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Pre-stimulus oscillatory signatures of tactile detection and attention

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Abstract

Oscillatory neuronal activity in the alpha band has been associated with both conscious perception and attention. Firstly, conscious perception of a weak sensory stimulus is preceded by alpha power decreases. Secondly, attention to a sensory event reduces alpha activity in the corresponding sensory regions. According to the widely accepted functional inhibition hypothesis, oscillatory neural activity in the alpha band reflects cortical excitability; in other words, a sensory region with low alpha power levels is more excitable. Several questions regarding the relationship between conscious perception, attention and alpha band activity have not been addressed so far. Firstly, it remained unclear whether brain states predisposing consciousness only comprise local pre-stimulus alpha power decreases, or also global network states. Secondly, it remained unclear whether alpha power decreases prior to conscious perception are confounded by fluctuations of attention or not. The goal of the current thesis is to address these two open questions in the tactile modality with two magnetoencephalography studies.

The first study explored brain states predisposing conscious tactile perception, with a particular focus on functional connectivity patterns in addition to alpha power modulations. To this end, a simple near-threshold detection paradigm was conducted, with weak tactile stimuli to the participants' left index finger. Findings revealed that conscious perception is preceded by a) a relative alpha power decreases in the somatosensory cortex contralateral to stimulation, and b) a spectrally specific pattern of functional connectivity in the primary somatosensory cortex. Based on the first study, it can be concluded that brain states predisposing consciousness comprise local cortical excitability changes as well as frequency-specific network patterns.

The second study focused on alpha power changes prior to conscious perception in the context of spatial attention. To this end, a near-threshold detection paradigm with a double-pulse target stimulus was combined with a spatial attention task. The results showed a) that spatial tactile attention modulates pre-stimulus alpha power, and b) that spontaneous alpha power fluctuations not explained by attention influence perception. These findings indicate that – while attention does affect pre-stimulus alpha power levels – spontaneous alpha power fluctuations predispose consciousness.

Taken together, we conclude that brain states predisposing conscious perception comprise spectrally specific functional connectivity patterns, and alpha power fluctuations distinct from attention-induced alpha power modulations.

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Author's Declaration

The studies presented in this thesis were conducted by the author, Julia Natascha Frey, under the supervision of Prof. Dr. Nathan Weisz and the support of a number of colleagues.

Study 1: The Tactile Window to Consciousness is Characterized by Frequency-specific Integration and Segregation of the Primary Somatosensory Cortex

Authors: Julia N. Frey, Philipp Ruhnau, Sabine Leske, Markus Siegel, Christoph Braun, Nathan Weisz

Currently submitted to Scientific Reports (26th October 2015)

I designed the study, collected and analysed the MEG data, made the figures, and drafted the manuscript.

Study 2: Alpha power in the Somatosensory Cortex Predisposes Conscious Perception in the Absence of Top-Down Influences

Authors: Julia N. Frey, Nathan Weisz

I designed the study, collected and analysed the MEG data, made the figures, and drafted the manuscript.

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List of Abbreviations

AI	Anterior Insula
ANOVA	Analysis of variance
CB	Change blindness
CSD	Cross-spectral density
DAN	Dorsal attention network
df	Degrees of Freedom
EEG	Electroencephalography
EPSP	Excitatory postsynaptic potential
ER	Event-related response
ERF	Event-related field
FEF	Frontal eye-field
FFS	Fast-forward sweep
FFT	Fast fourier transform
GNW	Global neural workspace
GW	Global workspace
Hz	Hertz
IFG	Inferior frontal gyrus
IPS	Intraparietal sulcus
IPSP	Inhibitory postsynaptic potential
ISI	Inter-stimulus interval
ITI	Inter-trial interval
LCMV	Linearly constrained minimum variance
LFP	Local field potential
LMF	Local magnetic field
MEG	Magnetoencephalography
MFG	Middle frontal gyrus
min	Minute
MNI	Montreal Neurological Institute
ms	Millisecond
MTG	Middle temporal gyrus
NCC	Neural correlates of consciousness

NCC-pr	Neural prerequisites of consciousness
NCC-co	Neural correlates of consciousness
nm	Nanometre
ROI	Region of interest
RP	Recurrent processing
s	Second
SFG	Superior frontal gyrus
SLF I-III	Superior longitudinal fasciculus (1st, 2nd & 3rd fibre tracts)
tACS	Transcranial alternating current stimulation
TMS	Transcranial magnetic stimulation
TPJ	Temporoparietal junction
VAN	Ventral attention network
VFC	Ventral frontal cortex
win2con	Windows to Consciousness

Chapter 1: Introduction

The present thesis investigates the neural basis of conscious perception and attention. Specifically, it addresses two open questions concerning the relationship between oscillatory neural activity in the alpha band, conscious perception, and spatial attention in the tactile modality. In the following sections, I will give a short introduction to the most relevant topics, including neural oscillatory activity, and the concepts of consciousness and attention. The introduction then finishes with an overview of the research questions addressed in this thesis.

Neural Oscillatory Activity

How do we perceive sensory stimuli from our surroundings? In a first step, the physical energy of external stimuli needs to be transformed to signals that can be processed by our neuronal system. Specialized receptor cells embedded in all sensory organs, e.g., mechanoreceptors in the skin, transform incoming stimuli into electrical signals. These so-called afferent action potentials are then transmitted along the receptor's axon and through synapses to the dendrites and somata of cortical neurons. Synapses – the junctions between neurons – consist of the membrane of the presynaptic neuron (on the axon), the synaptic cleft, and the membrane of the postsynaptic neuron. When an action potential arrives at a synapse, the electrical signal results in a release of neurotransmitters in the synaptic cleft. These, in turn, influence the postsynaptic membrane potential by binding to specific receptors. Two forms of neural activation can be distinguished: Fast depolarization of the postsynaptic membrane, and longer-lasting change of the membrane potential. Whereas the former results in another action potential elicited at the axon hillock within 1-2ms, the latter consists of a longer-lasting change in the postsynaptic membrane potential. Depending on the neurotransmitters, the involved receptors, and further characteristics of the synaptic interactions, this postsynaptic potential can either be excitatory

(EPSP) or inhibitory (IPSP) (see Hämäläinen et al., 1993; Lopes da Silva, 2010, 2013).

In healthy human participants, only the latter form of neural activity can be assessed by non-invasive recordings at scalp level using electroencephalography (EEG; Berger, 1929) and magnetoencephalography (MEG; Cohen, 1972). Both methods measure the synchronized postsynaptic potentials from the spatially aligned apical dendrites of pyramidal cells, which are oriented perpendicularly to the cortical sheet of the grey matter. Whereas EEG signals consist of the local field potentials (LFP) caused by the summated postsynaptic potentials, MEG signals consist of the corresponding local magnetic fields (LMF) around the electrical currents that are oriented tangentially to the scalp surface. Thus, EEG and MEG can be considered complementary. Whereas both methods have a very good temporal resolution in the millisecond range, MEG has a better spatial resolution than the EEG, because magnetic fields are not distorted by electric conductivity of tissues (see Hämäläinen et al., 1993; Lopes da Silva, 2010, 2013).

The recorded signals of EEG and MEG are oscillatory in nature and reflect rhythmic fluctuations of the summated postsynaptic membrane potentials. These fluctuations are influenced by the intrinsic membrane properties of the neurons, the connection strength between the neuronal populations, and neurotransmitter systems (Pfurtscheller and Lopes da Silva, 1999), and can be described with three features: Frequency, amplitude (power), and phase. Frequency information (measured in hertz, Hz) is obtained after deconstructing the complex signals of electrophysiological data into different oscillatory signals. Power and phase information can be used to describe neural activity within each frequency band on a local level, i.e. within a brain region, or on a more global level, i.e. across distant brain regions. Averaged across trials, power provides information about the synchronization strength of an oscillation in specific brain regions. In contrast, instantaneous phase reflects the angle of an oscillatory signal. Correlating neural activity (either power or phase) across different brain areas is used to approximate measures for neuronal communication, also called functional connectivity. For instance, two brain regions are functionally connected if their oscillatory signals share a consistent phase relationship (Lachaux et al., 2000; Varela et al., 2001).

The earliest rhythm described in the human encephalogram was the so-called alpha rhythm around 10Hz (Berger, 1929). When measured over posterior brain regions, the power of this rhythm increases when participants close their eyes, and decreases and when they are presented with visual stimuli. Neural activity in the alpha band was therefore thought to reflect the 'idling' rhythm of the brain, which dominates the oscillatory activity when the respective brain regions are at rest. Based on findings from the last decades, however, the alpha rhythm is ascribed a much more active role reflecting cortical excitability and a functional inhibitory mechanism (Klimesch et al., 2007; Jensen and Mazaheri, 2010; for a more detailed discussion of the alpha band rhythm see below, and Appendix B).

Numerous studies have shown that not only the alpha rhythm is associated with specific cognitive tasks but also oscillatory activity in other frequency bands including delta (2-4Hz), theta (4-8Hz), beta (14-30Hz) and gamma (>30Hz) (for a review see Wang, 2010). For instance, the low-frequency theta rhythm (4-8Hz) in the hippocampus and limbic structures is involved in encoding spatial information during exploration of the environment (e.g., O'Keefe and Conway, 1978; Geisler et al., 2007), as well as in forming and retrieving episodic and spatial memory (e.g., Hasselmo, 2005). Theta band activity in the neocortex has been shown to be associated with working memory (e.g., Raghavachari et al., 2001; Meltzer et al., 2008). Functions ascribed to the oscillatory activity in the beta band mainly include preparation and inhibitory control of movement (e.g., Murthy and Fetz, 1992; Sanes and Donoghue, 1993; Pfurtscheller and Lopes da Silva, 1999; Swann et al., 2009), but also other functions, such as long-distance coordination between brain regions (Siegel et al., 2012), rule learning (Buschman et al., 2012), and language processing (Hanslmayr et al., 2009; for a review of beta band activity see Engel and Fries, 2010). Particularly in the somatomotor cortex, beta band oscillations do not necessarily reflect a distinct rhythm from alpha band oscillations, as somatomotor alpha band activity (also called Rolandic mu rhythm) is very often arch-shaped (Gastaut, 1952; Gastaut et al., 1952), resulting in two peaks in the power spectrum in the alpha and the beta band. Finally, gamma band activity is associated with states of high attention (e.g., Engel et al., 2001; Fries et al., 2001; Fries, 2009) and with integration of sensory information (e.g., Tallon-Baudry et al., 1997; Singer, 1999). Taken together, the notion that cognition arises from temporally organized neural activity is widely accepted; in the next paragraph, I will briefly introduce oscillatory activity in the alpha band.

Neural oscillatory activity in the alpha band

The most prominent neural rhythm of the human brain is oscillatory activity in the alpha frequency band, and is particularly strong in posterior regions when participants close their eyes. In the electroencephalogram, the visual alpha rhythm can be identified without prior preprocessing, which led to its discovery as the first human brain rhythm (Berger, 1929). Similar rhythms were subsequently reported in the somatosensory modality, originally called 'mu' (Gastaut, 1952; Hari and Salmelin, 1997), and in the auditory modality, originally called 'tau' (Lehtelä et al., 1997). While alpha oscillatory activity was originally thought to reflect an 'idling' state of the human brain, there is a widespread consensus amongst neuroscientists for a more active role of oscillatory alpha activity.

According to the inhibition-timing hypothesis (Klimesch et al., 2007) oscillations in the alpha band reflect a top-down controlled mechanism, which exerts inhibitory influence in a tonic and pulsed manner (see Fig. 1A). Increased alpha power levels control cognitive processing by inhibiting cortical regions, whereas decreased alpha power levels reflect a general release of functional inhibition. Furthermore, the timing of neural processing is regulated by the phase of the alpha oscillations; whereas processing is facilitated during troughs, it is impaired during peaks of the oscillatory activity (Klimesch et al., 2007). Similarly, the gating-by-inhibition hypothesis (Jensen and Mazaheri, 2010) proposes that oscillatory activity in the alpha band plays a fundamental role in the functional architecture of the human brain (see Fig. 1B). Specifically, in accordance with the inhibition-timing hypothesis (Klimesch et al., 2007), alpha band activity is assumed to regulate information processing along sensory pathways by fluctuating amplitudes. Due to these fluctuations and the resulting inhibition, the gating-by-inhibition hypothesis postulates that incoming information is ‘gated’ into less strongly inhibited regions with relatively decreased alpha power levels. In other words, oscillatory activity in the alpha band can serve as a guide through the neural system by selectively inhibiting irrelevant areas along the sensory pathway.

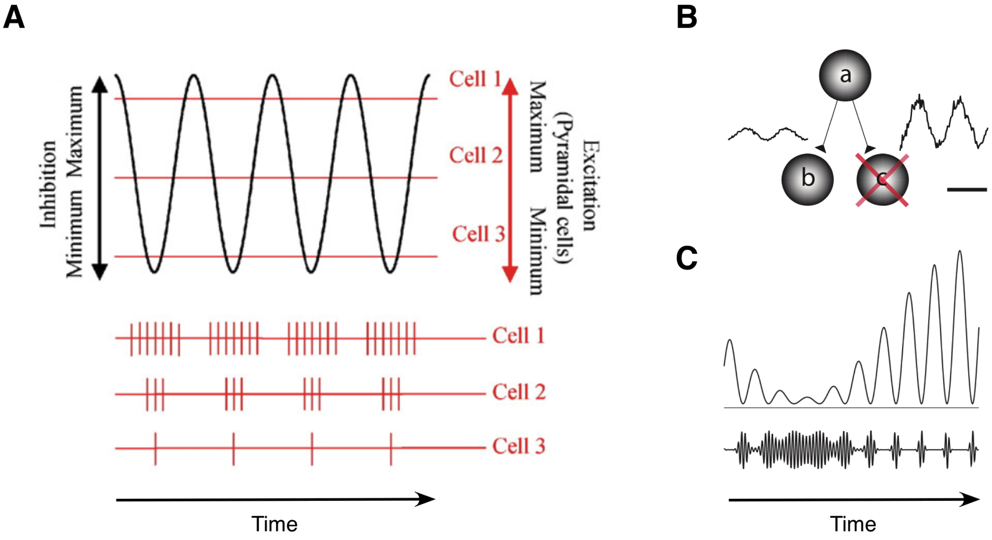

Figure 1. The inhibition-timing and the gating-by-inhibition hypotheses. **A** According to the inhibition-timing hypothesis, neural activity of pyramidal cells depends on their level of excitation and the phase of inhibitory oscillatory activity in the alpha band. During maximally inhibiting phases (peaks of black trace), neural activity is inhibited, particularly in cells with a low excitation level (Cell 3). Moreover, the greater the alpha amplitude, the stronger the inhibitory phase effect, such that neural activity in cells with a high excitation level (Cell 1) also becomes phase-dependent. (Reproduced with permission from Klimesch et al., 2007) **B** By functionally inhibiting activity in the node c with high alpha power, the information flow is gated from the node a to the node b. **C** Oscillatory activity in the alpha band (upper trace) modulates activity in the gamma band (lower trace) in a pulsed manner, particularly during episodes of high alpha power (adapted from Jensen and Mazaheri, 2010). (B and C reproduced with permission from Jensen and Mazaheri, 2010).

Consciousness

One of the major challenges of philosophy and neuroscience is to understand consciousness and its underlying brain processes. *Consciousness* is an ill-defined concept with a long history in philosophy, science, and folk psychology. As a term, *consciousness* is distinguished by a semantic ambiguity with an intransitive and a transitive use, complicating the discourse about the concept. Whereas the former refers to the states of a subject, including for instance coma, wakefulness, and alertness (e.g., 'to lose consciousness'), the latter needs a direct object and denotes being aware of something (e.g., 'to be conscious of a red rose'). In the current thesis, the term consciousness will always refer to its transitive meaning. Generally speaking, neuroscientific research aims to identify the neural mechanisms that underlie conscious perception (neural correlates of consciousness, NCC; Crick and Koch, 1990). In other words, how is neural activity caused by an external stimulus processed so that we become aware of the stimulus? For instance, when we look at a red rose, light with a specific wavelength (~650nm) enters our eyes, where photoreceptors convert it into electrochemical signals. These signals are then transmitted through the brain to visual areas in the occipital cortex. In specialized occipital regions, they elicit activity relating to the colour (red) and the shape (rose), amongst other features. The main question now arises whether this local posterior activity is sufficient for a conscious percept of the red rose, and if not, which additional neural processes are necessary for consciousness. In the following paragraphs, I will give a short introduction to the major debate in the study of consciousness, the main neuroscientific theories, and a description of pre-stimulus neural signatures of consciousness with a focus on oscillatory alpha activity.

The overflow-argument

The transitive concept of consciousness (i.e., 'to be conscious of a red rose') can be further divided into two aspects: subjective experience per se, and the cognitive access of the experienced information. Subjective experience is also called phenomenology or qualia, and describes *how* something feels, looks, or smells like. In contrast, cognitive access comprises all processes involved when a conscious experience becomes the subject of cognitive processes, such as memory consolidation or speech. A major debate in the study of consciousness revolves around the question whether conscious experience depends on cognitive function or whether consciousness is independent of cognition. The latter notion mainly rests on the intuitive assumption that we as experiencing subjects must be conscious of more than we can report. This sentiment agrees with widespread beliefs in folk psychology, and can be summarized by the statement ‘phenomenology overflows access’ (Block, 2007). Supporters of the so-called overflow-argument postulate two kinds of ‘consciousnesses’: a *phenomenal* consciousness referring to all phenomenological states (the qualia), and a *access* consciousness referring to any conscious content that is accessed by cognitive function.

Apart from intuitive assumptions, findings from a classical psychological experiment seemingly support the overflow-argument. In an influential study, Sperling (1960) conducted several experiments and showed that participants have more visual information available after a short stimulus exposure than they are able to report. Participants were presented with rows of letters for a very short time (50-500ms). In a first part, Sperling showed that participants were not able to report all presented letters when asked to do so (whole report), but only a fixed number, irrespective of stimulus duration or total number of target letters. He interpreted this finding as an expression of the short-term memory span (‘immediate-memory span’). To circumvent the limitations of short-term memory, Sperling then asked the participants in a second part to only report the letters of one randomly chosen row (partial report), which was cued *after stimulus offset*. This sampling procedure revealed that participants had more information available shortly after stimulus offset than the ‘whole report’ procedure would suggest.

At first glance, based on intuition and the Sperling task, the tenets of the overflow-argument – consciousness is richer than verbal reports – seem to be plausible to a certain degree. However, Sperling’s findings can be accounted for without postulating the existence of a phenomenal consciousness. Firstly, in line with Sperling's own interpretation, Cohen and Dennett (2011) argue for a transient information storage, which contains the presented but still unconscious letters until they become conscious because of the post-stimulus cue. This line of reasoning also accounts for other experimental findings, such as the change blindness (CB; Simons and Levin, 1997), in which participants are not able to report changes in a visual scene after it has been flickered on and off. CB is drastically reduced when the item that will be changed is cued, even *after* the offset of the visual scene, indicating a persisting unconscious representation of the scene. Secondly, a multi-access model of attention accounts for the impression of a rich phenomenology by stating that the world beyond focal attention is processed via distributed ('excess') attentional resources (e.g., Cartwright-Finch and Lavie, 2007; Lavie, 1995; Yi et al., 2004). Finally, the impression of rich phenomenology might also be due to a simple overestimation of subjective experience and sensory illusions (de Gardelle et al., 2009; Levin et al., 2000; see also Cohen and Dennett, 2011).

Importantly, from a scientific perspective, these alternative explanations have to be favoured over the overflow-argument. In the study of conscious perception with objective methods, a certain level of introspection is always necessary. Specifically, the experimenter has to rely on participants' reports to categorize the trials as consciously perceived or unperceived. As phenomenal consciousness is per definition not accessible by cognition, it cannot be scientifically tested or falsified, and remains outside the scope of science (Cohen and Dennett, 2011).

Taken together, based on intuitive assumptions and findings from studies using a post-cueing approach, supporters of the overflow-argument claim that the contents of consciousness are richer than what can be reported. As a consequence, however, this notion is per definition outside the scope of science, as any study of consciousness relies on some degree of introspection. In contrast, opponents of the overflow-argument propose alternative explanations accounting for the impression of a rich phenomenology. These include rapidly decaying information in an unconscious buffer, consciously perceived degraded information outside of focal attention, and sensory illusion of a rich phenomenology.

Neuroscientific theories of consciousness

Theories supporting the overflow-argument and postulating the existence of a phenomenal and an access consciousness are called *dissociative* theories, as they argue for a dissociation between consciousness and cognition. In contrast, theories opposing the overflow-argument are called *non-dissociative* (see Cohen and Dennett, 2011; Kouider et al., 2007). These theories only know one kind of consciousness, defined as the sum of reportable – or at least cognitively accessible – subjective experiences. In the following sections, I will present a short summary of the most dominant dissociative and non-dissociative neuroscientific theories of consciousness.

Dissociative theories. In an influential theory, Block (1995) conceptually distinguishes a phenomenal consciousness and an access consciousness. Whereas the former signifies the feeling of what something is like, e.g. the ‘redness of red’ or the ‘rosiness of a rose’, the latter reflects the content that is available for use in reasoning, action and speech (Block, 2005). Furthermore, Block argues that both putative types of consciousness have distinct neuronal correlates, and proposes two NCCs: A phenomenal NCC, and an access NCC (Block, 2005). In a similar vein to Zeki’s microconsciousness (Zeki, 2001; see below) and Lamme’s recurrent processing (Lamme, 2004; Lamme and Roelfsema, 2000; see below), Block defines his phenomenal NCC as local (recurrent) activity in regions processing a specific feature. For instance, activity in the human MT/V5 reflects the core phenomenal NCC of motion (Block, 2005). In addition, the total phenomenal NCC, comparably to Zeki’s macroconsciousness (Zeki, 2001), also contains activity in other local modules. The access NCC, in contrast, is defined as the neural basis of making content from the phenomenal NCC available to other brain systems, such as those underlying speech and action.

Similar to Block’s subdivision of core and total phenomenal NCCs, Zeki argues that there are many distinct consciousnesses, which are spatially and temporally distributed (Zeki and Bartels, 1999; Zeki, 2001, 2003). In fact, he repeatedly stated that 'the quest for the NCC will remain elusive' as long as it is considered to reflect a unified construct (Zeki, 2003). According to Zeki's theory of consciousness (mainly based on vision), sensory systems consist of several parallel, functionally specialized and autonomous processing systems, for instance, for colour or motion. Based on neuropathological findings, e.g. concerning akinetopsia or acquired achromatopsia, he argues that these processing systems also reflect *perceptual*, i.e. consciousness producing, systems. Furthermore, each processing system, in turn, contains distinct nodes, each of which produces a conscious correlate of only one visual feature. These so-called microconsciousnesses are, just like the underlying nodes, hierarchically organized, functionally specialized, and spatially and temporally distributed. Binding these microconsciousnesses together in a non-hierarchical fashion gives rise to so-called macroconsciousnesses, i.e. consistent, multimodal percepts (Zeki, 2003). A red rose, for instance, could elicit several microconsicousnesses (one for each visual feature, such as colour, shape, location), and one macroconsicousness, representing the whole rose.

Following the conceptual distinction proposed by Block (1995), Lamme also proposes several neural signatures of conscious perception, distinguishing four different stages of sensory processing (see Fig. 2). Processing with a feedforward sweep (FFS) occurs if a stimulus is masked and unattended. In contrast, deep FFS processing occurs if a masked stimulus is attended. Whereas this initial sweep of neural activity enables the extraction of information from, e.g., a visual scene, both processing stages do not cause conscious perception. As a third and fourth stage, Lamme (2010) proposes superficial (local), and deep (wide-spread) recurrent processing (RP), in which a sufficiently strong stimulus is unattended and attended, respectively. Only if there is an interaction between low-level brain regions (local RP), and feedback from higher-order areas (global RP), is a stimulus access conscious. If there is only local RP, a stimulus is phenomenally conscious.

As a response to the objection that phenomenal consciousness cannot be studied scientifically (Cohen and Dennett, 2011; see above), Lamme advances the debate regarding phenomenal vs. access consciousness by proposing to define consciousness entirely by neural activity, and not by any verbal or behavioural responses (Lamme, 2006). In fact, he disagrees with the notion that we know what we are conscious of ('psychological intuition'; Lamme, 2010). In a somewhat circular claim, he postulates that local recurrent processing is the definite neural signature of conscious perception (in contrast to the feedforward sweep, and activity in frontoparietal areas), and turns these neural correlates into 'neural arguments' for consciousness (Lamme, 2010). Thus, according to Lamme, whenever sensory input is associated with local recurrency, it is phenomenally conscious, even if the participant verbally denies a conscious percept (Lamme, 2006).

Taken together, supporters of the overflow-argument (i.e., the notion that phenomenology is richer than what can be reported) have proposed a series of dissociative theories, postulating distinct NCCs for a phenomenal and an access consciousness. Across all theories, the access NCC involves activity in sensory and higher-order regions, and feedback loops between these regions. In contrast, the phenomenal NCC is constrained to sensory areas and characterized by local recurrent processing. According to Lamme, this local activity even constitutes a 'neural argument' for conscious perception.

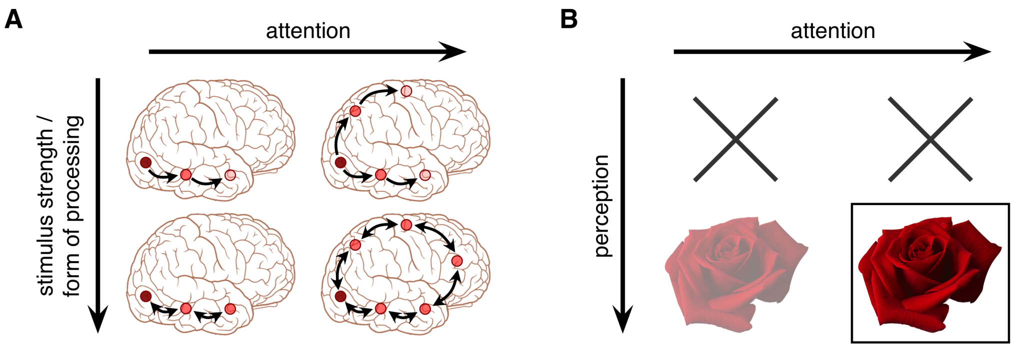

Figure 2. Four different stages of consciousness with resulting percepts. **A** Lamme as well as Dehaene propose four distinct stages of sensory processing depending on whether a stimulus is attended or not, and the stimulus strength (Dehaene et al., 2006) or the form of processing (Lamme, 2010). The first two stages (upper panel) are characterized by a feedforward sweep of activity. The depth of processing depends on the level of attention and the task set. The third stage (lower left) occurs when a stimulus is sufficiently strong but not attended. It is characterized by local recurrent activity confined to sensorimotor regions and local synchrony. The fourth stage (lower right) occurs when a stimulus is sufficiently strong and attended. It is characterized by sustained global recurrent activity including frontoparietal regions, top-down amplification of activity and global synchrony. (Adapted with permission from Dehaene et al., 2006; Lamme, 2010) **B** Schematic illustration of conscious content corresponding to the four stages of processing in A. The first two stages (upper panel) do not result in a conscious percept. The third stage (lower left) is thought of as phenomenally conscious in the context of dissociative theories (e.g., Lamme, 2010), whereas it is preconscious (i.e., potentially conscious) in non-dissociative theories (e.g., Dehaene et al., 2006). The fourth stage (lower right) is cognitively accessed, and is labelled access conscious in dissociative theories, and conscious in non-dissociative theories.

Non-dissociative theories. As discussed above, the idea of phenomenal consciousness is per definition outside the scope of science (Cohen and Dennett, 2011). After proposing the investigation of the NCC (Crick and Koch, 1990), Crick and Koch repeatedly stated that phenomenology is a topic that should be better left aside, and that the more fundamental questions – how we perceive at all – is of greater interest (Crick and Koch, 1990, 1995, 2003; Koch and Crick, 2001). In a comprehensive review article, they outline ten aspects of a framework to consciousness (Crick and Koch, 2003). Amongst others, these aspects include the notion of nodes, which respond to specific sensory features and form competing neural coalitions. Further, they propose that the activity within a coalition becomes conscious when it crosses a certain threshold, and that consciousness arises from discrete epochs, possibly related to slow frequency oscillations. Later, Koch and colleagues proposed that attention is neither sufficient nor necessary for conscious perception, and that sensory processing can occur in four different stages, depending on attention and consciousness (Koch and Tsuchiya, 2007a; Van Boxtel et al., 2010). Here, attention is defined as an *analyser* for stimulus selection, and consciousness as a *synthesizer* that summarizes all relevant information and makes in available to higher cognition such as language, theory of mind, and reasoning (Koch and Tsuchiya, 2007a, 2007b; Van Boxtel et al., 2010).

Another influential theory of consciousness is the global neuronal workspace (GNW) model (Dehaene et al., 1998; Dehaene and Naccache, 2001), which is based on the global workspace (GW) model by Baars (Baars BJ, 1988). The GW model revives the theatre as a metaphor for cognitive processing and consciousness. Whereas the stage represents working memory processes, the spotlight directed towards the stage represents selective attention, and the resulting bright spot focal consciousness. Furthermore, the zone behind the scenes and the audience reflect unconscious processes shaping conscious events and receiving information from consciousness, respectively. In other words, a subject becomes aware of sensory stimuli, thoughts and ideas (area behind the scenes), if they are available to multiple cognitive systems (the audience) in a global workspace (the stage). In contrast, anything that cannot be cognitively accessed remains unconscious.

In the GNW model by Dehaene and colleagues (Dehaene et al., 1998; Dehaene and Naccache, 2001), distributed and heavily interconnected neurons constitute a unique and global workspace, and locally organized neurons represent specialized and modular processors. Whereas in the latter computational space several representations can co-exist simultaneously (similarly to Zeki's microconsciousnesses and Lamme's local recurrent processing; see above), only one representation can be active in the global workspace at any given moment. Importantly, just as the GW model, the GNW model postulate that activity outside of the global workspace is not accessed by cognitive functions, and thus, remains unconscious.

A taxonomy of consciousness based on the GNW model differentiates conscious perception from two types of unconscious processing (Dehaene et al., 2006; see Fig. 2). Subliminal processing is present, if the bottom-up strength of an unattended stimulus is too weak for a conscious percept irrespective of attention. Brain activity reflecting subliminal processing comprises weak activation confined to primary sensory areas if attention is absent, and additionally strong feedforward activation if attention is present. Importantly, in both cases, there is no activation of frontoparietal regions. Preconscious processing is present, if the target stimulus is not attended, but strong enough to elicit intense activation, which is, however, confined to sensorimotor regions. Again, there is no reportability and no conscious perception. Lastly, conscious perception is present, if a target stimulus is sufficiently strong as well as attended. Neuronal correlates include all-or-nothing ignition of frontoparietal regions, amplified activation in sensorimotor regions, long-range cortico-cortical synchronization mainly in the beta band, late amplification in the gamma band, and increased causal connections between distant regions (Dehaene et al., 2006; Dehaene and Changeux, 2011).

Taken together, dissociative theories make a conceptual distinction between a putative phenomenal and access consciousness (Block, 1995), which can be related to different aspects of the NCC, such as micro- vs. macroconsciousness (Zeki and Bartels, 1999; Zeki, 2001, 2003), or local vs. wide-spread recurrent neural activity (Lamme and Roelfsema, 2000; Lamme, 2006). In contrast, non-dissociative theories differentiate between several stages of unconscious processing, but know only one type of conscious perception reflected in one NCC (Crick and Koch, 2003; Dehaene et al., 2006). In addition, non-dissociative theories highlight the role of consciousness in interpreting sensory input and making it available to higher-order cognitive functions (Dehaene et al., 2006; Van Boxtel et al., 2010). From this perspective, it follows firstly that consciousness per se and subsequent cognitive functions cannot be separated, and secondly that consciousness cannot be studied independently of cognition (Cohen and Dennett, 2011). The current thesis adopts the non-dissociative perspective of the GNW

(Dehaene et al., 1998), and operationalizes conscious perception via reportability.

Neural brain states and conscious perception

Despite the fundamental difference between the dissociative and non-dissociative theories discussed above, they share one important aspect: All of them focus on the processing of a stimulus, while completely ignoring pre-stimulus neural brain states and their impact on subsequent perception. Neural activity in pre-stimulus periods has conventionally been treated as irrelevant background noise without any meaning for sensory processing or cognitive function. However, recent studies have shown that oscillatory activity prior to, for instance, a weak sensory stimulus influences its perceptual fate, reflecting neural requirements for conscious perception. As pointed out by Aru et al. (2012), the NCC is, in fact, not a unified construct, but contains several distinct parts. These are the proper NCC, consequences of conscious perception, and, importantly, prerequisites of consciousness. The present thesis explicitly focuses on this pre-stimulus part of the NCC. In the following sections, I will give a short overview of previous literature with a focus on the alpha band, followed by an introduction to the framework windows to consciousness (Ruhnau et al., 2014; Weisz et al., 2014).

Oscillatory signatures of consciousness in the alpha band. In the visual and auditory modalities, alpha power increases in the corresponding sensory regions impair conscious perception. In the visual modality, alpha power over posterior recording sites are negatively correlated with conscious perception (Ergenoglu et al. 2004; Hanslmayr et al. 2007; van Dijk et al. 2008; Busch et al. 2009; Wyart and Tallon-Baudry 2009; see Fig. 3A). These power differences originate in the visual cortex (Romei et al., 2008; Lange et al., 2013) and more anterior parieto-occipital areas (Van Dijk et al., 2008). Using transcranial magnetic stimulation, Romei and colleagues showed that spontaneous oscillatory alpha band activity in the visual cortex reflects cortical excitability fluctuations (Romei et al., 2008). In the auditory modality, we were recently able to show that power in the alpha band was decreased prior to a consciously perceived stimulus (Leske et al., *in press*).

In addition to the findings regarding amplitude changes in the alpha band, stimulus detection correlates with alpha phase at stimulus onset (Mathewson et al., 2009). Moreover, the phase of oscillatory alpha activity can be entrained with rhythmically presented training stimuli prior to target presentation (Mathewson et al., 2010, 2011). However, in line with the functional inhibition hypothesis (Jensen and Mazaheri, 2010; Mazaheri and Jensen, 2010), both alpha phase dependency and alpha band entrainment were contingent on high pre-stimulus alpha power.

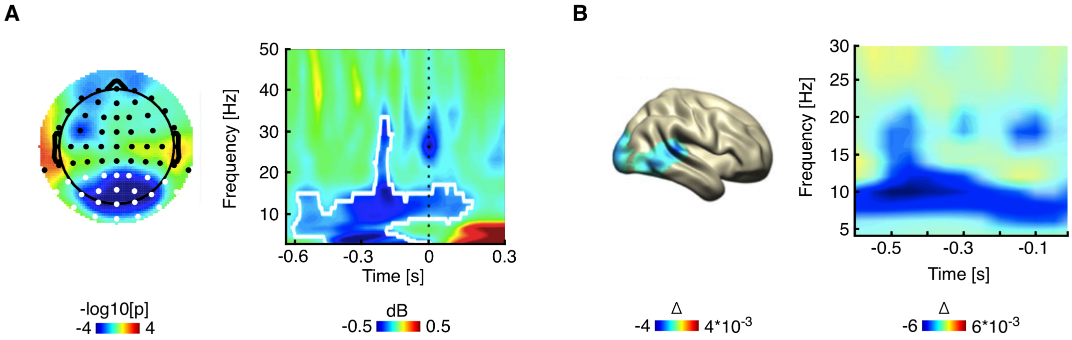

Figure 3. Oscillatory alpha power prior to conscious visual/auditory perception. **A** Topography (left) and time-frequency representation (right) of an alpha power decrease prior to consciously perceived visual stimuli. White electrodes markers indicate the channels used for the time-frequency representation; white outlines designate significant time-frequency points. (Reprinted with permission from Busch and VanRullen, 2010). **B** Source reconstruction (left) and time-frequency representation (right) of an alpha power decrease in the right auditory cortex prior to consciously perceived auditory stimuli. Transparency designates significant time-frequency points. (Reprinted with permission from Leske et al., 2015).

Similar findings regarding the impact of oscillatory alpha band activity on conscious perception have also been reported in the somatosensory modality. First of all, a combined EEG-TMS study showed that somatomotor alpha power reflects cortical excitability (Sauseng and Klimesch, 2008). Moreover, tactile conscious perception is preceded by relative alpha power decreases in the somatosensory cortices (Linkenkaer-Hansen et al., 2004; Schubert et al., 2008; Zhang and Ding, 2010; Ai and Ro, 2014; Weisz et al., 2014). In contrast to the relatively straightforward relationship between pre-stimulus alpha power and conscious visual perception, some studies reported an inverse U-shaped relationship between pre-stimulus alpha power and tactile perception (Linkenkaer-Hansen et al., 2004; Zhang and Ding, 2010; Ai and Ro, 2014; see Fig. 4A-B). This finding indicates that an intermediate alpha power level prior to stimulus presentation is optimal for conscious perception. Other studies, in contrast, reported a negative linear relationship similarly to the visual domain (Schubert et al., 2008; Weisz et al., 2014; see Fig. 4C-D).

Possible reasons for these discrepant findings could be found in the task requirements, experimental design, or data analysis. First of all, the studies reporting a quadratic function between pre-stimulus alpha power and conscious perception used a binning procedure to divide pre-stimulus alpha power into different levels. In this procedure, the first and the last bins are particularly influenced by extreme power values (see e.g., Ai and Ro, 2014), which, in turn, strongly influence the quadratic measure. Secondly, the experimental design varied considerably between the studies, with potential impact on general alpha power levels and signal-to-noise ratios. For instance, Schubert and colleagues (2008) presented a high-intensity distractor stimulus and provided explicit instructions to attend to the target finger. These instructions could have affected the spontaneous pre-stimulus alpha power fluctuations in a top-down manner, and possibly prevented extremely low or extremely high alpha power values. In contrast, in the earliest study participants were required to perform a demanding detection task for blocks of 20min while being blindfolded (Linkenkaer-Hansen et al., 2004), most likely increasing the occurrence of extreme alpha power values.

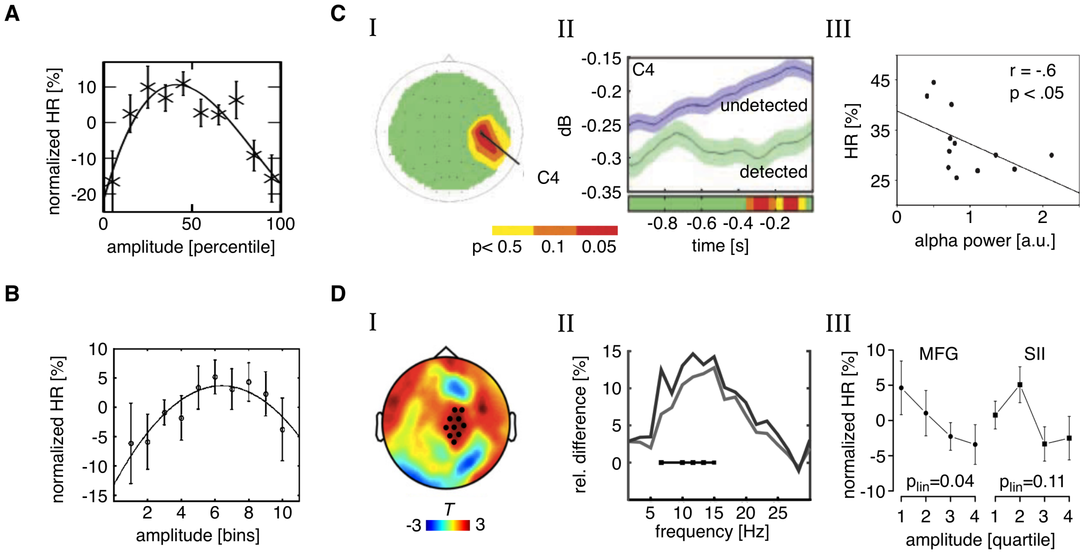

Figure 4. Oscillatory alpha power prior to conscious tactile perception. **A** and **B** The amplitude of sensorimotor alpha power was shown to have a parabolic relationship with detection rates of weak somatosensory stimuli. (Reproduced with permission from Linkenkaer-Hansen et al., 2004 and Zhang and Ding, 2010). **C** Topography of p-values for the contrast detected vs. undetected showing significantly increased alpha power prior to undetected somatosensory stimuli (**I**) and the corresponding time course of alpha power prior to undetected and detected stimuli (**II**). In contrast to A and B, alpha power was shown to have a linear relationship with detection rate (**III**). (Reproduced with permission from Schubert et al., 2008). **D** Topography of T-values for the contrast undetected vs. detected (**I**), showing significantly increased alpha power prior to undetected somatosensory stimuli, and the frequency spectrum (**II**) of the relative difference for the same contrast (lower grey trace). Here, oscillatory alpha power in the middle frontal gyrus (MFG) but not in the secondary somatosensory cortex (SII) contralateral to stimulation showed a negative linear correlation with the normalized hit rate (**III**). (Reproduced with permission from Weisz et al., 2014).

Regarding alpha phase, only a few studies have investigated the effect of phase on somatosensory perception. The first study reported a broadband phase-locking of detected stimuli relative to undetected stimuli, particularly in the alpha band, but with a focus on the post-stimulus period (Palva et al., 2005). Furthermore, somatosensory stimulus detection was found to be more likely during the descending, and less likely during the ascending alpha phase, however, only if the pre-stimulus alpha power level was generally high (Ai and Ro, 2014).

Taken together, findings from the somatosensory modality correspond to reports from the visual and the auditory modalities. Whereas low tonic alpha power in general enhances stimulus processing, and thus awareness, high alpha power exerts a stronger functional inhibition in a pulsed manner (Klimesch et al., 2007; Jensen and Mazaheri, 2010).

Windows to consciousness. As seen above, studies from the last two decades have revealed that alpha power decreases in sensory regions, reflecting increased cortical excitability, facilitate conscious perception. These findings were interpreted according the functional inhibition hypothesis (Klimesch et al., 2007; Jensen and Mazaheri, 2010). That is, if a stimulus enters the system when the relevant sensory neurons are already highly excitable, it is more likely to cause sufficiently strong activity in these regions to cross the perceptual threshold. Thus, alpha power decreases prior to stimulus presentation were proposed to reflect a brain state predisposing conscious perception.

This line of reasoning indirectly implies that conscious perception depends on a stimulus-driven bottom-up input sweep. Moreover, activity in sensory regions related to successful stimulus perception should become evident immediately. However, in contrast to these implications, studies investigating conscious processing do not report such immediate sensory activity. Furthermore, as discussed above, theories regarding conscious perception emphasize the importance of recurrent activity between sensory and higher-order regions for conscious perception. Specifically, it was proposed that sensory activity has to cross an ignition threshold, which is followed by an all-or-nothing activation of frontoparietal regions (Dehaene et al., 2006; see Fig. 2A). Across these empirical findings and theoretical accounts, it is highly unlikely that the prerequisite of conscious perception is limited to local excitability changes in sensory regions.

The window to consciousness framework (win2con; Ruhnau et al., 2014; Weisz et al., 2014) proposes an alternative account for brain states predisposing conscious perception (see Fig. 5). Specifically, this framework argues that – in addition to local excitability changes – pre-established functional pathways prior to stimulus onset predispose conscious processing. Along these lines, stimulus processing is facilitated and becomes more efficient, if an incoming stimulus encounters a sensory cortex that is functionally already well connected with higher-order areas. In other words, increased *local* neuronal excitability as well as *global* functional connectivity patterns prior to stimulus presentation constitute windows to conscious perception.

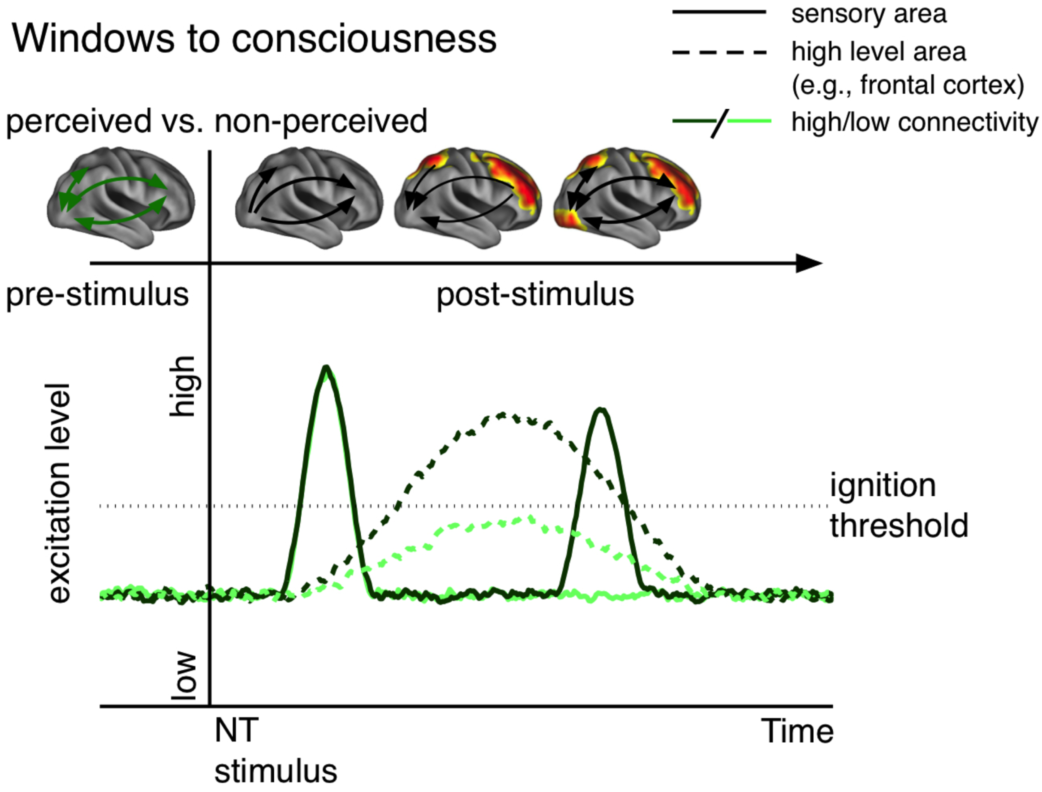

Figure 5. The window to consciousness framework. Pre-established functional pathways between sensory and higher-order regions (green arrows drawn on leftmost brain figure) predisposes the propagation of stimulus-related neural activity (black forward arrows), resulting in activity in frontoparietal regions (clusters in hot colours), top-down amplification (backward arrows) and recurrent activity (two-way arrows) between sensory and higher-order regions. Sensory activity immediately after stimulus onset can be observed irrespective of pre-stimulus functional connectivity (green traces) and conscious perception. Only if a sensory region is already well connected to higher-order regions prior to stimulation onset (dark green traces), will this activity be propagated and elicit activity in higher-order regions (dark green, dotted trace). This is not the case for regions that are not well connected prior to stimulus onset (light green, dotted trace). (Reproduced with permission from Ruhnau et al., 2014).

Attention

Attention has been at the centre of psychological and neuroscientific research for decades. Important advances were made in understanding the neural basis of attention, including its functional and structural anatomy (for reviews see Corbetta and Shulman, 2002; Corbetta et al., 2008; Ptak, 2012; Vossel et al., 2014; Wang, 2010), and its oscillatory signatures. Cortical oscillations associated with attention include local synchrony in the alpha band, but also local gamma power (Jensen et al., 2007), phase resetting/dependencies in the delta/theta band (Schroeder and Lakatos, 2009; Schroeder et al., 2010) and alpha band (Busch et al., 2009; Mathewson et al., 2010, 2009; for a review see Mathewson et al., 2011), and long-range coherence in the beta and gamma band (Siegel et al., 2008; for a general review see Gregoriou et al., 2015). An exhaustive discussion of all these aspects of attention lies outside the scope of the present thesis. Instead, to provide a theoretical context for the studies reported here, the following sections will focus on the functional and structural anatomy of attention and local oscillatory signatures of attention in the alpha band.

Functional and structural anatomy

According to a meta analysis, attention allocation recruits two largely distinct frontoparietal systems, the dorsal and ventral attention network (DAN, VAN; Corbetta and Shulman, 2002; see Fig. 6A). Whereas the DAN consists of bilateral areas along the precentral gyrus including the frontal eye fields (FEF) and the posterior parietal cortex along the intraparietal sulcus (IPS), the VAN is right-dominant and contains the temporaparietal junction (TPJ) and the ventral frontal cortex (VFC; Corbetta and Shulman, 2002; Corbetta et al., 2008; Vossel et al., 2014). Resting-state activity is highly correlated within each network (i.e., within the DAN and within the VAN), indicating a segregation of the systems. Nevertheless, the two networks are structurally connected via the superior longitudinal fasciculus (SLF; Ptak, 2012; see Fig. 6B). The first and third fibre tract of the SLF (SLF I and III) interconnect regions of the DAN and regions of the VAN, respectively, the SLF

II connects the inferior parietal cortex (including the TPJ) with the middle premotor cortex and dorsolateral prefrontal cortex (including the FEF).

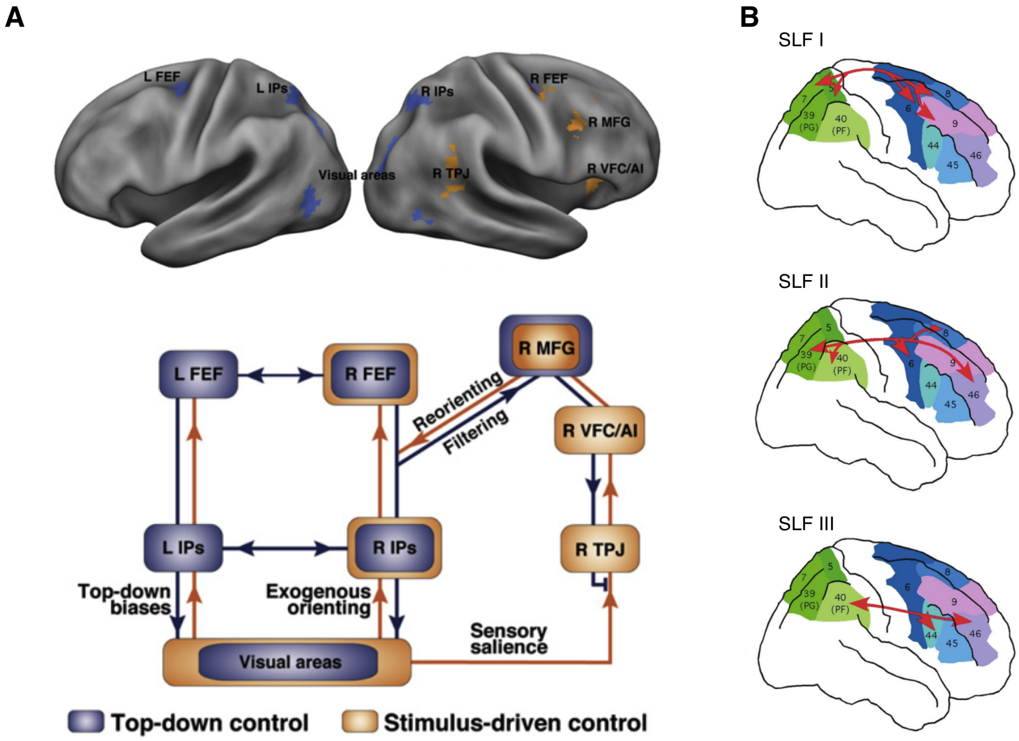

Figure 6. The dorsal and ventral attention networks. **A** Results from a meta analysis of activation data showing the dorsal / ventral attention networks in blue / orange (upper part), and a model of the interactions between the two networks during stimulus-driven reorienting. Whereas the dorsal network sends mainly top-down biasing signals (to visual areas and the ventral network), the ventral network processes sensory salience and sends a reorienting signal to the dorsal network. Communication between the two networks occurs via the middle frontal gyrus. (Reproduced with permission from Corbetta et al., 2008). **B** Subdivisions I, II, and III of the superior longitudinal fasciculus fibre tract, connecting regions within and between the two attention networks. (Reproduced with permission from Ptak, 2012).

Generally speaking, the DAN is activated during top-down biasing during goal-driven attention, for instance, during spatial or feature-based attention in cueing paradigms (Kastner et al., 1999; Corbetta et al., 2000; Hopfinger et al., 2000; Egner et al., 2008; Shulman et al., 2010). Concerning functional connectivity, visual areas are influenced by the bilateral IPS (Bressler et al., 2008; Vossel et al., 2012) and by the FEF (Bressler et al., 2008). Furthermore, transcranial magnetic stimulation on IPS and FEF modulated visual cortex activity (Ruff et al., 2006, 2008). In contrast, the VAN is activated by stimulus-driven attention, for instance, if a stimulus is behaviourally relevant, infrequent, or appears at an unattended (i.e. invalidly cued) location (Arrington et al., 2000; Corbetta et al., 2000; Macaluso et al., 2002; Shulman et al., 2010). Importantly, the VAN is only activated if a stimulus is also task-relevant, and not just if it is particularly salient (Corbetta et al., 2008). In the case of invalid cueing, the functional connectivity from visual areas to the TPJ is increased (Vossel et al., 2012).

Even though both systems within the frontoparietal cortex are largely distinct, they dynamically interact with each other during attention deployment. Whereas the VAN was originally conceptualized as a circuit breaker of attentional activity in the DAN (Corbetta and Shulman, 2002), subsequent research suggested that the DAN plays a more fine-grained role, for instance, as a filter mechanism (Corbetta et al., 2008) or as an evaluation process regarding top-down expectations (Vossel et al., 2014). Importantly, how the DAN and the VAN interact is task-dependent; their activity can either be anticorrelated, for instance during visual search, or positively correlated during spatial attention with invalidly cued targets (Vossel et al., 2014).

Alternative accounts for frontoparietal activity during cognitive tasks including, for instance, visual search have been proposed and include a task relevance map (Navalpakkam and Itti, 2005); a top-down salience map (Egner et al., 2008), or a priority map, (Ptak, 2012). While the concept of attention plays a certain role in these proposals, salience or priority go beyond simple attention by additionally involving stimulus properties and behavioural goals. Thus, these ideas propose alternative mechanisms, which optimally prepare for perception and adequate responses to environmental stimuli. In conclusion, much evidence supports the existence of two largely distinct, dynamically interacting functional networks for goal-driven and stimulus-driven attention.

Oscillatory signatures of attention in the alpha band

Research concerning oscillatory activity has provided a vast amount of evidence how brain oscillations support attention. As the reported studies in this thesis focus on alpha power modulations during attention and perception, this section will introduce how attention relates to local oscillatory activity in the alpha band, focusing on amplitude changes (for reviews see Foxe and Snyder, 2011; Frey et al., 2015, in Appendix B).

Amongst others, attention can be directed towards the locus, a feature, or the modality of a sensory stimulus, for instance based on an attentional cue (for a typical design of an attention study, see Fig. 7A). Experimental manipulation of attention leads to a relative alpha power decrease over regions processing the attended stimulus or stimulus feature. Conversely, relative alpha power increases were observed over regions processing potential distractor stimuli, for instance, on the opposite side or in a different modality (for an example, see Fig. 7B). Findings were reported in manifold experiments and tasks, for instance during spatial attention (e.g., visuospatial - Rihs et al., 2007; Thut et al., 2006; somatosensory - Anderson and Ding, 2011; Bauer et al., 2012; audiospatial - Frey et al., 2014 , in Appendix A; Müller and Weisz, 2012), or during sensory selective attention (e.g., audiovisual - Foxe et al., 1998; Fu et al., 2001; Wittekindt et al., 2014; visuotactile - Bauer et al., 2012). Intracranial recordings supported these findings by showing alpha power increases in the auditory cortex when attention was directed towards visual stimuli (Gomez-Ramirez et al., 2011).

Importantly, when attending to a specific stimulus, the strength of post-cue alpha power in regions processing the attended stimulus depends on the certainty with which a stimulus is presented (Haegens et al., 2011). As a consequence, by varying the reliability of an attentional cue, alpha power increases and decreases in sensory and attention-sensitive areas can be experimentally manipulated. As discussed above, oscillatory activity in the alpha band is widely accepted to reflect cortical excitability (Klimesch et al., 2007; Jensen and Mazaheri, 2010). Taken together, during attention deployment, alpha power modulations in sensory regions reflect a top-down preparatory mechanism that influences how efficiently an incoming stimulus will be processed.

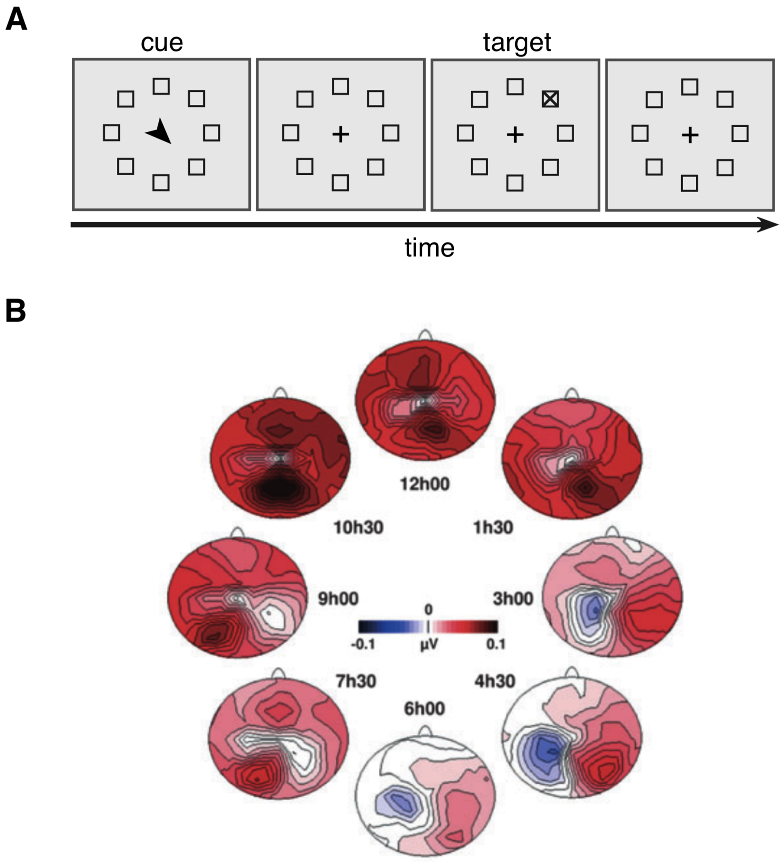

Figure 7. Paradigm and results of a classical attention study. **A** In each trial participants were required to attend one of eight spatial locations on a screen, cued by a central arrow. After a cue-target interval, a target was presented in one of these locations (in 88% of all trials, the target was validly cued), and participants had to respond with a button press as quickly as possible. Here, an invalidly cued trial is shown. **B** Topographies showing the baseline-corrected post-cue alpha power modulations when each of the eight locations was attended. Alpha power is relatively increased/decreased over regions that process the unattended/attended locations. (A and B reproduced with permission from Rihs et al., 2007).

Research Questions and Outlook

The overall goal of the present thesis is to elucidate the pre-stimulus oscillatory signatures of tactile conscious perception and attention. As discussed above, reduced alpha power precedes successful detection of a weak sensory stimulus. Therefore, decreased pre-stimulus alpha power is part of a brain state predisposing conscious perception. Based on empirical findings and theoretical considerations, however, it is unlikely that increased cortical excitability alone (reflected by decreased alpha power) predisposes consciousness. The first goal of the current thesis is to investigate the prerequisites of conscious perception in the tactile modality. In the study reported in Chapter 2, we address the question whether pre-established functional pathways between somatosensory regions and the whole system positively influence conscious perception, in addition to increased cortical excitability.

Moreover, we aim to understand the relationship between spontaneous alpha power fluctuations prior to conscious perception with attention-induced alpha power modulations. As summarized above, modulations of oscillatory activity in the alpha band are not only found prior to conscious perception, but also during top-down attention. Specifically, if stimuli from a specific modality are attended, alpha power in regions processing this modality is reduced. Until now, it remained unclear to what extent such attentional alpha band modulations play a role prior to conscious perception. Thus, the second goal of the current thesis is to investigate the relationship between consciousness, attention, and sensory alpha power. The study reported in Chapter 3 tests the assumption that spatial attention modulates alpha power, but that neural activity in the alpha band also spontaneously fluctuates predisposing conscious perception.

Chapter 2: The Tactile Window to Consciousness is Characterized by Frequency-specific Integration and Segregation of the Primary Somatosensory Cortex

Abstract

We recently proposed that besides levels of local cortical excitability, also distinct pre-stimulus network states (windows to consciousness) determine whether a near-threshold stimulus will be consciously perceived. In the present MEG study, we scrutinised these pre-stimulus network states with a focus on the primary somatosensory cortex. For this purpose participants performed a simple near-threshold tactile detection task. Confirming previous studies, we found reduced alpha and beta power in the somatosensory region contralateral to stimulation prior to correct stimulus detection as compared to undetected stimuli, and stronger event-related responses following successful stimulus detection. As expected, using graph theoretical measures, we also observed modulated pre-stimulus network level integration. Specifically, the right primary somatosensory cortex showed an increased integration in the theta band, and additionally, a decreased integration in the beta band. Overall, these results underline the importance of network states for enabling conscious perception. Moreover, they indicate that also a reduction of irrelevant functional connections contributes to the window to consciousness by tuning pre-stimulus pathways of information flow.

Introduction

Studies investigating pre-stimulus effects in near-threshold (NT) paradigms observed that correctly perceived stimuli (‘detected’) are preceded by low alpha power in task-relevant areas. This was shown for the visual (e.g., Ergenoglu et al., 2004; Hanslmayr et al., 2007; Thut et al., 2006; van Dijk et al., 2008) and the somatosensory cortex (Linkenkaer-Hansen et al., 2004; Schubert et al., 2008; Zhang and Ding, 2010; Ai and Ro, 2014; Weisz et al., 2014) depending on the task. These experimental observations are usually also interpreted according to the notion that alpha activity reflects the cortical excitability with strong alpha reflecting functional inhibition (Klimesch et al., 2007; Jensen and Mazaheri, 2010). The straightforward rationale, thus, states that an upcoming NT stimulus will become conscious when pre-stimulus local excitability (e.g., in the visual cortex) is high, so that a weak input causes ignition of relevant neural assemblies. Hence, the alpha power effects are interpreted mainly in local terms. Despite providing an intuitive explanation of pre-stimulus determinants of conscious perception that are well linked to a strong conceptual framework, this interpretation has a major shortcoming. As this viewpoint emphasizes local pre-stimulus cortical excitability, it predicts that successful stimulus detection depends on a bottom-up input sweep. In this case, effects in sensory regions should become evident immediately, as soon as an ignition threshold is crossed. Interestingly, evidence for this implicit prediction is rather scarce. In contrast, effects in sensory regions are reported to appear relatively late, probably due to recurrent activation from downstream areas (Dehaene and Changeux, 2011).

Apart from this empirical discrepancy of what should be expected if pre-stimulus effects were interpreted along the functional inhibition hypothesis, major neuroscientific frameworks of conscious perception stress a network perspective. For example the global neuronal workspace model (GNW; Dehaene et al., 1998) suggests that sensory stimuli only become conscious, if they are *globally* available for further cognitive processing. Recently, we have shown that conscious perception of a weak tactile stimulus is characterised by a stronger network integration of the secondary somatosensory cortex

(SII) already in the pre-stimulus period (Weisz et al., 2014). In an accompanying framework called Windows to Consciousness (win2con, Ruhnau et al., 2014; Weisz et al., 2014) we have argued that this enhanced pre-stimulus integration reflects pre-established pathways of information flow, facilitating a more efficient stimulus-related spread of information throughout a distributed network. By extending the straightforward interpretation of pre-stimulus effects in terms of local cortical excitability, our framework adds a conceptual contribution to bridge the gap between the pre- and post-stimulus divide (i.e. what would be predicted based on a local excitability hypothesis, and what is actually observed in the post-stimulus period). Specifically, it does not predict early activation in sensory regions to determine conscious perception (for detailed argumentation, see Ruhnau et al., 2014).

In our framework (Ruhnau et al., 2014; Weisz et al., 2014), we have specifically emphasized *increased* pre-stimulus integration reflecting pre-established pathways of information flow. We have argued that increased coupling and enhanced network integration make stimulus processing more efficient, and thus more likely to be consciously perceived (Leske et al., *in press*; Weisz et al., 2014). Stimulus processing, however, will also be optimized, if pre-stimulus functional connectivity is tuned to incoming sensory stimuli by *reducing irrelevant* connections. For instance, if task-relevant sensory areas (e.g., the primary somatosensory cortex in a unimodal tactile task) are strongly coupled with task-irrelevant areas (e.g., other sensory regions), processing of an incoming tactile stimulus could be impaired. Thus, it is likely that the tactile window to consciousness is not only characterized by improved coupling between sensory regions and task-relevant higher-order areas, but also by decoupling between sensory regions and task-irrelevant cortical areas.

In our pervious study (Weisz et al., 2014), we focused mainly on SII and its functional connectivity predisposing stimulus detection. Whereas sustained stimulus-related activity in SII has been shown to be essential for conscious perception (Wühle et al., 2010, 2011), a causal modelling study emphasized recurrent activity between SI and SII to underlie somatosensory awareness (Auksztulewicz et al., 2012). Most likely, stimulus-related activity in SI is necessary but not sufficient for conscious perception, whereas sustained activity in SII and recurrent processing between SI, SII, and higher-order areas form coalitions of neurons (Crick and Koch, 2003), resulting in a conscious percept. The exact roles, however, of SI and SII in the window to consciousness have not been explored so far, particularly regarding pre-established functional pathways.

Going beyond our previous study (Weisz et al., 2014), we investigated whether there are inverse pre-stimulus network patterns predisposing conscious perception as described above, with a particular focus on SI. To this end, we used a simpler NT detection task, and computed pre-stimulus time-frequency resolved global and local graph theoretical measures. In addition to previously described power decreases in the alpha and beta band in sensory areas prior conscious perception, here we report for the first time simultaneous functional integration and segregation patterns for the relevant sensory areas. Specifically, we found increased pre-stimulus integration of the right SI in the theta band (increased local efficiency and local degrees), and decreased integration in the beta band (decreased local efficiency) prior to conscious perception. Overall, these findings have far-reaching consequences in understanding the prerequisites (Aru et al., 2012) of conscious perception.

Methods

Participants

19 participants (6 females; mean age: 26.8 years, SD: 4.4 years) took part in the experiment after giving written informed consent. All participants were right-handed (Edinburgh Handedness Questionnaire, mean: 95.1, SD: 11.5; Oldfield, 1971) and had normal or corrected-to-normal vision. The experimental protocol was approved by the Ethical Committee of the University of Trento, Italy.

Task and design

To study conscious somatosensory perception, a NT tactile perception task was employed. Tactile stimulation was delivered to the tip of the left index finger, using one finger module of a piezo-electric stimulator (Quaerosys, Schotten, Germany) with 2x4 rods. These rods can be raised to variable degrees (maximal height 1mm); height was set for all participants independently to match their perceptual threshold. The module was attached to the finger with tape, and the participant's left hand was cushioned to prevent any unintended pressure on the module, which could have influenced stimulus intensity. Participants were asked to fixate a black cross on a grey screen throughout the whole experiment to minimise eye movements. To ensure that participants did not hear any auditory cues caused by the piezo-electric stimulator during tactile stimulation, binaural white noise was presented using a STIM2 system (Tip-300, Nicolet, Madison, WI, USA) and MEG-compatible tubal in-ear headphones.

In a training session prior to the main experiment, participants' individual perceptual threshold was determined in the shielded room using a 1-up / 1-down staircase procedure. Two randomly interleaved staircases (one up- and one downward) were used with fixed step sizes. Then, a short training run with 20 trials was conducted to ensure that participants had understood the task, and to control the accuracy of the threshold measurement.

The main experiment consisted of a NT tactile detection task (see Fig. 8A). Participants were told that on each trial a weak tactile stimulus could be presented on the tip of their left index finger at random time intervals. After 250ms, participants were prompted with an on-screen question to indicate whether they had felt the stimulus. The question was presented maximally for two seconds, or until participants responded. Responses ('yes'/'no') were given by using MEG-compatible response boxes with the right index and middle fingers. Overall, there were five to eight runs with 62 trials each. Each trial started with a variable inter-stimulus interval (2-5s, gamma-distributed) followed by an experimental stimulus (48 per run), a sham stimulus (12 per run) or a catch stimulus (2 per run) of 50ms each, presented at, clearly below, or clearly above perceptual threshold intensity, respectively. Each run lasted for approximately 5min; between the runs participants could take a break.

MEG data acquisition and preprocessing

Electromagnetic brain activity was recorded using a 102 triple-sensor (two planar gradio-, one magnetometer) MEG system (Elekta Neuromag, Helsinki, Finland). Data was sampled continuously at 1kHz. Prior to the experiment, the headshape of each participant was measured using a Polhemus FASTRAK 3D digitiser, relative to five coils (two on the left and right mastoid, three coils on the front). Head movement was monitored by passing small currents through these coils before each run. From most participants, an anatomical 3D structural image was obtained using a 4T magnetic resonance imaging (MRI) scanner (Bruker Biospin, Ettlingen Germany). All MEG data was analysed using the Matlab-based Fieldtrip toolbox (Oostenveld et al., 2011). Epochs of +/-2000ms length were extracted around stimulus onset and 1Hz highpass filtered. Then, the data was visually inspected to identify and remove noisy trials, channel jumps and ocular artefacts. After the artefact rejection, all trials were downsampled to 300Hz. In all further analyses, an equal number of detected and undetected trials was randomly selected to prevent any bias across conditions (Gross et al., 2013).

Sensor-level analyses

Sensor-level analyses were done for both sensor types separately and missing channels were interpolated. Neural activity event-related to stimulus onset was investigated by computing event-related fields (ERF). To this end, 30 Hz lowpass-filtered epochs were averaged, and normalized by subtracting the mean activity in a pre-stimulus baseline time window (-300 to -100ms). Furthermore, spectral power was estimated using a Fourier transformation on Hanning-tapered time windows from 1500ms pre- to 500ms post-stimulus (in steps of 50ms) from 2 to 30Hz (in steps of 1Hz). The length of the sliding time window was frequency dependent (6 cycles per frequency).

Source-level analyses

For all source-level analyses, the preprocessed data was bandpass-filtered between 2-30 Hz and projected to source-level using an LCMV beamformer analysis (Van Veen et al., 1997). For each participant, realistically shaped, single-shell headmodels (Nolte, 2003) were computed by co-registering the participants' headshape either with their structural MRI or – when no individual MRI was available (6 participants) – with a standard brain from the Montreal Neurological Institute (MNI, Montreal, Quebec, Canada; http://www.bic.mni.mcgill.ca/brainweb), warped to the individual headshape. A grid with 1.5cm resolution created based on an MNI template brain was morphed into the brain volume of each participant. A common spatial filter (for each grid point and each participant) was computed using the leadfields and the common covariance matrix taking into account the data from both conditions (detected, undetected). Using this common filter, the spatial power distribution was estimated for the detected and undetected trials separately.

For the source-level event-related activity, the covariance window for the beamformer filter calculation was based on 100ms pre- to 300ms post-stimulus. The resulting data was averaged relative to the stimulus onset in both conditions (detected and undetected), and baseline-normalized relative to a time-window from 300-100ms pre-stimulus. To eliminate polarity, statistics were computed on the absolute values of the source-level event-related responses (ER).

For the source-level analysis of spectral power and connectivity in the pre-stimulus time period, the LCMV beamformer filter was calculated based on a covariance window from 1000-100ms pre-stimulus. Spectral power was estimated using a multitaper FFT method on dpss-tapered time windows from 1500-0ms pre-stimulus (in 100ms steps) for 2-30Hz (in 2Hz steps) with a frequency smoothing of 3Hz. The length of the sliding time window was frequency dependent (5 cycles per frequency). Furthermore, functional connectivity was calculated using imaginary coherence (Nolte et al., 2004) and graph theoretical analysis was applied to the thresholded connectivity matrices (Bullmore and Sporns, 2009). Imaginary coherence values were obtained based on the spectral power analysis described above. Then, the absolute values of the resulting coherence spectra were thresholded for each frequency-band and across conditions to obtain binary adjacency matrices. Thresholds were determined by first identifying the smallest of all maximal coherence values per node within each frequency band and each condition. This procedure ensured that each node had at least one connection without underestimating actual connections. Then, the lower threshold of either condition was chosen and applied to both conditions. All coherence values below this were set to zero. For the individual nodes following graph theoretical measures were calculated: node degree (number of connections for one specific node), local efficiency (inverse of average path lengths of all direct connections of a node), local clustering (proportion of connections between direct connections of a node to the total amount of possible connections), and local betweenness (placement on many shortest paths of the network; Bullmore and Sporns, 2009; Sporns, 2014). While node degree reflects the overall connectedness of a node, local efficiency and clustering is more sensitive to its integration, and local betweenness reflects the importance of a node in the whole network (Bullmore and Sporns, 2009). We also computed global graph theoretical measures such as density, average path length, efficiency, and small-worldedness. However since no effects were obtained that survived correction for multiple comparisons we refrain from a detailed description of these measures for brevity's sake.

Statistical testing

Detection rates for the experimental trials were statistically compared to those from the catch trials as well as to chance level, using a dependent samples T-Test. Concerning the MEG data, the main statistical contrast was between trials in which participants reported stimulus detection, with trials in which they did not (detected vs. undetected). If not stated differently, these two conditions were statistically tested with a dependent-samples T-test, controlling for multiple comparisons with a non-parametric cluster-based permutation analysis (Maris et al., 2007).

Event-related activity was tested for a time-window from 0-1000ms post-stimulus on sensor and source level. Spectral power was tested for a 1000-100ms pre-stimulus time-window, and the theta, alpha and beta band frequency window (2-6 Hz, 8-14Hz and 16-26Hz). On sensor-level, this was done separately for the two sensor types with averaging over frequency-bands. On source-level, based on the sensor-level results, the statistical test was done only for the right hemisphere with averaging over the whole time-frequency windows.

Concerning graph theory, for the local measures, the data was averaged across the time-window of 1000-100ms pre-stimulus, and frequency-windows in the theta, alpha, and beta band (2-6Hz, 8-14Hz, 16-26Hz). The main contrast (detected vs. undetected) was then tested within an anatomically defined region of interests (ROI; the right SI) with a dependent-samples T-test using a non-parametric permutation analysis and a false-discovery rate correction for multiple comparisons across voxels (FDR; Benjamini and Hochberg, 1995).

Results

Behaviour

Across all participants (N=19), detection rate was 94% (SD: 5%) for catch trials, and 50% (SD: 9%) for experimental trials. The mean false alarm rate in sham trials was 7.5% (SD: 8.5%). Detection rate of experimental trials significantly differed from those of catch trials ($T_{1,18} = -20.7$, $p < 0.001$), but not from chance ($T_{1,18} = 0.087$, $p = 0.93$), indicating that stimulation at NT intensities was successful and participants were highly compliant.

Post-stimulus event-related neural activity

Sensor-level ERFs clearly show that stimuli reported as detected resulted in pronounced post-stimulus neuronal activity, whereas unreported stimuli did not (see Fig. 8B-C). The ERFs of both magnetometers and gradiometers were significantly different from around 0-500ms and 0-550ms post-stimulus, respectively, showing a first peak at 63ms and a second peak at 133ms. The first peak was relatively higher for the magnetometers (data not shown), suggesting a deeper source. This assumption was confirmed by reconstructing the sources of both peaks. Whereas the first evoked peak was localised to the somatosensory and motor areas contralateral to stimulation and the bilateral anterior cingulate gyrus, the second peak originated mainly in the right SI and SII (secondary somatosensory cortex), and the bilateral superior frontal gyrus.

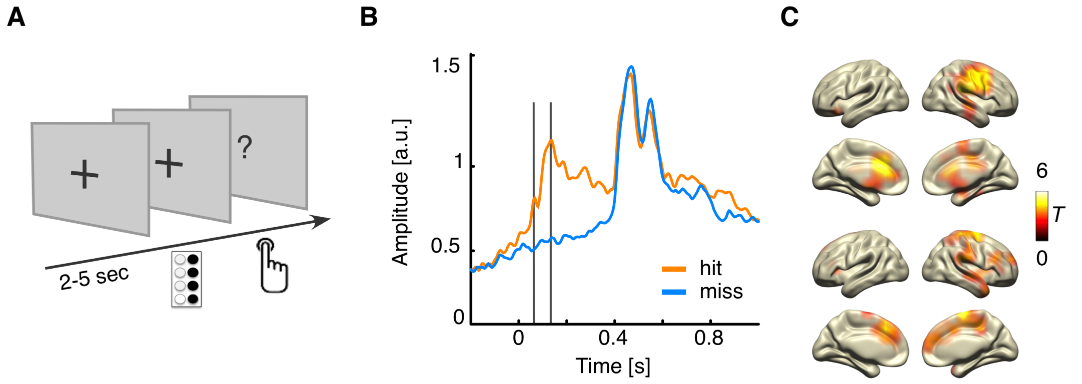

Figure 8. Paradigm and event-related responses. **A** After a variable inter-trial interval between 2-5s during which participants fixated a central cross, a tactile stimulus was presented on the tip of their left index finger for 50ms at individual perceptual intensity. After 250ms, stimulus presentation was followed by an on-screen question, and participants indicated their perception by pressing one of two buttons (‘detected’ or ‘undetected’). **B** Sensor-level event-related global field power in the detected (orange) and undetected (blue) condition for the gradiometer data. Marked with grey lines: First peak at 63ms, second peak at 133ms. **C** Source reconstruction of the two main sensor-level peaks marked in B at 63ms (top) and 133ms (bottom) for the contrast detected vs. undetected trials, masked at $p_{cluster} < 0.05$.

Pre-stimulus power effects

The main statistical contrast (see Statistical Testing) resulted in a significant negative cluster in both sensor types in the alpha band (gradiometers: $p_{cluster} = 0.032$, magnetometers: $p_{cluster} = 0.034$; data not shown)but not in the theta or beta band. The alpha effect seen in the peak magnetometer (MEG1311) lasted from around 700-100ms pre-stimulus and was maximal at 11Hz and 300ms pre-stimulus. In contrast, the effect seen in the peak combined gradiometer (MEG1112+1113) emerged earlier lasting from 800-100ms pre-stimulus, and was maximal at 11Hz and 600ms pre-stimulus. On a descriptive level, the topographies of the alpha effect in both sensor types were lateralised contralateral to the stimulation, and strongest in frontocentral sensors.

On source-level, the statistical analysis of spectral power resulted in significant relative alpha and beta band power decreases prior to stimulus detection ($p_{cluster} = 0.016$ and 0.01, respectively). No power modulations were found in the theta band. Both effects were distributed across the right post- and precentral gyri (BA3 and BA4), while the beta band effect also included the right middle cingulate cortex (see Fig. 9A). The time-frequency representation for the voxel with the maximal effect in both frequency bands reveals that the alpha band effect lasts from 900-200ms pre-stimulus with a peak from 800-700ms pre-stimulus at 12Hz (see Fig. 9B). Whereas the beta power effect also emerges around 900ms pre-stimulus, it becomes strongest shortly before stimulus presentation (after around 400ms pre-stimulus; see Fig. 9B).

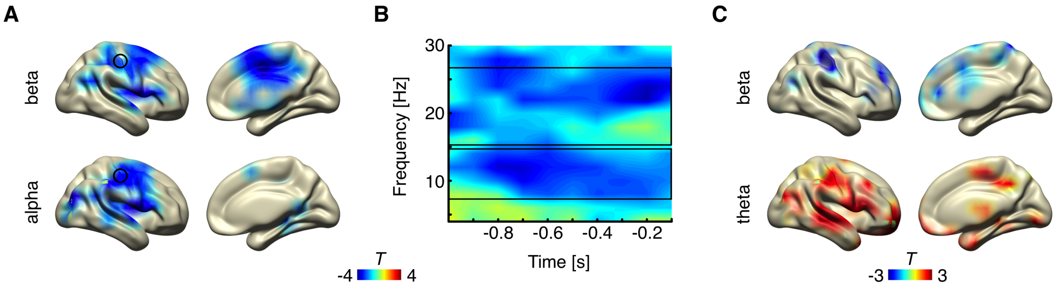

Figure 9. Pre-stimulus spectral power and functional connectivity. **A** Source reconstruction of the alpha (lower panel) and beta (upper panel) power effect ($p_{cluster} < 0.05$). Marked with a black circle is the voxel in SI with the maximal power effect in both frequency bands. **B** The time-frequency representation of the voxel with the maximal power effects marked with a black circle in A. Marked with black rectangles are the time-frequency windows that were used for the source-level power analysis (alpha: 8-14Hz; beta: 16-26Hz). **C** Local efficiency effect in the beta band (top) and in the theta band (bottom). For illustration purpose, the whole brain map is shown at $p_{uncorrected} < 0.05$.

Pre-stimulus functional connectivity

To investigate the functional network architecture in the time window of interest (1000-100ms pre-stimulus) we compared global and local graph theoretical measures (detected vs. undetected). There was no significant effect in any of the global graph theoretical measures (density, path length, efficiency, small-worldedness). Concerning the local metrics, we found significant effects for local degrees and efficiency in the right SI, but not for local clustering and betweenness. Local node degree and efficiency tested in the right SI was relatively increased prior to stimulus detection in the theta band ($p_{FDR} < 0.05$; see Fig. 9C), which were driven by relative increased values at 6Hz throughout the whole pre-stimulus period. In contrast, local efficiency in the right SI was relatively decreased prior to conscious perception in the beta band ($p_{FDR} < 0.05$; see Fig. 9C), which was mainly driven by negative values from 16-18Hz and 24-26Hz between 900-600ms pre-stimulus (data not shown). For illustration purposes, Figure 2C shows the whole brain map of both effects (local efficiency in the beta and theta band), masked at $p_{uncorrected} < 0.05$).

Discussion

In the present MEG study, we set out to investigate the pre-stimulus network integration of the task-relevant sensory area that predisposes conscious perception. First of all, we were able to replicate the well-established pre-stimulus alpha power modulations in task-relevant areas (e.g., Hanslmayr et al., 2007; Schubert et al., 2008; van Dijk et al., 2008; Weisz et al., 2014). In addition to the alpha power effect, we provide more support for our framework win2con, by demonstrating that conscious tactile perception is indeed preceded by a modulated functional integration of task-relevant regions into the network. Specifically, analysis in the SI contralateral to stimulation revealed enhanced network measures in the theta band, and diminished network measures in the beta band. We interpret this integration / segregation pattern as a tuning of pre-established functional pathways to the relevant sensory inputs. As stated in the win2con framework (Ruhnau et al., 2014), this tuning of the functional architecture optimizes stimulus processing and predisposes conscious perception.

Pre-stimulus alpha power in the right SI precedes conscious tactile perception

Here, we replicate previous findings concerning alpha power in task-relevant areas. Contrasting detected with undetected trials revealed relatively decreased alpha power in SI and SII, and distributed regions contralateral to stimulation. Oscillatory alpha activity is thought to reflect the cortical excitability state (Klimesch et al., 2007), and a mechanism to functionally inhibit brain areas (Jensen and Mazaheri, 2010). Thus, the relatively decreased alpha power prior to successful stimulus detection presented here can be interpreted as a release of functional inhibition of task-relevant areas, making stimulus processing more efficient and conscious perception more likely. This finding is in line with previous research regarding conscious tactile perception. Similar pre-stimulus alpha power modulations over posterior regions and the somatosensory cortices were shown to precede conscious somatosensory perception (Schubert et al., 2008; Weisz et al., 2014). Furthermore, alpha power effects in motor areas contralateral to stimulation were reported in a somatosensory discrimination task in monkeys (Haegens et al., 2011). Regarding other modalities, pre-stimulus alpha power modulations inversely related to conscious perception were also shown, for instance, in vision (Romei et al., 2008; Van Dijk et al., 2008; Lange et al., 2013).

Local efficiency modulations in the theta and beta band prior to conscious perception reflect integration and segregation of the right SI

In the present study, we set out to scrutinise our framework win2con (Ruhnau et al., 2014; Weisz et al., 2014), which predicts that enhanced integration of task-relevant sensory areas within the whole brain network determines upcoming conscious perception. In line with our framework, we expected to find more efficient integration of such regions prior to correctly detected stimuli. In the present study, we focused on SI contralateral to stimulation. Analysing functional connectivity with graph theoretical measures, we found higher pre-stimulus local efficiency and node degree values in the theta band in the right SI. Local node degree reflects the number of direct connections of a node, whereas local efficiency reflects the average path length between all directly connected nodes. Thus, these two measures strongly suggest that the contralateral SI is stronger and better integrated in the overall network. Enhanced integration of the SI enables the propagation of stimulus-related activity to higher-order areas. This propagation causes the functional network to ignite, and the stimulus to be globally accessible, resulting in a conscious percept (Dehaene et al., 2006; Dehaene and Changeux, 2011). In contrast to our previous report (Weisz et al., 2014), in which we reported connectivity effects in the alpha band originating from SII, here we specifically focused on SI contralateral to stimulation. To do so, we employed a simpler tactile detection task, boosting the functional role of SI. This change in paradigm most likely also accounts for the differences in global graph theoretical measures. Whereas we have previously reported a smallworldedness and a global efficiency effect (Weisz et al., 2014), no global differences were observed in the present study. Overall, enhanced integration of the right SI in the theta band reflects pre-established functional pathways prior to conscious perception, which represent crucial components of a tactile prerequisite of consciousness.

In addition to the increased local node degree and efficiency effects in the theta band described above, the graph theoretical analysis revealed relatively decreased pre-stimulus local efficiency in the beta band in the same area (contralateral SI). Even though, at first glance, this finding seems to disagree with the win2con framework (Ruhnau et al., 2014; Weisz et al., 2014), it not only integrates well with our hypotheses but also adds important insights. The win2con framework states that pre-established functional pathways determine conscious perception by guiding information flow. Specifically, we have argued that pre-established functional pathways increase the likelihood that a weak sensory stimulus crosses the perceptual threshold and stimulus-related neural activity propagates to the global neuronal workspace (Dehaene et al., 1998; Dehaene and Naccache, 2001).

Intuitively, our hypothesis seems to refer only to 'more' or 'better' pre-established functional pathways. However, stimulus processing is also arguably enhanced if pre-stimulus functional pathways are tuned to the processing of the incoming task-relevant sensory stimulus by *reducing* pathways that are detrimental to stimulus processing. Such irrelevant pathways could mean a) functional pathways between regions of no interest (spatial domain), or b) functional pathways occurring in an irrelevant time-frequency window (temporospectral domain). In either case, the reduction of irrelevant functional pathways benefits the processing of weak sensory stimuli by increasing the likelihood that the stimulus-related activity is propagated to relevant brain regions (for a similar argument for alpha power, see Jensen and Mazaheri, 2010; Tuladhar et al., 2007). Thus, the observed segregation of the right SI is seen as a tuning mechanism. Accordingly, the relative decreases in local efficiency in the beta band reported in this study are reflecting an essential part of the win2con framework.

Together, the increased theta band efficiency and the decreased beta band efficiency in SI prior to conscious tactile perception complement each other for optimal processing of weak stimuli. While the original win2con framework (Ruhnau et al., 2014; Weisz et al., 2014) focused on enhanced integration of task-relevant sensory areas prior to conscious perception, the present study provides important additional insights about spectrally specific connectivity patterns. As discussed above, the same task-relevant sensory region showed an inverse integration pattern in two frequency bands, suggesting a spectral shift in the connectivity patterns to be essential for the tactile window to consciousness.

The integration and segregation reflect processes distinct from local excitability

The integration / segregation effects reported here do not overlap in the time- or the frequency-domains with the pre-stimulus alpha power decreases. In the beta band, the local efficiency decrease was found in the same sensory region as part of the power decreases (right SI). While this could reflect a potential power confound, the power and the connectivity effects do not overlap in the time- or frequency-domains. Specifically, whereas the power effect was strongest in high beta shortly before stimulus onset, the local efficiency effect was most pronounced in low beta up to 600ms pre-stimulus. Moreover, graph theoretical measures were computed based on imaginary coherence, a conservative measure that is insensitive to volume conduction and does not suffer from power confounds (Nolte et al., 2004). Regarding the connectivity effects in the theta band, no corresponding power effect was observed. Thus, exceeding previous works, we show network mechanisms in the theta and beta band that reflect most likely additional processes distinct from power modulations in general, and from alpha band power modulations specifically.

This account is particularly well suited to link the pre-stimulus states with well-established theoretical frameworks of conscious perception concerning stimulus-related neural activity. According to the GNW model (Dehaene et al., 1998, 2006), weak sensory input will only be consciously processed if the activity in essential nodes, such as primary sensory areas, is propagated to higher-order areas, causing a global ignition. In contrast, activity constrained to an essential node will not result in a conscious percept (Dehaene et al., 2006). According to this reasoning, decreased local alpha power in a primary sensory area – an essential node with increased cortical excitability – prior to a weak stimulus will not guarantee a downstream spread of neural activity. However, without this propagation to higher-order areas neural activity would quickly fade away, and thus, would not suffice for conscious perception. Our results strongly suggest that this propagation of activity is only possible if relevant functional connections between primary sensory areas and higher-order regions are already contained in the pre-stimulus brain states whereas irrelevant connections are minimized. If this is the case, activity caused by a weak stimulus can be broadcasted effectively, leading to a conscious percept. Thus, as predicted by win2con (Ruhnau et al., 2014; Weisz et al., 2014) a pre-stimulus increased functional integration and a functional segregation provides a plausible explanation for subsequent conscious perception.

Conclusion

In the present study, we scrutinised our framework win2con (Weisz et al., 2014) using an NT tactile detection paradigm. We replicate that decreased pre-stimulus alpha power in task-relevant areas is related to the conscious perception of the NT stimulus. Importantly, we show that task-relevant areas are characterised by enhanced and more efficient network integration in the theta band, and less efficient integration in the beta band. In our view, these spectrally specific network patterns indicate a tuning of pre-stimulus pathways by establishing relevant and minimizing irrelevant connections. The resulting pre-stimulus functional pathways then influence how subsequent information can propagate to higher order areas and, therefore, within the global workspace. Taken together, these findings provide evidence for a tactile windows to consciousness characterised by a frequency-specific integration and segregation of the right SI into a distributed network.

Chapter 3: Alpha Power in the Somatosensory Cortex Predisposes Conscious Perception in the Absence of Top-Down Influences

Abstract

Studies investigating conscious perception have repeatedly reported relative alpha power decreases prior to successful stimulus detection. However, oscillatory activity in the alpha band is also strongly associated with experimental manipulation of attentional states. For this reason, conscious perception studies, which report alpha power modulations without explicitly manipulating attention, are often confronted with the claim that alpha power decreases prior to perception are due to differences in attention between conditions. In the present study, we set out to investigate whether and to what extent these alpha power modulations prior to conscious perception are influenced by attention. To this end, we combined a spatial attention and a conscious perception task. To experimentally manipulate the pre-stimulus levels of alpha power, the spatial cue could be fully informative, medium informative, or completely uninformative. As expected, the attention manipulation resulted in pronounced lateralized alpha power patterns, with strongest modulations after the fully reliable spatial cue, while conscious perception was preceded by a relative alpha power decrease in frontotemporal regions. Moreover, focusing on functionally defined regions of interest in the primary and secondary somatosensory cortex contralateral to stimulation, revealted that both attention and conscious perception are intricately related to pre-stimulus alpha power in these regions. Whereas top-down attention modulated pre-stimulus alpha power mainly in the fully informative condition, spontaneous fluctuations predisposed conscious perception particularly in the condition with an uninformative cue.

Introduction

It is now widely accepted that oscillatory activity in the alpha band reflects an inhibitory process (Klimesch et al., 2007). According to theoretical frameworks, this mechanism gates information flow throughout a distributed cortical architecture by inhibiting task-irrelevant areas (Jensen and Mazaheri, 2010). These accounts provide a fitting explanation for findings from attention studies, which have repeatedly reported power modulations in the alpha frequency band. Yet, because of this tight association between attention deployment and the inhibitory mechanism reflected by alpha band activity, it remained unclear whether alpha power modulations in other paradigms, for instance prior to conscious perception, is confounded by different levels of attention.

Oscillatory activity in the alpha band was repeatedly reported in attention studies (for reviews see Frey et al., 2015, in Appendix B, and Foxe and Snyder, 2011; Gregoriou et al., 2015; Jensen et al., 2007; Mathewson et al., 2011). When attention is directed towards a particular stimulus, activity in the alpha frequency band (~10Hz) is relatively decreased in cortical regions processing this (upcoming) stimulus, while alpha band activity is increased in regions processing distracting stimuli. This was shown for attention directed towards a specific modality (e.g., audiovisual: Foxe et al., 1998; Fu et al., 2001; Gomez-Ramirez et al., 2011; Wittekindt et al., 2014; tactile: Bauer et al., 2006; Haegens et al., 2011) as well as towards a specific presentation side (Thut et al., 2006a; Rihs et al., 2007; Haegens et al., 2010, 2011, 2012; Frey et al., 2014 , in Appendix A). Moreover, the strength of these alpha power modulations can be experimentally controlled by the reliability of the attentional cue, as in the classical Posner paradigm to study spatial attention. Alpha power modulations are strongest for fully informative cues, and nearly absent for uninformative cues (e.g., Haegens et al., 2011).

Oscillatory activity in the alpha band is not only modulated by attention but also by other paradigms, including conscious perception. Conscious perception is commonly investigated with a simple detection paradigm by contrasting detected vs. undetected near-threshold (NT) stimuli. These studies reported relative alpha power decreases in task-relevant areas prior to successfully detected stimuli, e.g., in the visual domain (e.g., Ergenoglu et al., 2004; Hanslmayr et al., 2007; van Dijk et al., 2008) and the somatosensory domain (e.g., Ai and Ro, 2014; Schubert et al., 2008; Weisz et al., 2014). Even though conscious access and attention are considered to be two separate theoretical entities (Baars, 1997; Koch and Crick, 2001; Koch and Tsuchiya, 2007a, 2007b; Van Boxtel et al., 2010), it could be claimed that relative alpha power decreases prior to conscious perception trivially reflect different levels of attention due to the tight association of oscillatory alpha activity with attention. The present study addresses the question whether and to what extent alpha power modulations prior to conscious perception are influenced by attention deployment.

To study the relationship between attention-induced alpha power modulations and alpha power changes prior to conscious perception, we combined a spatial attention task with a paired-stimulus detection task. This combination enabled the investigation of conscious perception during experimentally manipulated states of attention. Regarding the effects of the attention modulation on the pre-stimulus period, we expected firstly that the spatial attention deployment results in an alpha power lateralization, particularly in somatosensory regions, with relative alpha power decreases contralateral to the locus of attention. Secondly, we expected that the strength of this lateralization depends on the reliability of the attentional cue. Regarding conscious perception, we expected that the contrast between detected and undetected stimuli reveals alpha power decreases in the somatosensory cortex contralateral to stimulation. Taken together, we assumed that both experimental tasks (attention deployment and stimulus detection) affect alpha power contralateral to attention / stimulation side.

Methods

Participants

19 participants (9 females; mean age: 27 years, SD: 5 years) took part in the experiment after having given written informed consent. All participants

were right-handed (Edinburgh Handedness Questionnaire, mean: 99, SD: 4; Oldfield, 1971) and had normal or corrected-to-normal vision. The experimental protocol was approved by the Ethical Committee of the University of Trento, Italy.

Task and design

Spatial attention was experimentally manipulated using a classical Posner task (Posner, 1980) based on the paradigm used by Haegens and colleagues (2011), see Figure 10. A central arrow presented at the beginning of each trial indicated whether the tactile stimulus would be presented on the left or the right index finger. The reliability of the spatial cue was set to 50% (uninformative), 75% (medium informative), or 100% (fully informative). To study conscious somatosensory perception, the Posner paradigm was combined with a tactile paired-stimulus perception paradigm (see Weisz et al., 2014; Wühle et al., 2011, 2010). In this paradigm, two short tactile stimuli are presented in quick succession. While the first pulse could either be at near-threshold intensity (NT trial), or clearly below or above the perceptual threshold (sham or catch trial, respectively), the second pulse was always above the perceptual threshold. After the double-stimulation, participants were required to indicate whether they had felt one or two stimuli. This paradigm was optimal for the purposes of the present study, as it operationalizes conscious perception as the detection of a weak sensory stimulus while still enabling an experimental modulation of spatial cue reliability.

In combination with the spatial attention task, the paired stimuli were either presented on the left or on the right index finger. Taken together, this task design yielded four cue-stimulus congruency conditions (right valid, right invalid, left valid, left invalid) and three reliability conditions (50%, 75%, 100%). Each reliability condition consisted of 320 trials (10% sham and catch trials), and was presented in four consecutive blocks. Due to the different cue reliabilities and the sham/catch trials, there were 64, 96, and 128 validly cued near-threshold trials for each hand in the 50%, 75%, and 100% condition, respectively. The order of the reliability conditions was counter-balanced across participants, and at the beginning of each block, participants were reminded of the current reliability condition.

Each trial started with a black fixation cross on a grey background. After 800ms the central arrow was presented for 300ms, either cueing the right or the left index finger, followed by a jittered post-cue period (1000-1800ms) in which the central fixation cross was shown again. After the jittered period, the first and the second tactile stimuli were presented for 50ms each with an inter-stimulus interval (ISI) of 150ms. To reduce preparatory motor activity in the post-stimulus period, a 400ms break separated the offset of the second stimulus and the onset of the on-screen question, which was presented maximally for two seconds, or until participants responded. After the response, there was a 200ms blank screen before the next trial started again with the presentation of a fixation cross. Thus, depending on the cue-stimulus interval and the response time, the average trial length was around 4300ms seconds, resulting in a total scanning time of around 70min.

In a training session prior to the main experiment, participants' individual perceptual thresholds for both index fingers were determined in the shielded room using a 1-up / 1-down staircase procedure. Two randomly interleaved staircases (one up- and one downward) were used with fixed step sizes, separately for both fingers. During this session, the same trial structure was used as described above, so that participants could get used to it (however, only with valid cueing, and stimuli on either index finger). Tactile stimulation was delivered to the tip of the right or left index fingers, using two finger modules of a piezo-electric stimulator (Quaerosys, Schotten, Germany). Each module had 2x5 rods, which can be raised to variable degrees (maximal height 1mm). The rod height of the NT-trials was set for all participants independently to match their perceptual threshold. Both modules were attached to the fingers with Velcro tape. The participants' hands were cushioned to prevent any unintended intensity modulation by additional pressure on the modules. Responses ('one' / 'two') were given by using MEG-compatible response boxes with the right middle and ring finger (counter-balanced across participants). To minimise eye movements, participants were asked to fixate a black cross on a grey background whenever it was presented. To ensure that participants did not hear any auditory cues caused by the piezo-electric stimulator during tactile stimulation, binaural white noise was presented using a STIM2 system (Tip-300, Nicolet, Madison, WI, USA) and MEG-compatible tubal in-ear headphones.

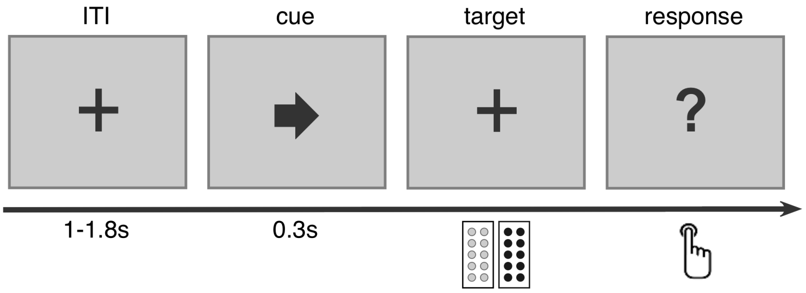

Figure 10. The combined tactile spatial attention / detection paradigm. After a jittered inter-trial interval (ITI), an arrow appeared on screen, cueing the finger participants needed to attend (left, right). Reliability of the spatial cue could be 100%, 75%, or 50%. The target consisted of a tactile paired stimulus with a first near-threshold stimulus and a second supra-threshold stimulus. Both were presented for 0.05s, with a 0.15s inter-stimulus interval (ISI). After 0.3s, participants were prompted with the question whether they had felt one or two stimuli.

MEG data acquisition and preprocessing

Prior to the experiment, the headshape of each participant was measured using a Polhemus FASTRAK 3D digitiser, relative to five coils (two on the left and right mastoid, three coils on the front). In addition, from each participant, an anatomical 3D structural image was obtained using a 4T MRI scanner (Bruker Biospin, Ettlingen Germany). Electromagnetic brain activity was recorded using a 102 triple-sensor (two planar gradio-, one magnetometer) MEG system (Elekta Neuromag), sampled continuously at a rate of 1kHz. All MEG data was analysed using the Matlab-based Fieldtrip toolbox (Oostenveld et al., 2011), and R Studio (R Development Core Team, 2008). Epochs from 1000ms pre-cue and 5000ms post-cue were extracted around cue onset, 1Hz highpass filtered and downsampled to 256Hz. Then, the data was visually inspected to identify and remove noisy trials, channel jumps and ocular artefacts. After the artefact rejection, stimulus-centred trials – which were used for all computed analyses – were created by shifting the time axis for the ISI duration, and the data from all files was appended.

Sensor-level analyses

Sensor-level data was analysed for the two sensor-types (gradiometers, magnetometers) separately, and missing channels due to artefact rejection were interpolated. Sensor-level event-related neural responses (ER) were computed by averaging 30Hz lowpass-filtered stimulus-centred epochs; however, were not further analysed because of a small but perfectly stimulus-locked stimulator-induced artefact.

Source-level analyses

The preprocessed, 5-30Hz bandpass-filtered data was projected to source-level using an LCMV beamformer analysis (Van Veen et al., 1997). Realistically shaped, single-shell headmodels (Nolte, 2003) were created by co-registering the participants' headshapes either with their structural MRI or – when no individual MRI was available (7 participants) – with a standard brain from the Montreal Institute of Neurology (MNI, Montreal, Quebec, Canada; http://www.bic.mni.mcgill.ca/brainweb), warped to the individual headshape. A common spatial filter (for each grid point and each participant) was computed using the leadfields and the common covariance matrix from all trials. Using this common filter, the spatial power distribution was estimated for all trials.

For the source-level event-related activity, the covariance window for the beamformer filter calculation was based on 0-500ms post-stimulus. The resulting data was averaged relative to the stimulus onset in all conditions. No baseline-normalization was applied. Importantly, this beamformer approach removed the stimulator-induced stimulus-locked artefact.

For the source-level analysis of spectral power, the LCMV beamformer filter was calculated based on a covariance window from 1000-100ms pre-stimulus. Spectral power was estimated using a multitaper FFT method on dpss-tapered time windows from 1500ms pre- to 500ms postimulus (in 50ms steps) for 2-30Hz (in 2Hz steps) with a frequency smoothing of 3Hz.

The length of the sliding time window was frequency dependent (5 cycles per frequency).

Statistical testing

For the entire data analysis, two different concepts were of interest: attention and conscious perception. For the attention conditions, all analyses were computed separately for trials in which attention was directed to the left and to the right, respectively (attL, attR) within each of the cue reliabilities and across the reliabilities (100%, 75%, 50%, all reliabilities), resulting in eight conditions (irrespective of cue validity, which depends on the actual stimulation side). The main statistical attention contrast was between attend left and attend right (attL vs. attR). For the detection conditions, analyses were computed separately for each stimulation side (stimL, stimR) for detected and undetected trials. Again, this was done within each cue reliability condition and across the reliabilities (100%, 75%, 50%, all reliabilities), resulting in 16 conditions (irrespective of cue side). The main statistical detection contrast was between detected and undetected trials.

Behavioural performance was statistically tested concerning the stimulus intensities of near-threshold trials, as well as detection and false alarm rates of the near-threshold, catch, and sham trials. Concerning stimulus intensity, a three-way repeated measures ANOVA was conducted irrespective of stimulus presentation side (cue side x cue reliability x detection). Concerning behavioural performance, overall detection rates were compared to chance level (for both near-threshold and catch trials), and false alarm rates were compared to chance level and zero using a T-test. In a second step, the detection / false alarm rates were analysed with a two-way repeated-measures ANOVA regarding effects of attention (cue reliability x locus of attention) and stimulus presentation (cue reliability x stimulation side). In all ANOVAs, a Mauchly’s Test for Sphericity was conducted, and if the assumption of sphericity was violated, a Greenhouse-Geisser correction was applied.

All analyses of MEG data were based on stimulus-centred epochs (time point zero was the onset of the first pulse of the paired target stimulus). Source-level event-related activity was tested for the main detection contrasts (detected vs. undetected; see above) on the absolute values of the event-related responses to eliminate polarity, for a time window from 0-500ms. Source-level spectral power was tested for both the attention and the detection contrasts (see above) for a 1000-0ms pre-stimulus time- and 8-14Hz frequency-window, using a dependent-samples T-tests, controlling for multiple comparisons with a non-parametric cluster-based permutation analysis (Maris et al., 2007). To investigate linear alpha power modulations due to the experimental attention manipulation, a dependent samples regression analysis was conducted on the source-level normalized alpha power changes. This was done across cue reliability (100%, 75%, 50%) of all conditions (for attention: [attL-attR]/[attL+attR]; for detection: [detected-undetected]/[detected+undetected] for each stimulation side).

Furthermore, to specifically investigate the influence of attention and detection on the alpha power modulations, a three-way repeated-measures ANOVA (cue side x cue reliability x detection) was conducted. In order to do so, power values were extracted from regions of interest (ROI) for the same time-frequency window as described above. The analysis was computed on log-transformed values, using a Mauchly's Test for Sphericity and a Greenhouse-Geisser correction if the assumption of homogenous sphericity was violated. This analysis specifically focused on alpha power in the somatosensory area contralateral to stimulation. Thus, in a first step, two ROIs were defined based on the maximal ER effect (detected vs. undetected) of right-sided stimuli within probabilistic anatomical maps of the left SI and SII (from now on: 'sensory ROIs'). Furthermore, to test the sensitivity of the three-way repeated-measures ANOVA to the effects under investigation (attention and detection), additional ROIs were defined. Concerning detection, the overall detection contrast of pre-stimulus alpha power described above (detected vs. undetected trials for right-sided stimuli, across all cue reliabilities) was used to define a ROI, which included frontotemporal regions (see Results; from now on: 'detection ROI'). Concerning attention, four additional ROIs were anatomically defined within the significant cluster revealed by the regression analysis of the attention conditions (from now on: 'attention ROIs'). They included the frontal eye field (FEF), the intraparietal sulcus (IPS), the inferior and middle temporal gyri (ITG/MTG), and the fusiform and parahippocampal gyri (FFG/PHG), all on the right hemisphere (see Results). In a second step, the resulting three-way interaction in the sensory ROIs (see Results) was further investigated by analysing the simple effects with a two-way repeated-measures ANOVA (detection x cue side) for each level of cue reliability separately.

Results

Behaviour

Overall stimulus intensity was 186 (+/-30) and 202 (+/- 35) micrometre for attend-left and attend-right conditions, and 180 (+/- 25) and 208 (+/-38) micrometre for the left and right finger stimulation, respectively. Stimulus intensities were analysed with a three-way repeated-measures ANOVA (cue side x cue reliability x detection) irrespective of stimulation side. This analysis revealed a main effect for the factors cue side ($F_{1,18} = 38.4$, $p < 0.001$) and detection ($F_{1,18} = 195.6$, $p < 0.001$) and a significant cue side x cue reliability interaction ($F_{2,36} = 13.3$, $p < 0.001$). Firstly, these results indicate that the intensity of the near-threshold stimulus was significantly smaller for attend-left than the attend-right trials with increasing cue reliability. This effect is mainly driven by the stimulus intensities of the left-sided stimulation (see Fig. 11A). Secondly, stimulus intensities were smaller in undetected compared to detected trials (see Fig. 11A). This result is a direct consequence of the adaptive staircase procedure used throughout the whole experiment. In this procedure, each detected stimulus was followed by an intensity decrease and vice versa (step size: ~6 micrometre).

Concerning stimulus detection performance, the overall detection rate across all participants (N = 19) and near-threshold conditions was 49.1% (SD: 2.2%) and did not significantly differ from chance level ($T_{1,18} = -0.98$, $p = 0.34$). The overall detection rate for catch trials was 87.9% (SD: 2.6%) and significantly differed from chance level ($T_{1,18} = 18.13$, $p < 0.001$). For sham trials, the mean false alarm rate was 4.3% (SD: 2%), which significantly differed from chance level ($T_{1,18} = -59.84$, $p < 0.001$), and from zero ($T_{1,18} = 5.57$, $p < 0.001$).

With regard to the effects of spatial attention on stimulus detection in near-threshold trials, the two-way repeated-measures ANOVA produced a significant main effect for locus of attention ($F_{1,18} = 5.6$, $p < 0.05$), indicating an increase in performance when attention was directed to the left side. Furthermore, no main effect for cue reliability, and no interaction cue reliability x locus of attention was found (see Fig. 11B). In the catch trials, no main effects and no interaction were observed. For the false alarms in the sham trials, there was no main effects, but an interaction cue side x cue reliability with a trend to significance ($F_{2,36} = 2.9$, $p = 0.07$), indicating higher false alarm rates with increasing cue reliability when attention was directed to the left.

Concerning the effects of cue reliability and stimulation side on detection rates in near-threshold trials, a two-way repeated-measures ANOVA resulted in a significant main effect of stimulation side ($F_{1,18} = 15.3$, $p < 0.01$), indicating significantly higher detection rates for stimuli presented on the left finger. There was no effect for cue reliability and no interaction cue reliability x stimulation side (see Fig. 11B). Concerning catch trials, there was no main and no interaction effects on detection rates. For false alarm rates in sham trials, there was no main effect of cue reliability, but a main effect of stimulation side with trend to significance ($F_{1,18} = 3.9$, $p = 0.06$), and a cue reliability x stimulation side interaction with a trend to significance ($F_{2,36} = 2.4$, $p = 0.1$), indicating that there were slightly more false alarms for left-sided stimuli with increasing cue reliability.

Taken together, participants' tendency to report a target as detected increased when the stimulus was presented on the left index finger, or when attention was directed to the left. This latter result was most likely due to the former, stronger effect, as cue side and stimulation side are not independent factors. Moreover, participants were more likely to give a false alarm when the cue was medium or fully informative and the stimulus was presented on the left finger, or when attention was directed to the left. Overall, it must be assumed that participants had a more liberal criterion for left-sided stimuli, and that their responses for left-sided stimuli are not sufficiently reliable.

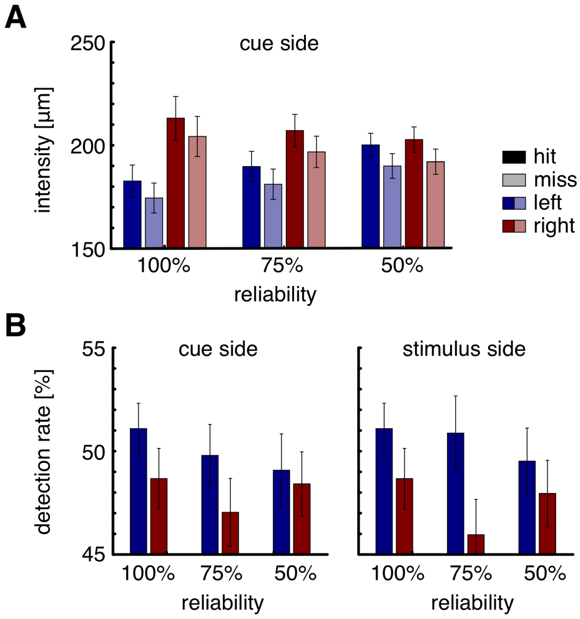

Figure 11. Stimulus intensities and detection rates across conditions. **A** Differences in stimulation intensity of the first near-threshold stimulus. **B** Differences in detection rate for trials sorted according to cued attention (left) and stimulation side (right).

Post-stimulus event-related neural activity

The main source-level detection contrast between event-related responses (ER) (detected vs. undetected across all cue reliabilities) yielded a positive cluster for the left stimuli as well as for the right stimuli ($p_{cluster}$ = 0.004 and $p_{cluster}$ = 0.002, respectively). The time courses of both clusters clearly show an ER increase for detected but not for undetected trials from around 80-150ms, with two peaks (94ms, 130ms). The source reconstruction at these two peaks revealed an effect originating mainly in the primary and secondary somatosensory cortices (SI and SII, respectively), contralateral to the stimulation. At 94ms, the source reconstruction showed additional, more distributed areas, including medial temporal and frontal regions for both stimulation sides, whereas at 130ms, the effect was concentrated to the somatosensory regions (data not shown). For illustration purposes, sources for both stimulation sides were reconstructed for a time period of 80-150ms, based on the event-related time courses irrespective of cue reliability (see Fig. 12A). Moreover, the significant voxels of these two main effects were used to compute the time courses of the event-related responses in the fully informative, the medium informative, and the uninformative condition (see Fig. 12B). Interestingly, the ER is stronger for right stimuli, which can be seen in the source reconstruction across all conditions as well as in the time courses within each reliability condition. Whereas right stimulation shows pronounced amplitude increases for detected but not for undetected stimuli, the left stimulation only shows small increases, mainly for the 100% and 75% condition.

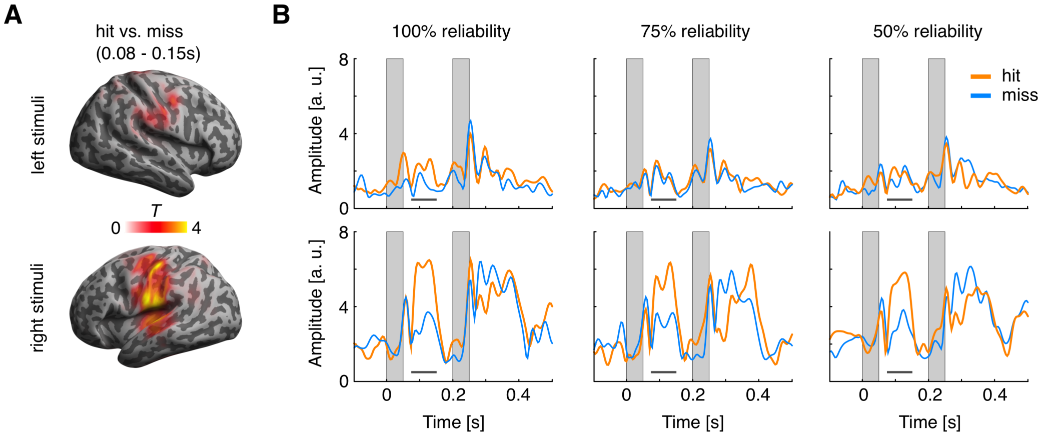

Figure 12. Event-related responses. **A** The source reconstruction from 80-150ms of the contrast detected vs. undetected across all cue reliabilities of the event-related responses of the left stimuli (upper figure) and the right stimuli (lower figure). **B** Time courses within each cue reliability for the left stimuli (upper panel) and the right stimuli (lower panel), showing the event-related responses for detected stimuli (orange) and the ER for undetected stimuli (blue). Vertical light grey rectangles mark the presentation duration of the two target stimuli; horizontal dark grey lines mark the time period from 80-150ms.

Pre-stimulus power effects: spatial attention

On source-level, the main statistical attention contrast (attL vs. attR; see Statistical Testing) resulted in strong lateralized alpha power effect (left-lateralized alpha power increases and right-lateralized alpha power decreases), particularly in the condition with the fully informative cue, and to a lesser extent in the condition with the medium informative cue (see Fig. 13A). However, none of the effects survived the permutation-based correction for multiple comparisons despite the evidently consistent modulation of alpha power. To investigate linear alpha power changes across the three conditions, a regression analysis was performed across 100%, 75%, and 50% cue reliability. This analysis resulted in a significant negative cluster ($p_{cluster} = 0.036$) in the left hemisphere, revealing regions with a linear modulation of alpha power (with the strongest modulation in the fully informative cue condition, and the weakest modulation in the uninformative cue condition, see Fig. 13B). The cluster was composed of the frontal eye field (FEF), the intraparietal sulcus (IPS), the inferior and middle temporal gyri (ITG/MTG), the fusiform and parahippocampal gyri (FFG/PHG), and the cingulate gyrus (CG).

Taken together, while simple contrasts (attL – attR) did not result in any significant clusters despite strong lateralized activity patterns, the regression analysis revealed brain regions in which alpha power was modulated the most in the condition with a fully informative cue, and the least in the condition with an uninformative cue. These results indicate that the experimental attention manipulation was successful in creating three attentional levels of different strength.

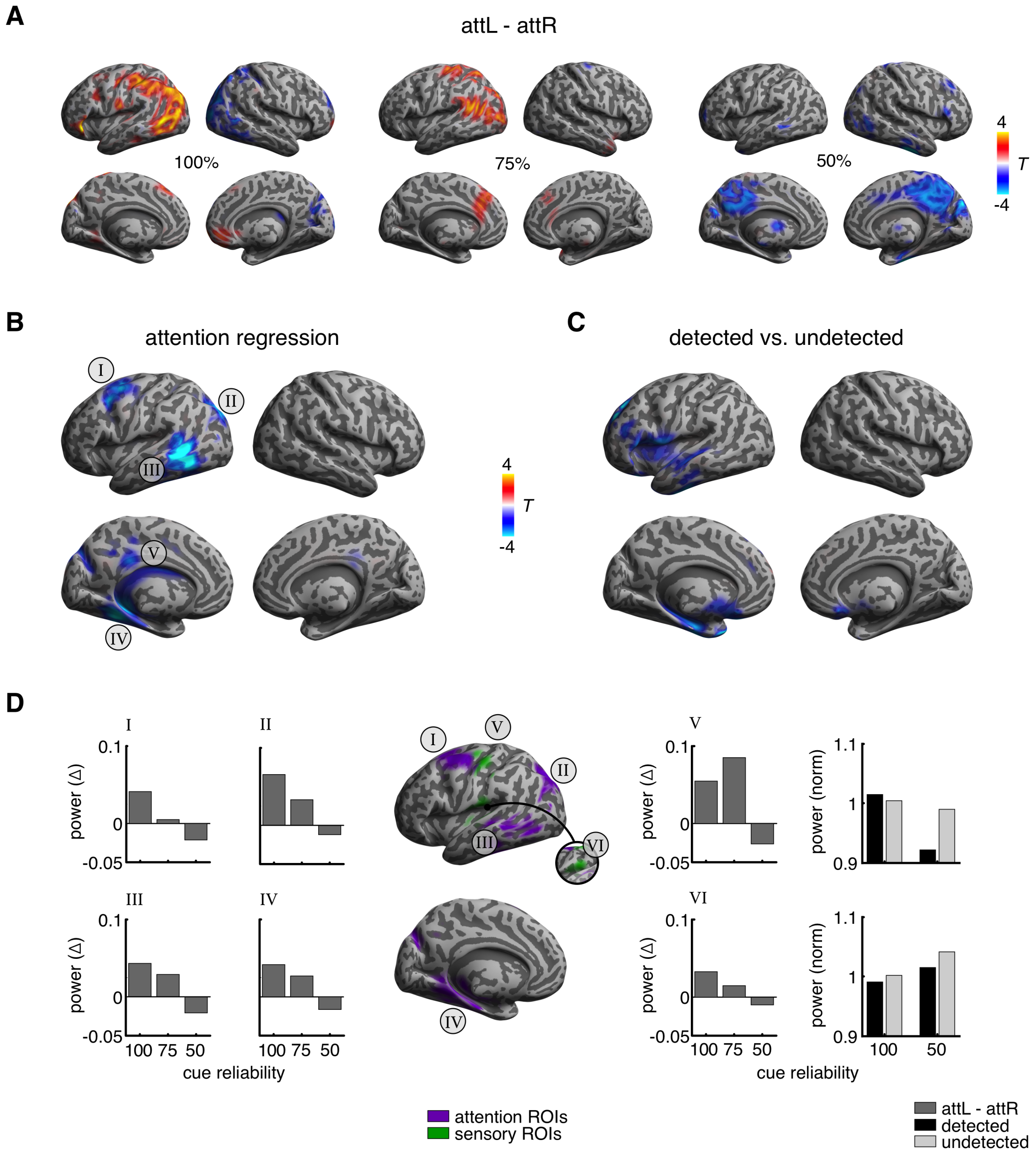

Figure 13. Pre-stimulus spectral power due to attention / prior to detection. **A** Source reconstructions showing the contrast attL vs. attR in all three cue reliability conditions (100%, 75%, 50%), masked at $p_{uncorr} < 0.05$. Alpha power is increased ipsilateral to attention. **B** Results of the regression analysis, showing the brain regions with a linear alpha power modulation decrease for the contrast attend left vs. attend right from 100% to 50% cue reliability, i.e. the strongest alpha power modulation was found in the condition with a fully informative cue. (**I**: frontal eye field, **II**: intraparietal sulcus, **III**: inferior / middle temporal gyri, **IV**: fusiform / parahippocampal gyri, **V**: cingulate). **C** Result from the main detection contrast (detected vs. undetected trials) for right-sided stimuli, showing a negative alpha power cluster in frontotemporal regions prior to conscious perception. **D** Results from the ROI analysis. The source plot shows the 'attention ROIs' (violet), which are based on the regression analysis shown in B, and the 'sensory ROIs' (green), which are anatomically and functionally defined based on the event-related response shown in Figure 12A. The bar graphs show selected power values to illustrate some of the ANOVA results. For the 'attention ROIs' (I-IV), power difference from the contrast attL vs. attR is shown for each cue reliability condition. For the 'sensory ROIs' (V: SI; VI: SII), the graphs illustrate the same power differences (left panel), and additionally, normalized power values for detected and undetected trials in the condition with a fully informative (100%) and an uninformative (50%) cue (right panel).

Pre-stimulus power effects: conscious perception

On source-level, the main statistical detection contrast irrespective of cue reliability (detected vs. undetected; see Statistical Testing) was conducted. For right stimuli and across all cue reliabilities, a negative cluster was found ($p_{cluster} = 0.04$), encompassing left frontal and temporal areas (see Fig. 13C). For left stimuli across all cue reliabilities, there was no significant effect. To investigate whether there was a linear alpha modulation across cue conditions like the one found in the attention contrasts (see above), a dependent-samples regression analysis was conducted for the left and the right stimuli separately. This analysis produced no significant effect, neither for the left or the right stimuli. In conclusion, the main detection contrast (detected vs. undetected) resulted in an alpha power decrease for right, but not for left stimuli. Moreover, the whole-brain regression analysis provided no evidence for a linear modulation of alpha power prior to conscious perception.

Pre-stimulus power effects: attention and perception

In addition to these two main analyses, the relationship of attention and conscious perception with pre-stimulus oscillatory alpha power was investigated with a three-way repeated measures ANOVA (cue side x cue reliability x detection). This analysis mainly focused on the left somatosensory region (with two ‘sensory ROIs’; see Methods), but included several additional ROIs to check whether it was sensitive to the main attention and detection effects (in ‘attention’ and ‘detection ROIs’; see Methods). The results for the ‘attention ROIs’ are summarized in Table 1, and those for the ‘detection’ and ‘sensory ROIs’ in Table 2 and Table 3.

Overall, across the ‘attention’ ROIs, the ANOVA revealed significant cue side x cue reliability interaction effects, and additionally, for the left cuneus a main effect for cue side. These findings are in line with the results of the regression analysis reported above, and show that the ANOVA is sensitive to the attention-induced alpha power modulations. In contrast, the ‘detection ROI’ revealed a main effect of detection, and an attention side x reliability interaction with trend to significance. This effect verifies that the ANOVA is sensitive to alpha power modulations prior to conscious perception.

In contrast to these straightforward effects, the ANOVA for the ‘sensory ROIs’ revealed more complex effects. The analysis in the functionally defined ROI in SI showed a main effect of attention side, an attention side x reliability interaction with trend to significance, and additionally, a 3-way interaction (detection x attention side x attention reliability). In contrast, concerning the ROI in SII, the ANOVA revealed no main effects, but significant interactions (attention side x attention reliability, and detection x attention side x attention reliability). To elucidate these main effects, additional two-way repeated-measures ANOVAs were run for each level of cue reliability separately (see Table 3). The results from these analyses indicate that alpha power spontaneously fluctuated prior to conscious perception when the cue was uninformative (50% reliable) in both SI and SII. In contrast, when the cue was fully informative, attention side modulated alpha power (relatively increased alpha power for left-sided cues). Taken together, these results provide evidence that both attention and detection are intricately associated with pre-stimulus alpha power in sensory areas, depending on the reliability of the spatial cue.

Table 1.
Analysis of Variance of power in ‘attention ROIs’.

		FEF			Cuneus			ITG / MTG			FFG			Cingulate		
	df	F	p		F	p		F	p		F	p		F	p	
Det	1, 18	43.18	0.52		0.52	0.48		1.23	0.28		1.56	0.23		0.48	0.5	
Rel	2, 36	1.20	0.31		1.49	0.24		0.74	0.48		0.57	0.57		1.95	0.16	
Side	1, 18	1.86	0.19		4.84	0.04	*	0.12	0.73		0.56	0.46		0.042	0.84	
Det x Rel	2, 36	19.56	0.82		0.16	0.85		0.10	0.35[a]		1.74	0.19		0.40	0.68	
Det x Side	1, 18	236.1	0.88		1.26	0.28		0.18	0.68		0.03	0.87		0.03	0.87	
Rel x Side	2, 36	6.12	0.005	**	3.86	0.03	*	6.71	0.003	**	5.84	0.006	**	3.31	0.048	*
Det x Rel x Side	2, 36	0.87	0.43		0.71	0.50		2.10	0.13		1.44	0.25		0.67	0.15	

Note. *p<0.05, **p<0.01

Det: Detection; Rel: Cue reliability; Side: Attention side; FEF: Frontal eye fields; ITG / MTG: Inferior / middle temporal gyrus; FFG: Fusiform gyrus

[a]corrected for inhomogeneous sphericity with Greenhouse-Geisser correction.

Table 2.
Analysis of Variance of power in ‘detection ROI’ and ‘sensory ROIs’.

		Cluster			SI			SII		
	df	F	p		F	p		F	p	
Det	1, 18	0.13	0.002	**	0.53	0.47		1.23	0.28	
Rel	2, 36	0.34	0.72		0.24	0.79		0.80	0.46	
Side	1, 18	0.95	0.34		5.91	0.026	*	2.62	0.12	
Det x Rel	2, 36	0.75	0.48		0.54	0.59		1.03	0.37	
Det x Side	1, 18	0.04	0.84		0.72	0.41		0.49	0.49	
Rel x Side	2, 36	3.05	0.06	º	3.10	0.06	º	3.68	0.035	*
Det x Rel x Side	2, 36	0.54	0.59		3.27	0.049	*	4.16	0.024	*

Note. ºp<0.1, *p<0.05, **p<0.01

Det: Detection; Rel: Cue reliability; Side: Attention side; Cluster: Region of interest based on significant cluster from the contrast detected vs. undetected stimuli; SI: Region of interest in primary somatosensory cortex; SII: Region of interest in secondary somatosensory cortex

Table 3.
Analysis of Variance (simple effects) of power in ‘sensory ROIs’.

			SI			SII		
Reliability		df	F	p		F	p	
50%	Det	1, 18	3.47	0.08	º	3.95	0.06	º
	Side	1, 18	0.37	0.55		0.94	0.34	
	Det x Side	1, 18	0.06	0.81		0.88	0.36	
75%	Det	1, 18	0.01	0.91		0.008	0.93	
	Side	1, 18	1.42	0.25		0.68	0.42	
	Det x Side	1, 18	5.36	0.03	*	0.32	0.58	
100%	Det	1, 18	0.06	0.81		0.38	0.54	
	Side	1, 18	10.09	0.005	**	7.19	0.015	*
	Det x Side	1, 18	3.14	0.09	º	7.32	0.014	*

Note. ºp<0.1, *p<0.05, **p<0.01

Det: Detection; Rel: Cue reliability; Side: Attention side; SI: Region of interest in primary somatosensory cortex; SII: Region of interest in secondary somatosensory cortex

Discussion

The goal of the present study is to investigate the relationship between attention, conscious perception, and sensory alpha power modulations observed in the pre-stimulus (post-cue) period. To this end, a spatial tactile attention task with three cue reliabilities (100%, 75%, 50%) was combined with a tactile paired-stimulus detection task. The experimental manipulation of attention resulted in a clear, lateralized alpha power modulation in the post-cue period. As hypothesized, the strongest modulation was observed in the condition with a fully informative cue (100% reliable), with a linear decrease across cue reliabilities in areas known to be involved in attention deployment. In contrast, conscious perception of right-sided stimuli was preceded by a relative alpha power decrease in frontotemporal regions. Moreover, focusing on the left somatosensory region, we found a intricate relationship between of alpha power levels, attention, and detection.

Left- and right-sided stimuli: Different behavioural and event-related neural responses

Both behavioural and event-related analyses revealed different effects for left- and right-sided stimuli. Detection rates and false alarm rates were higher for attend-left and left-sided stimuli, particularly in the condition with medium and fully informative cues. Moreover, a spatial cue towards the left side compared to the right side was followed by smaller stimulus intensities. Concerning the event-related neural responses, the difference for detected vs. undetected trials was small for left-sided stimuli, whereas those for right-sided stimuli were pronounced across and within all cue reliability conditions.

First of all, participants could have been more sensitive on the left finger, accounting for smaller stimulus intensities and higher detection rates. However, the higher false alarm rates for left-sided stimuli points towards a more liberal criterion and a tendency for unreliable responses for these stimuli, which also could have resulted in lower stimulus intensities. The poor performance of the participants for left-sided stimuli could also partly accounted for the small differences in event-related neural responses between detected and undetected trials. In addition, however, the piezo-electric device caused a perfectly time-locked artefact for left- but not right-sided trials. It is conceivable that due to this artefact the spatial filter of the LCMV beamformer analysis was sub-optimal for left-sided stimuli, resulting in poor estimates of post-stimulus activity. Taken together, it must be assumed that participants were either less able or willing to perform the task for left-sided stimuli and/or that a time-locked artefact lead to suboptimal estimates of source-level activity following left-sided stimuli.

Spatial attention resulted in linear modulation of alpha power in the dorsal attention network

Somatosensory attention was experimentally modulated with a spatial attention paradigm, in which a visually presented cue directed the participants' attention to the left or the right index finger. This cue could be fully informative (100% reliable), medium informative (75% reliable), or uninformative (50% reliable). Across all cue reliabilities, spatial attention deployment resulted in a lateralized alpha power modulation pattern with relatively increased alpha power ipsilateral and relatively decreased alpha power contralateral to the locus of attention. This pattern was distributed and included the somatosensory regions, dorsoparietal, occipital, and temporoparietal areas. These findings are in line with previous reports stating that somatosensory spatial attention modulated alpha power in sensors above or in the somatosensory cortices (Anderson and Ding, 2011; Bauer et al., 2006; Haegens et al., 2012, 2011; Jones et al., 2010; van Ede et al., 2011, 2010; Zhang and Ding, 2010; for a detailed review of alpha power modulations due to attention, also see Frey et al., 2015, in Appendix B).

Moreover, the main attention contrast (attend left vs. attend right) within each cue reliability condition showed that alpha lateralization was strongest for the condition with a fully informative cue and virtually absent for the condition with an uninformative cue. This pattern was supported by a regression analysis, which revealed a linear decrease of the attention-induced alpha power modulation across the three cue reliabilities. Specifically, whereas other studies reported similar linear effects in sensory regions (Haegens et al., 2011), the present data revealed linearly modulated alpha power levels in higher-order regions on the left hemisphere, including the frontal eye field (FEF) and the intraparietal sulcus (IPS). The FEF and IPS are well known as part of the dorsal frontoparietal attention network (DAN; Corbetta and Shulman, 2002; Vossel et al., 2014), which biases sensory regions during spatial and feature-based attention tasks towards stimulus detection in a top-down manner (Ruff et al., 2006, 2008; Bressler et al., 2008; Vossel et al., 2012). Furthermore, linear alpha power modulations due to attention were also observed in the inferior and middle temporal gyri (ITG/MTG), the fusiform and parahippocampal gyri (FFG/PHG), and the cingulate gyrus (CG) on the left hemisphere. A functional magnetic resonance study showed that the ITG/MTG and the FFG/PHG are transiently activated by a visually presented spatial cue (Corbetta et al., 2000). The present findings indicate that the strength of this transient activation not only depends on the cue side but also on the cue reliability, just as the activity in the dorsal attention network.

Whereas the overall lateralization pattern of the attL vs. attR contrast revealed alpha power modulations in the right and the left hemisphere, a linear modulation during spatial attention was only found in left-hemispheric regions DAN regions. Whereas the ventral attention network (VAN; Corbetta and Shulman, 2002) is right-dominant (Arrington et al., 2000; Shulman et al., 2010), the activation of the DAN does not have a lateralized dominance (Kastner et al., 1999; Corbetta et al., 2000; Hopfinger et al., 2000; Shulman et al., 2010). This body of research is, however, based on the visual domain, with generally weaker hemispheric lateralization. In the context of *somatosensory* spatial attention, it is conceivable that the DAN is in fact left-lateralized, particularly as all participants were right-handed. A relationship between DAN lateralization and handedness was shown by Petit and colleagues (2015), however, based on a visual task and only for left-handers. Alternative reasons for the absent linear modulation of right-hemispheric DAN regions could include the participants' attention strategy (instead of actively attending to the left side, they might have suppressed attention to the right side), incompliant behaviour for left-sided stimuli (also seen in relatively high false alarm rates), or noisy data on sensors over the right hemisphere.

Overall, alpha power changes were found in task-relevant somatosensory regions, posterior and medial areas, and in the dorsal frontoparietal attention network on the left hemisphere. In the latter regions, alpha power was modulated in a linear manner depending on the cue reliability.

Alpha power in frontotemporal regions precedes conscious perception

A tactile paired-stimulus detection task was used to enable the combined investigation of conscious perception and attention. Irrespective of cue reliability, the contrast of detected and undetected right-sided target stimuli produced a negative effect in the alpha band, whereas the same contrast for left-sided stimuli did not result in any significant effect. The negative alpha power cluster prior to consciously perceived right-sided stimuli was localized to frontal and temporal regions of the left hemisphere, not including the left SI and SII. This finding complements previous studies, which reported alpha power modulations prior to conscious perception mainly in the corresponding sensory regions in the visual modality (e.g., Busch et al., 2009; Ergenoglu et al., 2004; Hanslmayr et al., 2007; Romei et al., 2008; van Dijk et al., 2008; Wyart and Tallon-Baudry, 2009), the auditory modality (Leske et al., 2015) and the somatosensory modality (e.g., Linkenkaer-Hansen et al., 2004; Sauseng et al., 2009; Weisz et al., 2014).

In contrast to alpha power modulations in task-relevant sensory regions, the frontotemporal alpha power cluster reported in the current study likely reflects more abstract processing. The reported cluster is not confined to one anatomical area, but includes the middle temporal gyrus (MTG), the anterior insula (AI), and the inferior, middle, and superior frontal gyri (IFG, MFG, SFG) on the left hemisphere. In the current study, participants were asked to perform a cognitively demanding combination of a spatial attention task and a tactile detection task of a paired-stimulus target. In the IFG/AI region – representing an essential node in cognitive control – sensory, motivational, and interoceptive inputs are integrated (see Tops and Boksem, 2011). Moreover, this region has connections with somatosensory, limbic, and attentional areas to regulate their responsiveness for an appropriate behavioural response (for a review see Tops and Boksem, 2011). The anterior SFG is thought to be part of the working memory network implementing monitoring and manipulation, particularly to spatially oriented cognition (Boisgueheneuc et al., 2006). In the context of the current study, monitoring of behavioural goals in a spatially specific manner was necessary for successful stimulus detection, as participants had to remember the level of cue reliability (fully or medium informative, or uninformative), while at the same time attending to the cued side. Overall, most likely due to the complex task of the current study, oscillatory alpha power prior to conscious perception was modulated in frontotemporal regions contralateral to stimulation.

Alpha power in somatosensory regions is modulated prior to conscious perception and by attention.

The previous two paragraphs described the results from the main attention and the main detection contrasts in higher-order regions. In a further step focusing on the somatosensory region contralateral to stimulation, a three-way repeated-measures ANOVA was conducted, which revealed modulations of oscillatory alpha power. Specifically, in both SI and SII, the analysis showed complex interaction effects of cue side x cue reliability, and detection x cue side x cue reliability. Moreover, in SI, the analysis revealed a main effect of cue side. A follow-up analysis revealed that in both SI and SII, alpha power fluctuated spontaneously prior to conscious perception if the spatial cue was uninformative, whereas it was modulated by attention when the cue was fully informative.

First of all, these findings shed light on the roles of SI and SII during conscious somatosensory perception. Previously, it has been suggested that SII is an essential node in conscious perception (Wühle et al., 2010, 2011; Weisz et al., 2014), whereas SI was shown to be modulated by expectation (Van Ede et al., 2010). In the present study, the pattern of alpha power modulation did not strongly differ between SI and SII. Alpha power in both regions showed a three-way interaction between detection, attention side, and attention reliability. These effects indicate that not only cortical excitability in SII prior to stimulus presentation is essential for conscious perception, but also in SI. Most likely, stimulus processing in SI is necessary but not sufficient for conscious somatosensory perception. In line with the present findings, a dynamic causal modelling study showed that sensory awareness is best accounted for by increased recurrent processing between SI and SII (Auksztulewicz et al., 2012).

Secondly, the present findings indicate that alpha power modulations in sensory regions prior to conscious perception do not necessarily depend on top-down attention, as others have claimed (see e.g., Wyart and Tallon-Baudry, 2008). Whereas the attention effect (cue side x cue reliability interaction) was mainly driven by the condition with a fully informative cue, alpha power levels spontaneously fluctuated prior to conscious perception when the cue was uninformative (50% reliability). In other words, naturally fluctuating alpha power levels predispose conscious perception, as long as there is no additional information about the stimulus presentation. As soon as the system can exploit additional information (e.g., a spatial cue) cortical excitability (reflected by alpha power) is modified in a top-down fashion to enhance stimulus processing. Furthermore, such top-down modulation becomes stronger with increasing reliability of the additional information. Evidence for spontaneous, attention-independent fluctuations in somatomotor and visual regions was provided by Sauseng and colleagues (2009) and Romei and colleagues (2008). Using transcranial magnetic stimulation, they showed that motor evoked potentials and phosphenes, respectively, are elicited more easily when sensory alpha power immediately prior to the TMS pulse is low.

Taken together, this is to our knowledge the first MEG study that has investigated the relationship between spatial attention and conscious perception in the somatosensory modality, and oscillatory alpha power. Notably, we provided evidence that pre-stimulus alpha power levels do not necessarily reflect the level of attention. On the contrary, we show that alpha power, i.e. cortical excitability, spontaneously fluctuates while there is no additional exploitable information about stimulus presentation, and that this fluctuation predisposes conscious somatosensory perception.

Conclusion

The main goal of the present study is to disentangle the relationship between attention and conscious perception with pre-stimulus alpha power modulations. To this end, a spatial attention task was combined with a paired-stimulus detection task in the somatosensory domain. As hypothesized, alpha power in the left somatosensory region depended on both attention and detection. Specifically, alpha power levels were modulated by attention particularly in the condition with the fully informative cue, whereas they spontaneously fluctuated prior to conscious perception in the condition with an uninformative cue. In addition to this main finding, alpha power changes were also found outside of the somatosensory cortex. Attention linearly modulated alpha power in higher-order areas known to be involved in attention deployment. In contrast, prior to conscious perception, there was a relative alpha power decrease in frontotemporal regions contralateral to right-sided stimuli. Overall, these findings provide clear evidence that cortical excitability not only depends on top-down spatial attention, but that it spontaneously fluctuates in the absence of a spatial cue.

Chapter 4: Discussion

The main goal of this thesis is to elucidate the pre-stimulus oscillatory signatures of tactile conscious perception, and to understand their relationship with the activity during tactile attention. To this end, we conducted two MEG studies, which are reported in Chapter 2 and Chapter 3 of this thesis. In the following sections, I will briefly summarize the main results of both studies, and then discuss these findings in the context of previous literature introduced in Chapter 1.

Summary

The first study was conducted to characterize the pre-stimulus neural activity prior to conscious tactile perception with a focus on pre-stimulus oscillatory power and connectivity patterns. To achieve this goal, participants were asked to perform a near-threshold detection task. They were presented with short tactile stimuli at their individual perceptual threshold on the tip of their left index finger. After the stimulation, participants were required to indicate whether they had detected a stimulus or not. In line with previous studies, reduced alpha power in the somatosensory region contralateral to stimulation predicted conscious perception of a tactile stimulus. Furthermore, pre-stimulus network level integration of the right SI was modulated, showing an increased and decreased integration in the theta and beta band respectively.

In the second study, we focused on ongoing oscillatory activity in the alpha band by investigating whether and how relative alpha power reductions prior to conscious perception are influenced by attention. To this end, we combined a tactile detection task with a spatial attention paradigm. For the detection task a paired-stimulus target was used, consisting of a stimulus at individual perceptual threshold followed by a stimulus clearly above threshold. Furthermore, attention was manipulated using a fully informative, a medium informative, or an uninformative cue resulting in three attention levels. In each trial, participants were required to attend to either the left or right index finger, and after the double-pulse stimulation, indicate how many stimuli they had felt. As expected, both the attention and the perception task resulted in relatively decreased alpha power in distributed regions. Moreover, alpha power in the SI and SII contralateral to right-sided stimuli was associated with both attention and detection. Whereas ongoing alpha power fluctuations predisposed conscious perception particularly when the spatial cue was uninformative, attention (cue side) influence alpha power mainly when the cue was fully informative.

Overall, both studies showed alpha power decreases prior to conscious perception in brain regions contralateral to stimulation. Findings from the first study provided evidence for the functional role of alpha power modulations in SI and SII prior to conscious perception and underlined the importance of functional connectivity in SI for somatosensory awareness. The results from the second study complemented these findings by elucidating the relationship between spontaneous alpha power fluctuations and modulations due to attention. Taken together, while spatial attention lead to top-down changes of cortical excitability, ongoing fluctuations in the absence of such an influence in both SI and SII predisposed conscious perception. Moreover, pre-stimulus network states of SI were associated with conscious perception in a spectrally specific manner.

Windows to Consciousness

The findings presented in the current thesis support and expand the framework windows to consciousness (win2con, Ruhnau et al., 2014; Weisz et al., 2014), which states that conscious perception is facilitated by specific brain states. In line with previous literature, the win2con framework contends that reduced alpha power, a marker for cortical excitability, favours conscious perception of a sensory event. More importantly, given the emphasis on network integration as an essential mechanism underlying conscious perception (e.g., Crick and Koch, 2003; Dehaene et al., 2006), the win2con framework reasons that the prerequisites of consciousness are unlikely to be limited to mere local excitability changes, but also include pre-established functional pathways. According to this line of reasoning, conscious perception is more probable, if a weak stimulus enters sensory regions that are less inhibited and already well integrated in a distributed network. If this is the case, the stimulus-related activity is more likely to cross the perceptual threshold and to be propagated to a distributed network, igniting the global neuronal workspace (Dehaene et al., 2006; Ruhnau et al., 2014).

In the present thesis, we reported relative decreases of oscillatory alpha power in sensory regions (SI and SII) contralateral to stimulation when a subsequent stimulus is consciously perceived. Furthermore, in the context of attention we showed that these ongoing fluctuations in the alpha band arose only if the attentional cue was uninformative (see below). Previous research reported similar findings for the somatosensory modality (Schubert et al., 2008; Weisz et al., 2014), the visual modality (e.g., Ergenoglu et al., 2004; Hanslmayr et al., 2007; Thut et al., 2006; van Dijk et al., 2008), and the auditory modality (Leske et al., 2015). Oscillatory neural activity in the alpha band is widely accepted to reflect functional inhibition of neural processing and cortical excitability (Klimesch et al., 2007; Jensen and Mazaheri, 2010).

In addition, we presented findings concerning the network state prior to conscious perception of tactile stimuli. Specifically, we showed that SI is better integrated prior to successful stimulus detection in the theta band, and less efficiently integrated in the beta band. While the former finding provides further support for the win2con framework as describe above, the latter finding adds an important insight: Not only establishing additional functional pathways predisposes conscious perception, but also *minimizing* already existing pathways that are detrimental or irrelevant for stimulus propagation. Regarding the functional connectivity, the win2con could therefore be described as a spectrally specific tuning process prior to stimulus onset.

Attention vs. Consciousness

Attention and consciousness (defined via cognitive access; see Introduction) are two processes closely intertwined. For instance, Koch and colleagues consider them to be distinct processes with distinct neuronal signatures (for reviews see e.g., Koch and Crick, 2001; Koch and Tsuchiya, 2012; van Boxtel et al., 2010). In contrast, Posner and Dehaene and colleagues argue that consciousness critically depends on attention (Posner, 1994; Dehaene and Naccache, 2001; Dehaene et al., 2006), while Merikle and Joordens even claim that these processes are indistinguishable (Merikle and Joordens, 1997). The functional roles assigned to attention include selecting sensory information, activating ideas from the short term memory, and maintaining vigilance (Posner, 1994), integrating sensory features into coherent objects (Treisman and Gelade, 1980), or selecting sensory information for current behavioural goals (Van Boxtel et al., 2010). In contrast, consciousness does not select information, but summarizes it and makes it available to cognitive functions, such as decision making, language, and theory of mind (Dehaene et al., 2006; Van Boxtel et al., 2010). Overall, as suggested by Koch and colleagues, these roles point to a functional dissociation, with attention as an analyser and consciousness as a synthesizer (Van Boxtel et al., 2010)

As both concepts are intimately associated with oscillatory alpha power, the question arises whether the modulations seen prior to conscious perception reflect just a form of attention or part of the window to consciousness (Ruhnau et al., 2014; Weisz et al., 2014). Attention-induced alpha power modulations were observed after a cue (see e.g., Frey et al., 2014, 2015 in Appendeces A and B), while ongoing alpha power fluctuations were observed prior to upcoming weak stimuli (e.g., Ai and Ro, 2014; Ergenoglu et al., 2004; Hanslmayr et al., 2007; Leske et al., 2015; Weisz et al., 2014). In the second study reported in the present thesis (Chapter 3), we investigated the intricate relationship between attention, and conscious perception, and pre-stimulus alpha power. Specifically, we showed that spontaneous fluctuations of alpha power predisposed conscious perception, if there was no additional information about stimulus occurrence, such as a spatial cue, available. As soon as the system can exploit additional information, however, cortical excitability is modulated in a top-down manner, according to the expected stimulus occurrence. Importantly, most studies investigating conscious perception make sure to sufficiently jitter and randomize stimulus presentation, so that such additional information cannot be exploited. Consequently, relative alpha power decreases prior to conscious perception reported by these studies most likely reflect spontaneous fluctuations of cortical excitability, rather than top-down influences like attention. (N.B. Additional information does not only include top-down attention, but anything that can be exploited to facilitate stimulus processing and a relevant motor response; see e.g., the notions of the task relevance map (Navalpakkam and Itti, 2005), or the priority map (Ptak, 2012)).

Taken together, attention, a mechanism to select contents for conscious processing, affects cortical excitability, so that an upcoming stimulus is more efficiently processed and thus more likely to be consciously perceived. In the absence of attention, cortical excitability spontaneously fluctuates, creating temporal windows for facilitated stimulus processing conscious perception.

Future Research and Conclusion

The aim of the first study was to characterise the tactile window to consciousness with a focus on oscillatory neural activity in the alpha frequency band and functional connectivity, whereas the second study put more emphasis on one of these aspects – oscillatory alpha activity – and its relationship with top-down attention modulated activity.

In the study reported in Chapter 3 we showed that spontaneous fluctuations of cortical excitability exert most influence on perception, if no additional information about stimulus occurrence can be exploited. However, spontaneous fluctuations of cortical excitability also played a role during trials in which there was additional information, i.e. an informative spatial cue. In other words, top-down modulations of alpha power did not completely override ongoing alpha power levels. Instead, attention-induced and ongoing alpha power modulations seemingly share an intricate relationship, which remains unclear. For instance, the influence of top-down attention might depend on the level of spontaneous cortical excitability; if cortical excitability is already very low (high alpha power), top-down attention might not have the same effects as when cortical excitability is already high (or vice versa). Alternatively, ongoing alpha power fluctuations could depend on top-down attention.

To specifically test the causal link between oscillatory activity in the alpha band, attention, and conscious perception, additional studies could be conducted based on neuronal stimulation. For instance, transcranial alternating current stimulation (tACS) could be employed to manipulate levels of alpha while at the same time measuring MEG. Recently, Neuling and colleagues showed that the combination of these two techniques is feasible, and can be exploited to shed light on causality between neural oscillations as measured with MEG and behaviour (Neuling et al., 2015). This approach could be used together with a somatosensory near-threshold detection task, a somatosensory spatial attention task, or a combination of both tasks as reported in Chapter 3, to elucidate the causal influence of oscillatory activity in the alpha band on consciousness and attention.

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Appendix A. Selective Modulation of Auditory Cortical Alpha Activity in an Audiovisual Spatial Attention Task

Frey JN, Mainy N, Lachaux J-P, Müller N, Bertrand O, Weisz N (2014) Selective modulation of auditory cortical alpha activity in an audiovisual spatial attention task. J Neurosci 34:6634–6639.

Behavioral/Cognitive

Selective Modulation of Auditory Cortical Alpha Activity in an Audiovisual Spatial Attention Task

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Despite substantial research on attentional modulations of visual alpha activity, doubts remain as to the existence and functional relevance of auditory cortical alpha-band oscillations. It has been argued that auditory cortical alpha does not exist, cannot be measured noninvasively, or that it is dependent on visual alpha generators. This study aimed to address these remaining doubts concerning auditory cortical alpha. A magnetoencephalography study was conducted using a combined audiovisual spatial cueing paradigm. In each trial, a cue indicated the side (left or right) and the modality (auditory or visual) to attend, followed by a short lateralized auditory or visual stimulus. Participants were instructed to respond to the stimuli by a button press. Results show that auditory cortical alpha power is selectively modulated by the audiospatial, but not the visuospatial, attention task. These findings provide further evidence for a distinct auditory cortical alpha generator, which can be measured noninvasively.

Key words: alpha; attention; auditory

Introduction

Alpha oscillations are considered to reflect the excitatory–inhibitory (E–I) balance of sensory and motor areas, with high levels of alpha indicating inhibitory states (Klimesch et al., 2007; Weisz et al., 2007). This view is well established in the visual and sensorimotor domain (Thut and Miniussi, 2009). The first magnetoencephalography (MEG) evidence of an auditory cortical alpha-like rhythm was reported by Lehtelä et al. (1997); however, doubts continue concerning the functional relevance and measurability of an auditory alpha rhythm (Weisz et al., 2011). A concern, mainly based on scalp EEG recordings in audiovisual attention paradigms, is whether noninvasive methods are sensitive enough to measure cortical auditory alpha. In many audiovisual spatial attention tasks, attention is cued to lateralized visual or auditory sensory input, followed by a target stimulus. Studies reported occipitoparietal alpha power increases during auditory attention (Foxe et al., 1998; Fu et al., 2001), interpreted as inhibition of visual processing. Banerjee et al. (2011) offered further insights, reporting modality-independent topographical ("supramodal") effects in early time-windows, and late "modality-specific" topographical differences dependent on attended modality. Although posterior-attentional modulations have been consistently shown using scalp EEG, a recent intracranial study by Gomez-Ramirez et al. (2011) showed auditory cortical alpha-band modulations influenced by intersensory attention. This study underlines the general challenge of detecting cognitive auditory cortical alpha-band modulations using noninvasive tools (Weisz et al., 2011). However, this has been shown to be feasible. Examples include "tau" desynchronizations (Lehtelä et al., 1997); and working memory dependent modulations of auditory cortical alpha (van Dijk et al., 2010). With regards to attentional manipulations our group has repeatedly demonstrated the sensitivity of MEG, as well as EEG, to capture modulations of auditory cortical alpha (for review, see Weisz and Obleser, 2014). However, in these studies participants had to attend to the auditory modality only. Using a design similar to audiovisual EEG studies, which reported parietal modulations (Banerjee et al., 2011), we set out to demonstrate modality-specific effects of spatial attention on auditory cortical alpha.

We devised a multisensory Posner task (Posner, 1980), in which participants were cued to attend lateralized vision or audition. We predicted alpha effects in occipitoparietal regions independent of the attended modality. Beyond this replication, our main goal was to identify modality specific effects of spatial attention. Source localization would aid in uncovering auditory cortical alpha modulations during audiospatial attention (Weisz et al., 2011). In accordance with these hypotheses, we present here for the first time MEG data of a combined audiospatial and visuospatial attention task showing selective alpha modulations in the auditory cortex only when attention was deployed to the auditory modality.

Materials and Methods

Participants. Overall 11 healthy participants (7 females; mean age, 26.5 years; age range, 22–43 years) took part in the study after the experimental procedure was explained and written informed consent was obtained. No partic-

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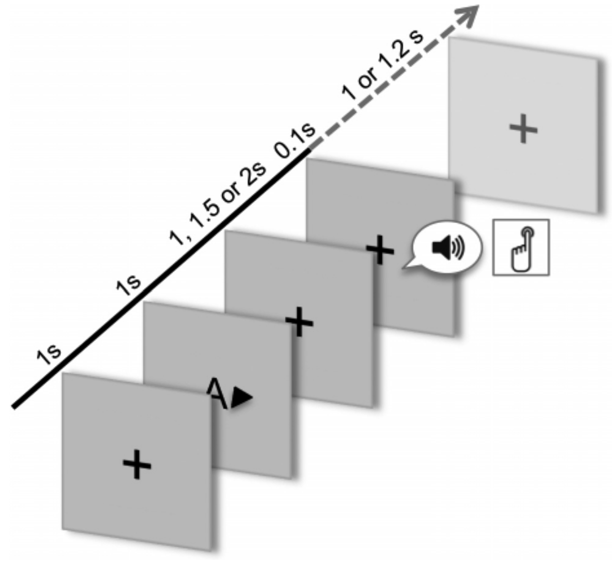

Figure 1. Schematic illustration of a trial. After a fixation cross, a cue indicating the modality (auditory or visual) and side (right or left) is presented, followed by a target stimulus. The figure depicts a valid right auditory trial. Participants were required to press a button as fast as possible after target presentation.

ipant had a history of neurological or psychiatric disorders or hearing/vision impairments. The experimental procedure conformed to the Declaration of Helsinki and was approved by the local ethics committee.

Experimental paradigm. The general outline of a trial is shown in Figure 1. Stimuli were presented with Presentation software (Neurobehavioral Systems). Each trial started with a white cross on a black screen; after 1000 ms a visual cue indicated the modality (auditory or visual; A or V) and the side (left or right ear/hemifield; ← or →) of a second stimulus (target). The target was presented after a pseudorandomized interstimulus-interval of 1000, 1500, or 2000 ms. In 80% of all trials, cues were valid, whereas 20% of the trials consisted of invalid cues (either concerning modality, side, or both). In the auditory condition, the second stimulus consisted of a noise burst of 100 ms (1 of 5 different pitches), and in the visual condition it consisted of a simple geometric figures (either an upward or downward triangle, a diamond, a circle, or a square). Participants were required to respond to all second stimuli by pressing a button as fast as possible. After 1000 or 1200 ms a new trial started. There were 6–9 blocks of 60 trials each (15 trials with each cue type) resulting in 360–540 trials in total. The whole experiment lasted for ~1.5 h.

Data acquisition. A 275 channel whole-head axial gradiometer system (CTF, VSM MedTech) was used for recording of electromagnetic brain activity, which was sampled continuously at a rate of 600 Hz (filtered online 0–150 Hz). Three coils were placed at nasion and the two preauricular points; passing small currents through these coils before and after each block allowing us to monitor head movements. From each participant we obtained an anatomical 3D MRI, using a 1.5 T Siemens Sonata scanner.

Behavioral data analysis. Task performance was computed with respect to reaction times (RTs), excluding all trials in which no response was given or in which response time was longer than 800 ms (on average 3.4%). Analysis was done using repeated-measures ANOVA with the four factors cue and target modality (auditory or visual), as well as cue and target side (left or right).

Preprocessing. Trials in which no response was given (on average 3.2%) were excluded from the data analysis. Epochs of ±2000 ms length were extracted around cue onset resulting in the four cue conditions: auditory right, auditory left, visual right, and visual left. A generous time-interval was chosen to diminish edge effects in the time-frequency estimates. Before an independent component analysis (ICA) to remove eye and heart artifacts, data were detrended, down-sampled to 400 Hz, and visually inspected to remove large muscle artifacts and channel jumps. The ICA was based on 300 randomly selected trials of the concatenated data; and two to five components were rejected in each dataset by visually inspecting the components' time course and topographies. After the ICA, a second visual artifact rejection was done to remove remaining artifacts, resulting in the rejection of 5–46% of all trials per subject. Following the artifact rejection, trial number across all four conditions was equalized for each participant to prevent any bias in subsequent data analysis across conditions (Gross et al., 2013). This was done by randomly selecting the same number of trials from each condition (i.e., the number of trials present in the condition with the fewest trials) resulting in 72–126 trials per condition and subject.

Sensor level. Spectral estimation (Fourier transformation) was performed on Hanning-tapered time windows from −0.5 to 1.5 s (in steps of 0.05 s) relative to the cue onset from 1 to 30 Hz (in steps of 1 Hz). The length of the sliding time windows was frequency dependent (5 cycles of the respective frequency). Postcue neuronal activity was then estimated as a relative power change with respect to a precue time window from −0.5 to −0.1 s. To test for direction-specific attention effects regardless of the modality, the power of the grand averages of the two auditory and two visual conditions (right vs left) was averaged and statistically compared regarding the time window from 0.3 to 0.9 s postcue and 8–16 Hz using a nonparametric cluster-based permutation analysis (Maris and Oostenveld, 2007).

To investigate whether there are alpha-band modulations in the auditory cortex in a main-modality contrast, we compared the auditory and visual condition regardless of locus of attention by concatenating all trials of each modality. For both conditions spectral power was estimated from −0.5 precue to 1.5 s postcue (in steps of 0.05) for 1–30 Hz (in steps of 1 Hz; sliding time window: 5 cycles per frequency). The postcue neuronal activity for the subsequent statistical test was estimated as relative power change with respect to the −0.5 to −0.1 s precue time window. Then we statistically contrasted the grand averages of the two conditions for the same time-frequency window (0.3–0.9 s, 8–16 Hz) using cluster-based correction for multiple comparisons.

Source level. To localize the probable generators of the sensor level effect, a time-frequency window was defined based on the time courses and power spectra of the respective peak sensors, and a source reconstruction was performed using a dynamic imaging of coherent sources beamformer (DICS; Gross et al., 2001). Cross-spectral density (CSD) matrices of all conditions were calculated using a multitaper FFT method with a center frequency of 11 ±3 Hz for a time period of 0.45–0.9 s after cue onset. For each subject, realistically shaped, single-shell head models (Nolte, 2003) based on individual structural MRI scans were computed. A grid with 1 cm resolution was normalized on a MNI template, and then morphed into the brain volume of each participant. Leadfields for all grid points and a CSD matrix based on the concatenated auditory and visual conditions (right and left) were used to compute a common spatial filter for each grid point and each participant. Using this common filter, the spatial distribution of power was estimated for all four conditions (modality × side). Dependent-sample t tests were calculated between the attention–direction (right vs left) in both modalities using the grand averages. Additionally, a conjunction/disjunction analysis based on the statistical maps of the source analysis was performed to illustrate modality-independent and -specific activation. In this way, regions active in both modalities (auditory and visual; conjunction) as well as regions specific to the auditory modality [auditory − (auditory and visual); auditory disjunction] and to the visual modality [visual − (auditory and visual); visual disjunction] were identified.

Additionally, to specifically investigate whether the alpha-band in the auditory cortex is modulated in the main modality contrast (auditory vs visual), we performed a second DICS beamformer analysis using all trials from the auditory and the visual condition, collapsed across spatial attention. Based on the sensor-level data, spatial filters were estimated for the 0.5–1 s time- and 10 ±3 Hz frequency-window. All other parameters were identical to the first beamformer analysis described above. In a second approach, all parameters (also the time-frequency window: 0.45–0.9 s, 11 ±3 Hz) were identical to the beamformer analysis described above. Because the main outcomes were virtually identical, in the present paper we restrict our description to the first approach. All offline treat-

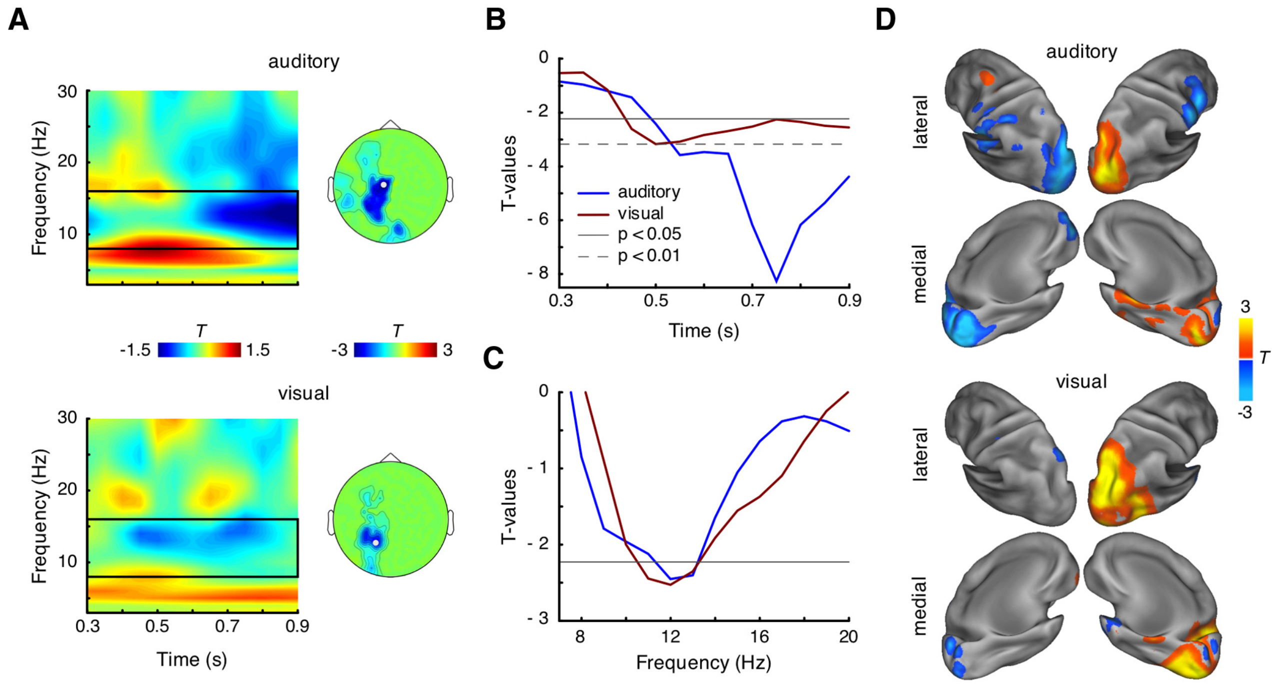

Figure 2. Modality-specific effects. Results of the contrast attend right versus attend left in the auditory and visual condition (positive and negative values refer to relative power increases and decreases, respectively). ***A***, Time-frequency plots and sensor-level topographies (masked at $p < 0.05$; corrected for multiple comparisons) showing the statistical contrasts attend right versus attend left for 300–900 ms post-cue and averaged across 8–16 Hz (marked with a solid black rectangle) in the auditory condition (top, $p = 0.001$) and visual condition (bottom, $p = 0.026$). ***C***, Time course and power spectrum of the auditory and visual contrasts (shown are the statistical values of the peak channels, marked with a white dot in A). ***D***, Statistical contrast attend right versus left (uncorrected) of the source reconstructions of the auditory (top) and visual conditions (bottom) for the 450–900 ms postcue time- and 11 ±3 Hz frequency-window (masked at $p = 0.05$).

ment of MEG data were performed using fieldtrip (http://fieldtrip.fcdonders.nl/; Oostenveld et al., 2011).

Results

Cue modality and cue side influence reaction time of target detection

An ANOVA with the four factors cue modality, cue side, target modality, and target side was applied to RTs. A main effect for the target modality was observed ($F_{(1,10)} = 439.44$, $p < 0.001$), with shorter mean RTs for auditory than visual targets. In addition, the allocation of attentional resources to the cued modality/side produced typical cost-benefit patterns, resulting in significant interactions between the cue and the target modality ($F_{(1,10)} = 48.28$, $p < 0.001$) as well as the cue and the target side ($F_{(1,10)} = 44.48$, $p < 0.001$). The effect of the cue-target modality interaction was particularly pronounced when an auditory cue was followed by a visual target due to the invalid cueing and generally longer reaction times for visual targets. Furthermore, we found a significant interaction between the cue side and the target modality ($F_{(1,10)} = 12.44$, $p < 0.01$).

Postcue alpha effects in audiospatial and visuospatial attention: sensor level

Nonparametric statistical contrasts in the auditory and the visual modality (attend right vs attend left) regarding the time-frequency window from 0.3–0.9 s after cue onset and 8–16 Hz (see Materials and Methods) resulted in significant negative auditory ($p < 0.001$) and visual ($p = 0.026$) clusters emerging at 0.5 and 0.45 s postcue, respectively (Fig. 2*A*,*B*). On a descriptive level, the topographies of both clusters were left-lateralized and strongest at parietal sensors. However, the auditory cluster spread to more posterior, and to left temporal and frontal sensors, whereas the visual cluster already emerged more posteriorly, with some later activation in left frontal sensors. The spectral profile of the peak channel of the auditory and the visual cluster indicated the effect to be centered ~11 Hz (Fig. 2*C*).

Postcue alpha effects in audiospatial and visuospatial attention: source level

To localize probable generators contributing to the sensor-level effect, we performed a beamformer analysis and subsequent *t* tests on the source level data contrasting attend right versus attend left (see Materials and Methods). Note in the following sections that alpha modulations are described as "relative", as they refer to a contrast, which does not provide conclusive information in which condition the alpha oscillations were modulated (e.g., increase for attend right, decrease for attend left, or both). In the auditory condition, we found relative alpha power decreases in the left auditory cortex (BA40-42 and postcentral gyrus), in the left primary, secondary, and associative visual cortices (BA17-19), the left superior frontal gyrus (BA11), and in the right inferior frontal and precentral gyri (BA44, BA6) when attention was directed to the right compared with the left side (Fig. 2*D*; positive and negative values refer to relative power increases and decreases, respectively). Additionally, when attending the right side, relative alpha power increases were identified in the left middle frontal gyrus (BA6) and right occipitoparietal regions (BA17, superior parietal lobule). Interestingly, no modulations of spatial attention were found in the right auditory cortex.

In the visual condition, when the right side was attended compared with the left side, we found small relative alpha power decreases in the left primary visual area (BA17), the left superior parietal lobule (BA7), and the right superior temporal gyrus

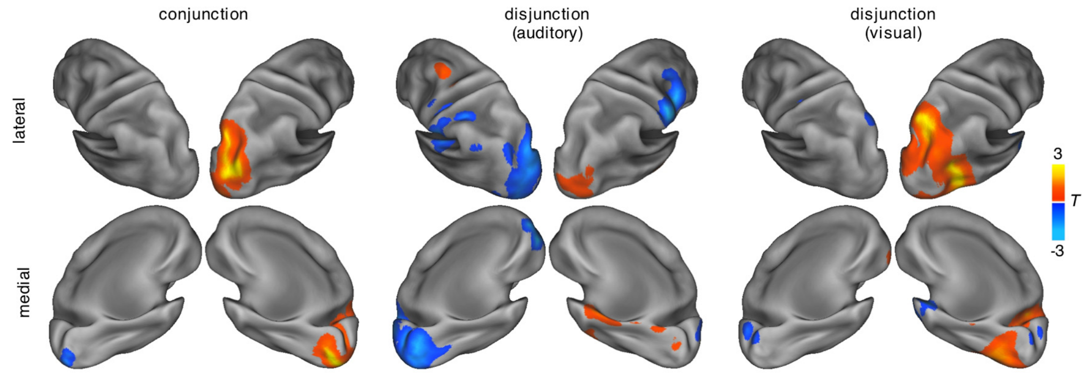

Figure 3. Results of the conjunction analysis based on the statistical maps of the source analysis (shown in Fig. 2*D*). Shown are source activity of the contrast attend right versus attend left common to both conditions (left), and specific to the auditory (middle), and the visual condition (right; positive and negative values refer to relative power increases and decreases, respectively).

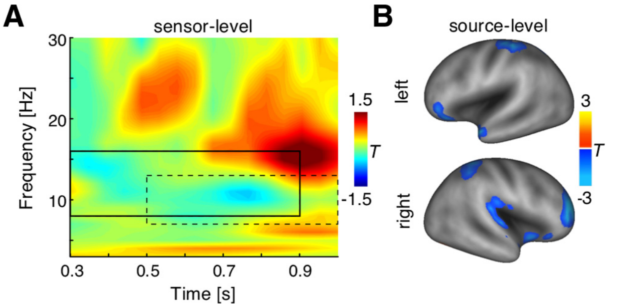

Figure 4. Main modality effects. ***A***, Time-frequency data from 3 to 30 Hz and 300–1000 ms postcue, showing the contrast between auditory and visual modalities. A nonparametric statistical test (cluster-based correction for multiple comparisons) was computed for the time-frequency window of 300–900 ms and 8–16 Hz (marked with a solid black rectangle). ***B***, Statistical contrast of the source reconstruction of the auditory and the visual condition using the time-frequency window of 500–1000 ms and 10 ± 3 Hz (marked in ***A*** with a dotted black rectangle). Shown are the lateral views (left and right) of inflated hemispheres thresholded at $p = 0.05$ (uncorrected).

(BA38). Similar to the auditory contrast, there were relative alpha power increases in the right occipitoparietal areas when attend right versus attend left. However, these increases were more extensive than in the auditory contrast including right primary, secondary and associative visual cortices (BA17-19), parts of the right fusiform gyrus (BA37), and the right superior parietal lobule (BA7; Fig. 2*D*). The conjunction analysis showed that relative alpha power decreases in the right primary and associative visual cortices (BA17, BA19), and the right superior parietal lobule (BA7), were common to both the auditory and the visual condition. Importantly, the auditory disjunction analysis clearly illustrated that the left auditory cortical alpha was solely modulated when attention was directed at acoustic input (Fig. 3).

Postcue main modality alpha effects: sensor and source level

On a descriptive level, the contrast between auditory and visual attention (in the 0.5–1 s time- and 8–16 Hz frequency-window) resulted in a negative pattern conforming to our expectations, however, without reaching statistical significance ($p = 0.53$; Fig. 4*A*). However, as outlined above circumscribed auditory cortical effects can be missed in the sensor level analysis especially when using cluster level correction (which favors broadly spread effects). Therefore, targeting the alpha frequency range (see Materials and Methods) a DICS was performed to scrutinize this issue in more detail. Indeed, the source reconstruction of the modality contrast shows an alpha-band modulation in the right auditory cortex (BA 41); however, interestingly, no similar modulation was found in the left auditory cortex (Fig. 4*B*). Furthermore, some additional modulations were found in bilateral parietal regions (postcentral gyri, right superior parietal lobule), frontal regions (right superior frontal gyrus, bilateral middle frontal gyri), and bilateral temporal regions (left temporal pole, right insular cortex). Also, in contrast to the spatial attention effect described in Figures 2 and 3, occipital effects were basically absent in the modality contrast.

Discussion

Audiospatial attention modulates cortical auditory alpha

For the first time we present noninvasively measured auditory alpha power modulations in an audiovisual attention paradigm. Audiospatial attention resulted in alpha power modulations in the left auditory cortex (and not in the right auditory cortex), whereas visuospatial attention mainly modulated alpha in visual areas, but not in the auditory cortex. Alpha band oscillations are thought to be a general mechanism regulating the excitability state of neural tissue (Klimesch et al., 2007) and a top-down driven mechanism to disengage cortical areas in stimulus processing (Jensen and Mazaheri, 2010). Importantly however, two potential mechanisms could influence auditory processing during an audiospatial attention task. On the one hand, processing of the unattended ear, mainly in the auditory cortex ipsilateral to attention, could be inhibited. On the other hand, processing of the attended ear, mainly in the hemisphere contralateral to attention, could be facilitated (Tervaniemi and Hugdahl, 2003). The statistical contrast reported in this study, however, does not disclose which mechanism was driving our effects (ipsilateral inhibition, contralateral facilitation or both). The present alpha modulations in the left auditory cortex could, therefore, reflect an inhibition of this region when the left ear was attended, or an increased excitability state of this region when the right ear was attended (or both). These results are in line with findings from the other modalities, in which relative alpha power increases were found in to-be-inhibited areas in visuospatial (Worden et al., 2000; Sauseng et al., 2005; Thut et al., 2006), visual feature-based (Snyder and Foxe, 2010), and somatosensory attention tasks (Haegens et al., 2011). Due to several difficulties in the study of cortical auditory alpha oscillations, particularly with scalp EEG recordings (e.g., the size and orientation of the auditory cortex, the blurring by simultaneous somatosensory and visual alpha fluctuations), it was either thought that the alpha-band modulations in auditory spatial attention studies resulted from posterior alpha generators, or that the increased sensitivity of intracranial recordings is necessary to measure them (Gomez-Ramirez et al., 2011). Using a very similar design as in aforementioned audiovisual studies (Foxe et al., 1998; Worden et al., 2000; Fu et al., 2001; Banerjee et al., 2011; Gomez-Ramirez et al., 2011), the current MEG study, however, clearly shows alpha-band modulations generated in the auditory cortex corroborating findings from previous research in the auditory modality (Weisz et al., 2011; Weisz et al., 2013; Müller and Weisz, 2012). These findings contribute to the field of auditory cognition on several levels. First, they provide more evidence for the existence of auditory alpha and that it can be measured with noninvasive techniques. Second, they show that its generation is separate from occipital alpha-band generators. Finally, they support the notion that auditory alpha is functionally relevant in auditory cognition, here in audiospatial attention; corroborating the notion that alpha possesses general similar functional properties.

Audiospatial attention is processed asymmetrically

When attending the right versus the left side alpha-band oscillations were modulated in the left but not the right auditory cortex. A reason for these results could be the asymmetries of the auditory system. Whereas the left auditory cortex mainly localizes stimuli in the contralateral space, the right auditory cortex processes stimuli in the whole space (Zatorre and Penhune, 2001; Spierer et al., 2009). Subsequently, there could have been similar alpha-band modulations in the right auditory cortex during audiospatial attention to the left and to the right side. Indeed, alpha-band oscillations in the right but not in the left auditory cortex are modulated when contrasting auditory versus visual attention regardless of locus of attention (Gomez-Ramirez et al., 2011). These results from the modality-specific audiospatial contrast and the main modality contrast are in line with previous results from our group (Müller and Weisz, 2012; Weisz et al., 2013), providing further evidence for asymmetries in the auditory system during audiospatial attention before stimulus onset.

Audiospatial attention modulates alpha outside of the auditory cortex

We hypothesized that spatial attention, regardless of modality, modulates alpha-band activity in posterior regions, reflecting a supramodal attention system (Banerjee et al., 2011). However, in addition to these common modulations, we report posterior alpha-band activity modulated by audiospatial but not visuospatial attention. It is worth noting that these modulations, in contrast to modulations in the auditory system, were symmetrical. As the current study focused on spatial attention within one modality, and as there was no simultaneous, to-be-ignored visual input during audiospatial attention, it is unlikely that these findings reflect a general disengagement of the visual system. On the contrary, they could reflect an automatic coactivation of visual areas during audiospatial attention either because the visual cue enhanced the salience of the spatial location regardless of the modality (Smith and Schenk, 2012), or because the visual and the auditory systems actively interact during audiospatial attention. Interestingly however on a behavioral level, dramatic costs in RTs were obtained when participants were wrongly cued to the auditory modality (i.e., a visual target appeared), meaning that this coactivation is not beneficial in a functional sense. Alternatively, also taking into account alpha power modulations in the posterior parietal cortex and the inferior and middle frontal gyri, these changes could reflect involvement of the dorsal and ventral attention networks (Corbetta and Shulman, 2002; Petersen and Posner, 2012; Wen et al., 2012). Involvement of both attention networks has been found in audiospatial attention tasks using fMRI and MEG (Degerman et al., 2006; Weisz et al., 2013; Kong et al., 2014; Lee et al., 2014). Together, the alpha-band modulations in regions outside of the auditory cortex could either reflect a coactivation of visual areas due to visual dominance or audiovisual interactions, or an involvement of the dorsal and ventral attentional networks.

Common posterior alpha-band modulations

The present study yielded interesting results concerning attention deployment across modalities in line with our hypotheses. The conjunction analysis showed that audiospatial as well as visuospatial attention modulated alpha-band oscillations mainly in right posterior areas. This activation could partly reflect automatic activation of visual areas during audiospatial attention (see above); however, it could also reflect a supramodal attentional system (Banerjee et al., 2011) or an interactive synergy between the auditory and the visual modality. The posterior parietal cortex has been suggested to play a central role in multisensory integration (Macaluso et al., 2003; Molholm et al., 2005) including auditory spatial attention (Wu et al., 2007; Hill and Miller, 2010; Smith et al., 2010, Banerjee et al., 2011). Additionally, the dorsal attention network, including parietal regions, has been suggested to be involved in visuospatial (Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002; Serences and Yantis, 2007; Capotosto et al., 2009) and audiospatial attention tasks (Degerman et al., 2006; Mayer et al., 2006; Shomstein and Yantis, 2006; Wu et al., 2007; Salmi et al., 2009; Lee et al., 2014; Weisz and Obleser, 2014). The present data are in line with these studies suggesting a parietal supramodal attention system (Banerjee et al., 2011; Ptak, 2012; Kong et al., 2014). Alternatively, neural substrates common to audiospatial and visuospatial attention could also represent an interactive synergy improving task performance in both or particularly the auditory modality.

Limitations

There are some limitations of the current design. First, the cues were presented visually in the audiospatial as well as the visuospatial attention task. To study the effects of attentional cues without any confounds of the cue modality, one could present them in a modality different from the target modalities. However, previous studies have used cues in the same modality as the target (Worden et al., 2000; Sauseng et al., 2005) as well as in a different modality (Fu et al., 2001; Thut et al., 2006; Haegens et al., 2011) showing no fundamental differences of cue modality on attentional effects. Also for our purposes of studying auditory cortical alpha, use of a visual cue poses no interpretational problems. Second, because alpha power is modulated by cue validity (Haegens et al., 2011), the observed effects could have been stronger and possibly clearer if all cues had been valid.

Conclusion

In accordance with the hypotheses, the present study has shown very selective noninvasively measured alpha-band modulations in the auditory cortex during audiospatial attention. Furthermore, visuospatial attention modulated alpha oscillations in visual areas but not in the auditory cortex, and both audiospatial and visuospatial attention resulted in effects in higher-order areas. These findings provide clear evidence that auditory cortical alpha modulations can be measured noninvasively and that there is a distinct alpha generator in the auditory cortex separate from occipital alpha generators. In addition, they support the notion that alpha-band oscillations possess general functional properties that are also relevant in auditory cognition.

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Appendix B. Not so Different After All: The Same Oscillatory Processes Support Different Types of Attention

Frey JN, Ruhnau P, Weisz N (2015) Not so different after all: The same oscillatory processes support different types of attention. Brain Res:1–15.

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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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Contents

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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

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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.

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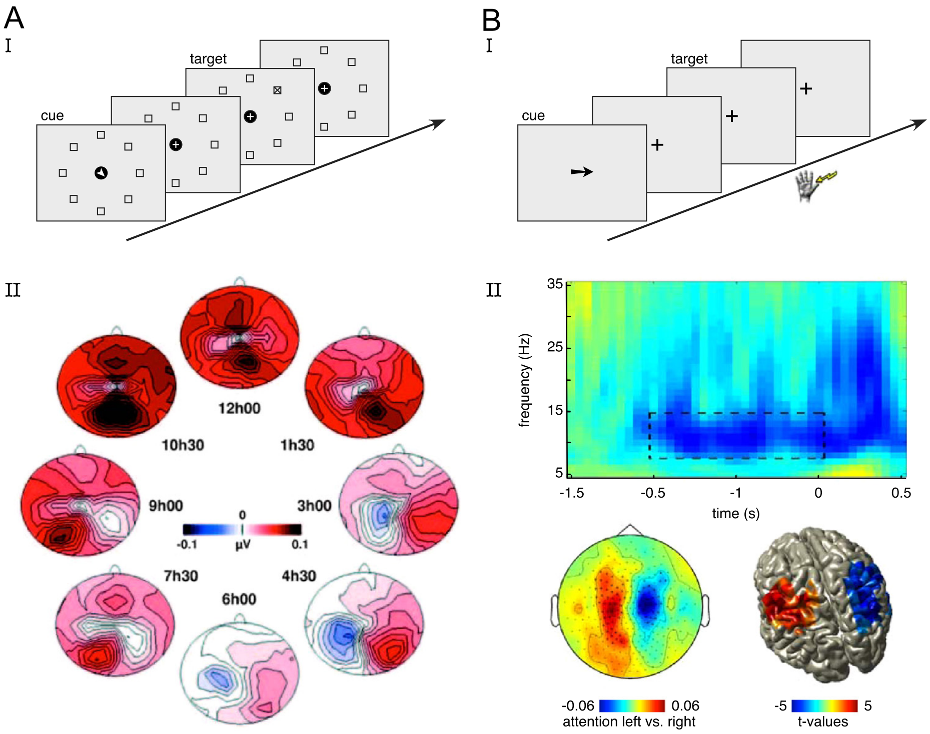

Fig. 1 – Alpha power modulations in visual (A) and tactile (B) spatial attention tasks. A (I) Depiction of one trial of a visual spatial attention task. Participants were cued by a central arrow (80 ms) to attend to one of eight peripheral locations. After a fixed prestimulus interval (1300 ms), a go-stimuus (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

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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

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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

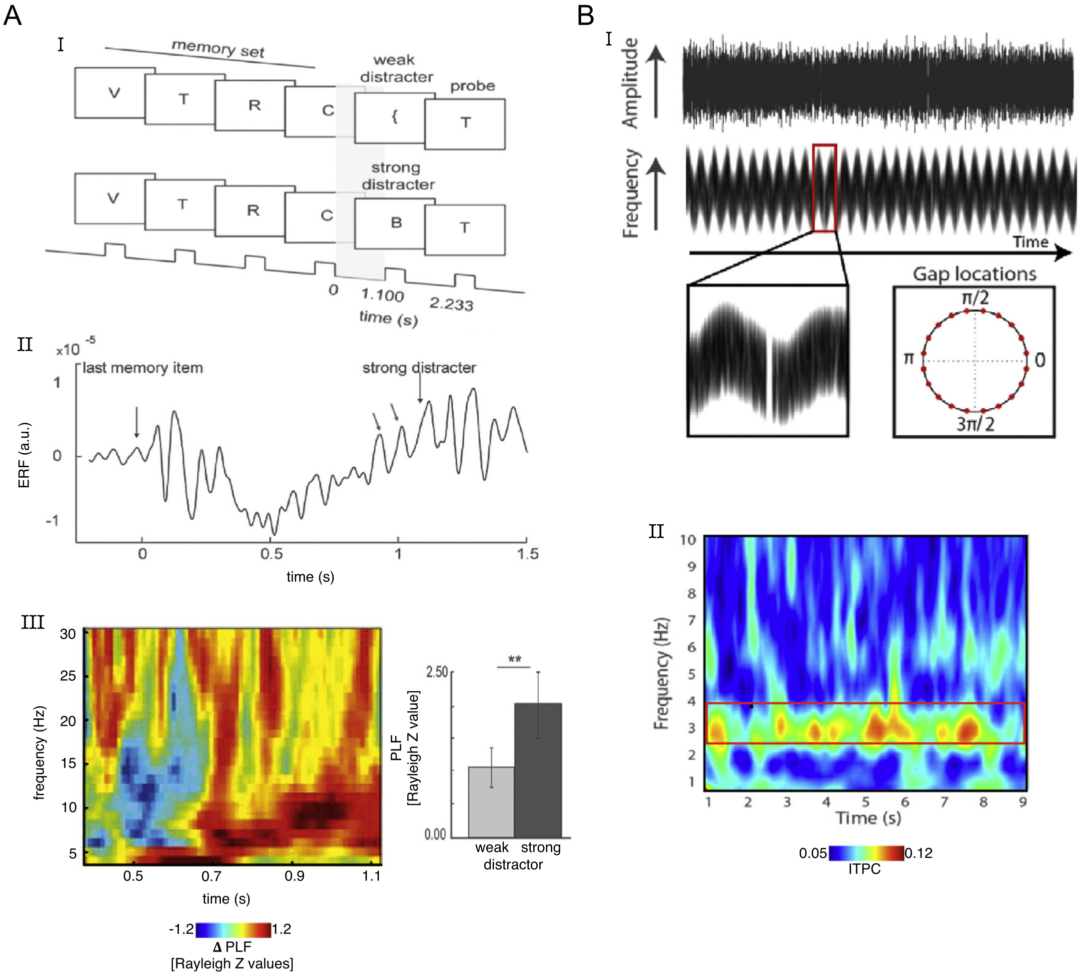

Fig. 2 – Phase resetting in an internal attention (memory) task (A) and auditory attention task (B). A (I) Depiction of one trial of an internal attention (memory) task using a conventional Sternberg paradigm. A memory set of four sequentially presented consonants had to be retained; during the retention 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).

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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

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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).

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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

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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

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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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