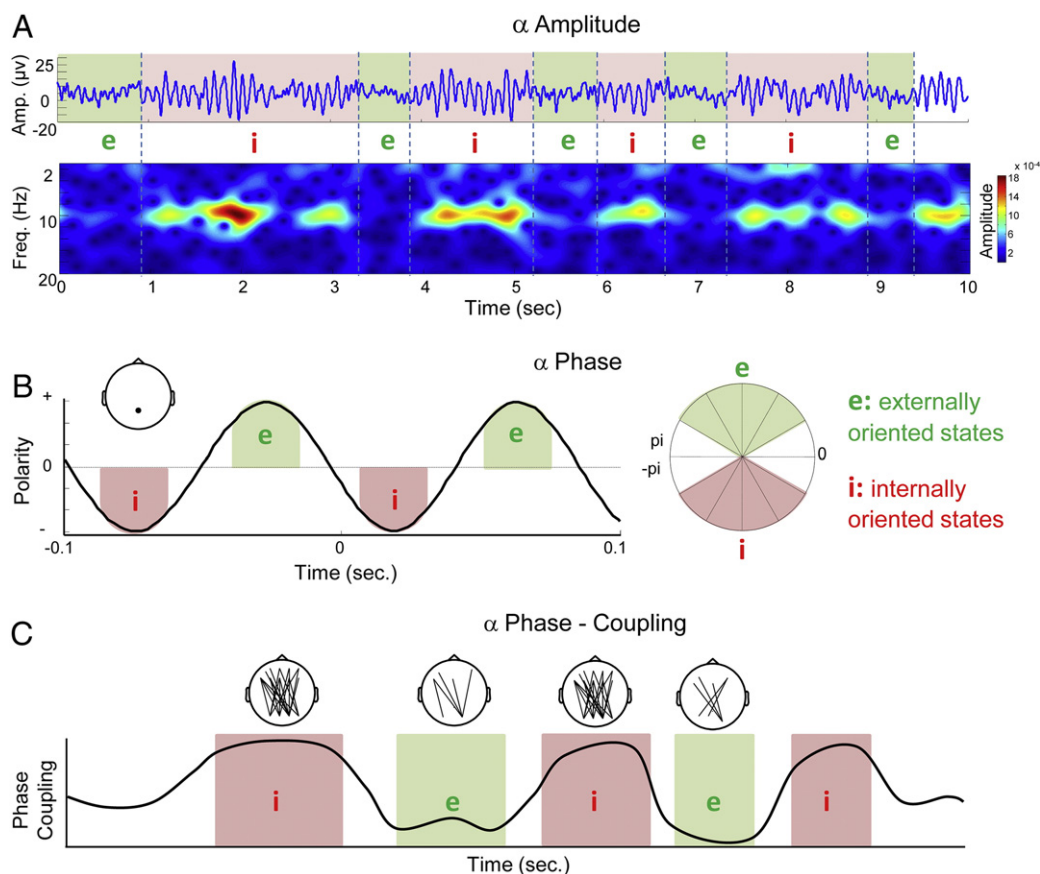


Fig. 4 – Three different parameters of alpha oscillatory activity indicate externally (e) and internally oriented (i) states. (A) The raw signal (upper panel) and time-frequency amplitude (lower panel) of a resting state EEG are shown for a parietal electrode. Note the waxing and waning pattern of alpha activity (10 Hz). Periods with low alpha amplitude indicate externally oriented states (green), whereas periods with high alpha amplitude indicate internally oriented states (red). (B) Alpha phase and its relation to externally (green) and internally (red) oriented states are shown. Peaks (positive polarity) indicate externally, and troughs (negative polarity) indicate internally oriented states. (C) Alpha phase-coupling and how it indicates externally and internally oriented states are illustrated. High periods of phase-coupling indicate internally oriented states (red), whereas low levels of phase-coupling indicate externally oriented states (green).

between-subjects level, comparable results were reported by Hanslmayr et al. (2007, 2005) who showed that subjects exhibiting poor performance in a visual perception task were characterized by high parieto-occipital alpha amplitudes.

The above cited studies investigated the role of prestimulus alpha amplitude utilizing a correlational approach, contrasting trials where the stimulus was perceived with trials where the stimulus was not perceived. Recently, a few studies have emerged that manipulated performance in a perception task by experimentally inducing states of high or low prestimulus alpha amplitude. Romei et al. (2010), for instance, employed repetitive TMS (rTMS) and were able to show that this type of stimulation applied at alpha frequency (and not in other frequencies) induced a decrease in visual perception performance (Romei et al., 2010). Another study used mood induction to manipulate prestimulus alpha amplitudes (Kuhbandner et al., 2009). Based on previous reports showing that mood is quite effective at modulating visual perception, with negative mood enhancing and positive mood decreasing performance (Phelps et al., 2006), Kuhbandner et al. reported that negative mood decreased, whereas positive mood increased, prestimulus alpha amplitude. Consistently, visual perception performance was better in the negative compared to the positive mood condition. These studies are a first hint that the relationship between prestimulus alpha amplitudes and perception is not a correlative but a causal one.

Taken together, the above reported findings provide strong evidence that alpha amplitude indicates different brain states, which have a bias either toward external or internal processing. Thereby, high alpha amplitudes may indicate internally oriented brain states, which make it hard for a briefly presented stimulus to be perceived; low alpha amplitudes may indicate externally oriented brain states, which bias the system toward processing information from the sensory channels (see Fig. 4A). In accordance with two recently proposed theories (Klimesch et al., 2007; Jensen and Mazaheri, 2010), the results suggest that parieto-occipital alpha amplitudes reflect the excitatory/inhibitory state of visual processing brain regions, thereby enhancing or diminishing, respectively, the likelihood of stimulus perception.

3.2. Alpha phase at stimulus onset

As mentioned above, the phase of an oscillation represents fine grained temporal windows of excitation and inhibition. It has been suggested that alpha oscillation in particular represents time frames of perception (Varela et al., 1981; VanRullen et al., 2006). It is thus reasonable to link the phase of alpha oscillations to the perceptual fate of a visual stimulus. Although a few recent studies have investigated this issue (Busch et al., 2009; Busch and VanRullen, 2010; Mathewson et al., 2009), the same idea was investigated far earlier (Varela et al., 1981; Callaway and Yeager, 1960; Dustman and Beck, 1965). For instance, Callaway and Yeager (1960) showed that faster responses to visual stimuli occur if the stimulus is presented at the positive phase of an alpha cycle (see Dustman and Beck, 1965; for similar results). Varela et al. (1981) presented two stimuli successively, with a very short interval in between, and showed that the subjects perceived the two stimuli as one, if they were presented at the positive peak of the alpha cycle.

Recently, Mathewson et al. (2009) reported comparable results by demonstrating that briefly flashed visual stimuli were more likely to be perceived when presented at the positive than when presented at the negative peak of the alpha phase. Interestingly, Mathewson et al. found that alpha phase predicted perception performance only in those trials where alpha amplitude was high. Thus, alpha phase and amplitude, though being mathematically independent measures, appear not to be empirically independent.

Similar results were reported by Busch et al. (2009) and Busch and VanRullen (2010), although their findings differ from the other studies in several ways: (i) Busch et al. found that alpha phase over fronto-central electrodes predicted perception performance, whereas other investigators (Mathewson et al., 2009; Varela et al., 1981; Callaway and Yeager, 1960) reported a parieto-occipital topography. (ii) In Busch et al.'s studies the effects were more pronounced around 7 Hz, at the crossover between theta and alpha frequency bands; not in the classical alpha band, around 10 Hz. (iii) Busch et al. failed to replicate the finding that the positive peak of the alpha cycle is optimal for perception performance, instead the phase of optimal perceptual performance varied considerably across subjects.

To our knowledge, only one study so far was designed to experimentally manipulate alpha phase at stimulus onset (Mathewson et al., 2010). In their study, Mathewson et al. presented a stream of stimuli flickering at 12 Hz, presumably inducing steady state visual evoked potentials in the alpha frequency range. A critical stimulus that had to be detected was presented at a variable interstimulus interval after the prestimulus flicker (32, 59, 82, 107, or 130 ms). The results showed that perception performance was best if the stimulus was presented at 82 ms, which exactly matches the period length of 12 Hz.⁴ Although Mathewson et al. (2010) did not measure the EEG, and thus cannot directly establish a link between alpha phase at stimulus onset and perception performance, their results are a first hint that the detection of a visual stimulus can be optimized by manipulating alpha phase at stimulus onset via steady state visual evoked potentials.

Despite the above reported discrepancies all studies come to the common conclusion that the phase of alpha oscillations represents temporally fine grained windows of internally or externally oriented brain states. The majority of these studies indicate that positive phases of EEG alpha oscillations over parieto-occipital regions indicate externally, whereas negative phases indicate internally oriented brain states (see Fig. 4B).

3.3. Alpha phase-coupling

Whereas several studies have explored how prestimulus alpha amplitude and phase at stimulus onset influence the perceptual fate of a visual stimulus, far fewer studies have investigated the role of prestimulus phase-coupling. One reason might be the extensive use of computational power that is required for calculating phase-coupling due to the many possible pairs of recording sites. For example a standard

⁴ The period length of a 12 Hz cycle is calculated as 1000 divided by 12, which is exactly 83.3 ms.

montage of 62 scalp EEG channels would result in 1953 possible couplings. Two recent studies, however, investigated the role of prestimulus phase-coupling on visual perception of a stimulus (Hanslmayr et al., 2007; Kranczioch et al., 2007).

In their study, Hanslmayr et al. (2007) presented one of four possible visual stimuli (p, b, d, or q) for a short duration (50 ms) and the subjects had to indicate which of the four stimuli they perceived. Contrasting trials in which the stimulus was perceived correctly, with trials in which the stimulus was not perceived, Hanslmayr et al. found a pronounced difference in prestimulus alpha phase-coupling. Perceived trials exhibited significantly lower levels of phase-coupling between frontal and parietal electrode sites than unperceived trials. Sorting the single trials according to prestimulus alpha phase-coupling, the authors showed that phase-coupling could account for a large range of the behavioral variance: ranging from 80% perception performance in the trials with lowest phase-coupling, to 40% perception performance in the trials with highest phase-coupling.

Kranczioch et al. (2007) utilized the attentional blink paradigm and investigated the difference between trials in which the second target was perceived correctly and in which the second target was missed. In line with the above cited findings, high levels of prestimulus alpha phase-coupling predicted a miss, whereas low levels of phase-coupling predicted correct perception of the second target stimulus. Whereas the two studies demonstrated that visual perception performance critically depends on the level of prestimulus alpha phase-coupling, no study has yet manipulated the levels of prestimulus phase-coupling experimentally.

Taken together, the above cited findings suggest that fluctuations in alpha phase-coupling indicate externally and internally oriented states, thus predicting the likelihood of whether a visual stimulus will be perceived or not. Therefore, high levels of alpha phase-coupling indicate internally oriented brain states, whereas low levels of alpha phase-coupling indicate externally oriented brain states (Fig. 4C).

4. Neurophysiological considerations of alpha oscillations

4.1. Alpha amplitude and phase at stimulus onset are controlled by thalamo-cortical loops

One of the main stations of the visual pathway is the lateral geniculate nucleus in the thalamus, in which information from the retina is transferred to the visual cortex by thalamo-cortical neurons. Several electrophysiological studies in animals revealed that dynamics in thalamo-cortical loops generate alpha oscillations in posterior brain regions (Lopes da Silva et al., 1980; Hughes et al., 2004; Hughes and Crunelli, 2007). Moreover, thalamo-cortical alpha oscillations gate signal transmission as demonstrated recently by Lorincz et al. (2009) who showed that the firing of thalamo-cortical neurons is phase-locked to the alpha cycle, with a majority of neurons firing at the negative peak of the alpha cycle. In humans, simultaneous EEG-fMRI studies demonstrated that fluctuations in alpha amplitudes are positively correlated with the BOLD signal in the thalamus (Sadaghiani et al., 2010;

Moosmann et al., 2003; Goldman et al., 2002). Moreover, intracranial recordings in human patients suggest that the pathological slowing of the alpha rhythm is due to abnormal thalamo-cortical network activity (Sarnthein et al., 2006; Sarnthein and Jeanmonod, 2007).

Together, these findings are consistent with the idea that alpha oscillatory amplitude and phase are generated by thalamo-cortical loops. By modulating alpha amplitude and phase at stimulus onset these loops likely gate the bottom-up flow of visual information from the thalamus to the cortex. As outlined above, alpha amplitude and phase at stimulus onset are not independent predictors of whether or not a visual stimulus will be perceived. Instead, the predictive role of alpha phase is positively correlated with alpha amplitude.⁵ Thus, alpha amplitude and phase at stimulus onset may both reflect externally oriented or internally oriented brain states at the thalamo-cortical level of the visual pathway, though in different time scales. Whereas alpha phase might reflect the fluctuations between these states at fast time scales, alpha power might reflect the more slower fluctuations between internally and externally oriented brain states.

4.2. Alpha phase-coupling reflects cortico-cortical communication

Phase-coupling between EEG/MEG sensors or brain regions can be regarded as a measure of communication between distant neural assemblies, because neuronal firing patterns are triggered by oscillatory phase (Canolty et al., 2010; Fries, 2005; Varela et al., 2001). Phase synchrony in the alpha frequency band in particular has been shown to reflect the top-down flow of information between cortical brain regions in cats (von Stein et al., 2000). In line with this result, a number of human EEG/MEG studies reported an increase in alpha phase-coupling during complex cognitive tasks, such as manipulation or maintenance of information in working memory (Sauseng et al., 2005; Palva et al., 2010), or perception of meaningful objects (Freunberger et al., 2008; Mima et al., 2001). Using sophisticated source localization methods Palva et al. (2010) demonstrated that alpha phase-coupling between fronto-parietal brain regions was parametrically modulated by visual working memory load and predicted individual working memory capacity. Such between-subject variations in working memory capacity have recently been shown to reflect successful filtering of relevant from irrelevant items during encoding and maintenance (Vogel et al., 2005). In visual perception paradigms, alpha phase-coupling between EEG sensors has been shown to index the perception of a meaningful object, which has been interpreted to reflect the integration of information into the semantic memory system (Freunberger et al., 2008).

Together, these studies strongly suggest that phase-coupling in the alpha frequency range may reflect top-down flow of information between cortical neural assemblies. Thereby, alpha phase-coupling likely indicates the action of higher order internal cognitive processes such as required

⁵ Note, however, that this effect can also arise from a higher signal to noise ratio in those trials with high alpha power.

during working memory or the perception of meaningful stimuli, as required by the AB task.

5. Explaining the attentional blink by alpha oscillations

To provide an account of the attentional blink in terms of alpha oscillations we begin with the assumption that in the typical AB paradigm, the series of events preceding T2 presentation, induces a brain state which is quite unfavorable for visual perception. Note, however, that the first target is also preceded by some of these events but is still much better perceived than T2, a point to which we will return below. Specifically, we contend that the AB paradigm influences all three parameters of alpha oscillatory activity such that they are maximally in their least favorable (i.e., internally oriented) state at the time the second target occurs. We unpack this argument as follows.

5.1. Alpha amplitudes

In the AB paradigm stimuli are usually presented at 10 Hz (ranging from 7 to 13 Hz). Stimulation at this frequency is known to induce steady state visual evoked potentials (Vialatte et al., 2010), which increase alpha amplitude at occipital brain regions. Although presently it is unclear whether such a stimulation induces neural activity that adds onto the ongoing intrinsic alpha oscillation, or whether it enhances alpha amplitudes by driving the intrinsic alpha oscillatory activity (Moratti et al., 2007), there is no doubt that such stimulation effectively enhances alpha amplitude over

visual processing regions. Previous studies demonstrated that ssVEPs increase in amplitude when attention is directed toward the stimulus stream (e.g. Müller and Hübner, 2002), which seems to be at odds with our argument that increased alpha power (e.g. due to ssVEPs) reflects an internally oriented processing mode. However, alpha oscillations might be in a resonant state during the AB task, as they are crucial for performing the task. Therefore, the external stimulus might lead to an increase of (internal) alpha power. As explicated above (Fig. 4A), this creates an unfavorable scenario for the perception of a visual stimulus.

5.2. Alpha phase at stimulus onset

By entraining the visual system in the alpha frequency range, the AB paradigm induces phase consistency over repeated trials, which can be seen in the ERP (Fig. 5). In Fig. 5 an example of an ERP dataset (averaged over 17 subjects) from our laboratory is shown for an occipital electrode (Oz) during a 10 Hz flickering stimulus. The data reveals strong phase locking to the stimulation frequency, as evident in the unfiltered ERP. Alpha oscillatory activity is entrained to the flickering stimulus such that the visual stimuli (squares) are presented exactly at the negative peak. As described above, this resembles an internally oriented brain state, which correlates with poor perceptual performance.

Thus, by presenting the stimuli at a regular frequency around 10 Hz the AB paradigm drives alpha amplitude and alpha phase at stimulus onset toward an internally oriented brain state, creating an unfavorable neural environment for the second target. Evidence to support this assumption comes from a recent behavioral study by Martin et al. (2011) who

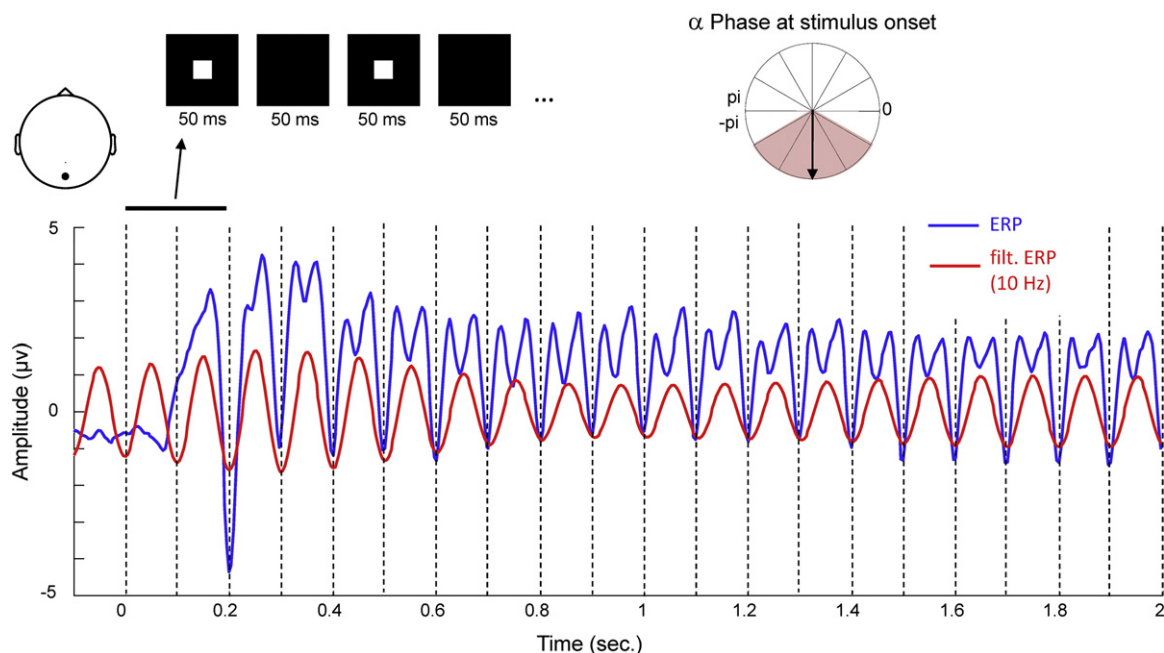


Fig. 5 – The ERP data (electrode Oz; averaged over 17 participants) is shown during a steady-state visual potential experiment. A stimulus (square) flickering at 10 Hz was presented. The blue line shows the unfiltered ERP, and the red line shows the bandpass-filtered ERP (8–12 Hz). Note, the constant negative phase at stimulus onset.

demonstrated that the AB effect can virtually be abolished by presenting the pretarget stimulus stream irregularly (using a random interstimulus interval). As such an irregular stimulation does not entrain alpha amplitude, nor does it induce phase consistency at stimulus onset, the results suggest that driving posterior brain regions in a 10 Hz frequency range is critical to obtain the AB.

Alpha amplitude and phase at stimulus onset, however, cannot alone explain why the AB occurs for the following two reasons: (i) Using a simplified version of the AB paradigm [Duncan et al. \(1994\)](#) presented only two targets successively, each masked, and separated by the same SOAs normally used to index the AB. Despite the fact that no pretarget stimulus stream was presented, the results revealed a prominent AB for the second target if presented around 250 ms after the first target. These results demonstrate that the induction of alpha evoked activity preceding the target presentation is not required for obtaining the basic pattern of the AB. (ii) In typical AB experiments 8 to 15 distracter items are presented before the first target. Alpha amplitude and phase at stimulus onset can thus be expected to resemble an internally oriented brain state already at the time the first target is shown. The first target, however, is usually perceived well, in 90% of the trials.⁶ Therefore, a third process, probably triggered by the perception of the first target must come into play to explain why the AB occurs.

5.3. Alpha phase-coupling

Phase-coupling in the alpha frequency range between frontal and parietal brain regions is typically triggered by complex cognitive processes such as working memory, or perception of a meaningful stimulus. In the AB paradigm perception of the first target likely relies on such processes. As outlined in section two, successful identification of a target stimulus requires the match between a template held in working memory and between the representation in posterior visual processing regions ([Enns and Di Lollo, 2000](#)). Because the target is quickly followed by a mask, this match has to be made internally within the working memory system. Thus, the perception of the first target likely induces an increase in cortico-cortical communication as reflected by alpha phase-coupling, which drives the brain toward an internally oriented state at the time the second target is presented. Indeed, [Mima et al. \(2001\)](#) showed that successful identification of a visual stimulus triggers increased alpha phase-coupling peaking at 250 ms, which perfectly mirrors the time course of the AB ([Fig. 2B](#)). As previously suggested, it is an externally, not internally, oriented brain state that is optimal for detection/identification of a sensory stimulus, thus conditions are in effect to bring about an attentional blink.

⁶ In the study by [Martin et al. \(2011\)](#) perception of the first target was reduced in the condition in which the pretarget stimuli were presented at a regular rate, compared to the condition in which an irregular stimulation frequency was used. These results further corroborate our assumption that inducing alpha oscillatory activity via ssVEPs drives the brain toward an internally oriented state.

6. Conclusions

Integrating recent studies, which reveal a strong link between ongoing alpha activity and perceptual performance, the current review suggests that the AB outcome can well be predicted by alpha oscillations. In particular, the rapid serial visual presentation aspect of the AB paradigm as the brain struggles with the first target drives alpha amplitude, phase at stimulus onset, and phase-coupling toward an internally oriented state, which makes it difficult for briefly presented stimuli to be perceived. Although performance for the second target is markedly reduced, it is important to note an AB is obtained in only about 50% of the trials,⁷ revealing the stochastic nature of the underlying brain processes creating the AB. However, the question of why an AB is obtained in some trials and not on other trials is not yet resolved. The currently proposed framework suggests that by combining the three different parameters of alpha oscillatory activity the occurrence of an AB can be predicted on a single trial level.

An intriguing remaining question is whether some parameters of alpha predict the occurrence of the AB better than others. Based on the above described studies, two hypotheses could be supported: (i) Alpha phase coupling is more critical than alpha power and phase. This hypothesis can be supported by the behavioral study by [Duncan et al. \(1994\)](#) which suggests that alpha amplitude and phase at stimulus onset alone cannot explain why the AB occurs. Moreover, phase-coupling has been shown to predict with very high accuracy whether or not a briefly presented visual stimulus is perceived ([Hanslmayr et al., 2007](#)). Assuming that alpha amplitude and phase at stimulus onset reflect thalamo-cortical activity, and that alpha phase-coupling reflects cortico-cortical communication, this hypothesis would be consistent with the finding that cortical processing is much more driven by cortico-cortical loops, than by thalamo-cortical loops⁸ ([Douglas and Martin, 2007](#)). (ii) The second hypothesis is that alpha power and phase are more critical than alpha phase coupling. Importantly, the first hypothesis assumes that alpha power and phase are not influenced by the cognitive processes triggered by the presentation of the first target. As no study has yet examined how the processing of the first target affects alpha power and phase consistency, we cannot rule out the possibility that the processing of T1 drives these two parameters even more strongly toward an internally oriented processing state. These hypotheses can be tested by future studies, hopefully shedding light onto the unresolved issues.

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⁷ In AB experiments the false alarm rate is typically quite low (around 10%) which indicates that the subjects correctly perceive the second target in about half of the trials.

⁸ Only 10–20% of the input layers in the cortex are thalamocortical, with the rest originating from other cortical pyramidal cells.

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