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Review

Not so different after all: The same oscillatory processes support different types of attention

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ABSTRACT

Scientific research from the last two decades has provided a vast amount of evidence that brain oscillations reflect physiological activity enabling diverse cognitive processes. The goal of this review is to give a broad empirical and conceptual overview of how ongoing oscillatory activity may support attention processes. Keeping in mind that definitions of cognitive constructs like attention are prone to being blurry and ambiguous, the present review focuses mainly on the neural correlates of 'top-down' attention deployment. In particular, we will discuss modulations of (ongoing) oscillatory activity during spatial, temporal, selective, and internal attention. Across these seemingly distinct attentional domains, we will summarize studies showing the involvement of two oscillatory processes observed during attention deployment: power modulations mainly in the alpha band, and phase modulations in lower frequency bands.

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1. Introduction

In approximately the last two decades, we have witnessed an impressive transformation of the assigned functional role of brain oscillations from an irrelevant background activity to a fundamental process that enables diverse cognitive processes. One of the main domains for changing this view has been research relating oscillatory processes to attention. The aim of the present review is to give a broad overview of how ongoing oscillatory activity may support attention processes (for in-depth reviews of specific issues see Foxe and Snyder, 2011; Jensen et al., 2007). Despite the over-cited Jamesian quote that "everyone knows what attention is" (James, 1890), researchers struggle to precisely define attention. Given the wobbly nature of the definition of attention, it is surprising how often one encounters discussions in cognitive neuroscience in which the work of someone is criticized as being 'confounded by attention'. Keeping in mind that definitions of constructs like attention are prone to being blurry and to evolve, in the present review we follow the pragmatic view of Summerfield and Egner (2009) by defining attention as a mechanism that "alleviates computational burden by prioritizing processing of that subset of [sensory] information deemed to be of the highest relevance to the organism's goals". Even though this definition includes endogenously employed attention ('top-down') as well as attention exogenously attracted to highly salient stimuli ('bottom-up'), we will specifically focus on 'top-down' effects. Specifically, we will summarize studies on two oscillatory mechanisms that are typically discussed independently and likely support top-down neural processes across a variety of attentional subdomains: namely power modulations mainly in the alpha band (see, e.g., Foxe and Snyder, 2011), and phase modulations in low frequency bands including the delta to alpha bands (see, e.g., Schroeder and Lakatos, 2009).

After the discovery of the occipital alpha rhythm (~8–12 Hz) by Berger (1929), oscillatory activity in similar frequency bands was reported also in the somatosensory modality, originally called 'mu' (Hari and Salmelin, 1997), and the auditory modality, denoted 'tau' (Lehtelä et al., 1997). Despite initially different names and slightly different frequency bands, evidence accumulated that suggested diverse alpha rhythms may reflect a modality-independent function. Contrary to earlier notions relating to states of 'brain idling' (Pfurtscheller et al., 1996), more recent theoretical approaches (Jensen and Mazaheri, 2010; Klimesch et al., 2007) grant oscillatory alpha activity an active role in cognitive processing. In particular, it is conceived that alpha is fundamental in inhibiting task-irrelevant regions and gating information throughout a distributed cortical architecture (see Box 1). Thus modulations of alpha power appear to enable the above mentioned aspect of 'prioritizing' (Summerfield and Egner, 2009) distinct neuronal assemblies as well as neural communication patterns. Consequently, it comes as no surprise that alpha power effects are consistently observed across diverse attentional domains, such as spatial, selective, and internal attention (Chapters 2, 4 and 5, respectively).

However, not only power but also phase of ongoing oscillatory activity is crucial for cognitive processing, as cortical excitability depends on the phase of neural oscillations (e.g., Lindsey, 1952). Attention can modulate the phase such that upcoming stimuli coincide with a phase of increased excitation. While this statement holds for isolated stimuli, its experimental investigation frequently employs rhythmic stimulation putatively 'entraining' the naturally occurring rhythms. The core notion is that oscillatory phase becomes aligned to rhythmic sensory stimulation(e.g., Spaak et al, 2014; for a critical discussion see Keitel et al., 2014). However, the exact phase relationship between stimulus and neural response is not only subject to bottom-up input, but can be modulated by attentional demands in order to optimize behavior. Research on temporal, selective, and internal attention (Chapters 3–5) delivered convincing evidence for phase modulation by attention.

In the present review, we will discuss modulations of oscillatory brain activity during different flavors of attention. In particular, we will focus on two main mechanisms observed during attention employment – alpha power modulations and phase resetting/entrainment – and aim to elucidate their relative contribution. To this end, we will adhere to the conventional psychological division of attention to aid the reader with integrating this review and the cited literature. Thus, the following sections will focus on a) spatial attention, in which participants attend to a spatial

location or body part, b) temporal attention, in which they attend to a point in time, c) selective attention, in which they either attend to a modality or one feature within a modality, and d) internal attention, in which they attend to an internal representation during working memory performance. However, in spite of this division, the discussed electrophysiological studies provide evidence that both mentioned oscillatory mechanisms play a role in all types of attention. In the discussion we therefore argue that for the neuroscientific study of attention, a division according to oscillatory mechanisms would be more sensible.

Box 1: Theories relating oscillations to attention

The main goal of this review is to give a broad overview of how attention processes are supported by ongoing oscillatory activity. While discussing the two major observations in neuroelectrophysiological attention research – power modulations and phase alignment – we refer to some well-established theoretical frameworks about oscillatory activity and attention. Here, we shortly summarize the main proposition of each theory.

Inhibition-timing hypothesis

The inhibition-timing hypothesis (Klimesch et al., 2007) postulates that oscillations in the alpha band reflect an inhibitory, top-down controlled mechanism. Based on the inherent nature of oscillatory activity, the hypothesis further states that this mechanism exerts its influence in a pulsed manner. Thus, increased alpha power controls cognitive processing and its timing, whereas decreased alpha power reflects a release of functional inhibition.

Gating by inhibition hypothesis

The gating-by-inhibition hypothesis (Jensen and Mazaheri, 2010) proposes that information processing along sensory pathways is regulated by fluctuating alpha band power in sensory and higher-order areas. In line with the inhibition-timing hypothesis (Klimesch et al., 2007), this framework postulates that alpha oscillatory activity represents an inhibitory mechanism, which blocks information processing within one area in a pulsed manner. In addition, it emphasizes that by doing so, alpha oscillations 'gate' the information into other, less strongly inhibited regions. Thus, oscillatory activity in the alpha band can serve as a guide through the neural system by selectively inhibiting irrelevant areas along the sensory pathway. On the other hand, the gating-by-inhibition hypothesis states that active processing within a given area is reflected by alpha power decreases accompanied by gamma power increases.

Oscillatory selection hypothesis and active sensing

The oscillatory selection hypothesis (Schroeder and Lakatos, 2009) states that attention can exploit the rhythmic nature of many environmental stimuli by forcing oscillatory brain activity to align with the sensory rhythm. By doing so, relevant stimuli will hit the system when it is in a more excitable state, benefitting stimulus processing. Furthermore, the oscillatory selection hypothesis postulates that attention will operate in such a 'rhythmic mode' whenever the incoming to-be-attended stimuli are rhythmic in nature. If this is not the case, attention will operate in a 'continuous processing mode'; the hypothesis proposes that this second mode is characterized by extended gamma power increase.

The concept of 'active sensing' is closely related to the oscillatory selection hypothesis, and, in the context of neuroscientific research, was also coined by Schroeder et al. (2010). Despite classic examples of active sensing in biological systems being well-known, including echo- and electro-location, other sensory systems (such as vision and audition) are traditionally regarded as passive (Schroeder et al., 2010). In contrast, active sensing is based on the observation that most sensory processing is controlled by rhythmic motor and sampling routines. Even if environmental stimuli are not rhythmic in nature, this sampling results in a rhythmic input to sensory systems, which can be consequently exploited by attention manipulation of inherent oscillations in these systems (as stated in the oscillatory selection hypothesis described above).

2. Spatial attention

Spatial attention is commonly investigated using the Posner paradigm, in which subjects are cued to attend to one of two spatial locations (Posner, 1980; see Fig. 1 for common designs). Shortly after the presentation of the cue, a target is shown in one of the two spatial locations, either congruent or incongruent to the cue (resulting in valid and invalid trials), to which participants have to react as fast as possible. Effects of successful attention deployment can then be studied by comparing reaction times in valid and invalid trials. Of particular interest in the study of attention is the post-cue time period, in which participants covertly shift their attention to the indicated location in the absence of any other external stimulation. Variations of the Posner paradigm can include more than two spatial locations of which one has to be attended, crossmodal tasks in which the cue is presented in a different modality then the target, or tasks more difficult than simple stimulus detection tasks. In the following section we will discuss modulatory effects of spatial attention on oscillatory activity and task performance in the visual, the somatosensory, and the auditory modality.

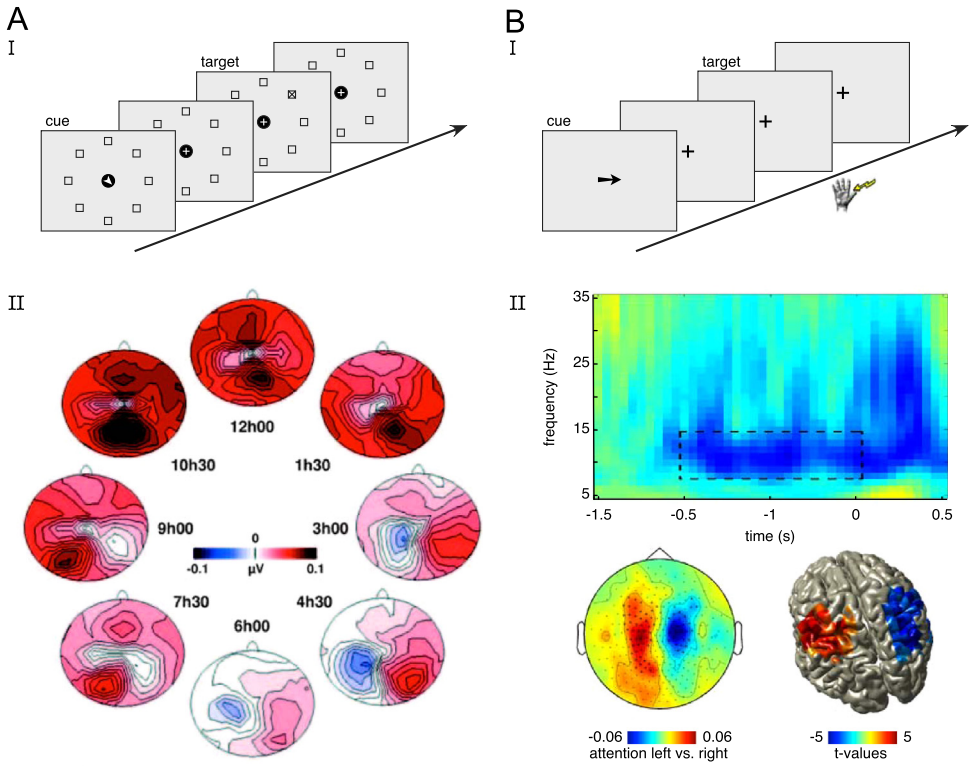

Fig. 1 – Alpha power modulations in visual (A) and tactile (B) spatial attention tasks. A (I) Depiction of one trial of a visual spatial attention task. Participants were cued by a central arrow (80 ms) to attend to one of eight peripheral locations. After a fixed prestimulus interval (1300 ms), a go-stimuus (x) or a no-go-stimulus (+) was presented in the cued (88%) or uncued (12%) location for 80 ms. (II) Prestimulus map topographies of baseline-normalized [log $_{10}$(prestimulus/precue)] alpha power changes. The display shows the data for all cued and attended spatial locations over the entire electrode array from −250 ms to stimulus onset. The topographies clearly indicate specific retinotopically organized alpha power increases ipsilateral to attended location. Reproduced with permission from Rihs et al. (2007). B (I) Depiction of one trial of a tactile spatial attention task. Participants were cued by a central arrow to attend to either left or right thumb. After a variable prestimulus period (1–1800 ms), participants had to discriminate between two possible frequencies of electrically presented pulse trains. (II) Prestimulus alpha power lateralization (attend left versus right hand) for 100% validly cued trials. The time-frequency representation shows alpha band power averaged across the significant sensors identified in a sensor-level analysis (using the same scale). The source reconstruction shows lateralized alpha activity in the sensorimotor cortex. Reproduced with permission from Haegens et al. (2011).

2.1. *Spatial attention modulates power of ongoing oscillatory activity in the cue-target interval*

Covertly orienting attention to a specific spatial location results in alpha band power modulations prior to target presentation in sensors over the corresponding sensory region. During visuospatial attention, alpha modulation is seen over posterior recording sites (Bauer et al., 2012; Busch and VanRullen, 2010; Frey et al., 2014; Händel et al., 2011; Kelly et al., 2006; Rihs et al., 2007; Roijendijk et al., 2013; Sauseng et al., 2005; Thut et al., 2006; Trenner et al., 2008; Worden et al., 2000; Wyart and Tallon-Baudry, 2008; Yamagishi et al., 2008, 2005, 2003; see Fig. 1A) and in visual areas (Buffalo et al., 2011; Fries et al., 2008, 2001) during somatosensory spatial attention over somatosensory cortices (Anderson and Ding, 2011; Bauer et al., 2012; Haegens et al., 2012, 2010; Jones et al., 2010; Van Ede et al., 2011, 2010; Zhang and Ding, 2010; see Fig. 1B). During audiospatial attention, alpha modulation is observed over temporal (Weisz et al., 2014) and parietal regions (Frey et al., 2014; Gomez-Ramirez et al., 2011). Some of these alpha modulations originate from sensory areas, as has been shown using source reconstruction (e.g., vision – Händel et al., 2011; somatosensory – Haegens et al., 2012; auditory – Frey et al., 2014).

Alpha band modulations are not only broadly observable during spatial attention, but they are also highly specific in their neuroanatomical location and their timing with respect to target occurrence. During visuospatial attention, alpha modulation was shown to be not only lateralized corresponding to the attended hemifields, but also retinotopically specific (Rihs et al., 2007; Worden et al., 2000; see Fig. 1A). Similarly, alpha/beta band modulations over somatosensory cortices during somatosensory spatial attention are lateralized (Bauer et al., 2012; Haegens et al., 2012, 2011; van Ede et al., 2011, 2010; see Fig. 1B) and topographically specific, with modulations in the hand and foot representation of the primary somatosensory cortex during attention to the corresponding body parts (Jones et al., 2010). Modulation of oscillatory activity near 10 Hz becomes evident after around 400 ms post-cue with increasingly stronger effects towards

target presentation in the visual (e.g., Foxe and Snyder, 2011; Thut et al., 2006; Worden et al., 2000), somatosensory (e.g., Bauer et al., 2012; van Ede et al., 2012, 2011) and auditory modality (e.g., Frey et al., 2014).

Furthermore, the observed modulations are specific to the attended modality and independent from cue modality. Whereas cue and target stimulus had the same modality in most visuospatial attention studies (but see Thut et al., 2006; Trenner et al., 2008), in somatosensory spatial attention studies cues were either visual (Anderson and Ding, 2011; Bauer et al., 2012; Haegens et al., 2012, 2011) or auditory (van Ede et al., 2012, 2011; Whitmarsh et al., 2014), and in audiospatial attention studies mostly visual (Frey et al., 2014; Müller and Weisz, 2012). Importantly, the main effects of covert spatial attention on post-cue oscillatory (alpha and beta band) activity were not affected by cue modality. On the contrary, they correspond well with the effects found in studies using unimodal attention paradigms. Taken together, these studies provide evidence for attention-dependent spatially, temporally and modally specific modulations of ongoing alpha oscillatory activity.

2.2. *Spatial attention can have effects across modalities and in supramodal regions*

Interestingly, the effects of spatial attention on post-cue oscillatory activity have been reported not only in sensory regions processing the cued but also in other – uncued and therefore effectively unattended – modalities. These effects were most often observed over occipital areas, for instance, during somatosensory (Anderson and Ding, 2011; Bauer et al., 2012, 2006; Haegens et al., 2012) and during audiospatial attention tasks (Frey et al., 2014). In the latter study, effects were found in parietal- and occipital cortex, some of which were specific for audiospatial attention. Similar activation of posterior regions during audio- and visuospatial attention indicates the involvement of a supramodal attention system (see Banerjee et al., 2011). Alpha power modulations in primary visual and parietal areas specifically affected by audio- but not visuospatial attention additionally indicate an involvement of the visual system or posterior auditory association areas during audiospatial attention. Overall, in addition to the findings discussed above, spatial attention can also modulate primary sensory areas of unattended modalities and supramodal regions.

2.3. *Function of alpha power modulations: target facilitation and distractor inhibition*

Whereas some studies in the visual modality reported alpha power decrease in the cue-target period contralateral to the attended side in human participants (Bauer et al., 2012; Roijendijk et al., 2013; Sauseng et al., 2005; Thut et al., 2006; Trenner et al., 2008; Wyart and Tallon-Baudry, 2008; Yamagishi et al., 2008, 2005), and in monkeys (Buffalo et al., 2011; Fries et al., 2008, 2001), other studies have reported an ipsilateral alpha power increase (Busch and VanRullen, 2010; Händel et al., 2011; Kelly et al., 2006; Rihs et al., 2007; Worden et al., 2000; Yamagishi et al., 2003). Similarly, in the somatosensory modality, most studies reported a contralateral decrease of alpha power (Haegens et al., 2010), alpha and beta power (Anderson and Ding, 2011; van Ede et al., 2012, 2011), or of beta power only (Bauer et al., 2012; van Ede et al., 2010). None of the somatosensory spatial attention studies reported solely ipsilateral alpha/beta power increases; however, Haegens et al. (2012) observed both (ipsilateral increase and contralateral decrease) in the alpha band simultaneously, and Jones et al. (2010) reported additional ipsilateral increase in the beta band over the hand area when attention was directed to the foot. Although all of these studies show an attention-related modulation of alpha (and beta) power prior to target presentation, it remains unclear which mechanism is the driving force of the observed effects: power increases, power decreases, or both.

These findings could reflect divergent but complementary processes that depend on the task requirements (Rihs et al., 2007; Thut et al., 2006; Worden et al., 2000). Rihs et al. (2007) suggested that in spatial attention, functional inhibition ipsilateral to the attended side gains importance if strong distractors on the unattended side have to be suppressed. Indeed, in the studies reporting ipsilateral alpha power increases, tasks were generally demanding and inhibiting strong distractors was essential for task performance (Busch and VanRullen, 2010; Händel et al., 2011; Kelly et al., 2006; Rihs et al., 2007; Worden et al., 2000; see Fig. 1A). This was also the case in the two somatosensory spatial attention studies, which reported additional alpha (and beta) power increases (Haegens et al., 2012; Jones et al., 2010). Moreover, some studies reported an advantage in task performance in the left hemifield (Thut et al., 2006; Worden et al., 2000), and more alpha power over left posterior recording sites (Rihs et al., 2007; Thut et al., 2006). Due to these baseline differences, Thut et al. (2006) proposed to use the normalized difference between the hemispheric alpha power as a lateralization index to express attention-related power modulations (see also next section). It was argued that the lateralization index reflects momentary visuospatial alpha power (Thut et al., 2006) or an individual's ability to attend one location and suppress distracting input from another location (Händel et al., 2011).

Taken together, the modulations of oscillatory alpha activity due to spatial attention are often evident as power suppression contralateral to the attended side. However, depending on task demand and baseline differences between the hemispheres, alpha power can also be ipsilaterally increased, which is thought to reflect active suppression of strong distracting information on the unattended side.

2.4. *Spatial attention and attention-related alpha/beta band activity modulate behavior and evoked neural activity*

Spatial attention has been shown to influence evoked responses during a somatosensory oddball task (Anderson and Ding, 2011), to decrease post-target alpha power (Händel et al., 2011), and to increase post-target gamma band activity (Bauer et al., 2006; Fries et al., 2008, 2001). Furthermore, spatial attention reduces reaction time (Frey et al., 2014; Haegens et al., 2010; Rihs et al., 2007; Wyart and Tallon-Baudry, 2008), increases visual stimulus detection (Wyart and Tallon-Baudry, 2008), improves task performance in a vibrotactile discrimination task (Haegens et al., 2010), and

improves performance in a tactile pattern discrimination task (van Ede et al., 2012). Interestingly, spatial attention has been shown to modulate task performance in a rhythmic pattern at around 4 and 7–10 Hz, indicating an underlying reset of low-frequency oscillatory activity (Landau and Fries, 2012).

Several studies have shown that attention-related oscillatory activity in the cue-target interval has effects on neuronal activity after stimulation presentation. For instance, Jones et al. (2010) reported an increase in magnitude of the evoked response after stronger pre-target alpha/beta suppression. Similarly, Anderson and Ding (2011) found a positive linear and a quadratic relationship between pre-target mu, and the P1 and N1 components of the evoked response, respectively. Furthermore, pre-target alpha modulation reduces target induced alpha (Händel et al., 2011) and theta power (Yamagishi et al., 2003), and enhances beta (Yamagishi et al., 2003) and gamma power (Buffalo et al., 2011; Fries et al., 2008, 2001; Wyart and Tallon-Baudry, 2008). Moreover, pre-target alpha power and alpha phase have both been shown to influence evoked global field power (Busch and VanRullen, 2010).

Concerning task performance, reaction time shortens after greater pre-target alpha suppression (Thut et al., 2006; Trenner et al., 2008 only for left targets). Thut et al. (2006) additionally reported a trial-to-trial correlation between the alpha lateralization index and reaction time for left and right targets. Visual perceptual sensitivity is influenced by pre-target alpha lateralization in invalidly cued trials (Händel et al., 2011), and by lower pre-target alpha power and higher inter-trial coherence (Yamagishi et al., 2008). Visual stimulus detection rate is predisposed by pre-target alpha phase (Busch and VanRullen, 2010; Thut et al., 2006), and is rhythmically modulated by visuospatial attention at 8 Hz (Landau and Fries, 2012) implying a phase reset of oscillatory alpha activity. In the somatosensory domain, alpha (beta) suppression in the cue-target interval contralateral to the attended side or a greater alpha lateralization improved vibrotactile discrimination performance (Haegens et al., 2012, 2010), stimulus detection (Jones et al., 2010), and tactile pattern discrimination (van Ede et al., 2012).

However, in contrast to simple reaction time, stimulus detection depends not only on preparatory processes, but also on reflexive reorienting (Thut et al., 2006; van Ede et al., 2012), which could account for generally high detection accuracy in invalid trials, despite longer reaction times. According to van Ede et al. (2012), reflexive reorienting is only effective if the stimulus is still present or easily retrieved from memory and at longer cue-target interval. They propose a preparatory mechanism reflected by post-cue alpha power modulations affecting task performance and reaction times at longer cue-target intervals, and a non-preparatory mechanism only affecting reaction times at very short cue-target intervals. Overall, these effects on evoked and induced neural activity and task performance are thought to reflect more efficient and efficacious stimulus processing (Fries et al., 2008, 2001).

2.5. *Conclusion*

Overall, spatial attention modulates oscillatory alpha (and in somatosensory tasks also beta) band activity after the presentation of a spatial cue. This modulation is independent from cue modality and is spatially, temporally and modally specific to the target. It is thought to reflect an active process, either suppressing sensory distractors on the unattended side (ipsilateral alpha power increases), enhancing stimulus processing on the attended side (contralateral alpha power decreases), or both. Furthermore, alpha (and beta) power modulation has been shown to correlate with evoked global field power and oscillatory activity in various frequency bands, and with task performance. Therefore, power modulations of alpha (and beta) band oscillatory activity reflect an anticipatory mechanism beneficial for perception, making stimulus processing more efficient and efficacious.

3. Temporal attention

In contrast to spatial attention tasks, in which attention is directed to a specific spatial location or a body part, in temporal attention tasks, attention is directed towards one specific point in time or towards a time interval (for a recent comprehensive review on temporal attention see Henry and Herrmann, 2014). Similar to other types of attention, cueing paradigms are often used to indicate the temporal point or interval towards which attention has to be directed. Attention to specific time points is strongly influenced by the hazard function of the paradigm and thereby highly related to expectation. A hazard function is defined as the conditional probability of an event occurring at a specific time given that it has not yet occurred (Nobre et al., 2007). For instance, if a stimulus is presented at one of two time points with equal probability, the probability of the first time point is 0.5, whereas when the stimulus does not occur at the first time point, the probability increases to 1 for the second.

Whereas temporal attention has been studied using fMRI (Coull and Nobre, 1998; Coull et al., 2000; Griffin et al., 2001; Henry et al., 2013) and electrophysiology with a focus on event-related potentials (Griffin et al., 2002, 2001; Miniussi et al., 1999), not many studies have looked at modulations of oscillatory activity (Henry and Obleser, 2012; Stefanics et al., 2010; van Ede et al., 2011).

3.1. *Temporal attention modulates ongoing oscillatory activity*

In a temporal attention task using tactile stimuli, participants were required to perform a pattern detection task on either the left or the right hand (van Ede et al., 2011). In one condition, stimuli were presented at one of two specific time points (1 or 3 s after the cue), whereas in a second condition, stimuli were presented 1, 2, or 3 s after the cue. In both conditions, hazard rates were manipulated so that they only differed on the last time point. Whereas the probabilities in the two-point condition were set to 0.33 and 1, in the three-point condition they were set to 0.33, 0.66, and 1. van Ede et al. (2011) showed that, similar to spatial attention, temporal attention to specific points in time results in alpha and beta power modulations. Specifically, they showed alpha and beta power suppression contralateral to the attended hand. Whereas alpha power modulations were only observed for the two-point hazard rate, and, therefore, could also reflect spatial attention, beta power was modulated in both

conditions with strongest contralateral suppression shortly before a potential event. These findings provide evidence for general anticipatory activity underlying spatial as well as temporal attention.

In another study investigating the effects of temporal attention on ongoing oscillatory activity, Stefanics et al. (2010) used a cueing paradigm to direct participants' attention to one of two specific time intervals, after which auditory target tones were presented. Each cue had a reliability of 0.8, that is, in 0.2 of the trials, the target tone was presented after the uncued time interval. As a result, the probability for the target tone presentation at the second time point was 1 in all trials, whereas for the early time point it was 0.8 after a short cue and 0.2 after a long cue. The authors reported a higher delta phase concentration and delta power prior to high-probability targets after the short interval. Thus, this study provides evidence that not only power but also phase of ongoing oscillatory activity is modulated by attention directed to specific temporal intervals. In support of this finding, a recent working memory study reported a phase adjustment prior to a temporally predictable distractor presentation in the alpha band (Bonnefond and Jensen, 2013, 2012; see

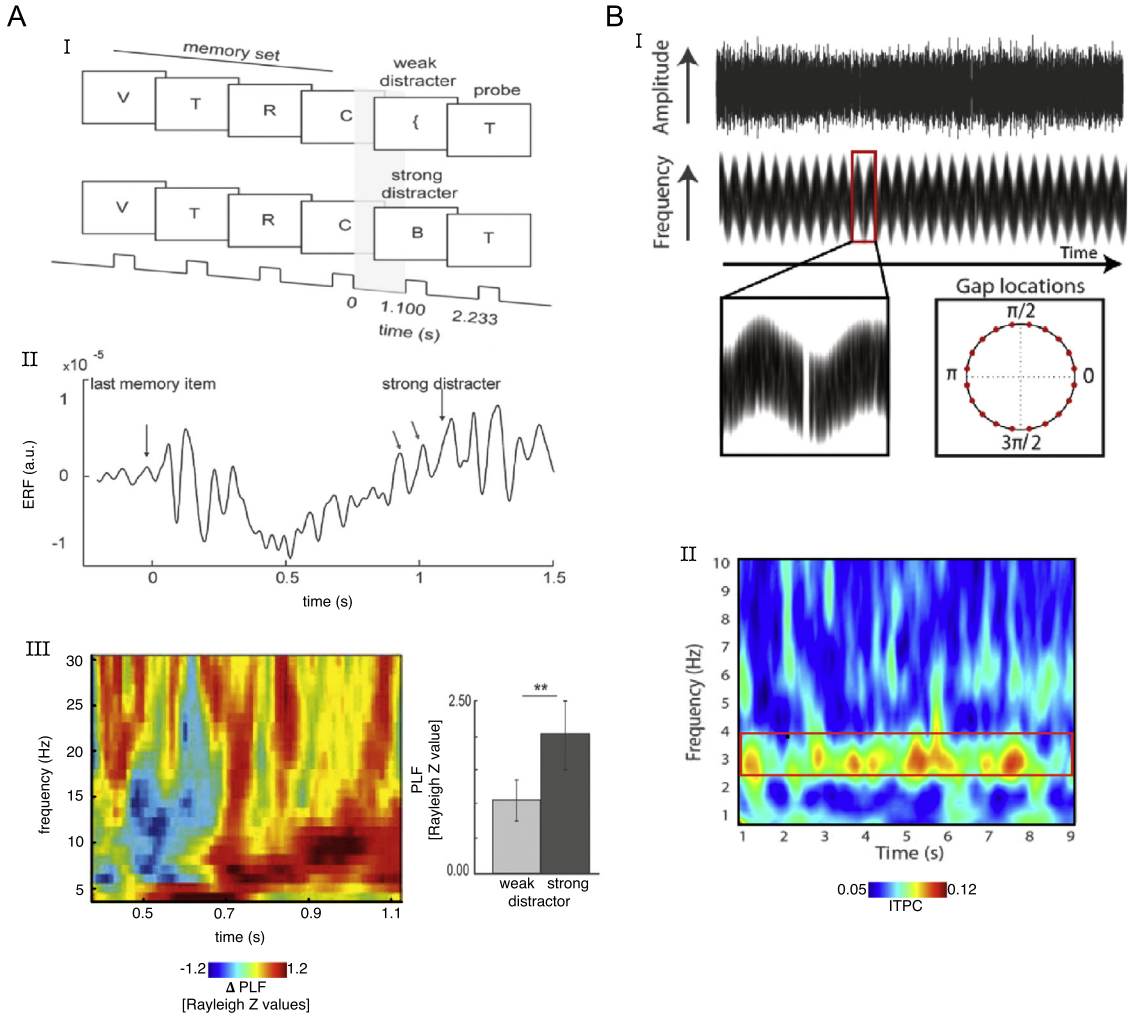

Fig. 2 – Phase resetting in an internal attention (memory) task (A) and auditory attention task (B). A (I) Depiction of one trial of an internal attention (memory) task using a conventional Sternberg paradigm. A memory set of four sequentially presented consonants had to be retained; during the retention period a weak (symbol) or a strong (vowel) distractor was presented at 1.1 s after the last memory item (distractor strength was predictable, as grouped into blocks). After presentation of the probe, participants had to indicate whether it was part of the memory set or not. (II) Time-locked responses (event-related fields) prior to the distracter averaged across all subjects showing a clear modulation in the alpha band (green arrows). (III) Time-frequency representation (left) of the difference in phase-locking factor (PLF; transformed to Rayleigh Z values) for the contrast strong versus weak distractors. A pronounced difference is clearly visible in the alpha band prior to distractor onset. Histograms show a more significant difference of the PLF prior to strong than weak distractors ($p<0.01$; error bars represent the SEM). Reproduced with permission from Bonnefond and Jensen (2012). B (I) Depiction of the paradigm of a delta entrainment study. Participants listened to a frequency-modulated sound (at 3 Hz; no amplitude modulation), in which they had to detect short gaps (2, 3, or 4 within a 10 s-stimulus). Gaps were distributed uniformly around the 3-Hz FM cycle. (II) Intertrial phase coherence (ITPC) over time across all electrodes. The frequency region with significantly increased ITPC is marked with a red rectangle. Reproduced with permission from Henry and Obleser (2012).

Fig. 2A). Furthermore, a study by Henry and Obleser (2012) showed that increasing phase alignment in slow oscillations (~3 Hz) to sensory inflow increased task performance, again highlighting the importance of phase as modulator of stimulus processing.

3.2. *Temporal attention modulates behavior*

Both studies (Stefanics et al., 2010; van Ede et al., 2011) investigating the effects of temporal attention on ongoing oscillatory activity reported beneficial effects on behavior, showing that higher hazard rates are linked to faster reaction times. Furthermore, temporally modulated beta power suppression contralateral to the attended hand during temporal attention also increased reaction time. Taken together, these two studies show that temporal information in a temporal attention task based on the hazard rates or informative cues can be exploited by the system, and that resulting preparatory mechanisms enhance task performance.

3.3. *Conclusion*

Modulations of oscillatory activity during temporal attention tasks are constituted by slow frequency (e.g., delta) phase alignment to the predicted target onset, and – similar to what occurs during spatial attention – by beta power suppression in somatosensory areas during a tactile pattern detection task. Importantly, these modulations are not general changes of a global attentive state, but are temporally, spatially and modality specific to the target stimulus. Oscillatory modulations are related to better task performance (faster reaction times), and are thought to reflect preparatory mechanisms in anticipation of the target occurrence positively affecting stimulus processing.

4. Selective attention

Attention can also be directed to features of sensory stimulations. Examples include (inter)modal attention and feature-based attention. In (inter)modal attention paradigms, stimuli from two modalities are presented simultaneously or in interleaved trials. Participants are required to attend to and perform a task in one modality, such as a sensory discrimination, stimulus detection or an oddball task, while ignoring the other modality. In feature-based attention paradigms, participants are usually presented with only one sensory stimulus, and have to attend to a specific characteristic of this stimulus, such as color, motion, or frequency. Similar to spatial attention tasks, the to-be-attended modality or feature is indicated with a cue prior to each block or to each trial, and the effects of attention can be studied in the cue-target time interval or during sensory stimulation. In the following sections, we will discuss the effects of (inter)modal and feature-based attention on (ongoing) oscillatory activity and task performance.

4.1. *Selective attention modulates the power of ongoing oscillatory activity*

(Inter)modal attention studies have employed audiovisual (Bollimunta et al., 2011, 2008; Foxe et al., 1998; Frey et al., 2014; Fu et al., 2001; Gomez-Ramirez et al., 2011; Mo et al., 2011; Wittekindt et al., 2014), visuotactile (Bauer et al., 2012), and vibrotactile tasks (Haegens et al., 2011). On sensor level, two studies have reported posterior alpha power increases when attention was directed to the auditory modality, power decreases when it was directed to the visual modality, and no alpha band modulations over auditory cortices (Foxe et al., 1998; Fu et al., 2001). In line with these findings, Wittekindt et al. (2014) and Bauer et al. (2012) reported relative alpha power increases in posterior sensors when attention was directed to the auditory and to the somatosensory stimulation, respectively. However, Bauer et al. (2012) also observed similar relative alpha and additional beta power increases over somatosensory cortices when attention was directed to the visual modality. These findings confirm that alpha oscillatory activity is modulated not only in posterior areas, but also in other sensory regions.

In support of these findings, alpha power increases in the auditory cortex were shown with intracranial recordings during a visual attention task (Gomez-Ramirez et al., 2011), and noninvasive relative alpha power decreases in the right auditory cortex in visual versus auditory attention were shown using MEG in combination with source localization (Frey et al., 2014). However, no modulatory effects of intermodal attention in the visual cortex were reported, due to co-activation of these areas during auditory attention. Furthermore, monkey studies have shown more alpha activity in V2 and V4 when attention was directed to auditory stimulation (Bollimunta et al., 2008), and decreased alpha power in low granular and infragranular layers, less alpha coherence and less Granger causality between layers of the visual cortex during increased visual attention (Bollimunta et al., 2011). Similarly, decreased alpha power in the somatosensory cortex was observed when monkeys attended the tactile modality to perform a vibrotactile discrimination task (Haegens et al., 2011). In contrast to these findings, Mo et al. (2011) found that during increased visual attention, both pre-target alpha power and multi-unit activity in the inferotemporal cortex (IT) were increased. Taken together, (inter)modal attention results in a modulation of alpha power in primary sensory areas. Specifically, decreases are observed in the areas processing the attended modality, while increases occur in the areas processing the unattended modality.

As in spatial attention, the effects of (inter)modal attention are independent of cue modality. In audiovisual tasks, an auditory cue (Fu et al., 2001), a visual cue (Foxe et al., 1998; Frey et al., 2014), and verbal instructions (Gomez-Ramirez et al., 2011) resulted in comparable alpha power modulations, which solely depended on the to-be-attended modality. In a visuotactile attention task, instructions on which modality to attend to were given verbally (Bauer et al., 2012), and in the feature-based selective attention task, visually presented words indicated whether color or motion should be attended (Snyder and Foxe, 2010). Taken together, the observed modulatory effects of oscillatory alpha power do not depend on

the modality in which the cue was presented either in (inter) modal or in feature-based attention tasks.

In a feature-based selective attention study, participants were required to either attend to the color or the motion of a random dot field array (Snyder and Foxe, 2010). As expected, attention to the color resulted in higher alpha power in dorsal areas, in which motion is processed, and vice versa. Interestingly, participants who only showed alpha power increase in the ventral or the dorsal stream had lower perceptual thresholds for motion or color perception. That is, if participants had to attend to the 'more difficult' sensory feature, the processing of the 'easier' feature was actively suppressed with alpha power increases in the corresponding cortical region. This study shows that feature-based selective attention also modulates ongoing alpha band oscillatory activity.

Overall, (inter)modal and feature-based attention affect oscillatory alpha band activity similar to spatial attention: relative alpha band power decreases can be observed over/in regions processing the attended modality or feature, whereas increases are seen over/in regions processing the unattended modality or feature, reflecting functional disengagement of these regions (but see Bollimunta et al., 2011; Mo et al., 2011). In line with findings from spatial attention studies, alpha power increases seem to be more relevant if distracting input has to be actively blocked.

4.2. *Selective attention modulates the phase of ongoing oscillatory activity*

In addition to attentional alpha power modulations, selective attention can also exploit the timing or the temporal rhythm of sensory stimulation. Timing information can lead to a phase adjustment prior to stimulus onset, for example in the alpha band (Bonnefond and Jensen, 2013, 2012; see Fig. 2A), whereas target detection in the attended modality resets ongoing oscillatory activity across multiple frequency bands (Lakatos et al., 2009). In contrast to phase adjustment and resetting, ongoing oscillatory activity can be entrained by rhythmic sensory stimulation in the same frequency band or its harmonics (Besle et al., 2011; Gomez-Ramirez et al., 2011; Henry and Obleser, 2012; Mathewson et al., 2012). Generally, entrainment and phase shifts are stronger with increased stimulation rhythmicity (Besle et al., 2011). As a result of entrainment, higher neuronal excitable phases are aligned to the stimuli in the attended sensory stream, enhancing stimulus processing. This effect has been mainly shown in the delta and theta range (Gomez-Ramirez et al., 2011; Lakatos et al., 2013, 2008; Ng et al., 2012). For example, when monkeys listened to an auditory stream with a specific spectrotemporal profile, neuronal ensembles in the primary auditory cortex tuned to the same frequency were entrained to the temporal dynamics of the auditory stream (Lakatos et al., 2013). Lakatos et al. (2013) suggested that by means of such 'spectrotemporal filters' specific auditory streams can be selected and segregated from other temporally or spectrally overlapping auditory streams, reflecting an essential mechanism for selective attention. While entrainment and phase resetting were reported mainly in primary sensory areas (Gomez-Ramirez et al., 2011; Lakatos et al., 2013, 2009, 2008), a study using the same audiovisual attention task as Lakatos et al. (2008) and intracranial recordings in human participants (Besle et al., 2011) showed that phase shifts and entrainment affect a distributed network, including the ventral visual, auditory and motor system, as well as parts of the parietal and frontal lobes. Furthermore, using human EEG and behavioral measures, Mathewson et al. (2012) showed that rhythmically presented visual stimuli (at 12 Hz, entrainers) increased detection performance of a hard-to-detect target when it occurred in phase with those as opposed to when the same pre-target stimuli were presented non-rhythmically. The entrainers also increased phase coherence at 12 Hz at the time of expected target onset. This indicates that specific phases of alpha oscillations are beneficial for stimulus perception. Overall, phase resetting and oscillatory entrainment reflect an attentional mechanism in addition to power modulation of ongoing oscillatory activity in the alpha and beta bands.

4.3. *Phase modulations due to selective attention can have effects across modalities*

Selective intermodal attention has been shown to have effects on regions processing the unattended modality (Lakatos et al., 2009). Oddball stimuli in an attended sensory stream reset not only the phase in the corresponding primary sensory region, but also in the region processing another, unattended modality. That is, a visual oddball in an attended rhythmic visual stream not only resets the phase in the visual but also the auditory primary cortices, and vice versa, across multiple frequency bands. Importantly, unattended oddball stimuli did not result in a similar effect. These findings are in line with earlier results regarding power modulations during spatial attention (see above). Correspondingly, the authors suggested that this phase reset enhances multisensory interactions.

4.4. *Selective attention influences behavior and evoked neural activity*

Attention to a specific modality has been shown to reduce reaction times for stimulus detection in the same modality (Frey et al., 2014). Yet, attention to one or another visual feature did not have any impact on detection rates (Snyder and Foxe, 2010). In monkey studies, visual alpha in V2 and V4 is negatively correlated with reaction times in an auditory discrimination task (Bollimunta et al., 2008).

Not many (inter)modal and feature-based attention studies reported effects of attention-modulated oscillatory neuronal activity on evoked and induced neuronal activity or task performance. Reaction time in a sensory oddball task was shown to be shortest when the target appeared in the trough of ongoing delta oscillations and vice versa (Lakatos et al., 2008), and reaction time and detection rate of target sounds embedded in background noise ('cocktail party effect') were shown to be best when oscillatory theta power was low and the target occurred at a beneficial phase (Ng et al., 2012). Moreover, miss trials had a stronger phase relationship than hit trials, suggesting that phase has an inhibitory role (Ng et al., 2012).

In line with findings concerning power and phase modulations, delta phase was shown to modulate alpha power (Gomez-Ramirez et al., 2011), and spike firing was stronger when visual alpha power was low and at the trough of ongoing alpha oscillations. Despite the small number of reports, selective attention and attention-related changes in ongoing oscillatory activity seem to impact task performance, similar to mechanisms during spatial and temporal attention. Furthermore, the two main selective attention effects – alpha power modulations and entrainment of low-frequency ongoing oscillations – seem to have a strong link.

4.5. *Conclusions*

Mechanisms underlying selective attention include power modulations of ongoing oscillatory activity in the alpha band similar to spatial attention, as well as phase resetting and entrainment of ongoing oscillations in lower frequencies as seen during temporal attention studies. Delta/theta band entrainment can be observed if stimuli are presented in a rhythmic pattern. As a result, sensory events coincide with the most excitable phase of the neuronal oscillations, increasing the probability that they are detected and efficiently processed. On the other hand, attention to randomly presented stimuli results in alpha band power modulation to facilitate and inhibit the processing of attended and unattended stimuli, respectively.

5. Internal attention

Thus far, we have discussed types of attention in which attention is directed towards external stimuli in the context of spatial, temporal, and selective attention paradigms. These paradigms manipulate the attention focus of study participants relatively directly and clearly, for instance, by using a cue or an oddball task. However, the physiological mechanisms underlying attention deployment in these common paradigms – modulation of ongoing alpha band oscillations and phase resetting/entrainment – also play a role in other cognitive functions. For instance, attention can also be directed away from external stimulation and towards internal processes in memory and cognition. For the sake of consistency and in the context of this review, we will call this form of attention deployment 'internal attention'. According to this working definition, 'internal attention' would complement 'external attention' including but not limited to spatial, temporal, and selective attention. Importantly, however, we do not intend to argue that memory and other cognitive functions can be reduced to 'internal attention'. Instead, we aim to highlight the similarities of the physiological mechanisms observed during attention deployment in common attention paradigms and in cognitive tasks without external stimulation, such as working memory.

In the following, we will discuss internal attention in the example of working memory tasks. Working memory is defined as the activated portion of long term memory in the focus of attention (see Cowan, 2000) or maintaining representations of events that are no longer present in the external world for a short period of time (Baddeley, 2003). Therefore, attentional processes are involved in working memory, as successful working memory performance essentially includes focusing on these representations, and blocking out distractors. The working memory studies reviewed in the following section used either a delayed match-to-sample task, or a modified Sternberg task. In the first case, participants are required to pay attention to a sample, maintain its representation for a short amount of time, and then compare it with a probe. In the Sternberg task, participants are given a set of stimuli which they have to encode, and after some time are asked whether a specific test stimulus was part of this set or not.

5.1. *Internal attention modulates the power of ongoing oscillatory activity*

Attending to internal representations and suppressing distracting information results in modulations of ongoing oscillatory activity in the alpha band, specifically in increases of alpha power over regions processing the distracting information. For instance, when participants were required to maintain the representation of face identities compared to face orientations, more alpha power was observed over the ventral visual stream. Source localization showed that this activity originated in the parieto-occipital sulcus (Jokisch and Jensen, 2007). Similarly, a study in which participants had to maintain the color of squares from one but not the other hemifield, more alpha power was observed during the retention period ipsilateral to the relevant information (Scheeringa et al., 2009). Moreover, alpha power increases were positively correlated with the number of the distracting squares. In the somatosensory delayed-match-to-sample task, similar results were obtained; however, instead of reporting only alpha power increases over the somatosensory cortex ipsilateral to stimulation, Haegens et al. (2010) also found posterior alpha power increases. In the auditory modality, van Dijk et al. (2010) found alpha power increases in left temporal regions during maintenance of auditory stimuli, potentially reflecting a disengagement of the left temporal cortex in this memory process.

However, not only alpha but also gamma band oscillatory activity is modulated by internal attention. When participants were asked to maintain the representation of face orientation instead of face identity, there was more gamma power in the occipital lobe (Jokisch and Jensen, 2007). Similarly, in the somatosensory delayed-match-to-sample task, Haegens et al. (2010) reported gamma power increases in the somatosensory cortex contralateral to stimulation and decreases ipsilateral to stimulation during the retention period. Taken together, these findings indicate that oscillatory activity in the alpha band reflects functional inhibition of areas processing distracting information, whereas gamma band oscillations reflect active maintenance of the memorized representations (Haegens et al., 2010; Jensen et al., 2002; Jokisch and Jensen, 2007; van Dijk et al., 2010).

5.2. *Internal attention modulates the phase of ongoing oscillatory activity*

Recently, Bonnefond and Jensen (2013, 2012) showed that internal attention modulates not only power but also phase

of ongoing oscillatory alpha activity (see Fig. 2A). The authors used a modified Sternberg task, in which participants had to memorize a string of letters. In alternating blocks, 1100 ms after the last sample letter, a weak or a strong distractor (a symbol or a letter) was presented. Participants were then asked whether a test letter was in the sample set or not. Prior to distractor onset, alpha power increased, but, more interestingly, alpha phase adjusted so that the distractor coincided with the least beneficial alpha phase for stimulus processing. They convincingly show that both alpha power and phase modulations resulted from anticipation of the distractor stimulus. These findings indicate that external stimuli result in phase shifts and entrainment not only of delta and theta oscillatory activity, but also of alpha. Furthermore, modulations become evident even prior to stimulus onset.

5.3. *Internal attention and attention-related oscillatory power and phase modulations influence evoked neural activity and behavior*

Modulations of oscillatory alpha activity predicted performance (Bonnefond and Jensen, 2013, 2012) in a modified Sternberg task. Furthermore, if there was strong alpha power increase over task-irrelevant areas, working memory performance improved (Haegens et al., 2010), and power enhancement of 10 Hz oscillations using rTMS ipsilateral to the relevant information improved working memory capacity and vice versa (Scheeringa et al., 2009). In addition to power effects, Bonnefond and colleagues (2012, 2013) showed that alpha phase adjustment prior to the onset of a distracting stimulus was linked to reduced reaction times.

5.4. *Conclusions*

During working memory tasks, attention deployment is essential for good task performance. In the present review, we have termed this allocation of attentional resources in the context of working memory 'internal attention'. In the preceding section, we reviewed papers investigating working memory and its influence on ongoing oscillatory activity. Effects of internal attention during working memory are strikingly similar to those observed during spatial, temporal, and selective attention. Areas processing distracting information are functionally inhibited by alpha power increases. Additionally, internal attention also resulted in temporally very specific alpha phase adjustments, so that a distracting stimulus coincided with the least excitable alpha phase. Whereas the phase adjustment in anticipation of a distracting stimulus reflects a preparatory mechanism similar to those in spatial and temporal attention, power modulations during the retention period reflect suppression of distracting information similar to modulations in selective attention.

6. Discussion

In the present review, we summarized research concerning attention and expectation effects on ongoing oscillatory activity. Traditionally, attention has been subdivided according to the contextual demands. While the structure of this review still adhered to this conventional division, it has hopefully become clear that two main oscillatory mechanisms – alpha power modulations and slow frequency phase effects – are not bound to one type of attention. We have discussed how neural oscillations are modulated during spatial, temporal, intermodal and feature-based selective, and internal attention. Whereas modulatory effects on alpha band power were observed mainly during spatial attention tasks, phase alignment (entrainment) of slow (delta and theta) oscillations was observed particularly during feature-based selective attention with a temporal component. Nevertheless, all different types of attention commonly engage both attention mechanisms, depending on task properties. Moreover, different types of attention oftentimes functionally overlap depending on paradigm and stimulus characteristics. Thus, for a scientific discourse of attention and the study of its underlying neural mechanism, the traditional distinction of attentional subtypes (e.g., spatial, temporal) seems rather impractical. Based on the electrophysiological findings outlined in this review, it seems more worthwhile to discuss attention deployment according to the actual neural mechanisms involved; that is, alpha power modulation and phase resetting/entrainment. In the next sections, we will discuss these two mechanisms and how they might relate to each other.

6.1. *Power versus phase modulations*

As a first mechanism, attention modulates power mainly in the alpha and beta frequency ranges, but also the gamma band (see Fig. 1 for examples). In spatial and selective attention paradigms, relative alpha power increases were most often observed in cortical areas processing an unattended location and modality, respectively. Furthermore, relative alpha power increases occurred between potential target onset times in temporal attention, and prior to the onset of distracting information during internal attention. Alpha oscillations have been related to so-called functional inhibition (Jensen and Mazaheri, 2010; Klimesch et al., 2007, see Box 1). According to this notion, alpha power increases in task-irrelevant regions can be interpreted as an increase in inhibition in these areas. In spatial attention tasks this is simply the ipsilateral sensory area, whereas in working memory tasks higher-level areas (parietal, temporal) show alpha modulations. Attention is making use of the inhibitory mechanism reflected by alpha power as proposed by the gating-by-inhibition hypothesis (Jensen and Mazaheri, 2010, see Box 1), by specifically blocking irrelevant areas and, even though less consistent, by reducing alpha power in relevant areas increasing excitability.

As a second mechanism, attention causes a phase reset and entrainment of oscillatory activity in slow oscillations (see Fig. 2 for examples). These mechanisms were mostly observed in temporal, selective (intermodal and feature-based), and internal attention paradigms, if the sensory stimulation exhibited a strong temporal regularity. Whereas phase reset without entrainment only occurs if a single sensory stimulus is presented, entrainment reflects general

phase alignment of ongoing oscillations to extended rhythmic sensory streams. However, both processes have the same consequences: more excitable phases of ongoing neural oscillatory activity are aligned to the stimulation onset (Lakatos et al., 2008). Thus, by causing phase resets and entrainment, attention enhances stimulus processing by tuning ongoing oscillatory activity to the attended sensory input. Simultaneously, non-attended sensory stimuli will more likely coincide with less excitable phases, effectively inhibiting processing of to-be-ignored stimuli (Lakatos et al., 2009). These observations are in line with the oscillatory selection hypothesis (Schroeder and Lakatos, 2009, see Box 1) and partly with the active sensing concept (Schroeder et al., 2010, see Box 1) as discussed in the next section.

6.2. *Continuous versus rhythmic processing*

In the following we would like to integrate the presented findings into a current theory by Schroeder and colleagues (Lakatos et al., 2008; Schroeder and Lakatos, 2009; Schroeder et al., 2010). In attention research, both mechanisms – power modulations in the alpha band and phase alignment/entrainment in lower bands – are seen as complementary to optimizing stimulus processing depending on stimulation characteristics. If stimuli are presented in a rhythmic pattern, the system will adopt a preferred 'rhythmic processing mode'; on the other hand, if the system cannot exploit any rhythmicity as the stimuli are presented randomly, it will adopt a 'continuous processing mode' (Henry and Herrmann, 2014; Schroeder and Lakatos, 2009).

The continuous processing mode is characterized by general power decrease of low-frequency oscillations and power increase of gamma band oscillatory activity over longer periods. This is metabolically relatively expensive and less efficient, and therefore arguably the less preferred processing mode (Schroeder and Lakatos, 2009). However, it accounts well for alpha modulations found in attention studies. Specifically for studies using arrhythmic stimulation, entrainment or a more efficient processing mode is impossible. Therefore, we would suggest that the majority of studies reporting power modulations are using designs where a continuous processing mode is beneficial. In other words, task relevant areas are generally alerted (and irrelevant areas inhibited); however, no temporally specific preparation is possible.

In contrast, the rhythmic processing mode is characterized by entrainment (phase alignment) of neural oscillations and pulsed stimulus processing due to hierarchical coupling, resulting in a generally more efficient stimulus processing because attended stimuli fall into more excitable phases, and because unattended potentially distracting stimuli fall into less excitable phases with more functional inhibition. Taken together, this approach argues that the system adopts a preferred rhythmic processing mode whenever it can exploit rhythmicity in the sensory input, and a less preferred continuous processing mode if this is not possible (Henry and Herrmann, 2014; Schroeder and Lakatos, 2009).

Taken together, the attentive brain adopts the processing mode resulting in the least metabolic cost and the most efficient stimulus processing. To do so, it will exploit any rhythmicity of the sensory stimulation. If there is none, it will adopt a continuous processing mode. However, rhythmic and continuous processing modes are most likely simultaneously involved in any type of attention, but to different degrees depending on the stimulation.

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