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The good, the bad, the complex: Investigating the behavioural consequences of EEG alpha oscillations in visual detection and selective attention

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A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy (PhD) in Psychology, The University of Auckland, 2016
Abstract

We heavily rely on vision to represent the world around us. Quite surprisingly, our ability to perceive identical visual stimuli varies considerably. Understanding why we sometimes miss a stimulus that we could easily see just a moment ago promises exciting insights into how we perceive and interact with the world. This variability has to depend at least to some extent on variability in the how the brain processes these stimuli. Recent research has related fluctuations in ongoing brain activity, especially in the alpha band (8-12 Hz) of the scalp-recorded electroencephalogram (EEG), with variability in the detection of visual stimuli. Lower alpha power over posterior cortex is generally assumed to lead to superior detection performance. It has also been shown that alpha oscillations play a role in the orienting of selective attention, which allows us to focus on task-relevant stimuli and to inhibit the rest. Alpha power is usually shown to be lower over the side of the head where the attended stimuli will be processed and higher over task-irrelevant sites (i.e. it is lateralised).

This thesis provides an in-depth investigation of the behavioural consequences of alpha power fluctuations in visual detection and selective attention. A series of three studies demonstrates that although alpha power fluctuations are related to the behavioural responses in visual tasks, low or high power cannot easily be related to either good or bad performance. Instead, lower alpha power is related to a less cautious and faster response. This association between alpha power and factors that are orthogonal to performance is similar regardless of whether alpha power fluctuates spontaneously or whether those fluctuations are controlled by attentional cues. In fact, the cue-related lateralisation of alpha power seems to index some other mechanism that is not directly related to the behaviourally relevant bias. We thus reveal the complexity of the relationship between alpha power fluctuations and behavioural performance in visual detection and selective attention tasks. EEG alpha oscillations influence how we respond to visual stimuli, and not directly their sensory coding.
Acknowledgments

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**Chapter 2. The manuscript is currently under review at the journal Psychophysiology**

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Chapter 1: General introduction – Investigating the Behavioural Consequences of EEG Oscillations in Visual Detection and Selective Attention

1.1 Introduction

“You will miss the best things, if you keep your eyes shut” (Dr. Seuss, 1978 p.30)

The world around us is full of wonderful things that we perceive though our senses. Even though everyone has a different understanding of what “the best things” to see are, we can probably all remember situations in which we marvelled at nature’s beauty, felt extremely happy at the sight of a loved person, or on the other hand were frightened when we were unable to see (be it during a sudden power cut or in a haunted house).

We heavily rely on the visual representation of the world in our everyday lives. We are immediately able to place ourselves in the environment and start to recognise and interpret what we are seeing when we open our eyes (Carrasco, 2011). The speed at which these processes occur gives us the illusion that we are able to perceive a very complex and complete representation of the world with relatively little effort. In fact it was commonly assumed in the 1960s and early 1970s that we would be able to build machines that could automatically interpret images within a couple of years. Over the last 60 years is has become increasingly clear though how over-optimistic that assumption was and how complex even the most basic visual processing mechanisms really are (Ballard, Hinton, & Sejnowski, 1983). Most importantly our perception of the world is much more than a passive representation of our surroundings and we can – at least to a certain extent - control what we are seeing. Even when we are directly ‘looking’ (so we are not controlling what enters the eyes by turning them away or closing them) our perception is shaped by our goals and
experiences (Awh, Belopolsky, & Theeuwes, 2012; Treue, 2001). Dr. Seuss (1978) is obviously right in saying we have to open our eyes first, but the processes that enable us to see the best things are more complex.

Perception of our visual surroundings is thus an active and constructive process (e.g. Ballard et al., 1983; Carrasco, 2011; Goldstein, 2014; Treue, 2001) and our ability to perceive stimuli varies much more from moment to moment than it might appear at first (Fechner, 1860). We often fail to detect stimuli and changes in the environment that we might easily perceive at different times. We overestimate our visual abilities and assume that we are seeing much more than we actually do (e.g. Azzopardi & Cowey, 1993; Rahnev et al., 2011). To be able to act upon sensory information in a timely and meaningful fashion we furthermore focus only on a small amount of the plethora of available stimuli and select those that are important for us at that moment (Carrasco, 2011). The processes underlying our visual perception are therefore much more complex and at the same time considerably more fascinating than at first sight.

Both the primacy of visual information and the complexity of its processing are reflected in the structural and functional architecture of our brains. The human cerebral cortex consists of roughly 25 billion neurons, about a fifth of which (ca. five billion) are involved in visual processing (Pakkenberg & Gundersen, 1997; Wandell, Dumoulin, & Brewer, 2007). This leads to the further question of how visual percepts arise from this vast number of neurons and how the processing is organised. Even though we have a good basic understanding of how the eyes work and convert the rays of light entering the retina into neuronal signals, we are only starting to understand the highly complex cortical processing mechanisms that underlie the resulting percepts. The question of flexible neuronal communication (e.g. Buzsáki, 2006; Fries, 2005) is strongly intertwined with the problem of how neuronal activity leads to the rich and vivid impressions of our visual environment.
CHAPTER 1: EEG OSCILLATIONS VISUAL DETECTION SELECTIVE ATTENTION

To date a range of powerful non-invasive techniques exist to study brain activity in awake humans. One of those techniques is the electroencephalography (EEG) that allows us to investigate brain activity at the time scale of actual neural processing (e.g. Cohen, 2014; Lopes Da Silva, 2013; Luck, 2005) and can help us to reveal how visual input is processed in the human brain. As the same visual stimulus can lead to various percepts, this variability has to stem from differences in its processing and arguably even from differences in brain activity before the stimulus is presented (e.g. Britz, Diaz Hernandez, Ro, & Michel, 2014; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Wyart & Tallon-Baudry, 2009).

A core topic in this thesis is how the ‘brain state’ around the time of stimulus presentation shapes its perception. The brain state is referred to as ‘cortical excitability’, cortical activation or excitation. Although these terms are often used in the literature, they are seldom defined in a clear manner. In the context of this thesis a state of heightened cortical excitability is meant to reflect that an external stimulus has a greater influence on ongoing processing than the same stimulus would have under lower excitability. A weak stimulus would for example more likely be seen under high compared to low excitability. Cortical excitability thus implies a degree of tuning to the environment.

This thesis specifically focuses on behavioural performance in visual detection and visuospatial attention tasks. The three studies are designed to broaden our understanding of how and why our perceptual performance varies and how this variability relates to the concept of cortical excitability. The remainder of this introductory chapter focuses on common theories that run throughout the thesis: basic characteristics in the organisation of the visual system, variability in perception, selective attention, and EEG oscillations as a possible manifestation of this variability. The chapter will conclude with a brief description of the three studies conducted for this thesis.
1.2 Basic Overview of Visual System

The dominant role of vision for our interactions with the environment is demonstrated by the structural and functional architecture of our brains. About a fifth of the cortical neurons are predominately utilised for visual processing (Pakkenberg & Gundersen, 1997; Wandell et al., 2007). In comparison, areas predominately assigned to auditory, somatosensory and motor processing occupy only about 7-8% each (Van Essen, 2004). The processing of visual information is a complex process that is optimised to enable meaningful interactions with the environment. A veridical representation of our visual surroundings is often sacrificed to enable the selection and prioritisation of behaviourally relevant information (e.g. Treue, 2001). The following four processing characteristics are important for the upcoming discussion: 1.) a disproportionally large amount of cortical processing is allocated to input from the central spot on the retina, the fovea (cortical magnification), 2.) the spatial configuration of the input is preserved in visual areas (retinotopy), 3.) processing is organised hierarchically, although the connections between visual areas are reciprocal and 4.) visual input is processed in parallel streams.

The photoreceptors on our retina, which are responsible for converting the rays of light into neuronal signals, are distributed and connected in a way that strongly prioritises input that falls onto the fovea, the central spot of the retina. To perceive fine visual details (e.g. when reading this page), the stimulus of interest has to be brought into the fovea via fast and accurate eye movements (Yarbus, 1967). The fovea covers only about 0.3 mm (~1%) of the human retina, but has by far the highest density of cones (which are the photoreceptors that enable colour vision and perception of fine details) and no rods (which are responsible for vision under dim light). Furthermore the cones in the fovea have ‘exclusive’ access to ganglion cells, meaning that each ganglion cell only relays information from a single cone (on average input from 6 cones and 120 rods converge to one ganglion cell) (Goldstein,
This primacy of information from the fovea is continued throughout most visual areas. Homes (1918) and Inouye (1909) discovered at the beginning of the 20th century that information from the fovea is represented by a significantly larger proportion of cortical neurons than the same sized space in the periphery, an organisational principle called cortical magnification.

Input from neighbouring locations on the retina is processed by neighbouring locations in the visual cortex. This organisational principle is called retinotopy. Wandell and colleagues (2007) point out that the spatial configuration of any visual scene is absolutely necessary for its recognition. Even if the size, colour or orientation of an image changes, we are still able to recognise the objects; however we are not able to do so if the spatial configuration is changed. Therefore it is not surprising that the spatial layout of the input is preserved during its processing. Another (spatial) organisational principle is that each hemisphere mainly processes input from the contralateral visual field. Exceptions are higher visual areas (see below), which often include information from the ipsilateral visual field as well due to their larger receptive fields (which can cover both visual hemifields) (Tootell, Mendola, Hadjikhani, Liu, & Dale, 1998).

Retinotopy mainly concerns the organisation of information within a cortical area. Across visual areas, the processing is organized hierarchically in that the complexity of the analysed characteristics increases in areas later in the processing stream (Van Essen & Maunsell, 1983). Areas V1 and V2 are often characterised as lower visual areas and areas such as V3, V4, MT and IT as higher areas. Neurons in V1 respond to simple features such as orientation and location (Hubel & Wiesel, 1962), while higher areas represent whole objects or classes of objects (e.g. Van Essen & Maunsell, 1983). The neurons’ receptive fields are smallest in V1, which means that they only process information from a very small part of visual space. Receptive field sizes increase along the hierarchy and higher areas are able to
integrate information from increasingly larger proportions of visual field (e.g. Hochstein & Ahissar, 2002; Ungerleider & Pasternak, 2004).

The areas along the visual hierarchy are highly interconnected and historically there was a strong focus on the feedforward streams and processing of visual input seemed to be a rather sequential process (Van Essen & Maunsell, 1983). However there are many feedback projections from higher to lower areas and it is now commonly accepted that higher areas influence the processing in early areas (Felleman & Van Essen, 1991; Hochstein & Ahissar, 2002; Treue, 2001). For example it is no longer assumed that only higher visual areas are influenced by ‘top-down’ factors such as selective attention or perceptual learning. Although the influence of such factors is greater in higher areas, it has been shown repeatedly that, for example, attention can modulate processing even in low visual areas that were assumed to be ‘purely sensory’ until a couple of decades ago (Hochstein & Ahissar, 2002; Kastner, 2004; Kastner, Pinsk, Weerd, Desimone, & Ungerleider, 1999; Luck, Chelazzi, Hillyard, & Desimone, 1997; Luck, Woodman, & Vogel, 2000; Treue, 2001).

Visual processing is not only distributed across the visual hierarchy, it is also parallel (e.g. Ballard et al., 1983) and arguably the separation into parallel processing streams originates in the retinal ganglion cells (Livingstone & Hubel, 1988). Following V1 there are two major parallel processing streams: the ventral stream reaching the temporal lobe and dorsal stream reaching the parietal lobe (Mishkin & Ungerleider, 1982). Areas in the ventral stream are tuned to object properties such as colour, shape and texture (the ventral stream is often referred to as the “what” pathway), and areas in the dorsal stream are tuned to spatial aspects and the direction and speed of motion (often referred to as the “where” pathway). Along the hierarchy, visual areas in the ventral stream get increasingly invariant to modulations of size, viewpoint or illumination, which take place if the observer or objects move (Ungerleider & Pasternak, 2004). These streams arguably originate in retinal ganglion
CHAPTER 1: EEG OSCILLATIONS VISUAL DETECTION SELECTIVE ATTENTION

cells. A popular theory by Goodale and Milner (1992) holds that the information in the dorsal stream is optimised for motor action whereas information in the central stream is optimised for object recognition and conscious perception (Ungerleider & Pasternak, 2004). However there is ongoing debate about whether or not the internal representations used for action and perception actually differ (for a review see Franz & Gegenfurtner, 2008).

1.3 Variability in Perception

The understanding of our complex visual processing mechanisms is further complicated by the fact that our perception is highly variable. Moment-to-moment variability is one of the fundamental truths in perception, leading Ashby and Lee (1993) to propose “[…] trial-by-trial variability in the perceptual information obtained from every object or event” (p. 370) as an axiom. There are multiple sources of this variability, and the distinction between functionally relevant ‘noise’ and pure-noise is fundamental to the understanding of variability, and of great significance for (systems) neuroscience (Ratcliff, Philia
tides, & Sajda, 2009).

Ashby and Lee (1993) suggest three causes for variability if the observer, object, and viewing conditions are fixed. In natural conditions where both the observer and the objects can move as well as where viewing conditions can differ, the variability is disproportionately high. The sources of variability are variability in the physical stimuli (such as the variable number of photons emitted by a light source), perireceptor noise (such as the scattering of light as it passes through the cornea), and variability due to fluctuations of brain activity. It is important to give special attention to variability that is introduced by fluctuations of activity within the brain. This kind of activity is highly complex (Parker & Newsome, 1998; Ratcliff et al., 2009) and appears to influence perceptual performance at different stages (Ratcliff et al., 2009). While some of these fluctuations might be spontaneous and rather random, others are probably linked to changes in attention and momentary task requirements (Prado, Carp, &
Weissman, 2011). It has been shown that if a stimulus is attended to or relevant for goal-directed behaviour, it evokes a different response to when it is not in the focus of attention (for a review see Carrasco (2011)). The influence of noise and variability on perceptual performance also depends on additional factors, for example the categorisation of high contrast objects is probably not affected by variability in the physical stimulus (Ashby & Lee, 1993).

Variability in response to nominally identical stimuli is most obvious for near-threshold stimuli and therefore usually neither obvious nor hindering interaction with the environment in everyday life. However, in psychophysiological experiments the presentation of identical stimuli near the detection threshold reliably leads to variability in the responses; response times vary from trial to trial and often participants fail to detect a stimulus that they could easily see before. Although this variability has puzzled psychologists for over 150 years (Fechner, 1860), it has often been downplayed as the inevitable consequence of perceptual noise. Only in more recent years have researchers started to investigate the underlying causes of the variability in neuronal processing (e.g. Busch, Dubois, & VanRullen, 2009; Chaumon & Busch, 2014; Mathewson et al., 2009). It is assumed that understanding why responses to identical stimuli vary will enhance our knowledge of visual processing and general cognitive processing greatly (Bellgrove, Hester, & Garavan, 2004; Prado et al., 2011; Weissman, Roberts, Visscher, & Woldorff, 2006).

It has even been suggested that the response to a sensory stimulus tells us more about the current brain state than it does about the stimulus (Buzsáki, 2006). Our brains constantly cycle through different states of excitability or awareness (e.g. Lindsey, 1952) and this excitability state is assumed to be one important source of behavioural variability in response to identical stimuli. At times we seem to be very tuned to the outside world and are able to easily notice what is happening in our surroundings. However, at other times we seem to focus
more on internal processes (e.g. memory, imagery), which probably results in being less tuned to the outside world. Periods or states of external orientation, when we are tuned to the outside world, seem to co-vary with states of reduced internal orientation/processing and vice versa (Hanslmayr, Gross, Klimesch, & Shapiro, 2011). These fluctuations between externally and internally oriented states are assumed to occur spontaneously (Monto, Palva, Voipio, & Palva, 2008). The research in this thesis focuses on how behavioural performance is affected by changes in excitability (i.e. between externally and internally oriented states) prior to stimulus presentation. We will focus on the variability due to fluctuations in brain activity, disregarding other noise sources that probably affect the available information from nominally identical stimuli (such as perireceptor noise see Ashby and Lee (1993)).

1.4 Selective Attention as a Source of Variability

Selective attention is a core topic in cognitive neuroscience. According to Carrasco (2011), visual attention “is the mechanism that turns looking into seeing” (p. 1484). In natural environments we are constantly surrounded by more stimuli than we can process at any given time. Selective attention is understood as a potential mechanism that prevents us from being constantly overloaded and enables us to select certain stimuli for more detailed processing and to inhibit others or delay their processing (e.g. Broadbent, 1958; Buschman & Miller, 2010; Carrasco, 2011). This selection is probably also needed due to both the high energy costs of neural activity and other characteristics of the visual system (e.g. Attwell & Laughlin, 2001; Carrasco, 2011; Lennie, 2003; Treue, 2001; Tsotsos, 1990; Van Essen & Maunsell, 1983). How crucial selective attention is for goal-directed behaviour and interactions with the environment is furthermore shown by the link between abnormal selective attention and brain disease. Pathological conditions including neurodegenerative diseases such as Parkinson’s, traumatic brain injury, and focal lesions, often result in attentional deficits that are particularly disabling (Manohar, Bonnelle, & Husain, 2004).
In a typical spatial selective attention task, participants perform some sort of a visual
discrimination task at a particular spatial location. Performance is compared between trials on
which participants received a valid cue before the brief target presentation (i.e. the cue
correctly indicated the target location) and trials in which they either received no cue or a cue
to a different and thus incorrect location (Posner, Snyder, & Davidson, 1980). The same
stimulus is perceived faster and more accurately if it is attended (Posner et al., 1980) and
neuronal populations are more active when the stimulus they are processing is attended
compared to the same stimulus being unattended (Desimone & Duncan, 1995). This
enhancement comes with the cost of decreased performance at unattended locations (Posner
et al., 1980). Various studies have shown that stimuli at the attended side are not only
processed faster and more accurately, but that the high level of attention can furthermore
change the appearance of low level features such as contrast sensitivity and spatial resolution
(e.g. Carrasco, Giordano, & McElree, 2006; Carrasco, Penpeci-Talgar, & Eckstein, 2000;
Giordano, McElree, & Carrasco, 2009; Herrmann, Montaser-Kouhsari, Carrasco, & Heeger,
2010; Lu & Dosher, 1998; Luck et al., 1994; Yeshurun & Carrasco, 1998). Attention can also
increases the flow of information between early and late sensory processing areas (Friston &
Buchel, 2000).

Often the stimulus displays are lateralised, so that the targets appear either on the left
or right side of the screen. Lateralised displays have proven to be very useful for the
investigation of neural processes in attention, as stimuli presented on the left side are
predominately processed in the right hemisphere and stimuli presented on the right side are
predominately processed in the left hemisphere. Attention to the left should therefore mainly
influence the processing in the right hemisphere and vice versa. This is especially important
for the investigation of the effects of attention on neuronal activity with techniques that have
low spatial resolution (e.g. EEG).
Although much research focuses on the effects of attentional deployment, visuospatial attention has been shown to influence the ongoing or baseline activity in early visual areas, even before a stimulus is presented (e.g. Kastner et al., 1999; Luck et al., 1997). It is assumed that the orienting of attention is due to a mechanism that initiates a ‘bias’ or ‘baseline shift’ in activity that in turn underlies the improved perception of attended stimuli and starts before the stimulus is presented (e.g. Wyart & Tallon-Baudry, 2009). Interestingly, this baseline shift might be due to local changes in excitability. In response to an attentional cue, excitability seems to be increased contralaterally and decreased ipsilaterally (e.g. Foxe & Snyder, 2011). The behavioural effect of cue related changes in cortical excitability will be investigated in Chapters 3 and 4.

1.5 EEG as a Measure of Cortical Activity

The electroencephalogram (EEG) was discovered in the early 20\textsuperscript{th} century (Berger, 1929) and developed as a technique to measure brain activity in the ensuing decades. Electrodes are placed on the surface of the scalp and measure changes in electrical potential presumably produced by the activity of cortical neurons. EEG can measure changes in scalp potential with high temporal resolution and is therefore a very valuable technique in the field of cognitive neuroscience. It is used to link neuronal activity with various behavioural and cognitive phenomena, such as memory, attention, sensory perception, language or emotion (e.g. Cohen, 2014; Lopes Da Silva, 2011b). As discussed in more detail below, the EEG signal oscillates, which means that it rhythmically alternates between different states. Recently, EEG research has increasingly examined the oscillatory nature of the EEG as the oscillations may potentially be very important for the transfer of information within the brain, and index general processing mechanisms (e.g. Buzsáki, 2006; Buzsáki & Draguhn, 2004; Cohen, 2014; Klimesch, 1999; Lopes Da Silva, 2013).
The biophysical basis of the signal is not entirely understood. The EEG signal is thought to be dominated by postsynaptic activity of pyramidal neurons that are the most common excitatory cell type in the human cortex. They are thought to play an important role in cognitive processing, as they constitute the major output from the cortex and their axons form cortico-cortical or cortico-subcortical projections (Felleman & Van Essen, 1991; Luck, 2005). As all neurons, a pyramidal neuron fires an action potential if it is stimulated to a certain threshold. When this action potential arrives at a synapse (the contact point with another neuron), neurotransmitters are released from the axon terminal and bind to the postsynaptic membrane. This results in intra- and extracellular current flows as ion channels open or close, leading to further changes in the electrical potential along the membrane of the postsynaptic neuron. This flow of currents generates an electrical field that is called Local Field Potential (LFP) and most likely underlies the EEG signal (Buzsaki, Anastassiou, & Koch, 2012; Cohen, 2014; Lopes Da Silva, 2013; Luck, 2005). If thousands of neurons are active at the same time and are oriented in the same direction, the fields generated by their postsynaptic currents summate and can create electrical fields large enough to be picked up by electrodes placed on the surface of the scalp. Postsynaptic activity in pyramidal neurons is the most likely cause of the scalp-recorded EEG signal firstly because they are oriented perpendicular to the scalp and organised in assemblies that are activated synchronously. This offers the opportunity for electrical fields to summate enough to be recorded on the scalp. Secondly, their dendrites branch out in the superficial cortical layers, which makes the propagation of the electrical field onto the surface of the scalp more feasible (Lopes Da Silva, 2011a; Luck, 2005).

As electric fields propagate nearly at the speed of light, EEG enables the recording of changes in the electric field caused by neuronal activity essentially instantaneously. This millisecond precision makes it a very valuable technique in human neuroscience,
especially for the investigation of temporal properties of cognitive processing (Cohen, 2014; Luck, 2005). However, its spatial resolution is poor and is in the range of several centimetres. While traveling through the brain, electrical fields spread and have to pass through different tissue layers before they reach the surface of the scalp. These layers (i.e. cerebrospinal fluid, skull and skin) have different electrical properties and geometries that lead to smearing of the signal. Therefore it is impossible to directly infer the sources of the activity from the electrical fields recorded on the scalp (Lopes Da Silva, 2013).

The majority of EEG research in perceptual and cognitive psychology focuses on event-related potentials (ERPs), which are calculated by averaging the EEG signal in response to certain stimuli or tasks over many trials. It is assumed that each stimulus or task presentation (i.e. each trial) gives rise to a systematic brain response that is time-locked to the presentation or event. This systematic response is embedded in ongoing brain activity that is not time-locked to the event and therefore cannot be seen in a single trial. By averaging over many trials, this ongoing activity should cancel out and only the systematic and time-locked response should remain. In ERP studies, the variability in each individual trial is thereby considered noise (Sauseng & Klimesch, 2008). However, recent research suggests that the ongoing activity may be a very meaningful index of cognitive processing. Trial-by-trial fluctuations in ongoing activity are believed to be responsible for a least parts of the variability seen in behavioural performance and to represent dynamics of cognitive processing (Buzsaki et al., 2012; Buzsáki & Draguhn, 2004; Cohen, 2014; Fries, 2005; Lange, Keil, Schnitzler, van Dijk, & Weisz, 2014; Lopes Da Silva, 2013; Palva & Palva, 2007). Due to the non-invasive nature of EEG recordings, the investigation of ongoing EEG activity therefore offers a unique opportunity to study these dynamics in the active human brain.
1.6 EEG Oscillations as an Index of Cortical Processing

Brain activity is changing all the time. These continuous fluctuations are reflected in the EEG signal, which shows repetitive parameter variations between positive and negative voltages (Luck, 2014). In general such repetitive and often rhythmic variations between two or more extreme values are called oscillations. Like any other time-varying signal, EEG activity can be analysed and conceptualised as a mixture of overlaid oscillations at various frequencies. Although the presence of oscillatory activity in the EEG signal could just be due to the time-varying nature of underlying signal, there is an increasing amount of literature suggesting that oscillations seen in the ongoing EEG signal are a reflection of neuronal oscillations and are modulated by behavioural and cognitive states (Buzsáki, 2006; Cohen, 2014; Lopes Da Silva, 2013). Neuronal oscillations are presumably related to both the functional architecture of the brain as well as to variability in responses to stimulation and interactions with the environment (Arieli, Sterkin, Grinvald, & Aertsen, 1996; Chaumon & Busch, 2014; Fox & Raichle, 2007; Fox, Snyder, Zacks, & Raichle, 2005; Thut & Miniussi, 2009; von Stein, Chiang, & König, 2000; von Stein & Sarnthein, 2000). To strengthen the claim that EEG activity shows ‘true’ oscillatory activity, a spectral peak for a relatively narrow band of activity and not simply power across a wide band of frequencies should be shown (Lopes Da Silva, 2013; Luck, 2014).

A popular hypothesis for the role of neuronal oscillations in cortical processing is that they might enable highly dynamic and effective communication within and between distant brain areas (Singer, 1999). Our brains consist of distributed systems that allow us to flexibly adapt our behaviour in response to the environment (e.g. Dehaene, Kerszberg, & Changeux, 1998; Fries, 2005; van den Heuvel & Sporns, 2013). Much of the information processing occurs in local specialised neuronal assemblies. These assemblies have to communicate with each other to form representations that are the foundation of our perceptions, thoughts, and
actions (e.g. Singer, 1999; van den Heuvel & Sporns, 2013; von Stein & Sarnthein, 2000). Often the same input has to be processed differently depending on the task at hand, such as when attention is sequentially focused on different aspects of a visual scene (e.g. Buschman & Miller, 2007; Fries, 2005). Therefore neuronal assemblies have to be connected to a variety of target regions (Fries, 2005; Jensen & Mazaheri, 2010; van den Heuvel & Sporns, 2013) and at the same time be able to dynamically change at which of those regions they target the information at (Friston et al., 1997; Jensen & Mazaheri, 2010). One possibility to enable this flexible communication is via the synchronisation of their activity. Synchronisation between neuronal assemblies could thus result in a more effective connectivity between them (Fries, 2005; Lopes Da Silva, 2013; Singer, 1999; Uhlhaas & Singer, 2006; Varela, Lachaux, Rodriguez, & Martinerie, 2001). Oscillations are a mechanism by which neuronal assemblies could flexibly synchronise their activity with one another, thereby supporting the creation of dynamic networks, and flexible as well as effective communication structures within the brain.

Synchronisation is assumed to increase neuronal communication, because synchronised neuronal activity has larger effects on targeted neurons and neuronal assemblies. Neurons are able to integrate input over certain time windows (Salinas & Sejnowski, 2001; Usrey, Reppas, & Reid, 1998) and therefore reach their threshold to fire faster if they receive input from multiple neurons in tight temporal and spatial coordination (Fries, 2005; Lopes Da Silva, 2013; Singer, 1999; Uhlhaas & Singer, 2006; Varela et al., 2001; von Stein & Sarnthein, 2000). Furthermore, a neuron’s membrane potential fluctuates periodically, which leads to temporally distinct fluctuations in its excitability (Amzica & Lopes Da Silva, 2011). Therefore, there are times during which the influence of incoming information on subsequent processing is greater (if the neuron is in a more excited or excitable state and the membrane potential is closer to a firing threshold) than during other
times when the neuron is less excitable and further away from a firing threshold (Buzsáki et al., 2012). Due to these two properties of neurons and neuronal assemblies, a target neuron can be influenced most effectively, if the input is sent synchronously from several neurons and arrives at the peak of the target neuron’s excitability (Buzsáki, 2006; Salinas & Sejnowski, 2001; Usrey et al., 1998). As argued by Buzsáki (2006), the most efficient way to establish dynamic synchronisation between neuronal populations is via oscillations. Therefore these general processing principles make a strong case for the role of oscillations in cortical processing (Fries, 2005; Singer, 1999; Uhlhaas & Singer, 2006; Varela et al., 2001).

Intracranial recordings in non-human animals actually show that oscillations modulate neuronal spiking activity (Buzsáki & Draguhn, 2004; Gray & Singer, 1989; Haegens, Nácher, Luna, Romo, & Jensen, 2011; Lee, Simpson, Logothetis, & Rainer, 2005; Singer, 1999) and that artificially induced high frequency oscillations synchronise spontaneous neuronal activity leading to a temporally more precise response pattern (Cardin et al., 2009). This suggests that oscillations might also help to organise and stabilise processing in our highly complex brains (Buschman & Miller, 2010; Salinas & Sejnowski, 2001). Synchronised neuronal activity may furthermore lead to more effective communication by matching of excitability cycles of distant neuronal assemblies (Buschman & Miller, 2010; Fries, 2005) and thus facilitating the gating of information through the brain (Fries, 2005; Jensen & Mazaheri, 2010; Salinas & Sejnowski, 2001).

Based on this research showing oscillations at the neuronal level and the hypothesis that they might be involved in enabling effective communication between distant neuronal assemblies, oscillations seen in the EEG emerge as a very interesting tool to investigate cortical processing in humans (Buzsáki, 2006; Buzsáki & Draguhn, 2004; Lopes Da Silva, 2013). Traditionally, ongoing EEG activity is subdivided into different frequency bands and these bands are associated with different states of arousal or excitability and cognitive
functions (Lopes Da Silva, 2013). Each of those EEG frequency bands ranging from slow
delta oscillations (0.2 – 4 Hz) to fast gamma oscillations (> 30 Hz), will be introduced below.
However, these subdivisions can be artificial at times and a broader understanding may be
gathered by considering the interactions between different frequency bands (Lopes Da Silva,
2013).

Every oscillation is defined by its frequency, amplitude (or power), and phase, which
is the current position in an oscillatory cycle (Hanslmayr et al., 2011). Relationships between
all three of these oscillatory parameters, as well as their interactions, and cognitive processing
have been established. The frequency likely depends on the size of the network (or more
precisely on the amount of connections within a network) and the distance between the nodes
(Hanslmayr et al., 2011). Smaller networks tend to oscillate at higher frequencies (> 40 Hz),
whereas larger networks show lower frequency oscillations (< 20 Hz). In a very simplistic
model, lower frequencies are likely to represent communication between distant regions (e.g.
for top-down modulation), whereas higher frequencies most likely index local processing as
they reflect short-range projections (Buzsáki & Draguhn, 2004; Hanslmayr et al., 2011;
Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; Lopes Da Silva, 2013; Sauseng &
Klimesch, 2008; Schroeder & Lakatos, 2009; von Stein & Sarnthein, 2000). Another factor
that might influence the frequency is laminar specificity, where certain oscillatory
frequencies are more commonly observed in one cortical layer compared to another. In early
sensory cortex it has been shown that faster oscillations are most common in superficial
layers and slower oscillations in deeper layers (e.g. Buffalo, Fries, Landman, Buschman, &
Desimone, 2011; Siegel, Donner, & Engel, 2012; Wang, 2010). Although it is not clear if and
how this laminar specificity would affect the scalp recorded EEG activity, this may help
explain the association between frequency bands and their assumed function, as for example
deeper layers are associated with feedforward connections and higher frequency oscillations,
whereas superficial layers are associated with feedback connections and lower frequency 
oscillations (Buffalo et al., 2011). Lower frequencies might thus be important for longer 
range feedback neuronal communication, whereas higher frequencies might be more 
important for local feedforward processing (von Stein & Sarnthein, 2000).

The overall neuronal activity level in the brain is relatively constant (Clarke & 
Sokoloff, 1999) and changes in amplitude in a given frequency band are therefore presumed 
to reflect changes in the synchrony of active neurons (Hanslmayr et al., 2011; Palva & Palva, 
2007; Varela et al., 2001). Numerous studies show that the amplitude (and the phase) of 
ongoing oscillations at the time of stimulus presentation modulates both the neuronal and 
behavioural response (Bishop, 1933; Busch et al., 2009; Busch & VanRullen, 2010; Buzsáki 
& Draguhn, 2004; Drewes & VanRullen, 2011; Dugué, Marque, & VanRullen, 2011; Haig & 
Gordon, 1998; Kruglikov & Schiff, 2003; Lakatos et al., 2008; Mathewson et al., 2009; 
Rajkai et al., 2008; Schroeder & Lakatos, 2009; Thut et al., 2011). Depending on the 
frequency band either a decrease or an increase in synchrony is commonly related to higher 
excitability and better perceptual performance. However one has to be careful when arguing 
that changes in amplitude reflect changes in synchrony on a neuronal level (Palva & Palva, 
2007). Even in one of the earliest EEG studies, it has been discussed that decreases in alpha 
amplitude (commonly related to increases in excitability) could be due to out-of-phase firing 
of the underlying oscillators and not just less synchrony (Adrian & Matthews, 1934). The 
assumption has been supported by recent in vitro recordings in the cat’s thalamus. Hughes 
and colleagues showed in a series of experiments that the reconfiguration of phase 
relationships in thalamic pacemaker neurons leads to an amplitude decrease in alpha (Hughes 
& Crunelli, 2007; Hughes et al., 2011; Hughes et al., 2004). This shows that amplitude can 
decrease, even if there is no change in the total synchrony (Palva & Palva, 2007) and stresses 
that although EEG oscillations are most likely an index of neuronal activity, the relationship
between neuronal activity and synchrony/ oscillations is complex and does depend on various other factors that are potentially not reflected in EEG activity.

As pointed out by several authors (e.g. Hanslmayr et al., 2011; Mathewson et al., 2011; VanRullen, Busch, Drewes, & Dubois, 2011), the nature of oscillations argues for not only changes in the amplitude but also in the phase being important for cortical processing and an index of changes in cortical excitability (Bishop, 1933; Neuling, Rach, Wagner, Wolters, & Herrmann, 2012). Indeed it has been shown on a neural level that the phase of an oscillation is related to the spike timing. Intracranial recordings in non-human animals and humans show that the probability for a neuron to fire depends on the phase of the oscillatory rhythm (Haegens, Nácher, et al., 2011; Jacobs, Kahana, Ekstrom, & Fried, 2007; Lee et al., 2005; Lisman, 2005). Phase dynamics might thereby be essential for dynamic neuronal communication and provide a mechanism to structure spiking activity, and enable precise temporal coordination between distant assemblies (Fries, 2005; Jensen & Mazaheri, 2010; Palva & Palva, 2007, 2011). However, it should be noted that the analysis of oscillatory phase in non-invasive EEG data is not unproblematic, as phase estimates have been shown to critically depend on analysis parameters, which might render the description of peaks and troughs quite arbitrarily (Britz et al., 2014).

Neuronal processing is thus likely to lead to and be shaped by the various oscillatory characteristics and their interactions. Neuronal networks underlying cognitive functions such as attention, working memory, and perception are thought to differ in their size and distribution (Dehaene et al., 1998; Friston, 1994; van den Heuvel & Sporns, 2013). These differences in network sizes may potentially lead to the association of different frequencies with these functions (e.g. von Stein & Sarnthein, 2000). As higher cognitive functions rely on interactions between these networks, the relationships between different frequency band oscillations call for further investigation. These relationships could be analysed by focusing
on the phase coupling between cortical areas oscillating at different frequencies (Sauseng & Klimesch, 2008) or by investigating the amplitude-phase relationships that are also assumed to carry important information about the functional connectivity between the areas. The phase of slower oscillations has been shown to modulate the amplitude of faster frequencies (Canolty et al., 2006). In addition, higher amplitudes could increase the phase reliability within a single frequency, and hence support the precise timing required for neuronal communication (Klimesch, Sauseng, & Hanslmayr, 2007).

In summary, EEG oscillations offer the opportunity to investigate general cortical processing mechanisms in a variety of tasks (Cohen, 2014). Research into oscillations on a neuronal level has established their potential role in the organisation of communication patterns between spatially distant neuronal assemblies (Buzsáki & Draguhn, 2004; Fries, 2005; Gray & Singer, 1989; Haegens, Nácher, et al., 2011; Lee et al., 2005; Singer, 1999). EEG oscillations have traditionally been divided into different frequency bands that are associated with different states and functions. However, these subdivisions may be too artificial or arbitrary, and different frequencies may be important either for processing at different spatial scales (e.g. higher frequencies for local processing, lower frequencies for communication between spatial distinct areas), or for carrying different input (such as lower frequency oscillations being related to the retention of shape information) (Buschman & Miller, 2010; Fries, 2005; Johnson, Sutterer, Acheson, Lewis-Peacock, & Postle, 2011). In the following sections, each of the traditional EEG frequency bands and their assumed functional relevance will be introduced. Although each of the traditional frequency bands will be discussed separately, it is important to keep in mind that in the active human brain they are to some degree present most of the time, and concurrently. Depending on general arousal states and/or task requirements, their contribution to the general EEG signal varies, but the brain does not show activity in a single frequency band at any one time.
1.6.1 EEG Oscillatory Frequency Bands

**Delta.** Oscillations in the 0 – 4 Hz frequency band are termed delta oscillations. Recent evidence suggests that a subdivision into narrower sub-bands might be useful to account for different functional processes associated with these oscillations (Lopes Da Silva, 2011b). Delta oscillations seem to be of cortical origin and are especially prominent during slow wave sleep (Amzica & Lopes Da Silva, 2011). Slow wave sleep is characterised by oscillations with a centre frequency of 0.8 Hz and it is functionally associated with hippocampus-dependent declarative memory consolidation (Marshall & Born, 2007; Marshall, Helgadottir, Molle, & Born, 2006; Stickgold, 2005). These oscillations are assumed to support or enable the distribution of memory traces throughout the brain during these sleep states (Diekelmann & Born, 2010). Marshall and colleagues (2006) showed increased memory performance when they artificially increased delta activity during sleep with transcranial direct current stimulation (tDCS). This supports the suggested causal role of delta oscillations for memory consolidation.

Delta oscillations seem to play a role in wakeful behaviour as well. They are associated with large-scale cortical integration and modulations of excitability, which might affect behaviour in a variety of tasks and situations (Bruns & Eckhorn, 2004; Monto et al., 2008). This is in close agreement with the previously presented idea that communication in larger networks is facilitated by low-frequency oscillations. Furthermore, the phase of infraslow oscillations (0.01 Hz- 0.1 Hz) has been shown influence not only behavioural performance (e.g. in detection tasks) but also the amplitude of faster oscillations at 1- 40 Hz (Monto et al., 2008).

**Theta.** Theta oscillations are defined as oscillations in the 4 to 7 Hz frequency band and can be found in the human cortex and hippocampus. The intracranially recorded hippocampal theta is usually slower (around 4 Hz) than the theta activity recorded from the
sculpt (around 7 Hz). There is an ongoing debate about whether or not the intracranial and scalp-recorded theta oscillations are produced by the same or different generators (e.g. Hughes et al., 2004; Kahana, Seelig, & Madsen, 2001). Similar to delta oscillations, theta is prominent during sleep. Theta oscillations are especially present during rapid eye movement (REM) sleep phases that are associated with hippocampus-independent, implicit or non-declarative memory, and usually follow slow wave sleep. Research has shown that REM sleep and thereby theta oscillations are important for local synaptic consolidation of memories (Laureys, Peigneux, Perrin, & Maquet, 2002; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002).

The cognitive functions associated with theta during wake states are manifold and increased theta power is associated with higher cognitive performance in general (for a review see Klimesch, 1999). Theta oscillations are more specifically associated with spatial navigation and orientation (Caplan et al., 2003; Kahana, Sekuler, Caplan, Kirschen, & Madsen, 1999) and memory. They have been reported to increase during the successful encoding of new information and with greater memory load (e.g. Jensen & Tesche, 2002; Klimesch, 1999; Mecklinger, Kramer, & Strayer, 1992; Sederberg, Kahana, Howard, Donner, & Madsen, 2003) and are therefore considered as a neuronal basis for memory processing. Theta oscillations seem to reflect dynamic communication between the hippocampus and neocortex, which might further argue for a common generator of hippocampal and cortical theta (Bastiaansen & Hagoort, 2003; Lopes Da Silva, 2011b). Guderian and Düzel (2005) showed increased theta activity during a face recollection task within a network that included prefrontal, medio-temporal and occipital areas. Correct responses in the recollection task might result from successful binding of these areas. This would again support the hypothesis that slow oscillations are important for information transfer and processing in large brain networks.
**Alpha.** The alpha rhythm is the most prominent feature of the EEG of relaxed-but-awake humans and oscillates at about 8-12 Hz (Berger, 1929). As this thesis focuses on the role of alpha oscillations in visual processing, alpha band oscillations will be discussed in more depth than the other frequency bands. Alpha band activity has been related to cortical excitability ever since its first description in the early 20th century (Berger, 1929; Bishop, 1933; Lindsey, 1952). Berger discovered that the amplitude of the occipital alpha rhythm decreased substantially when the participant opened his eyes. Further research expanded this notion and associated decreases in alpha power with cortical activation and interaction with the environment during task processing and sensory stimulation (e.g. Berger, 1929; Klimesch, 1999; Klimesch, Doppelmayr, Pachinger, & Russegger, 1997; Pfurtscheller, 1992; Pfurtscheller & Lopes Da Silva, 1999; Sauseng, Klimesch, Doppelmayr, et al., 2005). Increases in alpha power on the other hand are often associated with the inhibition of sensory inputs or cortical processing (e.g. Foxe & Snyder, 2011; Jensen & Mazaheri, 2010).

The alpha rhythm is, however, not a unitary phenomenon. There are multiple cortical sources with different spatial distributions (Başar, 2012; Lopes Da Silva, 2011b). At least three independent sources of activity in the alpha frequency band have been discovered in the human cortex. This review will focus on the occipito-parietal alpha rhythm which is associated with visual processing. The other two alpha rhythms are: central alpha, also known as mu which is related to the somatomotor system; and temporal alpha, known as tau. Tau is difficult to detect in healthy humans with the EEG and is most prominent over bone defects (Niedermeyer, 1990). The neuronal or behavioural relevance of tau still remains unknown.

An inhibitory role for high alpha power is supported by its neurophysiological source. Intracranial recording in non-human animals show that oscillations in the alpha frequency emerge when the output of the main pyramidal neurons to other cortical areas is suppressed (Lopes Da Silva, 2011b; Silva, Amitai, & Connors, 1991). There is an ongoing debate on the
role of the thalamus in creating the scalp-recorded EEG alpha activity. Originally it was assumed that an increase in alpha power reflected a “closed” thalamic gate as thalamic neurons were shown to fire at alpha frequencies at times. The information transmission during these thalamic alpha bursts seemed to be imprecise, which was taken as evidence of a disruption in the relay of visual input from the thalamus to early cortical areas (e.g. Lopes da Silva, van Lierop, Schrijer, & Storm van Leeuwen, 1973). However, more recent work shows that although the thalamus seems to be involved in the generation of alpha oscillations, increase in alpha power do not necessarily index unreliable information processing (Hughes & Crunelli, 2007; Hughes et al., 2011; Hughes et al., 2004), which questions not only current models of alpha power generation but also the inhibitory role of these oscillations in general. However, the BOLD (blood oxygenation level dependent) signal acquired with functional magnetic resonance imaging (fMRI) correlates negatively with alpha power, which means that an increase in alpha power coincides with a decrease in hemodynamic activity and supports the assumed inhibitory function (Goldman, Stern, Engel, & Cohen; Goncalves et al., 2006; Laufs, 2003; Laufs et al., 2003; Moosmann, 2003).

Therefore states of high alpha power will be understood as an index of low cortical excitability throughout this thesis, which may be related to the inhibition of sensory input. Similarly, low alpha power will be taken as an index of high cortical excitability. The assumption that alpha oscillations are an important index of inhibition does not mean that they index cortical inactivity or ‘idling’ as proposed originally in relation to the closed thalamic gate (Pfurtscheller, 1992, 2001). More recently it has been suggested that the inhibition shown by high alpha power might play an active role in cortical processing and act as a “gating” or control mechanism that supports processing and the flow of information (Jensen, Bonnefond, & VanRullen, 2012; Jensen & Mazaheri, 2010; Johnson et al., 2011; Lopes Da Silva, 2011b; Palva & Palva, 2007, 2011). Increases in alpha power might for
example support the flow of information by inhibition of task-irrelevant regions (Jensen & Mazaheri, 2010). Palva and Palva (2011) suggest that the functions of alpha oscillations might even change along the visual hierarchy. Whereas decreases in amplitude have been related to better performance in early visual processing areas, in higher areas increased alpha amplitude has been shown to be related to superior neuronal processing (Mo, Schroeder, & Ding, 2011; von Stein et al., 2000). Decreases in alpha power have also been shown to co-occur with increases in inter-area alpha-band phase synchrony, which might index increased information processing within those areas and suggest a rather active role of alpha oscillations in neuronal communication (Doesburg, Green, McDonald, & Ward, 2009; Palva & Palva, 2011).

As will be discussed in more detail in sections 1.7 and 1.8, alpha oscillations have been functionally associated with signal detection and attention. Several EEG and magnetoencephalogram (MEG, which measures the magnetic activity produced by cortical activity and therefore relies on similar physiological properties as EEG (Lopes Da Silva, 2013)) studies show that stimuli are less likely to be detected if the stimulus is presented during high alpha power (i.e. decreased cortical excitability) (Busch et al., 2009; Ergenoglu et al., 2004; Mathewson et al., 2009; van Dijk, Schoffelen, Oostenveld, & Jensen, 2008). Alpha power seems to also play a role in the spatially selective orienting of attention and spatial cues have been consistently shown to modulate alpha power over the posterior cortex (for a review see Foxe & Snyder, 2011). In a lateralised stimulus display, alpha power is typically reduced over the side of the head contralateral to the attended side of space. It has been suggested that the decrease in alpha power enables focal attention by increasing local excitability, and thereby optimises processing at the attended side (represented in the contralateral cortical hemisphere) (Thut, Nietzel, Brandt, & Pascual-Leone, 2006).
Increases in alpha power have also been observed during delay periods in memory tasks, when stimuli have to be either retained in memory or manipulated (Jensen, Gelfand, Kounious, & Lisman, 2002; Johnson et al., 2011; Klimesch, 1999; Sauseng, Klimesch, Doppelmayr, et al., 2005). The increase in alpha power has often been interpreted as the inhibition of task-irrelevant areas to support the retention of the stimuli as it is presumably easier to retain information without interference from other stimuli (Jensen & Mazaheri, 2010). However, due to limited knowledge about which areas are relevant for which processes, high interconnectivity between areas, and the limited spatial resolution of EEG, this assumption has been questioned. More recent studies argue that, in addition to an inhibitory role, increased alpha power may also be actively involved in memory processing, especially in the retention of shape or orientation information (Anderson, Serences, Vogel, & Awh, 2014; Johnson et al., 2011; Myers, Stokes, Walther, & Nobre, 2014; Palva & Palva, 2007). The memory system is likely distributed over many cortical areas and increased alpha activity during retention could also be associated with increased communication between these regions.

In summary, there is a strong history of research over the last century and in particular over the past 15 years or so that suggests that alpha oscillations play an important role in cognitive processing. Alpha oscillations might be generally involved in the gating of information between neuronal assemblies, which could explain their relationship to performance in a variety of cognitive tasks (Jensen & Mazaheri, 2010; Lopes Da Silva, 2013; Palva & Palva, 2007, 2011). They seem to index cortical excitability and influence neuronal processing and the resulting behavioural performance in stimulus detection, selective attention, and working memory. Generally, lower alpha power is supposed to be beneficial for performance in detection tasks and higher alpha power might be beneficial in tasks that rely on the retention or manipulation of sensory information.
**Beta.** The beta rhythm is defined as oscillations between 14 and 30 Hz. Beta oscillations are associated with the output of deep layer pyramidal neurons and are found in most cortical areas (Lopes Da Silva, 2011b). They are generally associated with cortical activation and seem to be especially important for the programming and execution of voluntary motor movements (Feurra et al., 2011; Neuper & Pfurtscheller, 2001). More specifically they are associated with the attention needed for fine and demanding movements and not necessarily the physical movement as such (Lopes Da Silva, 2011b; Murthy & Fetz, 1996). The association between beta oscillations and attention is further stressed by current research showing increased beta band activity in tasks that do not involve the planning of voluntary movement. These studies show that beta band activity increases during attentional tasks and suggest that this increase may index the strengthened communication within and between task-relevant brain areas (Bekisz & Wróbel, 2003; Gross et al., 2004; Wróbel, Ghazaryan, Bekisz, Bogdan, & Kamiński, 2007). Aside from movement control, coherence in the beta frequency band between prefrontal and posterior parietal cortex has been found to increase during tasks that require top-down attention (e.g. when a target has to be found among distractors) (Buschman & Miller, 2007). Buschman and Miller (2010) conclude in a further study that top-down attention, and especially the shifting of the focus of attention, are associated with the beta rhythm.

In combining evidence for the role of beta oscillations in both motor and cognitive processes, Engel and Fries (2010) hypothesise that beta oscillations could reflect the processes required to maintain the current state. In this view beta oscillations are enhanced if the current status, be it sensorimotor or cognitive, has to be maintained and decreased if a change occurs or is expected. Among other sources, support for their hypothesis stems from research with Parkinson’s disease patients. One of the four cardinal motor symptoms of Parkinson’s disease is bradykinesia or the slowness of movement. Bradykinesia has been
associated with increased levels of beta band oscillations that are prominent in Parkinson’s patients (Bronte-Stewart et al., 2009; Cassidy et al., 2002; Kühn et al., 2004). Deep brain stimulation can be used to treat some symptoms of Parkinson’s disease. Chronic high-frequency stimulation at pulse rates around 130 Hz are applied to the basal ganglia and lead to decreases in beta band oscillations over motor areas when either recorded with EEG on the scalp or intracranially at the stimulation site. This decrease in beta band activity correlates with an improvement of movement capabilities (Kühn et al., 2008; Wingeier et al., 2006). Engel and Fries (2010) interpret the Parkinson’s disease’s symptom of bradykinesia as extreme problems with the modification of the current state that manifests as pathologically increased beta power.

**Gamma.** The gamma rhythm, usually defined as oscillations between 30 and 80 Hz (but sometimes up to 100 Hz or higher), has been the focus of many neuroscientific investigations over the last 25 years. The interest in gamma activity was inspired by the hypothesis that it may be the mechanism by which various features that are processed in spatially distinct cortical areas get bound together to form coherent object representations, known as the ‘binding-by-synchrony’ hypothesis (Eckhorn et al., 1988; Gray, König, Engel, & Singer; Gray & Singer, 1989). Further research has associated activity in the gamma band with many cognitive functions, and such research has focused particularly on its role in perception and attention. Gamma oscillations are shown to be modulated by spatial, feature and temporal selective attention (Bichot, Rossi, & Desimone, 2005; Fries, Reynolds, Rorie, & Desimone, 2001; Fries, Womelsdorf, Oostenveld, & Desimone, 2008; Lima, Singer, & Neuenschwander, 2011; Müller, Gruber, & Keil, 2000; Taylor, Mandon, Freiwald, & Kreiter, 2005) and are associated with the memory representations in different modalities (Gruber, Tsivilis, Montaldi, & Müller; Kaiser, Heidegger, Wibral, Altmann, & Lutzenberger, 2008;
Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998; Wyart & Tallon-Baudry, 2009); for a review see (Jensen, Kaiser, & Lachaux, 2007).

However, the functional role of gamma oscillations for cognitive function has been critiqued on various bases. Firstly, recording gamma band activity on the human scalp via EEG is very difficult due to technical limitations and the nature of the signal. Microsaccades and muscle movements give rise to signals that look very similar to gamma band activity and it is therefore difficult to distinguish cortically produced gamma from noise in scalp recordings (Nunez & Srinivasan, 2010; Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008). The second important critique regarding the focus on gamma oscillations has been raised by Nunez and Srinivasan (2010), who argue that most of the research focusing on gamma oscillations is relying on intracranial recordings in non-human animals. However, these recordings of single neurons or neuronal populations do not take into account the complexity of the large-scale brain processing (Ballard et al., 1983; van den Heuvel & Sporns, 2013) as complex cognitive processes cannot be inferred from activity in a single neuronal population. Finally, physical variability such as brain size and the length of axonal delays influences the oscillatory signatures of processing. Thereby higher frequency oscillations may play a different and more important role in smaller species than they do in humans (Nunez & Srinivasan, 2010).

Furthermore, the question of whether gamma oscillations are actually functionally involved in the cognitive tasks they are associated with, or whether they just index a state of cortical activation, has been raised (Merker, 2013). High gamma power is associated with heightened arousal (Herculano-Houzel, Munk, Neuenschwander, & Singer, 1999) and a considerable volume of research shows that an increase in gamma band power co-occurs with a decrease in alpha power, which is a further index of heightened arousal (e.g. Fries et al., 2001; Jensen et al., 2012; Jensen et al., 2007; Jensen & Mazaheri, 2010; Lima et al., 2011).
On a neurophysiological level it has been shown that gamma oscillations enhance the synchronisation of neuronal spikes (Fries, Nikolić, & Singer, 2007; Roelfsema, Engel, König, & Singer, 1997) and thereby facilitate the spread of activity across a network (Bruno & Sakmann, 2006). A dense clustering of neuronal spikes is likely to enhance the effect at targeted postsynaptic neurons. This may enable fast routing of information, optimise the output efficiency, and/or increase the temporal precision needed for dynamical information processing (Fries et al., 2007; Fries et al., 2001). Gamma therefore is assumed to be especially important for the coordination of neural activity on a local level but may also have a role in optimising synchrony and thereby may facilitate communication between spatially separate cortical areas (Roelfsema et al., 1997; Rose, Sommer, & Büchel, 2006). However, whether the role of gamma oscillations stays on this level of infrastructural support (Merker, 2013) or is actually involved in the implementation of cognitive functions is still a matter of debate.

Although the precise roles played by oscillations in cognitive processing is not clear yet, functional relationships between oscillatory modulation and cortical processing have been reliably established. The brain is a very complex and dynamic system and some of its complexity might be understood by focusing on oscillatory dynamics (Jensen et al., 2012; Jensen & Mazaheri, 2010; Palva & Palva, 2007; Varela et al., 2001; von Stein et al., 2000; von Stein & Sarnthein, 2000). Oscillations seem to be especially important in the modulation of cortical activity, and for facilitating communication between spatially distant neuronal populations (Lopes Da Silva, 2013; Salinas & Sejnowski, 2001). The precise signature of an oscillatory correlate depends on various properties like the size of the network involved, its cortical source and maybe also the input that is processed (Hanslmayr et al., 2011; Johnson et al., 2011). Alpha activity, which has been consistently shown to be related to behavioural
performance in signal detection and visuospatial attention tasks, is the focus of the thesis. The ‘special’ role for oscillations around 10 Hz in perceptual tasks is possibly due to the nature of the underlying processing mechanisms and the neural circuits involved (e.g. the size of the cortical networks and the length of their connections) (e.g. Gratton, 2014; Jensen & Mazaheri, 2010; Palva, Kulashekhar, Hamalainen, & Palva, 2011; Palva & Palva, 2007). Oscillations at different frequencies might reflect conceptually similar processing mechanisms at different scales or in different systems.

1.7 **Alpha-Band Oscillations and Spontaneous Fluctuations in Visual Stimulus Detection**

Our ability to perceive sensory stimuli varies largely from moment to moment and it is assumed that understanding this variability will lead to a better understanding of the general processing mechanisms in the brain (Ashby & Lee, 1993; Prado et al., 2011). In psychophysical experiments, performance varies between trials, which usually means within a couple of seconds, but performance also varies on longer timescales of several minutes or even throughout the day (Fechner, 1860; Kam et al., 2011; Weissman et al., 2006). EEG oscillations are a potential biological marker of these fluctuations at various timescales and seem to be especially useful in explaining variability in detection performance. For example, Monto and colleagues (2008) found a strong correlation between the phase of infraslow oscillations (0.01 – 0.1 Hz ) and somatosensory detection performance, whereas various other studies report a significant relationship between alpha oscillations (8- 12 Hz) and trial-to-trial fluctuations in detection (e.g. Busch et al., 2009; Ergenoglu et al., 2004; Mathewson et al., 2009; van Dijk et al., 2008). Alpha oscillations presumably index different levels of cortical excitability and therefore are an attractive candidate to explain variability in stimulus detection.
It is assumed that a weak stimulus can be detected more easily if cortical excitability is high (Lange et al., 2014; Lange, Oostenveld, & Fries, 2013; Romei, Gross, & Thut, 2010). Decreases in alpha power are usually seen during task-related processing and sensory stimulation (e.g. Berger, 1929; Klimesch, 1999; Klimesch et al., 1997; Pfurtscheller, 1992; Pfurtscheller & Lopes Da Silva, 1999; Sauseng, Klimesch, Doppelmayr, et al., 2005) and low levels of alpha power are thought to reflect high levels of cortical activity. Indeed, research has shown that stimulus detection and discrimination are enhanced if there is relatively low alpha power in the interval directly preceding the presentation of the target (Busch et al., 2009; Dombrowe & Hilgetag, 2014; Ergenoglu et al., 2004; Hanslmayr et al., 2005; Hanslmayr, Klimesch, et al., 2007; Mathewson et al., 2014; Mathewson et al., 2009; van Dijk et al., 2008).

The association of alpha power with cortical excitability and thus detection of sensory stimuli has been further strengthened by EEG-TMS studies. Transcranial magnetic stimulation (TMS) sends pulsed electromagnetic currents through a coil placed over the scalp. If positioned over the occipital cortex, these pulses can elicit illusory percepts, called phosphenes, by inducing activity in visual neurons (e.g. Cowey & Walsh, 2000; Merton & Morton, 1980). As with visual stimuli, the same TMS input strength is not effective in eliciting a phosphene on every trial. Romei and colleagues (2008) showed that the effectiveness of TMS pulses is related to the amplitude of ongoing alpha oscillations: TMS pulses delivered during low alpha power are more effective in eliciting phosphenes than those sent during high alpha power. This strengthens the hypothesis that cortical excitability is heightened during decreased alpha power as induced activity is more likely to elicit a percept. High excitability as indexed by low alpha power might thus make us more susceptible to stimulation (Lange et al., 2014).
A further study by Romei and colleagues (2010) demonstrated the causal role of alpha power for the perception of brief visual stimuli even more directly. They modulated oscillatory power in specific frequencies by applying rhythmic-TMS (rTMS) to occipital or parietal regions. Previous research has shown that rTMS modulates and entrains natural oscillations (Thut et al., 2011). Applying rTMS at 10 Hz is therefore assumed to increase alpha power around the site of stimulation. Romei and colleagues found that the detection of briefly presented stimuli was impaired contralateral to the side of rTMS stimulation, but only if the stimulation frequency was in the alpha band (10 Hz). rTMS applied at 5 or 20 Hz did not affect perception. By experimentally and selectively increasing alpha power they could thereby show that an increase in alpha power is causally related to a decrease in detection performance.

Although it seems to be a very consistent finding that lower alpha power leads to increased performance, there are also some contradictory results and alternative viewpoints have been expressed around the relationship between cortical excitability and perceptual performance. Some studies suggest that intermediate levels of alpha power are most beneficial for the detection of near-threshold stimuli and thereby question the monotonic relationship between alpha power and detection found in other studies (e.g. Lange, Halacz, van Dijk, Kahlbrock, & Schnitzler, 2012; Linkenkaer-Hansen, Nikulin, Palva, Ilmoniemi, & Palva, 2004; Rajagovindan & Ding, 2011; Zhang & Ding, 2010). Interestingly, three of those studies, with the exception of the study by Rajagovian and Ding (2011), who only reported an increase in early ERPs and no behavioural effect of an alpha power increase, used somatosensory stimuli and investigated alpha rhythms anterior to the occipital cortex. Scalp recorded alpha rhythms have multiple generators (Başar, 2012) and a different function for the more occipital versus a more medial alpha rhythm could explain these conflicting results.
Furthermore, a recent study by Lange and colleagues (2013) suggests that higher cortical excitability (as indexed by low alpha power) does not necessarily mean better or more veridical perceptual performance. Their task paired visual stimuli with task-irrelevant tactile stimuli, which sometimes lead to the illusory perception of a second visual stimulus. Participants were more likely to report to have seen two stimuli (instead of one) when alpha power was low. By showing this, the researchers argue that higher excitability leads to higher susceptibility to stimulation which does not necessarily mean better performance. The finding by Chaumon and Busch (2014) that alpha power affects the response gain points in a similar direction as they argue that alpha power does not influence the ‘input’ to the sensory areas but rather the ‘decisional stage’ and inter-areal communication. Our study in Chapter 2 was also motivated by trying to find a more accurate behavioural correlate of changes in alpha power. The earlier reports on a monotonic relationship between a decrease in alpha power and an increase in performance across multiple tasks seemed to be a bit too simplistic given the complex relationships between oscillations, cortical processing and behavioural performance.

In addition to alpha power the phase of alpha at stimulus presentation and the coherence between different cortical areas in the alpha band have been related to perceptual performance. Phase analysis promises a more realistic view of the role of alpha in cognitive processing as it takes into account its oscillatory nature (e.g. Mathewson et al., 2011; VanRullen et al., 2011). In a backward-masking task, Mathewson and colleagues (2009) showed that the phase of the alpha rhythm predicts detection during periods of high alpha power. In this task, the detection of a target is made difficult by presenting a second stimulus shortly after the target. In addition to replicating earlier findings that detection is enhanced in trials that are preceded by low alpha power, they showed that stimuli were more often detected if they were presented at the peak of the alpha oscillation. Interestingly, this
relationship was only found during periods of high alpha power. Based on these results they established their “pulsed inhibition theory” in which they claim that detection is facilitated during two different states. During low alpha power, which is assumed to reflect high cortical excitability, detectability is high in general. During high alpha power states, detectability is only high at the precise time point during the peak of the oscillations (Mathewson et al., 2014; Mathewson et al., 2009; Mathewson et al., 2011). This is in agreement with the claim by Klimesch and colleagues (2007) that high alpha power increases the reliability of phase measures and thereby offers precise timing information for cortical processing.

This ‘pulsed inhibition’ theory might be able to reunite the conflicting theories of alpha oscillation as either inhibiting cortical processing or rather actively enabling it (Mathewson et al., 2011). Alpha oscillations could index both inhibition and facilitation depending on the relationship between power and phase. An interesting and consistent idea by Jensen and colleagues (2012) is that the increase in excitability during certain phase within the alpha oscillations could allow for unattended – but salient and behaviourally relevant information - to reach awareness. The peak of the oscillation during high alpha power could be a short release from the inhibition to allow these unattended but important stimuli to reach awareness. Importantly, as pointed out by them and several others (Osipova, Hermes, & Jensen, 2008; Palva & Palva, 2007) the processing of sensory information likely depends on a coupling between alpha and gamma oscillations. It is assumed that the local information processing is supported by an increase in gamma power that has been shown both during decreased alpha power and at certain phases of the alpha oscillation (e.g. Fries et al., 2001; Lima et al., 2011). In addition to strengthening the pulsed inhibition theory this also stresses the importance of the relationship between different frequencies.

In agreement with Mathewson and colleagues, Busch, Dubois and VanRullen (2009) also found that target detection is influenced by both the phase and power of oscillations.
However, they analysed their data with a higher frequency precision and claim in contrast to Mathewson and colleagues that the phase effects are independent of the power effects. The power effects were most strongly pronounced in the alpha range of about 8.2 Hz, which is in close agreement with the result reported by Mathewson and colleagues, but the phase effects were pronounced most strongly around 7 Hz which is within the theta range and slightly below the alpha range of 8-12 Hz. This could either be interpreted as a functional difference or might raise the question of how useful it is to break EEG into distinct bands of oscillatory activity. Furthermore their power and phase effects were most strongly pronounced at anterior locations, whereas Mathewson and colleagues focused their investigation on a central-parietal location.

Some of these conflicting results may be explained by the differences in the tasks utilised. Busch and colleagues presented the stimulus at an individually determined threshold, whereas Mathewson and colleagues used a mask to hinder detection on every trial. Successful masking might depend on a mismatch between the current information in early areas when the mask is presented and the template (e.g. the target) that constitutes the feedback from higher areas (Di Lollo, Enns, & Rensink, 2000). This dependence on feedback to early visual processing might explain why Mathewson and colleagues found their effects posterior to the location found by Bush and colleagues. Busch and colleagues also presented the targets in the periphery of the visual field (7° visual angle) and the participants were asked to delay their response until a prompt was given (1500 ms after target presentation), whereas in the Mathewson study the target was presented centrally and the participants were asked to respond immediately. There are many differences between processing of centrally and peripherally presented stimuli (e.g. cortical magnification) and it is not clear yet whether alpha power affects both processes in a similar fashion. Furthermore a study by Grent-‘t-Jong and colleagues (2011) showed that alpha power is especially related to the perceptual
outcome, if an immediate – and not a delayed - response is requested. Although Bush and colleagues showed a relationship between a delayed response and pre-stimulus alpha power, it is possible that this was tapping into different processes than those investigated by Mathewson and colleagues. The role of these and other task requirements in determining the behavioural effect of alpha power fluctuations will be investigated in more detail in Chapters 2, 3 and 4.

Despite these conflicting results, especially concerning the relationship between power and phase effects, there is further evidence from different techniques and paradigms that stresses the importance of oscillatory phase in predicting detection performance. A recent TMS study shows that phosphene detection was modulated not only by alpha power but also by alpha phase in the pre-stimulation interval and thereby establishes a causal link between alpha phase and detection performance (Dugué et al., 2011). Earlier studies also show that stimuli that are presented at the peak of the alpha oscillation are perceived more precisely and faster (Callaway & Yeager, 1960; Dustman & Beck, 1965; Nunn & Osselton, 1974; Valera, Toro, John, & Schwartz, 1981). Furthermore, there is physiological evidence from animal models that support the notion that the phase of alpha oscillations influences excitability. Haegens and colleagues (2011) showed that the firing rate of neurons in the sensorimotor network in monkeys was modulated by both alpha power and phase. The firing rate decreased as the alpha power increased and was highest at the trough of an alpha cycle. These findings are crucial in understanding the importance of oscillations for cortical processing on the neuronal level as they demonstrate a tight link between the phase of the alpha oscillations and neuronal firing.

Although it has not been established yet how those intracranial recorded oscillations are related to those measured on the surface of the scalp (e.g. firing was highest at the trough in intracranial recordings, whereas superior behavioural performance was related to the peak
of the alpha cycle), it shows that oscillatory processes are able to directly modulate neuronal processing. However, a recent finding byBritz and colleagues (2014) highlights some methodological issues which EEG sensor-level derived phase measures: Although they were able to show phase differences between detected and undetected stimuli, whether the peak or the trough was related to increased performance depended on the chosen reference scheme. This questions the assumption that phase measures are a more direct index of neuronal oscillatory activity than for example amplitude measures (e.g. Palva & Palva, 2007).

It has also been shown that the phase-coherence, which is the similarity between phases across distant brain areas, indexes detection performance (for recent reviews see Hanslmayr et al., 2011; Siegel et al., 2012). Phase-coherence or coupling between brain areas is interpreted as a measure of inter-areal communication (e.g. Fries, 2005; Siegel et al., 2012). This communication may be more effective if spatially distant areas align their phases systematically and thereby increase the impact that they can have on each other. In their recent review, Hanslmayr and colleagues (2011) suggest that decreased phase coupling in the alpha frequency band indexes externally orientated states and increased phase coupling indexes internal processing states (and thereby increased information transfer between certain neuronal populations). This is in line with two further studies that also found increased detection performance during periods of decreased phase coupling between posterior and anterior regions in the alpha band (Hanslmayr, Aslan, et al., 2007; Kranczioch, Debener, Maye, & Engel, 2007). In addition, Kranczioch et al. (2007) showed that increased coherence within the beta band enhanced detection.

Taken together this research shows that there is a complex interplay between oscillatory parameters and variability in detection performance. Oscillations in the alpha band seem to index different cortical excitability states, which can predict whether a stimulus is going to be detected or not (Busch et al., 2009; Dombrowe & Hilgetag, 2014; Ergenoglu et
al., 2004; Hanslmayr et al., 2005; Hanslmayr, Klimesch, et al., 2007; Mathewson et al., 2014; Mathewson et al., 2009; van Dijk et al., 2008). Detection seems to be enhanced during externally oriented states, which in turn are indexed by low alpha power, but also by the peak of the oscillations and/or reduced phase coupling between anterior and posterior brain regions (Hanslmayr et al., 2011). Although low pre-stimulus alpha power has been related to increases in stimulus detectability a variety of questions in regard to the precise behavioural effect remain. Several findings hint at the possibility that decreases in alpha power do not affect the early sensory processing of the stimuli but rather the decision-making processes that presumably happens at later processing stages (Chaumon & Busch, 2014; Grent-’t-Jong et al., 2011; Lange et al., 2013). The behavioural effect of alpha power modulation will be further investigated in the studies in Chapter 2 and 4.

1.8 Alpha-Band Oscillations as a Mechanisms of the Orienting of Visuospatial Selective Attention

In addition to its role in detection performance, ongoing EEG activity in the alpha band has also been related to the orienting of attention. Whereas earlier studies have mainly focused on the behavioural effect of attention (e.g. see Carrasco 2011 for a current review), EEG oscillations can be used to investigate the mechanisms underlying the orienting of attention. It is assumed that the benefit for attended stimuli stems from a baseline shift that prioritises the attended location or stimulus even before its onset (Kastner et al., 1999; Luck et al., 1997). Several studies suggest that the cue-related modulation of alpha power could index such a baseline shift. Usually these studies show that alpha power either decreases contralateral to the cued side and/or increases ipsilaterally (e.g. Kelly, Lalor, Reilly, & Foxe, 2006; Rihs, Michel, & Thut, 2009; Sauseng, Klimesch, Stadler, et al., 2005; Thut et al., 2006; Trenner et al., 2008; Worden, Foxe, Wang, & Simpson, 2000; Wyart & Tallon-Baudry, 2009; Yamagishi, Goda, Callan, Andersen, & Kawatoa, 2005). The decrease in alpha power
contralateral to the attended side is interpreted as a top-down modulated increase in cortical excitability in preparation for the upcoming stimulus. Along the same line the ipsilateral increase is taken as an index of inhibition of the unattended side (Foxe & Snyder, 2011; Thut et al., 2006). Capotosto and colleagues (2009) showed that this lateralisation is under control from the fronto-parietal attention network. TMS pulses to those fronto-parietal areas (e.g. the frontal eye fields) at the time of the cue did not only disrupt the contralateral alpha decrease, but also slowed the behavioural response to validly cued targets. This strengthens the suggestion that the lateralisation of alpha power indexes the mechanism underlying the orienting of attention.

This role for the lateralisation in the orienting of attention is further corroborated by the following properties: firstly, the strength of the alpha modulation seems to be flexibly determined by the cue reliability such that the more reliably the cue, the stronger the alpha modulation and the better the performance (Dombrowe & Hilgetag, 2014; Gould, Rushworth, & Nobre, 2011; Haegens, Händel, & Jensen, 2011). Secondly, the modulation is specific in time and peaks just before the expected target presentation (Rohenkohl & Nobre, 2011). This strengthens the assumption that alpha lateralisation is necessary for the perceptual benefit that stems from knowing not only where but also when a target is likely going to appear. Thirdly, the lateralisation seem to present a general cortical processing mechanism as is has also been shown to the orienting to tactile stimuli (Haegens, Händel, et al., 2011), different modalities and features of interest (Foxe, Simpson, & Ahlfors, 1998; Synder & Foxe, 2010).

Although most studies (that use a lateralised stimulus display and spatial cues) show a difference in alpha power over the contralateral compared to the ipsilateral hemisphere (i.e. a lateralisation), there are at least two important questions remaining. The first of these is whether the lateralisation is driven by a contralateral decrease or an ipsilateral increase or by their combination. This might even vary in response to certain task specifics like the length of
the cue-target-interval, the cue reliability or the presence of distractors. Secondly, it is not clear yet how and to what extent the lateralisation is related to the behavioural benefit seen for attended targets. Again there are contradictory results as to whether the contralateral decrease or ipsilateral increase influences behaviour and several task specifics are discussed as potential modulators of the effects. Additionally the lateralisation is affected by individual differences.

An important factor in determining the direction of the alpha modulation (i.e. contralateral decrease or ipsilateral increase) following an attentional cue seems to be length of the cue-target interval. Studies have recently found that if attention has to be sustained at a certain location, the initial decrease of alpha power contralateral to the attended side is followed by an increase over the ipsilateral side at around 700 ms (J. J. Green & McDonald, 2010; Rihs et al., 2009). This temporally specific interplay between alpha power decreases and increases might suggest that there are at least two different processes that underlie the modulation and potentially the orienting of attention. Rihs and colleagues argue that the orienting starts with facilitation contralateral to the attended side and is then followed by inhibition ipsilateral to the attended side later on. The ipsilateral increase of alpha power might help to prevent the reflexive reorienting of attention known as the inhibition of return effect (Rihs et al., 2009).

Capilla and colleagues (2014) were indeed able to differentiate between two cortical sources for the ipsi- and contralateral modulation in the dorsal and ventral streams that had different time courses and behavioural correlates. They showed that the ipsilateral increase could be localised to the dorsal stream, likely area V6. Interestingly this increase was only transient and disappeared 300 ms after the cue offset. The contralateral decrease was sustained over the length of the cue-target interval and localized to an area in the ventral stream, likely V4, which is involved in the detection and recognition of digits that was
required in their task. Although this seems to contradict the earlier findings that show that the ipsilateral increase follows the contralateral decrease (J. J. Green & McDonald, 2010; Rihs et al., 2009), Capilla and colleagues argue that the transient increase might reflect an initial inhibitory process that is discontinued later on. They argue that as they were using a probabilistic cue and targets could sometimes appear at the ‘unattended’ side, participants could not disengage their attention completely from that side and might therefore discontinue its inhibition.

This highlights two additional factors that could determine the direction of the alpha modulation, namely the cue reliability and the presence of distractors. Several authors suggest that an ipsilateral increase is only seen if the unattended side can be ignored completely (i.e. using instructional cues, and either only showing targets at the attended locations or only asking for responses to those at the attended location) or if there are bilateral displays that include distractors at the unattended locations (Foxe & Snyder, 2011; Händel, Haarmeier, & Jensen, 2010; Kelly et al., 2006; Worden et al., 2000). They argue that only under those conditions the unattended location/side can be ignored and an inhibition of that side could optimise performance.

In addition, Rihs and colleagues (2009) reported that only the subset of their participants who had high baseline alpha power showed the cue-related alpha lateralisation. Interestingly, all participants, regardless of whether or not they showed the cue-related alpha power lateralisation, demonstrate the attentional effect behaviourally. This brings us to the second question, namely the behavioural relevance of the alpha power lateralisation. The finding that the behavioural effect is seen even without the lateralisation suggests that although it might index an important mechanism during the orienting of attention, it does not seem to be the only determinant of the behavioural benefit due to knowing where the stimulus will appear. This is in line with a study by van Ede, Köster and Maris (2012) that
found that only 29% of the attentional improvement can be explained by the alpha modulation.

Performance in the attention tasks is usually measured as accuracy and response time and behaviourally selective attention has been shown to lead to both more accurate and faster responses (Carrasco, 2011). Some studies show that the lateralisation of alpha predicts both measures of performance (Haegens, Luther, & Jensen, 2012; Kelly et al., 2006), while others show effects only in response time and not accuracy (Thut et al., 2006; Trenner et al., 2008). Furthermore under some conditions the lateralisation is not related to the behavioural benefit for validly cued targets at all (Dombrowe & Hilgetag, 2014; Gould et al., 2011; Händel et al., 2010; van Ede, Szebenyi, & Maris, 2014). Similar to the discussion about the driving force behind the lateralisation, some studies claim that both the contralateral decrease and ipsilateral increase are important for optimal performance (Haegens, Händel, et al., 2011; Händel et al., 2010), while other studies have only found a behavioural effect of the contralateral decrease (e.g. Capilla et al., 2014; Gould et al., 2011). Taken together this suggests that although the lateralisation is a very consistent finding, it seems to be rather difficult to find a clear behavioural correlate.

Whereas the bulk of the studies in the attention literature focused on effects of alpha power, there is also some research stressing the role of alpha phase for attentional orienting. Busch and VanRullen (2010) investigated the effects of oscillatory power and phase in a visuospatial attention study. Besides the well-known effect of alpha decrease at the attended side, they also found that the phase of the oscillation interacted with behaviour only at the attended side (where the strongest phase effects were around 7 Hz). They argue that although perceptual performance is generally enhanced at the attended side, it still varies depending on alpha phase. This contradicts the above mentioned “pulsed inhibition theory” by Mathewson and colleagues (2009, 2011). Applying their theory to an attentional design, a stronger
interaction between alpha phase and behaviour would be expected at the unattended side, where alpha power should be larger (VanRullen et al., 2011). However as targets could also appear at the “unattended” location and they did not report an actual increase of alpha power over the ipsilateral side (Mathewson et al., 2011), it is not clear how these results fit with the pulsed inhibition theory.

In summary, current research has begun to investigate the underlying mechanisms of the orienting of visuospatial attention in more detail. The lateralisation of alpha power in response to attentional cues has been put forwards as an index of such a mechanism. Alpha power has been shown to decrease contralaterally and/or increase ipsilaterally to the attended location (Foxe & Snyder, 2011). Although this lateralisation could in theory help to optimise performance by locally increasing excitability at the attended location, the behavioural effects of the lateralisation seem to be harder to establish than the lateralisation itself. By taking individual differences into account and controlling the response requirements, we will investigate this behavioural effect in more detail in Chapter 3. In Chapter 4 we will compare the behavioural effect of alpha power modulations between a detection and selective attention task.

1.9 Summary and Outlook

This chapter has focused on the putative role of EEG oscillations in cognitive processing and especially on the role of alpha oscillations in detection and visuospatial attention tasks. Research suggests that the processes resulting in the moment-to-moment fluctuations in detection performance and the orienting of selective attention might be indexed by both spontaneous and evoked modulations of alpha power (for recent reviews see Foxe & Snyder, 2011; Mathewson et al., 2011; VanRullen et al., 2011). Although detection and selective attention tasks are often discussed separately, similar mechanisms may underlie the variability in performance seen in both of tasks. Most of the discussed studies focus on
the perception of nominally identical stimuli (near the perceptual threshold) and variability in their perception seems to be related to the state of cortical excitability at the time of stimulus presentation (Mathewson et al., 2009; Romei et al., 2010). Stimuli presented during highly excitable states, as indexed by low alpha power, are assumed to be perceived faster and more in depth. Studies on attention, on the other hand, show that we can voluntarily shift our attention to certain stimuli and perceive them faster and/or in more detail than other stimuli (Posner et al., 1980). These attentional shifts are presumably also indexed by a lateralisation of alpha power, leading to lower alpha power on the side of the head that is contralateral to the attended side (Rihs, Michel, & Thut, 2007; Rihs et al., 2009; Thut et al., 2006).

Although the contribution of this lateralisation to the behavioural benefit of attentional orienting is not clear yet, it is thought that either the contralateral decrease facilitates performance at the attended side or that performance is optimised by an inhibition of the unattended side – indexed by an ipsilateral increase of alpha power. Therefore attentional shifts may be interpreted as mechanisms that control the variability in perceptual performance, and attention and detection may be relying on the same cortical mechanism. In detection, we may see random fluctuations in cortical excitability, whereas we might be able to control those fluctuations and increase local excitability in anticipation of attended targets. This suggestion is supported by a recent study showing that the alpha decrease indicated in detection performance stems from the cuneus region and is under control from the dorsal-parietal attention network (Corbetta & Shulman, 2002; Mathewson et al., 2014).

In a series of three studies we will investigate the behavioural consequences of alpha power fluctuations in more detail and directly compare the role of these fluctuations in detection and selective attention. In Chapter 2 we will investigate the behavioural effect of pre-stimulus alpha power oscillations in a visual detection task. It has been reported consistently that lower pre-stimulus alpha power leads to increased performance. This first
study aims to replicate and expand upon these experiments and applies a more in-depth behavioural analysis, as previous research mostly focuses on hit rate, a rather limited description of behavioural performance. Our results show that alpha power may not merely influence performance as much as it influences the evaluation of the sensory evidence. This suggests that in a state of reduced cortical excitability, as indexed by increased alpha activity, we may be more cautious about reporting a stimulus as present than during a highly excited state as indexed by decreased alpha activity. Being more cautious during reduced cortical excitability may help to prevent us from making too many false alarms. This finding challenges the notion of a simple and monotone relationship between alpha power and performance and will be further expanded upon in the following Chapters.

Chapter 3 investigates the behavioural effect of cue-related alpha modulation in a visuospatial attention task. Previous research has shown a lateralisation of alpha power after an attentional cue. Usually alpha power is decreased over the side of the head contralateral to the attended side (for a review see Foxe & Snyder, 2011). However a clear behavioural correlate of this lateralisation has not been established yet (Dombrowe & Hilgetag, 2014). To control for differences in task instructions, which could contribute to the problem of establishing a clear behavioural correlate, we modulated the speed-accuracy trade-off by using three different response-deadlines. We replicated earlier findings that only a subset of participants lateralised their alpha power in response to the cue (Rihs et al., 2007). However, both groups, those with low and high power at baseline, show similar performance, which we will argue poses a problem on the assumed function of alpha power lateralisation as an index of the orienting of attention. Additionally, on an individual level the change in alpha power predicts the behavioural change across experimental manipulations, strengthening the relationship between variability in alpha power and performance in visual tasks. It
furthermore shows that more demanding task requirements might mask a direct effect of alpha power fluctuations on behavioural performance.

In Chapter 4 the behavioural effect of alpha power modulations is compared between a discrimination and selective attention task. Even though a similar role of alpha power is suggested in both of these tasks, this has not been investigated directly yet. On a trial-by-trial basis participants were either informed of the upcoming target location or received a neutral cue, which did not hold any information as to the target location. Results show that variability in performance is related to similar modulations of alpha power under both conditions. A decrease in alpha power is related to a faster response. Importantly there is a significant speed-accuracy trade-off in this task, showing that accuracy is lower in fast compared to slow trials. This strengthens the suggestion made in Chapter 2 that the relationship between alpha power and performance in visual perception tasks is complex and a decrease in alpha power does not simply index an increase in performance. A close inspection of both task requirements and behavioural measures is important to understand the role of alpha oscillations in visual perception.
Chapter 2: Pre-stimulus alpha power influences response criterion in a detection task

2.1 Chapter Prologue

In this first experimental chapter we aimed to replicate and expand a study by Mathewson and colleagues (2009) that showed that the ability to detect a masked stimulus critically depended on both the power and phase of oscillatory activity in the alpha band prior to stimulus presentation. Although their findings were supported by a study published around the same time (Busch et al., 2009), we noticed that behavioural performance was not analysed in much detail, with both of these studies only reporting hit rate as their dependent variable. However hit rates are an incomplete measure of performance and do not allow the differentiation of, for example the sensitivity to the stimulus and the willingness to report it as present (D. M. Green & Swets, 1966; Macmillan & Creelman, 2005). We therefore found it premature to suggest that fluctuations in alpha power are related to perceptual sensitivity as they might well be related to other processes underlying the overt behavioural response.

Other researchers have similarly identified this issue and there are more recent reports that question whether alpha power fluctuations really influence the sensitivity to the visual input or other aspects of the behavioural response (e.g. Chaumon & Busch, 2014; Lange et al., 2013).

The manuscript included in this chapter is currently under review for the journal *Psychophysiology*. The only differences between the submitted version and this version is the change from American English to British English and the use of ‘alpha’ instead of its Greek letter to ensure consistency in the thesis for the submitted manuscript. A follow-up experiment in which we changed the response scheme from a simple “seen/ not seen” response to a 6-point scale which included the confidence in the seen/not seen decision will
be described in the chapter epilogue. Due to the null-result the follow-up was neither included in the manuscript nor will it be discussed in-depth.

2.2 Abstract

Recent studies have linked variability in near-threshold stimulus detection to fluctuations in the pre-stimulus EEG alpha power (~ 8-12 Hz). Typically, these studies rely on hit rate as a measure of detection performance, and show that detection is enhanced when alpha power is low compared to when it is high. However, hit rates are determined by both sensitivity to the stimulus and the placement of the response criterion. Here, we investigated the relationships between pre-stimulus alpha power and variability in these two measures. We confirm earlier reports that detection is inversely related to alpha power. However, our results show a stronger relationship between alpha power and response criterion than with sensitivity. Higher alpha power was related to a more conservative response criterion (i.e., more “no” responses). A response criterion that varies depending on alpha power might help to optimise performance in an excited state and protect against false positives in a relatively disengaged state.

2.3 Introduction

We perceive the world around us rapidly and seemingly without effort. Subjectively, we experience a very complex and relatively complete picture of the world. However, it has long been understood that this experience relies heavily on memory and construal, and that our ability to perceive environmental stimuli varies dramatically from moment to moment (Fechner, 1860). We often fail to detect stimuli and changes in the environment that we were able to perceive before, and we sometimes even think that we are seeing much more than we actually do (e.g. Azzopardi & Cowey, 1993; Rahnev et al., 2011). The reasons for the variability in perception still remain elusive, but recent work suggests that at least part of this
variability can be explained by fluctuations in the excitability of the cerebral cortex (Hanslmayr et al., 2011; Lange et al., 2014).

Oscillations in the alpha frequency band (~8-12 Hz) of the electroencephalogram (EEG) are often understood as an index of the current excitability of the cortex with lower power indexing higher excitability (Lange et al., 2013; Romei et al., 2008). Several recent studies have investigated the relationship between power in the alpha frequency band before stimulus presentation and detection performance. Typically, these studies show that detection is more likely for stimuli presented during intervals of low alpha power than for those presented during high alpha power (Busch et al., 2009; Ergenoglu et al., 2004; Mathewson et al., 2014; Mathewson et al., 2009; Roberts, Fedota, Buzzell, Parasuraman, & McDonald, 2014; van Dijk et al., 2008). This is taken to suggest that alpha power is predictive of visual perception and that low alpha power leads to increased sensitivity to visual stimuli. A recent study using optical imaging combined with EEG found that those alpha power modulations can be localised to the cuneus and precuneus regions and are modulated by fronto-parietal attention networks. This suggests a top-down modulation of sensory processing via modulation of oscillatory power in the alpha-band (Mathewson et al., 2014).

Thus far the studies on the relationship between pre-stimulus oscillatory power and visual performance have reported hit rate (i.e., the proportion of correctly detected stimuli) as the dependent measure of psychophysical performance. However, according to a signal detection theory (SDT) approach, hit rates are an incomplete description of performance (D. M. Green & Swets, 1966; Macmillan & Creelman, 2005). In a simple detection task, participants have to decide whether or not a target is presented on a given trial. SDT assumes that this decision is based on the strength of some internal signal, like sensory activity. On average sensory activity is higher if the target is presented (“signal”) compared to when it is not presented and the trial just includes “noise”. However, noise levels randomly fluctuate
CHAPTER 2: ALPHA POWER RESPONSE CRITERION

from trial to trial and sensory activity is thus necessarily variable even if the physical stimulus itself remains constant. Occasionally a target presentation will only evoke low sensory activity and at other times noise level will be high leading to comparably high activity even without a signal being present.

On a given trial the participant perceives some level of sensory activity, without knowledge of whether it stems from the noise alone or from the presentation of a stimulus, and needs to evaluate the evidence for the presence of a signal. In its simplest form, SDT assumes a Gaussian distribution of sensory noise, to which a constant value is added when the stimulus is present (see Figure 2.1b). Thus, the participant’s task is to decide whether a given level of sensory activity is likely to have arisen from noise alone or from the signal-plus-noise distribution (D. M. Green & Swets, 1966; Macmillan & Creelman, 2005; Parker & Newsome, 1998). Sensitivity ($d'$) is defined by the difference in the average sensory activity levels between the two distributions. This parameter is high if target presentations increase sensory activity substantially compared to noise presentations, which leads to less overlap of the underlying distributions and less ambiguity when evaluating the evidence. SDT hypothesises that the participant sets a response criterion ($c$) at some level of sensory activity in order to respond. If the activity on a given trial exceeds the criterion level, the participant reports having seen a target. Criterion placement therefore determines how much activity is needed to report a target as present and influences which mistakes are likely to occur. A liberal criterion means that relatively low sensory activity is sufficient to report the presence of a signal. When there is overlap between the noise and signal-plus-noise distributions, there may be some misclassifications of noise presentations as targets (false alarms), but most targets will be reported (few misses). A conservative criterion (i.e. high activity is needed to report a target as present) on the other hand leads to more misses, meaning that targets are classified as noise, but fewer false alarms.
CHAPTER 2: ALPHA POWER RESPONSE CRITERION

According to this framework hit rates are influenced by both of those parameters: sensitivity to the stimulus, $d'$, and the placement of the response criterion, $c$. This has important implications for the proposed role of pre-stimulus alpha power in detection performance as increased hit rates during low alpha power states do not have to index improved visual sensitivity as such (i.e. a greater difference in sensory activity between noise and target presentations) but could also reflect differences in criterion placement (i.e. different levels of activity are needed to report the stimulus as present). A more liberal criterion during lower alpha power would lead to both a higher hit and false alarm rates without a change in sensitivity - an effect overlooked when focusing solely on hit rate.

Here we investigated the role of pre-stimulus alpha power in a backward-masking task based on that used by Mathewson and colleagues (2009). Rather than relying on hit-rate as a measure of performance, we employ a SDT analysis to investigate how varying states of cortical excitability (as indexed by alpha power) influence the sensitivity and criterion placement parameters. We report effects of both within and between participant variability in alpha power on detection performance.

2.4 Materials and Methods

2.4.1 Participants

Twenty-four students from The University of Auckland participated in this study and received NZD 20 for their participation. Five participants were excluded because of their behavioural performance and data from five additional participants was excluded because of excessive noise in the EEG data (see Results). Data from the remaining 14 participants were analysed ($M = 23.64$ years, $S.D. = 3.95$ years, 8 women). All participants reported normal or corrected-to-normal vision and 13 were right-handed. Participants provided written informed consent and all research protocols were approved by The University of Auckland Human Participants Ethics Committee.
2.4.2 Stimulation and Procedure

Participants were seated in a darkened booth. Experimental stimuli were presented on a 21-inch LCD (60 Hz refresh rate) monitor using E-Prime 2.0 Professional presentation software (Psychology Software Tools Inc., Pittsburgh). The monitor was positioned at 57 cm in front of the participant and the viewing distance was maintained through the use of a chinrest.

Participants completed 16 blocks of a backward-masking task that was closely matched to the task used by Mathewson and colleagues (2009). On each trial, participants indicated via button press whether or not they saw a grey diamond-shaped target that was presented centrally. The target was presented in 50% of the trials and followed by a mask. The mask was the outline of the diamond and was shown in both target-present and target-absent trials, which were presented in random order. In target-absent trials the screen remained blank during the target interval. The stimuli were grey and presented on a light grey background (luminance: 23.6 cd/m²). The target was lighter (21.35 cd/m²) than the mask (7.08 cd/m²) to increase task difficulty. These parameters were fixed for all participants and were chosen based on pilot work indicating hit rates of about 65 – 75%.

Each block consisted of 72 trials with self-paced breaks between blocks (in total 576 target-present and 576 target-absent trials). The timeline for each individual trial is shown in Figure 2.1a). The length of the inter-stimulus-internal (ISI) was chosen randomly (400, 800 or 1200 ms) with equal distribution between target-present and target-absent trials to hinder precise anticipation of target presentation. Behavioural results showed no difference in performance between different ISIs and trials were pooled together for analysis, independent of ISI. Prior to the experiment, participants were given both written and verbal instructions and performed a practice block consisting of 40 trials, after which they received verbal feedback. Participants were not informed about the probability of target appearances. Trials
in which participants failed to respond (on average 1%) were excluded from further analysis.

The experiment took about an hour in total, depending on the duration of the self-paced breaks.

<table>
<thead>
<tr>
<th>a) Fixation</th>
<th>ISI</th>
<th>Target</th>
<th>ISI</th>
<th>Mask</th>
<th>Response</th>
</tr>
</thead>
<tbody>
<tr>
<td>250 ms</td>
<td>400, 800 or 1200 ms</td>
<td>16.7 ms</td>
<td>50 ms</td>
<td>33.3 ms</td>
<td>1483.3 ms</td>
</tr>
</tbody>
</table>

Figure 2.1: Experimental design and signal detection theory account for detection performance. a) Timeline for each trial. The target subtended 1° visual angle and the mask 2°. The target was presented at low contrast to increase task difficulty. The length of the ISI between fixation and target presentation was selected randomly on each trial. b) Distributions of underlying sensory activity according to signal detection theory (c.f. Macmillan & Creelman, 2005). $d'$ is the distance between the centres of the two distributions, and reflects sensitivity to the signal (target stimulus); $c$ is the response criterion against which an observation is matched. On average, target presentations lead to higher sensory activity. If the activity in a given trial exceeds the criterion, $c$, the participant responds that the stimulus was present (‘yes’). If the target stimulus was in fact presented in this trial, the response is classified as a hit, if it was not presented, the response is a false alarm. A trial in which the activity does not reach the criterion leads to a ‘no’ response, which is classified as either a miss (if target was present) or a correct rejection (if target was absent). The criterion shown here is set left of the intersection of the distributions, representing a conservative response pattern. c) Two scenarios that can lead to change in criterion. Upper: An increase in activation elicited by both signal and noise (‘activity gain’) leads to a more liberal response criterion (although the criterion remains at the same level of sensory activity). Lower: Shift in criterion placement, with no change in the signal and noise distributions.
2.4.3 Electrophysiological Recording and Pre-processing

The electroencephalogram (EEG) was recorded using a 128-sensor Geodesic Sensor Net and Net Amps 300 amplifiers (Electrical Geodesics Inc., EGI, Eugene, Oregon, USA). It was digitised at 1000 Hz and acquired with respect to the vertex electrode. Individual sensor impedance was kept below 40 kΩ and measured both prior and half way through the experiment. Offline the EEG was down sampled to 250 Hz and analysed using EEGLab toolbox (Delorme & Makeig, 2004) and custom-written scripts for Matlab (The Math Works Inc., Natick, Massachusetts). Continuous EEG was first digitally high-pass filtered at 0.1 Hz using a finite impulse response filter.

The continuous EEG was segmented into 2060 ms segments, starting 1460 ms before target presentation to 600 ms after target presentation. Segments were first manually reviewed for artefacts. Segments containing blinks immediately before or after stimulus presentation were discarded, as well as segments containing noise (e.g. non-stereotypic artefacts and muscle activity). On average 85% of the trails were accepted (range 74% to 94 %). Each condition held at least 38 trials (with false alarms being the condition with the fewest trials, range 38 to 413 trials) and there was no significant difference between trials accepted in the target present versus target absent conditions (average 485 trials, \( t(13) = 0.176, p = 0.893 \)). Five participants were excluded because more than 25% of trials were rejected and not all conditions had at least 35 trials. After artefact rejection, data were decomposed using an independent component analysis (ICA) as implemented in EEGLab. Components that were identified as relating to eye blinks were not included into the remixing of the data (1-2 components per participant). Channels that contained excessive noise were discarded prior to the ICA and interpolated afterwards (using spherical-spline interpolation as implemented in EEGLab). Data were re-referenced to the nasion electrode and analysis focused on two electrode clusters (consisting of 3 electrodes each) over left and right
occipital-parietal cortex. These electrodes were chosen based on the scalp distribution across all trials at 10 Hz (see Figure 2.2c) and previous literature (Stokes, Atherton, Patai, & Nobre, 2012; Thut et al., 2006). They are positioned between electrodes P7 and O1 (left) and between P8 and O2 (right) of the 10-20 system.

2.4.4 EEG data analysis

**Individual alpha frequency bands.** To account for individual differences in the alpha band (e.g. Başar, 2012; Haegens, Cousijn, Wallis, Harrison, & Nobre, 2014; Klimesch, 1999; Pfurtscheller & Lopes Da Silva, 1999) we adjusted the alpha frequency band individually to encompass +/- 2 Hz around the individual alpha frequency (IAF). The IAF was defined as the frequency with the maximal power in the 7-14 Hz frequency band (Gould et al., 2011; Thut et al., 2006) determined by a Power Spectral Density estimate via Welch's method (using the spectopo function implemented in EEGLab). We conducted this analysis for the whole length of each epoch regardless of outcome, which resulted in a frequency resolution of 0.5 Hz. The peak frequency was averaged across the 6 electrodes chosen for analysis. The resulting mean IAF was 9.3 Hz (SE = 0.32). The average alpha frequency band (7.3 Hz to 11.3 Hz) is close to bands chosen in other studies, although a bit lower (e.g. Gould et al. 2011 7.9 – 11.8 Hz, Thut et al. 2006 7.8 – 13.8 Hz, Worden et al. 2000 8-14 Hz). All the following analyses use this IAF band if not indicated otherwise.

**Time-frequency analysis.** Single-trial power was estimated using a modified Morlet wavelet transformation (Delorme & Makeig, 2004). The length of the wavelets varied from 3 cycles at 5 Hz to 14 cycles at 60 Hz. This analysis resulted in estimates for 200 time points (from 1125 ms prior to target onset to 261 ms afterwards) and 28 log-spaced frequencies. As describe above the analysis focused on the individual alpha band, centred on the IAF. The squared absolute value was taken for each estimate (i.e. power) and averaged over a 200 ms pre-stimulus time-window (-300 to -100 ms) (Wyart & Tallon-Baudry, 2009). Due to the
temporal down-sampling of the wavelet analysis, this window will necessarily include small amounts of post-stimulus activity. However we did not choose a time window further back in time to limit differences between ISIs (the fixation cross offset always occurred at least 100 ms before the start of the pre-stimulus analysis window (400ms ISI in 1/3 of the trials)). To show that our effects are not driven by post-stimulus activity we repeated our analysis with power estimates derived from a Discrete Fourier Transformation (see below). This analysis eliminates the influence of post-stimulus activity in the pre-stimulus activity. Single-trial power was averaged based for each of the four possible outcomes of the detection task (hits, misses, correct rejections and false alarms) and log-transformed. We investigated whether there was a significant difference in pre-stimulus power between outcomes. Furthermore we sorted single trials into quintiles based on pre-stimulus alpha power per participant. For each of the 5 bins we calculated the hit and false alarm rates as well as d’ and c. For the calculation of d’ and c, the hit and false alarm rate were first normalised via a z-transform. d’ is defined as the difference between the normalised hit and false alarm rates (d’ = z(H) - z(FA)) and the criterion c is their negative mean (c = -0.5 * (z(H) + z(FA)) (Macmillan & Creelman, 2005). We investigated whether these performance indexes changed as a function of alpha power. To investigate between participant effects of pre-stimulus alpha power, we also correlated these indexes of performance with general pre-stimulus alpha power across the experiment.

To replicate earlier findings (Mathewson et al., 2009) and avoid the problem of post-stimulus activity in the pre-stimulus power estimates, an additional analysis using Discrete Fourier Transforms (as implemented in the fft function in Matlab) was applied. A FFT was applied to the 200 ms window immediately preceding target presentation. Power estimates (absolute value squared) at 10 Hz were extracted for each trial, outcome and participant and log transformed. The same analyses as described above (both within participant comparisons between outcomes and the single trial analysis; as well as the between participant
correlations) were performed on these power estimates. As a post-hoc exploratory analysis we furthermore compared pre-stimulus power between outcomes in the surrounding frequency bands (5-30 Hz in 5 Hz steps).

2.4.5 Statistical Analysis

To investigate whether modulations of pre-stimulus alpha power influences the behavioural performance in our task, we firstly performed a 2 x 4 repeated-measures ANOVA with the factors Hemisphere (left, right) and Outcome (hit, hiss, false alarm, correct rejection). We followed this analysis up with planned comparison using two-tailed pairwise t-tests to compare power preceding hits versus misses and false alarms versus correct rejections for each electrode cluster. The resultant \( p \)-values were Bonferroni-corrected to account for multiple comparisons. This analysis was performed for power in the 300 to 100 ms pre-stimulus window in the individual alpha-frequency band for the wavelet analysis as well as for power at 10 Hz in the -200 to 0 ms pre-stimulus window derived from the FFT (see above for a justification of those time windows). We furthermore conducted a 6 x 4 repeated-measures ANOVA with the factors Frequency (5-30 Hz) and Outcome on the FFT power estimates to test whether the same effect can be seen in adjacent frequency bands. We followed these up with the planned comparisons we described above.

To investigate the influence on pre-stimulus alpha power on behavioural performance in more detail, we furthermore compared behavioural indexes (hit rate, false alarm rate, d’ and c) across power quintiles. As we did not have specific hypothesis regarding the hemispheres, we averaged power estimates across electrode clusters and sorted single trials into quintiles based on that. For each behavioural index we conducted a repeated-measures ANOVAs with the factor Quintile (5 levels). We conducted this analysis both on the single-trial estimates from the wavelet as well as the FFT analysis. These ANOVAs were followed up by Bonferroni-corrected planned comparisons between each of the quintiles. To account
for a violation of the assumption of sphericity, the degrees of freedom were corrected using Huynh-Feldt estimates of sphericity, whenever Mauchly's test for sphericity indicated such a violation.

2.5 Results

2.5.1 Behaviour

Hit rate, $d'$ (sensitivity measure) and $c$ (response criterion) were calculated for all participants. 95% confidence intervals were calculated around $d'$ to ensure that only participants who could perform the task better than chance were included in the analyses (Gourevitch & Galanter, 1967). Four participants, for whom this interval included 0, were excluded from all further analyses. One additional participant was excluded because the performance was too high (hit rate of 95%, which led to too few misses and false alarms). Five additional participants were excluded because of excessive noise in the EEG data. The remaining 14 participants had an average hit rate of 59.94% (S.D. = 16.63), $d'$ of 1.25 (S.D. = 0.66), and $c$ of 0.35 (S.D. = 0.28). We did not find any differences between behavioural performance (hit rate, false alarm rate, $d'$, response criterion) in the first and second half of the experiment (paired $t$-tests all $p_{corr} > .09$). There were also no significant differences in performance between the different ISIs and trials were pooled independent of ISI in the following analyses.

2.5.2 Electrophysiology

The scalp distribution of pre-stimulus power at 10 Hz across all trials from 300 to 100 ms prior to target presentation showed peaks over the lateral occipital-parietal areas (see Figure 2.2c) middle insert for scalp distributions at IAF bands (mean 9.3-11.3 Hz). Two electrode clusters, averaged across three electrodes over left and right occipital-parietal cortex each, were chosen for all following analyses. Those electrode clusters differ from the
electrode side (Pz) chosen by Mathewson and colleagues (2009). We chose those electrode sides based on both the scalp maxima and prior research on pre-stimulus alpha power in visual tasks (Stokes et al., 2012; Thut et al., 2006). Figure 2.2 shows the results of the time-frequency analyses. Single-trials power estimates from the wavelet analysis were sorted based on the outcome of the detection task (hits, misses, false alarms and correct rejections). A 2 x 4 repeated-measures ANOVA with the factors Hemisphere (left and right cluster) and Outcome (hit, miss, false alarm, correct rejection) revealed a significant main effect for Hemisphere ($F(1, 13) = 6.018, p = 0.029$), indicating that there was more pre-stimulus power over the right compared to the left hemisphere, and a significant effect for Outcome ($F(1.977, 25.702) = 5.574, p = 0.01, \epsilon = 0.659$), showing that pre-stimulus power (-300 to -100 ms) differed significantly between the outcomes. There was no significant interaction. The test of within-subjects contrasts showed a significant cubic trend for outcome ($F(1,13) = 8.275, p = 0.013$) suggesting that power preceding hits and false alarm was lower than power preceding misses and correct rejections. This can also be seen in Figure 2.2c and d and suggests that alpha power influences the response criterion (i.e. how willing the participant was to respond with ‘yes’). Two-tailed pairwise t-test confirmed that there was significantly less power preceding hits than misses at the left cluster (left: $t(13) = -3.065, p_{corr} = 0.036$), suggesting that lower occipital alpha power prior to stimulus presentation is associated with superior detection. The other comparisons did not reach significance after correction for multiple comparisons. However there was a trend for a significant different between power preceding hits versus misses at the right electrode cluster (left: $t(13) = -2.880, p_{corr} = 0.052$).
Figure 2.2: Pre-stimulus alpha activity in a visual detection task. Results are shown averaged across both occipital-parietal electrode clusters. a) Power across all conditions shows a peak in alpha power across time. 0 ms indicates target onset. The average alpha band window is indicated with the dotted box. Per participant the frequency band for analysis was based around the individual alpha frequency b) The pre-stimulus power derived from discrete Fourier transform (200 ms) shows a peak at 10 Hz across conditions as well as significant differences between outcomes. Error bars represent SEM. c) Scalp distributions of pre-stimulus alpha power. Middle inset shows alpha power across outcomes and the black triangles indicate the location of the electrode clusters used for analysis. Alpha power is significantly lower preceding hits than misses at the left electrode cluster d) Differences in power between hits and misses and false alarm and correct rejections across times and frequencies averaged for both electrode clusters. 0 ms indicates target onset and the dotted box the analysis window. For display purposes power estimates were baseline-corrected by 10*log10(Power (per time frequency point)/ average power across all conditions at -300 to -100 ms). * p < 0.05.

For the Signal detection analysis (SDT) analysis we sorted single trials into quintiles based on pre-stimulus alpha power. As we did not have specific hypotheses as to the role of
the hemispheres and the power at both hemispheres was highly correlated ($\rho = 0.945, p < 0.0001$), we sorted trials based on average alpha power across electrode clusters. We then compared hit and false alarm rates, as well as $d'$ and $c$ across bins (see Figure 2.3) via repeated-measures ANOVAs. There was a significant main effect of Quintile for Hit rate ($F(4, 52) = 4.347, p = 0.004$; linear trend: $F(4, 52) = 8.606, p = 0.012$), False alarm rate ($F(4, 52) = 3.951, p = 0.007$; linear trend: $F(4, 52) = 3.548, p = 0.083$; quadratic trend: $F(4, 52) = 6.991, p = 0.02$) and criterion ($F(4, 52) = 7.714, p < 0.0001$; linear trend: $F(4, 52) = 7.523, p = 0.017$). $d'$ did not differ between power quintiles ($p > 0.6$). As can be seen in Figure 2.3, hit and false alarm rates decreased with increasing power, whereas the criterion increased across bins. This suggests that the lower hit rates during higher alpha power, which were reported previously, might be explained by a more conservative criterion, leading to more “no” responses. Especially the 5th quintile seems to be different from the others, suggesting a non-linear relationship between alpha power and performance. The results of the planned comparisons between the quintiles are indicated in Figure 2.3a).
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a) Within participant effects of pre-stimulus alpha power

![Graph showing within participant effects of pre-stimulus alpha power.](image)

\[ p_{\text{corr}} = 0.075 \]

b) Between participants effects of pre-stimulus alpha power

![Graph showing between participants effects of pre-stimulus alpha power.](image)

\[ p = 0.745^{**} \]
\[ p = 0.222 \]
\[ p = 0.037 \]
\[ p = 0.446 \]
\[ p = 0.019 \]

Figure 2.3: Pre-stimulus alpha power and SDT parameters. Figure shows results based on pre-stimulus power estimates from the wavelet analysis. Alpha power was averaged across both electrode clusters per participant. a) Within participant effects of single-trial alpha power on detection performance. Single-trial alpha power across electrode clusters was sorted into quintiles. Significant linear trends are shown for the relationship between
quintile and hit rate as well as criterion. Bonferroni-corrected planned comparisons were conducted between the bins. Significant differences are indicated in the upper part of each diagram. *$p_{corr} < 0.05$, **$p_{corr} < 0.01$. Error bars represent SEM. b) Pre-stimulus alpha power across all conditions was correlated with performance. Spearman’s rank correlation coefficients are shown for mean power across electrode clusters and indices of performance *$p < 0.05$, **$p < 0.01$.

We furthermore applied a non-parametric Spearman’s rank correlation test to determine, whether there was a relationship between overall alpha power across trials and performance (Figure 2.3b). In contrast to the previous tests, this investigates the influence of pre-stimulus alpha power at a between participant level. Similar to the single trial analysis described above we conducted this analysis on alpha power averaged across electrode clusters. We found significant correlations between alpha power and hit rate and criterion (Hit rate: $\rho = -0.745, p = 0.002$; c: $\rho = 0.618, p = 0.019$). Similar to the within participant effects of single-trial alpha power we found that higher alpha power across the experiment was correlated with a decreased hit rate and an increased criterion. In contrast to the single-trial analysis, there was also a significant negative correlation between alpha power and d’ ($\rho = -0.560, p = 0.037$) and no significant correlation between pre-stimulus alpha power and false alarm rate.

To eliminate the influence of post-stimulus power in the pre-stimulus window due to the temporal down-sampling in the wavelet analysis, we also decomposed the time-frequency information by using a discrete Fourier transform on the 200 ms directly preceding target presentation (-200 to 0 ms). We applied the same tests to the power estimates at 10 Hz as before. Since we only found a power difference between the clusters (the right cluster seems to have more power than the left) but no interaction and similar results across hemispheres, the following analyses were conducted for power estimates averaged across both electrode clusters. As can be seen in Figure 2.2b the results match those of the previous wavelet analysis. A repeated-measures ANOVA showed that pre-stimulus alpha power differed
significantly between the outcomes ($F(3, 39) = 9.976, p < 0.001$). We again found a
significant cubic trend ($F(1,13) = 15.233, p = 0.002$) suggesting that alpha power preceding
hits and false alarms was lower than alpha power preceding misses and correct rejections.
Two-tailed pairwise t-test confirmed that there was significantly less power preceding hits
than misses ($t(13) = -3.3.81, p_{corr} = 0.001$) and preceding false alarms than correct rejections
($t(13) = -3.450, p_{corr} = 0.008$). The signal detection analysis revealed very similar results to
the wavelet analysis. There was a significant main effect of quintile for Hit rate ($F(4, 52) =
4.948, p = 0.002$; linear trend: $F(4, 52) = 11.763, p = 0.004$), False alarm rate ($F(4, 52) =
4.276, p = 0.005$; linear trend: $F(4, 52) = 10.323, p = 0.007$) and criterion ($F(4, 52) = 8.227, p
< 0.001$; linear trend: $F(4, 52) = 20.283, p = 0.001$). d' did not change depending on power
quintile ($p > 0.6$). The hit and false-alarm rates decreased with increasing power, whereas the
criterion increased with increasing power. The Spearman rank test showed significant
correlations between alpha power and hit rate, d' and criterion (Hit rate: $\rho = -0.767, p =
0.001$; d': $\rho = -0.560, p = 0.037$, c: $\rho = 0.684, p = 0.007$). There was no significant correlation
with the false alarm rate. As can be seen in Figure 2.2b the effects of pre-stimulus power on
performance do not seem to be limited to the alpha frequency band. We therefore conducted a
4 x 6 repeated-measures ANOVA with the factors Outcome (hit, miss, false alarm, correct
rejection) and Frequency (5-30 Hz in 5 Hz steps). There was a significant main effect of
Outcome ($F(3,39) = 16.474, p < 0.001$). We again found a cubic trend ($F(1,13) = 34.775, p <
0.001$) suggesting that across those frequency bands, power was lower preceding hits and
false alarms than misses and correct rejection. There was also a significant main effect of
frequency ($F(1.373, 17.846) = 41.948, p < 0.001, \varepsilon = 0.275$) showing less general power in
the higher frequency bands and a significant Outcome x Frequency interaction ($F(7.625,
99.121) = 3.724, p = 0.001, \varepsilon = 0.508$). When corrected for multiple comparisons, only the
difference between hits and misses at 15 Hz ($t(13) = -4.326, p_{corr} = 0.012$; trend at 5 Hz: $t(13)$
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\( t(13) = -3.381, p_{\text{corr}} = 0.06 \) and false alarms and correct rejections at 10 Hz \( t(13) = -3.450, p_{\text{corr}} = 0.048 \) remained significant. Without correction, the difference between hits and misses was significant at all frequency bands from 5-20 Hz and the difference between false alarms and misses was significant at 10 and 25 Hz.

2.6 Discussion

We investigated the effect of modulations in pre-stimulus alpha power (~8-12 Hz) over occipital-parietal cortex on performance in a backward-masking task based on that used by Mathewson and colleagues (2009). Earlier research has shown an inverse relationship between pre-stimulus alpha power and hit rate (Busch et al., 2009; Ergenoglu et al., 2004; Hanslmayr, Aslan, et al., 2007; Hanslmayr et al., 2005; Mathewson et al., 2009; Roberts et al., 2014; van Dijk et al., 2008). Our data confirm these reports and show that participants were more likely to detect a visual stimulus if power in the alpha frequency band before the target presentation was low. This relationship was shown both between participants and on a single-trial level. However by applying a signal detection approach, we showed that this difference in hit rate is likely due to pre-stimulus alpha power modulating criterion placement more strongly than sensitivity. The criterion became more conservative (i.e. an increase in the probability of “no” responses), with increasing power in the alpha frequency band. A significant relationship between increases in pre-stimulus alpha power and sensitivity was only found between participants but not on a single trial level. Different behavioural effects of modulations in alpha power between participants and between trials within a participant might suggest that alpha power influences different levels or aspects of performance. Participants with lower levels of alpha power might show superior detectability of visual stimuli in general (Hanslmayr, Aslan, et al., 2007; Klimesch et al., 2007) whereas the trial-by-trial fluctuations might reflect top-down influences on visual processing by fronto-parietal
attention networks (Capotosto, Babiloni, Romani, & Corbetta, 2009; Mathewson et al., 2014) on a moment-to-moment basis.

These results strengthen the suggestion that variability in the perception of constant stimuli can be explained by ongoing EEG activity before stimulus presentation. We show that on a single trial level this relationship is probably based primarily on modulations of response criterion (or modulations of sensory activity leading to changes in response criterion, see below) and therefore do not support the suggestion that modulations of alpha power over the course of the experiment index or enable increased visual sensitivity. These findings hint at the possibility that the visual system might operate differently depending on its current excitability state (as indexed by the trial by trial fluctuations of power in the alpha frequency band). Lower excitability is indexed by increased alpha power (Romei et al., 2008) and seems to lead to a more conservative response criterion (i.e. a preponderance of ‘no’ responses). In signal detection terms this means that more sensory activity is needed to elicit a positive response (Figure 2.1b). This more conservative criterion for high-power states might protect against false positives or unnecessary actions when the system is relatively disengaged from the world.

During reduced alpha power states, which correspond to higher excitability, the criterion was more liberal and therefore less sensory activity was needed to elicit a positive response. Further research needs to determine whether the more excited state leads to a more liberal or a more balanced criterion or whether the placement of the criterion might even depend on the task requirements (e.g. see below for a discussion on the use of masking tasks and selective attention designs). A balanced criterion maximises the hit rate and minimises both false alarms and misses if – as in our task - the target is presented in half the trials. On the other hand a liberal criterion is a beneficial strategy if the goal is to maximise hits and the costs of a miss are higher than that of a false alarm (Macmillan & Creelman, 2005). A liberal
criterion during excited states might therefore reflect the tuning to the environment and
greater readiness to accept weak signals as meaningful. The relationship between alpha
oscillations and response criterion seems to suggest that the state of cortical excitability
influences our response to the sensory input more strongly than the sensitivity to target
stimuli, which is in agreement with a current study by Chaumon and Busch (2014).

Furthermore our results suggest that there is no simple linear relationship between
alpha power and performance but rather that there are two different states (high and low
cortical excitability) between which performances differs. Performance seems to differ
especially in trials preceded by the highest level of alpha power (Figure 2.3a). We think that
this might be due to the non-normal distribution of spectral data, which is skewed towards the
lower power values. This non-continuous relationship between alpha power and performance
is also evident in the study by van Dijk and colleagues (2008) who show that performance for
trials preceded by the highest level of alpha power is different from the others. As revealed
by an exploratory analysis, the effect of oscillatory power on the outcomes of a detection task
seems to be present across a range of low frequency bands and not limited to alpha frequency
band.

We understand this result of a relationship between pre-stimulus power in the alpha
frequency band and response bias as an extension of previous reports, which show a
relationship between alpha power and hit rate, and do not think that our results are necessarily
incompatible with those. In fact we replicate the finding that lower power in the pre-stimulus
window is related to a higher hit rate. However our experimental design, which included the
same number of target present and target absent trials, allowed us to do a more nuanced
analysis of behavioural performance. Previous studies have either limited their analysis to
target present trials (Busch et al., 2009; Ergenoglu et al., 2004; Mathewson et al., 2009;
Roberts et al., 2014; van Dijk et al., 2008) or used a discrimination task (Hanslmayr, Aslan, et
al., 2007; Hanslmayr et al., 2005), which usually leads to a balanced criterion (Macmillan & Creelman, 2005). These experimental designs therefore impeded the investigation of response criterion. We suggest that especially the restriction to target present trials in the analysis (most likely due to the low number of target absent trials in the above mentioned studies) limits the ability to understand variability in detection performance. Understanding why noise is at times perceived as a target is arguably as important for the understanding of variability in perception as understanding why a target is missed. Future research needs to determine whether alpha power influences response criterion in designs similar to those used in the above mentioned studies (e.g. for the detection of low contrast/threshold stimuli).

To our knowledge, Wyart and Tallon-Baudry (2009) conducted the only other study that explicitly looked at the relationship between oscillatory power and response bias. They report a relationship between response bias and γ-oscillations (48-64 Hz) and did not find evidence for a relationship in the alpha band. There are several distinctions between our study and theirs that might help to understand these different results. As we will discuss below one major difference between the studies is their use of a visuospatial attention task that might affect the role of alpha power on performance. Their task was also harder (average hit rate of 46.6 %, d’ = 1.04 compared to 60% and 1.25 in our task) and it has been shown that harder tasks lead to decreases in alpha power (Haegens et al., 2012; Min & Herrmann, 2007; Roberts et al., 2014). This might have led to a lower variability in alpha power in their study and consequently might have masked the effects (Drewes & VanRullen, 2011; Lou, Li, Philiastides, & Sajda, 2014). Most importantly though, they used a different theoretical framework and the decision bias, which was found to be influenced by gamma power, was defined as the pre-stimulus power that predicted the seen-unseen decision (again only on target present trials) and was uncorrelated to the post-stimulus activity (as a measure of sensory activity elicited by target presentation). This decision bias was differentiated from a
baseline shift, another kind of bias that depends on the correlation of pre- and post-stimulus activity and was influenced by modulations of alpha power. We did not distinguish between different kinds of biases in the current analysis and focused solely on pre-stimulus activity.

A recent study by Lange and colleagues (2013) made a similar suggestion to ours on the relationship between pre-stimulus alpha power and performance in perceptual tasks. They questioned whether reduced pre-stimulus alpha power led to increased sensitivity to stimulation in the sense of more veridical perception or whether it influenced other aspects. In their study participants reported whether they perceived one or two visual stimuli, which were accompanied by tactile stimuli. Interestingly, pre-stimulus alpha power derived from magnetoencephalography (MEG) predicted the number of perceived visual stimuli regardless of whether the response was correct. Participants were more likely to respond ‘two’ when pre-stimulus alpha activity was low. The authors interpret reduced alpha power as an index of increased cortical excitability and suggest that this leads to a greater responsiveness to heteromodal stimulation. Although the authors did not explicitly perform a signal detection analysis, we suggest that their findings could be accounted for by a shift in response criterion. Reporting two stimuli instead of one during low pre-stimulus alpha power could be interpreted as the result of a more liberal response criterion, which matches our results. However it should be noted that other studies show that this phenomenon, known as the Double Flash Illusion, is a perceptual effect that influences sensitivity (Lange, Oostenveld, & Fries, 2011; Violentyev, Shimojo, & Shams, 2005) or both sensitivity and criterion (McCormick & Mamassian, 2008). This suggests that a shift in criterion due to modulations of alpha power could probably not account for the entire effect. It would be interesting to investigate the relationship between oscillatory power and SDT measures of performance with this paradigm in more detail, both on a between and within participant level. Our results
show an effect of alpha power on $d'$ only between participants and an effect on criterion both between participants and on a trial-by-trial basis.

In their recent review of the above mentioned and other studies using illusory stimuli in different modalities, Lange and colleagues (2014) conclude that low alpha power indexes increased sensory excitability, which leads to a lower threshold for neuronal activation. Due to this lowered threshold stimulation is more likely to activate neuronal populations or as in the above described case, those populations are more likely to respond to heteromodal input. Our findings add to this conclusion and show that this change in threshold is possibly reflected by a change in response criterion behaviourally. This interpretation argues for an ‘activity gain’ during states of heightened excitability as shown in the upper panel of Figure 2.1c). According to this interpretation the change in criterion placement is brought about by higher activation elicited by both signal and noise under decreased alpha power. Assuming that the criterion stays fixed at a certain level of sensory activity, the criterion would be reached more often under high versus low excitability states. Based on the current analysis, we cannot determine whether the observed change the criterion placement is due to a change in ‘activity gain’ or to a shift in criterion placement, while level of sensory activity stays fixed (Figure 2.1c). To our understanding a change in ‘activity gain’ could be consistent with a ‘baseline shift’ as found by Wyart and Tallon-Baudry (2009). Consistent with this interpretation of our results they report an influence of alpha power on the baseline shift. Furthermore Chaumon and Busch (2014) show that alpha power influences the response gain in detection task and in agreement with our results argue that alpha power modulations thereby influence the ‘decisional stage’.

It should be noted that the choice of a masking task might not be ideal to find modulations of sensitivity as successful detection in those tasks relies on the representation of the target and the mask stimulus (e.g. Di Lollo et al., 2000; Ro, Breitmeyer, Burton, Singhal,
Increased excitability during decreased alpha power would most likely have a similar effect on sensory activation elicited by both the target and mask stimuli. This general increase in activation would not necessarily improve performance, as that relies on a differential increase of target relative to mask activation. This poses an interesting question for further research. Studies investigating the influence of pre-stimulus alpha power mostly use near-threshold stimuli to measure variability in detection performance. Studies have either used masked stimuli (e.g. Hanslmayr, Aslan, et al., 2007; Mathewson et al., 2014; Mathewson et al., 2009; van Dijk et al., 2008) or low threshold stimuli (e.g. Busch et al., 2009; Ergenoglu et al., 2004; Roberts et al., 2014) to limit detectability of the targets. Both of these paradigms led to the same conclusion that lower alpha power increases detectability (or discriminability as in Hanslmayr et al. (2007) using a 4 alternative forced choice task). As mentioned above, further research should investigate whether decreases in performance during increased alpha power can be explained by a more conservative response criterion in paradigms using unmasked near-threshold stimuli.

A different relationship between alpha power and response criterion might be inferred from the selective attention literature. It has been shown consistently that the orienting of attention leads to specific modulations of alpha power. In spatial attention designs there is usually more alpha power over the ipsilateral compared to the contralateral occipital-parietal cortex (e.g. Foxe & Snyder, 2011; Gould et al., 2011; Kelly et al., 2006; Rihs et al., 2009; Sauseng, Klimesch, Stadler, et al., 2005; Thut et al., 2006; Trenner et al., 2008; Worden et al., 2000; Yamagishi et al., 2005). A TMS study by Capotosto and colleagues (2009) showed that this modulation of alpha power is controlled by the dorsal fronto-parietal network that is indicated in attentional mechanisms (e.g. Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Corbetta & Shulman, 2002). These experimentally induced modulations of alpha power are not limited to spatial locations, but are also reported for feature-based and modality
based selection (Foxe et al., 1998; Synder & Foxe, 2010). However as with simple detection tasks, response criterion has not been in the focus of most of these investigations. This is probably also due to the fact that most of these studies use discrimination (such as a two alternative forced choice task) and not simple detection tasks, which usually lead to balanced criterion. However, if our present results were applicable to a selective attention task, we would hypothesise a more liberal criterion for attended stimuli (i.e. where alpha power has been shown to be decreased). In a recent behavioural study Rahnev and colleagues (2011) found a more conservative criterion for the attended stimuli, which contradicts our hypothesis. Furthermore as described above Wyart and Tallon-Baudry(2009) reported that alpha power affected sensitivity, but gamma power influenced response criterion. Future research is needed to investigate whether the role of alpha oscillations in perception might differ between these different tasks. Simple detection and selective attention tasks usually differ across a range of parameters, for example there are often two or more possible peripheral target locations in selective attention tasks whereas there is usually only one central location in detection tasks. As pointed out by Rahnev and colleagues (2011) the subjective experience of the visual periphery often seems more vivid and detailed than could be expected from the resolution and colour sensitivity (Abramov & Gordon, 1977; Azzopardi & Cowey, 1993). This could potentially lead to differences in criterion placement for central and peripheral locations.

Several studies on the role of alpha oscillations on visual performance also show that in addition to power, the phase of the alpha oscillation is predictive of visual perception. It has been shown repeatedly that detection is more likely at a certain point on the alpha wave (Busch et al., 2009; Busch & VanRullen, 2010; Drewes & VanRullen, 2011; Dugué et al., 2011; Hamm, Dyckman, McDowell, & Clementz, 2012; Jensen et al., 2012; Mathewson et al., 2009). Although the analysis of alpha phase is beyond the scope of the current
investigation it would be very interesting to investigate whether the indices of the behavioural performance used here can be predicted by variation of alpha phase.

In conclusion, our study provides further evidence that random fluctuations in pre-stimulus activity influence visual perception. We show that spontaneous fluctuations in pre-stimulus alpha power affect the response criterion. Response criterion is more conservative during less excited states (as indexed by increased alpha power), explaining the reduced hit and false rate by a preponderance of ‘no’ responses. These findings hint at the possibility that the visual system might operate differently depending on its current excitability state, as indexed by power of low frequency oscillations. During reduced power states, which probably correspond to higher excitability, the system might accept stimuli as present more willingly than in less excited states. A more conservative criterion for high-power states might be protective against false positives when the system is relatively disengaged from the world. Furthermore our results suggest that different aspects of performance might be influenced by differences in oscillatory power between participants and modulations on a moment-to-moment basis within a participant. Participants with higher alpha power in general show both a more conservative response criterion and a decrease in sensitivity. However, there was no relationship between sensitivity and moment-to-moment fluctuations in alpha power.

2.7 Chapter Epilogue

In a follow-up experiment 17 participants did a backward-masking task that was very similar to one used before to investigate the relationship between pre-stimulus alpha power and behavioural performance in more detail. The only major difference was that participants had to rate how sure they were that they saw or did not see the target on any given trial on a 6-point scale instead of just indicating whether or not they saw it. The introduction of a rating scale allows the creation of Receiver Operating Characteristics (ROC) curves. According to
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SDT different Hit and False Alarm rate pairs can lead to the same sensitivity estimate and a single Hit and False Alarm rate pair (as in the first experiment) does not necessarily provide a reliable measure of sensitivity and response criterion. In a rating task, the different response levels or confidence ratings can be used to create Hit and False Alarm rate pairs and therefore several points on the ROC curve (e.g. for the first point on the ROC curve, only responses of ‘1’ are scored as a ‘no’ response and responses ‘2’ to ‘6’ are scored as ‘yes’. For the second point responses ‘1’ and ‘2’ are scored as ‘no’ and ‘3’ to ‘6’ as ‘yes’ as so forth. A 6-point response scale leads to 5 ROC points, see Figure 2.4). Multiple points on the ROC curve can be used to better visualise and analyse behavioural performance (Macmillan & Creelman, 2005).

Based on our previous results, we hypothesised that different levels of pre-stimulus alpha power would lead to similar sensitivity estimates (all points would fall on the same ROC curve), but that the actual points would move along the curves. As can be seen in Figure 2.4, our preliminary analysis suggests that this is not the case. We sorted single trial power in the alpha band (in this analysis a general band of 8-12 Hz, only right hemisphere) into a low and high power bin and plotted the different Hit and False Alarm rate pairs. Although the results seem to support our finding that different levels of pre-stimulus alpha power do not affect sensitivity (the ROC curves for different alpha power levels are mainly overlapping), there is also no effect on response criterion (the points are overlapping). We were thus not able to show a significant difference between performance in high and low power trials in this experiment. We hypothesise that this might be due to the task requiring a more complex and possibly delayed response. As has been suggested earlier, alpha power might only be a good predictor of performance for immediate responses in relatively simple tasks (Drewes & VanRullen, 2011; Grent-’t-Jong et al., 2011; van Ede et al., 2014).
Figure 2.4: Rating Scale Follow-Up experiment. a) The experimental design was similar to the previous one, except that participants had to rate how sure they were that the target was presented on a 6-point scale. b) Mapping of different responses on decision space. The 6 responses lead to 5 different response criteria and thus 5 points on the ROC curve. See Figure 2.1 for a more detailed description of the SDT model. c) Empirical ROC curves based on pre-stimulus alpha power. A median split was performed on single-trial pre-stimulus alpha power. Results are shown for the right hemisphere. Hit and False Alarm rates were calculated for different ratings and averaged across participants.
Chapter 3: Alpha Power Modulation but not Lateralisation Reflects the Balancing of Task Requirements in a Selective Attention Task

3.1 Chapter Prologue

In this chapter we investigated the behavioural effect of alpha power lateralisation in a selective attention task. As outlined in Chapter 1, alpha power has been shown to be lower over the contralateral compared to the ipsilateral hemisphere in response to spatial cues. This is in line with the commonly assumed role of fluctuations in alpha power. The decrease over the contralateral hemisphere is interpreted as an increase in local excitability in preparation of the target. On the other hand the ipsilateral increase could support the suppression of distracting input at the unattended side. The lateralisation of alpha power could thereby index the mechanism that is responsible for the orienting of attention and explain why performance is increased at the attended side (e.g. Foxe & Snyder, 2011; Thut et al., 2006; Worden et al., 2000). However, as we have shown in Chapter 2 the relationship between pre-stimulus alpha power and performance is not that simple and at close inspection of the literature the behavioural effect of the lateralisation in attention tasks seems to be rather complex as well.

We were intrigued by the apparent lack of observation of the inconsistencies when it comes to the behavioural effect of the lateralisation in the field: At times the lateralisation is related to changes reaction time, at others to accuracy; sometimes there even is no relationship between the lateralisation and performance; it is sometimes reported that the cue-related modulation in both hemispheres determines behaviour (i.e. it is a truly bilateral process), whereas others claim that only the contralateral or the ipsilateral change is behaviourally relevant. To systematically investigate the effect of the lateralisation we modulated the speed-accuracy trade-off and asked participants to either make a fast and potentially incorrect response or respond accurately but more slowly. We hoped that this
manipulation could help to establish whether the lateralisation is more closely related to a correct, a fast or maybe even a fast and correct response.

There is some debate about whether the lateralisation is driven by an ipsilateral increase, a contralateral decrease or a combination of both. Although we do not investigate or differentiate between these sources, we will discuss some of the potential modulating factors. We use the term ‘alpha lateralisation’ to indicate that there is a difference in power between the ipsilateral and contralateral hemispheres. We use the term ‘alpha modulation’, when we specifically refer to a change in the ipsilateral or contralateral hemisphere. The analysis techniques are similar to those used in the previous chapter, with the exception that the task design allowed the application of a baseline-correction and thereby the investigation of the relative changes in alpha power in response to the spatial cues.

3.2 Abstract

Recent research has related the orienting of selective attention to the lateralisation of posterior EEG alpha power (~8 to 12 Hz). In response to a cue, alpha power is typically reduced over the side of the head contralateral to the cued side of space. However it is not clear yet whether this lateralisation indexes a behaviourally relevant neuronal mechanism. Here, we recorded the EEG from 28 participants, who performed a spatially cued visual discrimination task under three different response-deadline conditions to investigate the relationship between alpha power lateralisation and behavioural performance in more detail. Behavioural data show that participants were more accurate but slower if they had more time to respond, and faster but less accurate under a stricter response-deadline. As in an earlier study, only a subset of participants –those with high baseline alpha power – show the alpha power lateralisation. Performance is strikingly similar across groups and importantly even participants who do not lateralise their alpha power in response to the cue show the behavioural benefit of attention. However, our data suggests that participants with low
baseline power might be more sensitive to task instructions. Strengthening the link between pre-target alpha power modulation and behavioural variability we furthermore show that the cue-related change in alpha power across response-deadlines was related to the behavioural change across response-deadlines; participants who show a greater decrease in alpha also show a greater decrease in accuracy under increased time-pressure.

3.3 Introduction

Selective attention is understood as the sort of process that enables us to select certain stimuli for more detailed processing and to disregard or delay the processing of others (e.g. Broadbent, 1958; Buschman & Miller, 2010; Carrasco, 2011; Desimone & Duncan, 1995). Attention thereby compensates for our limited processing capabilities, which are most likely due to the high energy costs of neural activity and other processing characteristics of the visual cortex (e.g. Attwell & Laughlin, 2001; Carrasco, 2011; Kastner et al., 1999; Lennie, 2003; Tsotsos, 1990; Van Essen & Maunsell, 1983). Selecting relevant stimuli and disregarding other information is crucial for goal-directed behaviour and interactions with the environment that presents us with an overwhelming plethora sensory input at any given moment (e.g. Treue, 2001). We have, at least to some degree, conscious control over which stimuli we want to focus our attention on (e.g. Posner et al., 1980). A baseline shift or bias in neural activity even prior to stimulus presentation is discussed as a potential mechanism that could lead to the increase seen in the neuronal and behavioural response to attended stimuli (Desimone & Duncan, 1995; Kastner et al., 1999; Luck et al., 1997). Modulations of ongoing EEG activity in the alpha band (~8-12 Hz) in response to attentional cues have recently been proposed as an index of the mechanisms underlying this voluntary orienting of attention.

Voluntary shifts of visuospatial attention (usually in experimental designs using lateralised stimulus displays in which a spatial cue indicates that a target is more likely to appear on the right or left side of the screen) have consistently been shown to modulate
posterior alpha power. Usually alpha power is lateralised, and is shown to be lower over the contralateral compared to the ipsilateral hemisphere (e.g. Capilla et al., 2014; Gould et al., 2011; Kelly et al., 2006; Rihs et al., 2009; Sauseng, Klimesch, Stadler, et al., 2005; Thut et al., 2006; Trenner et al., 2008; Worden et al., 2000; Yamagishi et al., 2005). This matches the idea of an attentional baseline shift, as alpha power seems to index changes in cortical excitability and has been shown to influence sensory detection (e.g. Mathewson et al., 2009; Romei et al., 2008). According to this idea, decreases in alpha power in response to a spatial cue are interpreted as a manifestation of top-down influence on sensory areas, which increases cortical excitability (i.e. decreases alpha power) over the side that will process the stimulus (Capilla et al., 2014; Kastner et al., 1999; Thut et al., 2006). Similarly, the ipsilateral increase has been interpreted as a mechanism to suppress unattended and potentially distracting information (Foxe & Snyder, 2011). Evidence for a top-down modulation of the alpha lateralisation by areas in the dorsal fronto-parietal attention network (Corbetta & Shulman, 2002) comes from a study by Capotosto and colleagues (2009). They applied TMS to fronto-parietal areas (e.g. intraparietal sulcus and frontal eye fields) during a visuospatial attention task and showed that TMS pulses at the time of the cue did not only disrupt the spatially selective alpha decrease, but also slowed the behavioural response to validly cued targets.

The alpha power lateralisation is sensitive to a variety of experimental manipulations, which furthermore strengthens the suggestion that it is under top-down control and functionally involved in the orienting of visuospatial attention (Haegens, Händel, et al., 2011). The strength of the alpha lateralisation has been shown to be flexibly determined by cue reliability, where the more reliably the cue predicts the target location, the stronger the lateralisation and the better the performance (Dombrowe & Hilgetag, 2014; Gould et al., 2011; Haegens, Händel, et al., 2011); the lateralisation is tightly related to temporal
expectancies and peaks just before the expected target presentation (Rohenkohl & Nobre, 2011) and it is also shown for orientation to tactile stimuli (Haegens, Händel, et al., 2011) and seems to be specific for the feature of interest (Synder & Foxe, 2010) or attended modality (Foxe et al., 1998). These findings suggest that alpha lateralisation indexes processes that underlie the perceptual benefit, which stems from knowing not only where but also when a target is going to appear.

However, despite the well-established finding of alpha power lateralisation in these studies of selective attention, its relationship to behavioural performance is still a matter of debate. Whereas some studies show that the lateralisation of alpha predicts both accuracy and response time (Haegens et al., 2012; Kelly et al., 2006), others show effects only in response time and not accuracy (Thut et al., 2006; Trenner et al., 2008). Van Ede and colleagues (2012) recently suggested that the effect of the attentional cue on accuracy can be predicted by preparatory increases in excitability as indexed by the contralateral alpha power decrease, whereas the effect on reaction time has to rely on at least one additional process.

Furthermore, while some studies claim that both the contralateral decrease and ipsilateral increase in alpha power are important for optimal performance (Haegens, Händel, et al., 2011; Händel et al., 2010), other studies have found only an increase or a decrease independent of one another (e.g. Rihs et al., 2007; Sauseng, Klimesch, Stadler, et al., 2005; Worden et al., 2000). Using source localisation techniques, Capilla and colleagues (2014) found distinct sources and behavioural correlates of the ipsilateral and contralateral modulation. They found that the contralateral decrease was generated in the ventral stream, sustained during the cue-target interval and related to successful recognition of validly cued targets. The ipsilateral increase on the other hand was localised to the dorsal stream, transient and not related to performance. Interestingly the recognition of invalidly cued targets seemed to be affected by the relative balance of ipsilateral and contralateral activity (better
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performance if there was less lateralisation). There are also reports in which the attentional benefit shown in the behavioural data cannot be related to the alpha power lateralisation (van Ede et al., 2014) or at least not under certain experimental manipulations (Dombrowe & Hilgetag, 2014; Gould et al., 2011; Händel et al., 2010).

Taken together this suggests a rather complex relationship between alpha power lateralisation and behavioural performance. There is additional evidence suggesting that this relationship is influenced by both individual differences in baseline power (Rihs et al., 2009), and other task specifics such as difficulty (Grent-'t-Jong et al., 2011; Haegens et al., 2012; Roberts et al., 2014) or transient versus sustained allocation of attention (van Ede et al., 2014). Rihs and colleagues (2009) found that only a subset of their participants – those with high baseline alpha power - showed the cue-related alpha power lateralisation. This is especially interesting because all participants (independent of the lateralisation) showed a similar behavioural benefit of the cue. The process underlying the alpha power lateralisation might therefore index certain aspects of the orienting of attention, but not be required for the development of the behavioural benefit. Furthermore, both Haegens and colleagues (2012) and Roberts and colleagues (2014) found a modulation of alpha power by task difficulty (decreased power for harder conditions), whereas Grent-'t-Jong and colleagues showed that alpha power modulation was not sensitive to increases in task difficulty but rather to response mode (stronger decrease in alpha power for immediate compared to delayed responses). The sensitivity to modulations of task difficulty is interesting as some studies suggest that alpha oscillations may not be a good predictor of performance if the tasks are very difficult (Drewes & VanRullen, 2011; Lou et al., 2014).

The difficulty in establishing a clear behavioural correlate of the cue-related alpha power lateralisation may be partly due to the use of a variety of different task designs, instructions and behavioural measures used in earlier studies. The accuracy of perceptual
decisions is often higher for slow compared to fast responses, indicating a speed-accuracy trade-off (SAT (Bogacz, Wagenmakers, Forstmann, & Nieuwenhuis, 2010). The SAT seems to indicate that it takes time to accumulate enough information to make a correct response. However the amount of time that can be spent on this accumulating information probably depends on the situation (e.g. the apparent urgency of a reaction versus the cost of a mistake). Effective behaviour depends on the right balance between the conflicting requirements of responding fast and taking time to accumulate enough information to respond correctly (Chittka, Skorupski, & Raine, 2009; Schouten & Bekker, 1967; Wickelgren, 1977). One systematic way to investigate whether the behavioural effect of alpha power lateralisation differs depending on task demands, is therefore to constrain reaction time by giving participants several response-deadlines (Heitz & Engle, 2007) and investigate whether the relationship between the lateralisation and performance is affected by this.

Here, we investigate alpha power modulation in a cued visuospatial discrimination task under three different response-deadline instructions. Firstly, we are interested in whether alpha power lateralisation is sensitive to manipulation of speed-accuracy trade-off similarly to modulations seen for different levels of cue reliability (Gould et al., 2011; Haegens, Händel, et al., 2011) and difficulty (Haegens et al., 2012; Roberts et al., 2014). Additionally, we want to investigate how changes in task instructions might affect the relationship between the lateralisation of alpha power and behavioural performance. We hypothesise that if alpha was more strongly related to accuracy than reaction time, there should be a stronger relationship between the lateralisation and performance when participants are asked to respond slowly and accurately. Earlier research furthermore established that only a subset of participants –those with high baseline power - showed the alpha lateralisation but that the behavioural benefit was independent of the modulation (Rihs et al., 2007). We therefore aim
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to investigate whether alpha power lateralisation indexed changes in behaviour on both within- and between-participants level.

3.4 Methods

3.4.1 Participants

Thirty-two students from The University of Auckland participated in this study and received NZD 20 for their participation. Four participants were excluded because of excessive noise in the EEG data (see Results). Data from the remaining 28 participants were analysed (M = 23.79 years, S.D. = 4.42 years, 19 women). All participants reported normal or corrected-to-normal vision and 20 were right-handed. Participants provided written informed consent and all research protocols were approved by The University of Auckland Human Participants Ethics Committee.

3.4.2 Stimulation and Procedure

Participants were seated in an electrically-shielded, darkened booth. Experimental stimuli were presented on a 21-inch LCD (60 Hz refresh rate) monitor using E-Prime 2.0 Professional presentation software (Psychology Software Tools Inc., Pittsburgh). The monitor was positioned at 57 cm in front of the participant and the viewing distance was maintained through the use of a chinrest.

Participants completed 15 blocks of a spatially cued discrimination task under three different response-deadlines. Participants were instructed to keep fixation on a central fixation cross that was displayed throughout the whole trial. The outlines of two squares in the lower left and lower right visual field remained present throughout the whole trial and served as placeholders for the targets. Each trial started with the presentation of the fixation array (fixation cross and two placeholders). After 250 ms an arrow-head appeared for 170 ms on either the left or right leg of the fixation cross and pointed to one of the placeholders. The
subsequent cue-target interval, during which the participants were instructed to covertly shift their attention to the cued location, lasted for a randomised time between 1000 and 1500 ms. The target was then presented for 50 ms. The target was a modified ‘Landolt c’, a stimulus that is often used in the assessment of visual acuity. The Landolt c’s used as targets here were the outline of a square that had a small gap (0.1°) either on the left or the right side.

Following the target-mask interval of 50 ms, the outline of the square was presented for 100 ms and served as the mask to interfere with target discrimination (see Figure 3.1 for a schematic representation of the stimuli and timing). Participants had to indicate via button-press on a standard keyboard whether the opening was on the left or right side of the target square (index fingers of left and right hand for opening on the left or right side respectively). The cue pointed to the left and the right on half of the trials and was valid in 80% of the trials (i.e. when the cue pointed to the left, the target appeared at that location on 80% of the trials and at the opposite, right, location on 20% of the trials). The target was equally likely to be open to the left and the right, and the side of the opening was determined independently of its location on the screen. Therefore the cue only indicated the target location (left or right placeholder) but not response (i.e. the side of the gap). The stimuli were black and presented on a light grey background (luminance: 23.6 cd/m²).

Figure 3.1: Experimental task. The placeholders were positioned at 2° below and 4° to the left and right of fixation. The target spanned 0.5° visual angle. Participants had to indicate via button press whether the gap in the target was on the left or right. The cue indicated the correct target location in 80% of the trials. Figure not drawn to scale.

Response-deadline instructions (three levels see below) varied between blocks. Each block started with an instruction of whether participants had either the ‘longest’,

<table>
<thead>
<tr>
<th>Fixation</th>
<th>Cue</th>
<th>Cue - Target</th>
<th>Target</th>
<th>Mask</th>
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<tbody>
<tr>
<td>250</td>
<td>170</td>
<td>1000 - 1500</td>
<td>50</td>
<td>100 ms</td>
</tr>
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85
‘intermediate’, or ‘shortest’ time to response in the upcoming block. These will be referred to as the slow, medium and fast block. At the beginning of the experiment participants were instructed verbally that during the blocks in which they had the longest time to respond, they should focus on making an accurate response whereas they should focus on making a fast response during the blocks in which they had the least time to respond. Participants received a warning (‘Too slow, respond faster’), when their reaction time was longer than the deadline in current block and received feedback on their performance (%corr) twice within a block. The feedback was presented for 5 s and reinstated the response-deadline instruction by stating that they should either focus on accuracy, speed or both in the current block.

The response-deadline for the “slow” block was 1000 ms for all participants. Response-deadlines for the “medium” and “fast” blocks were determined individually according to performance in two practice blocks before the experiment. The median response time over the two practice blocks plus 50 ms was taken as the deadline for the medium blocks and the median of the fastest 50% trials was taken as the deadline for the fast blocks (25% fastest trials). The minimum deadline in the fast block was 450 ms and deadlines were adjusted so the deadlines for the fast and medium block differed by at least 50 ms. On average the deadline for the medium block was 585 ms (S.D. = 88.52) and 485 ms (S.D. = 74.34) in the fast blocks. Participants completed 5 blocks of 40 trials each per deadline (600 trials in total, 200 per response-deadline). There were self-paced breaks (with a minimum duration of 30 s) between blocks and each block started with a 10 s countdown during which participants were instructed to settle into the chin rest and to get ready for the task.

Before the practice blocks and the start of the experiment participants were given both written and verbal instructions. They were especially instructed to not move their eyes but to covertly shift their attention to either the left of the right placeholder. Trials in which participants failed to respond (on average 0.4 %) were excluded from further analysis. The
experimental duration was approximately one hour, depending on the duration of the self-paced breaks.

### 3.4.3 Electrophysiological Recording and Pre-processing

The electroencephalogram (EEG) was recorded using a 128-sensor Geodesic Sensor Net and Net Amps 300 amplifiers (Electrical Geodesics Inc., EGI, Eugene, Oregon, USA). It was digitised at 250 Hz and acquired with respect to the vertex electrode. Individual sensor impedance was kept below 40 kΩ and measured both prior and half way through the experiment. Offline the data was analysed using EEGLab toolbox (Delorme & Makeig, 2004) and custom-written scripts for Matlab (The Math Works Inc., Natick, Massachusetts). Continuous EEG was first digitally high-pass filtered at 0.1 Hz using a finite impulse response filter.

The continuous EEG was segmented into 2710 ms segments, starting 550 ms before cue presentation to 2160 ms after. Each segment contained the cue, target and mask presentation regardless of the length of the cue-target interval. Segments were first visually reviewed for artefacts. Segments containing blinks immediately before or after stimulus presentation were discarded, as well as segments containing noise (e.g. non-stereotypic artefacts and muscle activity). On average 80% of the trails were accepted (range 75% to 89%). The valid conditions held at least 105 trials per participant (range: 105 – 149) and the invalid conditions at least 20 (range 20-38). There were no significant differences between trials accepted for the different response-deadlines (average 159 trials, $F(2,27) = 0.306, p = 0.737$). Four participants were excluded because more than 25% of trials were rejected. After artefact rejection, data were decomposed using an independent component analysis (ICA) implemented in EEGLab. Components that were identified as relating to eye blinks were not included into the remixing of the data (1-2 components per participant). Channels that contained excessive noise were discarded prior to the ICA and interpolated afterwards (using...
spherical-spline interpolation implemented in EEGLab). Following this, data were re-referenced to the nasion electrode and analysis focused on two electrode clusters over left and right occipital-parietal cortex (see Figure 3.3). They are positioned between electrodes P07 and O1 (left) and between P08 and O2 (right) of the international 10-20 system. These electrodes were chosen both based on the scalp distribution of alpha power across conditions and literature showing that attention related effects in alpha power are maximal over posterior-occipital electrode locations (e.g. Dombrowe & Hilgetag, 2014; Thut et al., 2006).

3.4.4 EEG Data analysis

Individual alpha frequency. The frequency band used for analysis was determined individually to account for individual differences in the alpha frequency band (e.g. Başar, 2012; Haegens et al., 2014; Klimesch, 1999; Pfurtscheller & Lopes Da Silva, 1999). The frequency with the maximal power in the 7-14 Hz frequency band was defined as the individual alpha frequency (IAF) (Gould et al., 2011; Thut et al., 2006). Power was determined by a Power Spectral Density estimate via Welch's method (using the spectopo function implemented in EEGLab) and the individual alpha band was chosen to encompass +/- 2 Hz around the IAF. We determined the IAF on the whole length of each epoch regardless of condition. The peak frequency was averaged across the six electrodes chosen for analysis. The resulting mean IAF was 9.7 Hz (SE = 0.23). The average alpha frequency band (7.8 Hz to 11.4 Hz) is similar to bands chosen in other studies (e.g. Gould et al. 2011 7.9 – 11.8 Hz, Thut et al. 2006 7.8 – 13.8 Hz, Worden et al. 2000 8-14 Hz). Power averaged in this IAF band will be used in all following analysis and regarded to as alpha power.

Time frequency analysis. Single-trial power was estimated using a modified Morlet wavelet transformation (Delorme & Makeig, 2004). The length of the wavelets varied from 3 cycles at 5.4 Hz to 13.8 cycles at 50 Hz. This analysis resulted in estimates for 400 time points (from 240 ms prior to cue onset to 1904 ms afterwards) and 25 log-spaced frequencies.
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Analysis focused on the alpha band, which was individually determined as described above. The squared absolute value was taken for each estimate (i.e. power). A 100 ms pre-cue time-window (-150 to -50 ms, during the presentation of the fixation cross) was chosen as the baseline. Single-trial power was averaged based on response-deadline and cue direction, resulting in six averages (valid and invalid in the slow, medium and fast blocks) per electrode cluster. These time-frequency averages were then averaged across electrode clusters resulting in an ipsi- and contralateral average per response-deadline condition and dB baseline corrected. Analysis focused on a 500 ms time window in the cue-target interval (450-950 ms), over which power in the alpha frequency band was averaged. We investigated differences in power modulation over the ipsi- and contralateral hemisphere across response-deadline blocks. We furthermore calculated a lateralisation index that takes power over the ipsi- and contralateral hemisphere into account (Haegens, Händel, et al., 2011; Thut et al., 2006). As the index increases, the higher the power over the ipsilateral hemisphere is, compared to the contralateral. The index is calculated as:

\[
\frac{\text{ipsilateral} - \text{contralateral alpha power}}{\left(\text{ipsilateral} + \text{contralateral alpha power}\right)/2}
\]

Additionally, we split participants in a high and low power group based on a median split of their baseline power across both electrode clusters and investigated whether there were group differences in both the alpha modulation in response to the cue and behavioural performance. We furthermore wanted to assess the relationship between an individual’s change in behaviour and alpha modulation across the response-deadline manipulation. Only valid trials were chosen for this analysis. Both single-trial behaviour and alpha power (baseline-corrected to single-trial baseline activity) were correlated with the block. For accuracy, a negative correlation means that the participant modulated their behaviour according to the instructions, responding more accurately in the slow (1) compared to the fast (3) block. A negative correlation for alpha power means that power was lower in the fast
compared to the slow block (stronger decrease). These two correlations (which could be understood as the strength of change across blocks) were then correlated with each other to assess whether a change in alpha power was accompanied by a comparable change in behaviour. The correlations were conducted for ipsi- and contralateral alpha power as well as for accuracy and reaction time. This procedure was derived from a similar analysis performed by Gould, Rushworth and Nobre (2011), relating the change in alpha activity to a change in behaviour.

3.4.5 Statistical Analysis

We conducted a 3 x 2 repeated-measures ANOVA with the factors Block (slow, medium, fast) and Validity (valid, invalid) to test for the influence of the behaviour manipulation on accuracy and response times. To test for differences in alpha power modulation we firstly performed a repeated-measures ANOVA with the factors Block (slow, medium, fast) and Hemisphere (ipsi-, contralateral). We then added Group as a between-participants factor in this ANOVA to test whether the modulation was influenced by the baseline power level. We furthermore used non-parametrical Spearman rank correlations to investigate the relationship between alpha power at baseline and the cue-related modulation.

Although the behavioural analysis did not reveal a significant interaction with baseline group, we conducted an exploratory analysis, in which we analysed the behavioural data separately for participants with high and low level of alpha power. To account for a violation of the assumption of sphericity, the degrees of freedom were corrected using Huynh-Feldt estimates of sphericity, whenever Mauchly’s test for sphericity indicated a violation of this assumption. Non-parametric Spearman rank correlations were used to assess the relationship between the change in alpha power and behaviour across response-deadlines.
3.5 Results

3.5.1 Behavioural Results

Our results show that both the response-deadline and attentional manipulation affected behaviour. Results of the 3 x 2 repeated-measures ANOVA with the factors Block (slow, medium, fast) and Validity (cue valid, cue invalid) showed a significant main effect for Block ($F(1.573, 42.472) = 32.336, p < 0.001, \varepsilon= 0.787$) and Validity ($F(1, 27) = 50.757, p < 0.001$) as well as a Block x Validity interaction ($F(2, 54) = 6.234, p = 0.004$) for accuracy. Participants were most accurate for validly cued targets in the slow condition and least accurate for invalidly cued targets in the fast condition. The interaction indicates that the cost for invalidly cued targets is largest in the fast condition. Reaction times showed a significant main effect for Block ($F(1.567, 42.309) = 58.386, p < 0.001, \varepsilon= 0.783$) and Validity ($F(1, 27) = 82.841, p < 0.001$) but no interaction. Participants were fastest for validly cued targets in the fast condition and slowest for invalidly cued targets in the slow condition (see Figure 3.2).

Figure 3.2: Behavioural performance across response-deadlines and attention conditions. Bars represent accuracy, lines reaction time. Both dependent measures were significantly influenced by both experimental manipulations of validity and response-deadline. Error bars represent SEM.
Although the side of the target opening was not related to its presentation side, we nevertheless tested whether the congruency between the side of the target opening and presentation affected behaviour. The so-called ‘Simon effect’ (Simon & Wolf, 1963), suggests that participants would be faster and more accurate when the side of the target opening was congruent to the target location (i.e. faster response to a target that is opened to the left and presented on the left side demanding a response with the left hand, compared to it being presented on the right and demanding a left response). We conducted a 3 x 2 x 2 repeated-measures ANOVA with the factors Block, Validity and Congruency (congruent, incongruent). In addition to the above mentioned effects we found a significant Block x Congruency ($F(2, 54) = 3.397, p = 0.041$) interaction for accuracy indicating that incongruency was most harmful under higher time pressure in the fast block. For reaction time we found a significant Validity x Congruency ($F(1, 27) = 13.508, p = 0.001$) interaction indicating that whether or not the target opening was congruent to its presentation side had a greater effect on reaction time for invalidly cued targets. Similar to the above described results, this might suggest that accuracy and reaction time are influenced differentially by our task manipulations. Although reaction time differed between blocks, the effects of validity and congruency are similar at all levels. On the other hand, accuracy was differentially affected by both validity and congruency depending on the block.

### 3.5.2 Electrophysiology

We found that the attentional cue had a significant effect on alpha power lateralisation over the occipital-parietal cortex. Following the cue onset there was less power over the contralateral compared to the ipsilateral hemisphere. This effect was present across all blocks and over the duration of the cue-target interval (see Figure 3.3). As can be seen in Figure 3.3 the effect was pronounced most strongly in the alpha band (~8-12 Hz). There was a significant main effect of Hemisphere ($F(1,27) = 25.992, p < 0.001$), indicating less power
over the contralateral compared to the ipsilateral hemisphere (3 x 2 repeated-measures
ANOVA with the factors Block (slow, medium, fast) and Hemisphere (ipsi-, contralateral)).
There was no effect of Block, indicating that the modulation of alpha power was similar
across response-deadlines. We calculated a lateralisation index (Haegens et al., 2014; Thut et
al., 2006) that depends on the relative difference between power over the ipsilateral and
contralateral hemisphere. The index is significantly greater than 0, indicating relatively more
power ipsilaterally, in all three response-deadline blocks (slow (0.0585): $t(27) = 3.784, p_{corr}=
0.003$; medium (0.0755): $t(27) = 6.4, p_{corr} < 0.001$; fast (0.0551): $t(27) = 3.779, p_{corr} = 0.003$).
This further indicates a lateralisation of alpha power in response to the cue.
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Figure 3.3: Cue-related modulation of alpha power. a) Difference between ipsilateral and contralateral power averaged across all blocks averaged across participants. 0 ms indicates cue onset. Dotted box indicates average time-frequency analysis-windows (frequency band used for analysis was chosen individually to encompass ±2 Hz of the IAF). Earliest target onset was at 1170 ms after cue. b) Scalp distributions of alpha power show that the effect is localised to the occipital-parietal cortex. Triangles indicate electrode clusters used for analysis. The first two scalp maps represents data averaged across all participants at baseline and during the cue-target interval. Activity over the left and right hemisphere was averaged across cue conditions and ipsilateral and contralateral activities are shown on the left and right hemisphere respectively. Participants were divided into two groups based on their alpha power at baseline. The third scalp map shows activity in the cue-target interval for participants with low baseline power and the forth (most right) map shows activity for the high baseline group. Note the different power scales used to display the effects per group.

Earlier research has indicated that alpha power at baseline might influence the cue-related lateralisation of alpha power (Rihs et al., 2009). To test for this effect we firstly correlated baseline power with the attentional alpha modulation and then sorted participants into a high and low group based on a median split of baseline alpha power. There was a significant positive Spearman rank correlation between baseline alpha power and the lateralisation index ($\rho = 0.534, p = 0.003$) (Figure 3.4a), indicating that participants with high baseline power showed a stronger lateralisation of alpha power in response to the cue. We
then investigated whether the attentional alpha power lateralisation was modulated by alpha power across experimental blocks by adding the between participants factor Group to the above described 3 x 2 repeated-measures ANOVA. In addition to the main effect for Hemisphere, we found a significant Hemisphere x Group interaction ($F(1,26) = 5.387, p = 0.028$), suggesting that participants with high baseline alpha power showed a larger difference between power over the ipsi- and contralateral hemisphere (Figure 3.4c). As shown by the lateralisation index, participants with low baseline power only showed a significant lateralisation in the medium block ($t(13) = 3.470, p_{corr} = .024$), whereas participants with high baseline power show a significant lateralisation in all blocks (slow: $t(13) = 4.343, p_{corr} = .006$; medium: $t(13) = 5.923, p_{corr} < .001$; fast: $t(13) = 3.677, p_{corr} = .018$).

We furthermore investigated whether behaviour differed between baseline groups. Therefore we first added Group as a between-participant factor to the above described 3 x 2 repeated-measures ANOVA. There were no significant interactions with group for neither accuracy nor reaction time ($p > 0.2$). We nevertheless conducted an exploratory analysis in which we analysed accuracy separately for baseline power groups. The data for all participants indicated that the cost for invalidly cued targets increased from the slow to the fast block (significant Block x Validity interaction). By investigating the cost (valid accuracy – invalid accuracy) per group we show that this is only the case for participants with low baseline power (repeated-measures ANOVA for Costs (slow, medium, fast block), $F(2,26) = 7.671, p = 0.003$, linear trend $F(1,13) = 12.56, p = 0.004$).

For participants with high baseline power, the cost does not change across blocks ($F(2,26) = 2.072, p = .126$). There were no differential effects for reaction time.
Figure 3.4: Effect of baseline power on cue-related alpha lateralisation and behavioural response. a) Significant positive Spearman rank correlation was found between baseline power and lateralisation index. The lateralisation index is positive if power is larger over the ipsilateral compared to the contralateral hemisphere. b) Effect of baseline power on accuracy. The lower graphs illustrate the exploratory analysis in which we analysed the difference in cost for invalidly cued targets separately for the baseline power groups. Cost is similar across blocks for high baseline group but increases under higher time pressure for high baseline group. Error bars represent SEM. c) Alpha power modulation separately for low and high baseline power group. 0 indicates cue-onset. Earliest target presentation was at 1170 ms. *p < 0.05, **p < 0.01.
3.5.3 Brain-Behaviour Correlations

We aimed to investigate whether alpha power lateralisation can predict behaviour if we take the response-deadline manipulation into account. We therefore correlated the change in alpha power across blocks with the change in behaviour across blocks (see Methods). Due to the low number of invalidly cued trials, we focused this analysis only on the validly cued trials. Furthermore these should be the trials where the alpha modulation is most effective in predicting behaviour as other processes such as reorienting of attention are taking place in invalidly cued trials and might impede with the effect of anticipatory alpha power on performance (Corbetta & Shulman, 2002; Thut et al., 2006). There were significant positive Spearman rank correlations between the change in accuracy across blocks and the change in ipsi- and contralateral power across blocks (ipsi: \( \rho = 0.398, p = .036 \); contralateral: \( \rho = 0.431, p = 0.022 \); see Figure 3.5). Participants who decreased their power more under higher time pressure (negative correlation between block and power) also showed a greater decrease in behavioural performance from the slow to the fast block (negative correlation between block and accuracy). A larger change in both power and accuracy could be interpreted as being more sensitive to the task instructions. This relationship was similar for both the change in ipsi- and contralateral alpha power suggesting that the alpha power modulation and not its lateralisation influences behaviour. There were no significant correlations for reaction time.
Figure 3.5: Relationship between behavioural and alpha power modulation across response-deadline blocks (only valid trials). X-axis represents the change in power across blocks (negative means less power under higher time pressure) and y-axis represents change in accuracy (negative values mean smaller accuracy under higher time pressure). A significant correlation between those measures indicates that a change in power across blocks predicts a change in accuracy across blocks.

3.6 Discussion

We investigated the behavioural consequences of cue-related alpha power modulations in a spatially cued visual discrimination task under three different response-deadlines. It is well established that alpha power is lateralised over posterior cortex in response to an visuospatial attentional cue (e.g. Capilla et al., 2014; Gould et al., 2011; Kelly et al., 2006; Rihs et al., 2009; Sauseng, Klimesch, Stadler, et al., 2005; Thut et al., 2006; Trenner et al., 2008; Worden et al., 2000; Yamagishi et al., 2005). We wanted to assess whether increasing the time-pressure to respond influences the modulation of alpha power and the relationship between the lateralisation and behavioural performance. Behavioural performance was effectively manipulated by both the attentional validity and the response-deadline instructions: Participants were slower and less accurate for invalidly cued trials. Furthermore, they were more accurate but slower when they had more time to respond and faster but less accurate under higher time pressure, demonstrating a speed-accuracy trade-off (SAT). Alpha power was also affected by the attentional modulation in the predicted manner. Posterior alpha power was lower over the contralateral compared to the ipsilateral hemisphere.
in the interval following the cue. However, the response-deadline manipulation did not affect this alpha power lateralisation and it was similar across the different deadline blocks.

Other factors and task instructions that affect the top-down modulation of attention have previously been shown to modulate the alpha power lateralisation or alpha power level. In particular, the top-down modulation of cue reliability has been shown to influence the lateralisation of alpha power. Both for visual (Dombrowe & Hilgetag, 2014; Gould et al., 2011) and tactile stimuli (Haegens, Händel, et al., 2011) alpha power is lateralised more for cues with a higher predictive value. This has been taken to suggest that alpha power modulation is under top-down control. Interestingly though the relationship between alpha power lateralisation and behavioural performance was only established for highly predictive cues in those reports (Dombrowe & Hilgetag, 2014; Gould et al., 2011; Haegens, Händel, et al., 2011). Even though the behavioural benefit for validly cued trials is also shown if the cue is only correct in 60-75% of the trials, this benefit could not be related to the alpha power lateralisation. Furthermore Pastötter and colleagues (2012) modulated SAT on a single trial basis, by telling their participants to either respond either quickly or accurately in the upcoming trial. Their data shows a decrease in alpha power when participants were asked to respond accurately compared to responding quickly. However in contrast to the present study, they investigated alpha power in response to the ‘instruction’ cue (speed vs accuracy) and did not investigate effects of the spatial cues. Furthermore, we changed the SAT instructions between blocks and not on a single-trial level. Our results indicate that although there is behavioural effect of the response-deadline modulation, this is not reflected in the alpha power lateralisation averaged across participants.

In accordance with previous research (Rihs et al., 2009) we show that the alpha power level at baseline is strongly related to the lateralisation of alpha power: Only participants with a relatively high level of alpha power at baseline show a strong cue-related lateralisation.
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However, whether or not participants lateralise their alpha power is not strongly related to task performance and all participants show the benefit for validly cued targets. This result challenges the notion that the cue-related lateralisation of alpha power indexes the mechanism responsible for the behaviourally relevant orienting of attention.

The first report of individual differences in alpha lateralisation (Rihs et al., 2009) also failed to find such a difference in the behavioural performance between groups. Rihs and colleagues argue that participants might use different strategies in the task. Those different strategies could affect the lateralisation of alpha power, but ultimately lead to similar performance. Although we did not find an overall difference in behaviour between groups, we investigated the influence of the task instructions separately per group. This exploratory analysis suggests that participants with low and high baseline power might in fact use different strategies. Participants with low alpha power at baseline show a greater interaction between the behavioural effects of the attentional and response-deadline instructions. They show a relatively small cost for invalidly cued targets in the slow condition, suggesting that they are able to spread their attention across both potential target locations effectively. However this costs increases if there is more pressure to respond fast. The cost for invalidly cued targets remains fairly stable across blocks for participants with high baseline power. Even though this difference is rather subtle, it is the first demonstration of a behavioural difference between groups of participants who show the attentional modulation of alpha power and those who do not. The behavioural effect of alpha power modulation thus is dependent on further constraints of the task. A stronger modulation of performance (a more difficult task or stricter response-deadlines) might help to establish further differences between participants and investigate whether and what kind of different strategies they might be using.
Lower alpha power is an index of increased cortical excitability, which seems to be beneficial in visual detection and discrimination tasks (e.g. Busch et al., 2009; Ergenoglu et al., 2004; Mathewson et al., 2009; van Dijk et al., 2008). Participants with lower alpha power at baseline indeed demonstrated superior performance in our task in the slow block, as they show smaller cost for invalidly cued targets. Interestingly, participants with higher baseline power show similar performance for validly cued targets in the slow blocks but their performance for invalidly cued targets is lower. Results under this response-deadline thus match the supposed function of the attentional alpha power modulation. Participants with high power at baseline show stronger alpha lateralisation, which could explain the cost for the invalidly cued targets (as they are presented to the side over which alpha power is increased). This could suggest that when participants are asked to respond slowly, lower baseline power is related to an overall increase in performance (both validly and invalidly cued targets) showing that participants are able to spread their attention across the visual field. However, if baseline power is high (which seems to be detrimental for performance), performance for validly cued targets could be optimised by processes that are indicated by the lateralisation of alpha power (but on the flip-side leading to lower performance for invalidly cued targets).

Under higher time pressure the cost for invalidly cued targets are similar for both baseline groups. This suggest that the mechanisms underlying the alpha power lateralisation cannot be the only mechanism underlying the attentional orientation as the lateralisation is only present in a subset of participants and behavioural performance is affected by both the modulation of attention and response-deadline. Further, it suggests that the effect of the alpha power lateralisation is most strongly observed if participants are not doing a time-pressured task. The different behaviour for alpha power groups is only shown for accuracy but not for reaction time. This is in line with the finding that the time course of the change in contralateral alpha modulation follows the time course of the deployment of the attention
benefit in accuracy, but that others factors play a role in the effect of attention on reaction time (van Ede, de Lange, et al., 2012).

We furthermore wanted to investigate whether the change in behaviour across experimental manipulations can be explained by a differential modulation of alpha power on a single-trial level. We found that on an individual level the change in alpha power can indeed predict the change in behaviour across response-deadlines blocks. Participants whose alpha power change more strongly to the response-deadline instructions, i.e. who show a stronger decrease in both ipsi- and contralateral alpha power from the slow to the fast blocks, also show a stronger change in accuracy (a greater decrease in performance from slow to fast blocks). This suggests that the modulation of alpha power is functionally related to changes in behaviour and that the strength of this relationship critically depends on task demands and is modulated by individual differences. We found similar effects for the ipsilateral and contralateral change. In agreement with Dombrowe and colleagues (2014) this might suggest that a general decrease in alpha power is a better predictor of performance than the lateralisation. By applying source localisation (in contrast to our sensor-level analysis) Capilla and colleagues (2014) could show that different generators might underlie the ipsilateral and contralateral modulation. The contralateral decrease was localised to area V6 in the ventral stream, which is supposedly involved in the recognition of digits as required in their tasks, whereas the ipsilateral increase was localised to area V6 in the dorsal stream that could be involved in the inhibition of the ipsilateral side of space. They claim that behavioural performance for validly cued trials is predicted by the contralateral decrease, whereas performance for invalidly cued trials is contingent on the relative difference between power over the ipsilateral and contralateral hemisphere. However they also report a high correlation between ipsilateral and contralateral power, questioning whether the lateralisation is really the behaviourally relevant factor.
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Taken together, the decrease in alpha power has a stronger behavioural effect than the cue-related lateralisation. Although only a subset of participants shows the lateralisation, all participants show the behavioural benefit of validly cued trials. Furthermore the lateralisation is not affected by the response-deadline manipulation (even though the manipulation has a behavioural effect and is shown to interact with the validity effect), but the decrease in accuracy under increased time-pressure to respond is predicted by the decrease across blocks over both the ipsilateral and contralateral hemisphere. Given the numerous reports of alpha lateralisation in response to attentional cues (e.g. Capilla et al., 2014; Gould et al., 2011; Kelly et al., 2006; Rihs et al., 2009; Sauseng, Klimesch, Stadler, et al., 2005; Thut et al., 2006; Trenner et al., 2008; Worden et al., 2000; Yamagishi et al., 2005) a relationship between attentional orienting and the cue-related modulation of alpha power cannot be disregarded. However there might be mechanisms other than the behaviourally relevant shifting of attention that could explain this relation. One – admittedly highly speculative – alternative hypothesis might be that the lateralisation indexes mechanisms of saccadic suppression or the anticipatory re-mapping of visual space (Findlay & Walker, 1999; Medendorp et al., 2007; Posner et al., 1980; Rizzolatti, Riggio, Dascola, & Umilta, 1987; Smith & Schenk, 2012), which does not necessarily have to result in the behavioural benefits accruing to avoid looking. Future research should investigate the relationship between saccadic eye movements and modulations of alpha power in more detail.

Alternatively the failure to establish a clear behavioural correlate of the alpha power lateralisation could also be due to other specifics of the task. For example it has been claimed that the ipsilateral increase is an index of suppression of input at the unattended side (Foxe & Snyder, 2011). Suppression should therefore primarily occur if the unattended side can really be ignored and there are no ‘invalidly cued targets’ (e.g. Foxe et al., 1998; Foxe & Snyder, 2011; Worden et al., 2000). Along the same lines, the presence or absence of distracting
stimuli is also discussed as a modulating factor of the alpha lateralisation. It is assumed that having to ignore distracting stimuli further strengthens the ipsilateral increase (e.g. Händel et al., 2010; Kelly et al., 2006). A strong lateralisation (that involves both a contralateral decrease and an ipsilateral increase) might not be found in our design, as we used probabilistic cues and there were no distractors. We cannot distinguish whether the difference in alpha power over the ipsilateral and contralateral hemisphere is driven by a contralateral decrease or an ipsilateral increase (after the initial increase shown over both hemispheres).

Nevertheless we find it intriguing that although the difference in power between hemispheres is only shown for a subset of participants, the behavioural effect seems to be largely independent of this. Even if the group differences in the slow condition were taken to suggest that people with high baseline power suppress the unattended side more than participants with low baseline power, it does not explain why the same difference in lateralisation between baseline groups is shown under high time pressure, without an effect on behavioural performance.

In conclusion our results show that although there was a behavioural effect of the response-deadlines, causing participants to either make fast but less accurate or slow and accurate responses, this modulation was not reflected in the cue-related lateralisation of alpha power. In line with previous research alpha power was shown to be decreased over the contralateral compared to the ipsilateral hemisphere. However, the lateralisation was the same for all response-deadlines and only shown for participants with relatively high alpha power levels at baseline. Performance was similar regardless of lateralisation, although participants with low power seem to be able to spread their attention more if they have a long time to response, shown by a lower cost for invalidly cued trials in the slow compared to the fast block. This could also be interpreted as them being better able to balance the task requirements, as they show better performance for both validly and invalidly cued targets.
when asked to respond accurately and adapt their response pattern more strongly across the blocks. However, the results strongly suggest that although the cue-related lateralisation of alpha power indexes aspects of the orienting of visuospatial attention, it does not seem to index those that are behaviourally relevant or are associated with the speed-accuracy trade-off. On an individual level, we show that the more alpha power changes in response to task instructions, the higher the change in performance. This further indicates that alpha power is indexing behaviourally relevant processes and the ability to adapt behaviour in response to task requirements.

3.7 Chapter Epilogue

Below we report on two additional findings that although not reported in the main analysis might support our claim. The change in single-trial alpha power across response-deadline conditions has been shown to predict the change in accuracy across them. This suggests that pre-stimulus alpha power influences performance. However, this relationship is not as direct as the one we reported in the previous chapter. In the previous chapter, lower pre-stimulus alpha power was related to a higher hit and false alarm rate as well as to a decrease in response criterion. Such a direct relationship between pre-stimulus alpha power and behavioural performance (indicated by hit rate) was not shown in the data for this experiment (see Figure 3.6).

Accuracy was not only similar across participants with high and low alpha power at baseline, but also for trials preceded by high and low power. There was no significant effect or interaction with power (when we included it in a 3 x 2 x 2 repeated-measures ANOVA with the within-subject factors of Block, Validity and Power and the between-subjects factor Baseline Group). If at all, the results in Figure 3.6 might suggest that performance might be influenced by single-trial alpha power for invalidly cued trials and more so for participants with high baseline power. However, the trial numbers for the invalidly cued trials are rather
low and the averages might not be reliable estimates, especially if the trials are split between high and low pre-stimulus power. We also did not find any differences between baseline groups or low and high single-trial power for $d'$ and $c$ that were shown to be related to alpha power in the previous chapter. In contrast to the detection task in Chapter 2, we use a discrimination task here. Performance is usually less biased in a discrimination task (Macmillan & Creelman, 2005), which might explain why we were not able to establish the relationship between alpha power and response criterion here.

Performance in validly cued trials in this task was higher than in the task used in Chapter 2. Such high performance might interfere with the ability to find a relationship between alpha power modulations and performance. In addition, we suggest that alpha power might not have a simple relationship to performance in this task due to the more complex task requirements. Alpha power might be related to performance especially in task that require an immediate and rather simple response (see epilogue to chapter 2 and Drewes & VanRullen, 2011; Greent-'t-Jong et al., 2011). Having two experimental manipulations (attention and SAT) arguably increases the task demands and might therefore mask the effect of alpha power fluctuations on behavioural performance.
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Figure 3.6: Relationship between alpha power (between and within participants) and accuracy. See Figure 3.4 for a relationship between alpha power at baseline and behaviour. The same data is shown here, with the additional split into low and high power in a single trial basis. There was no effect of single-trial alpha power for neither baseline group on accuracy. Error bars represent SEM.

Alpha power at baseline might indicate how well participants can adapt to this increased load and we suggested that participants with low alpha power might be able adapt their behaviour more in response to the task requirements. Figure 3.7 shows the correlation between the change in accuracy and the change in reaction time across response-deadlines. This analysis is similar to the ones shown in the main analysis, with the difference that instead of correlating the change in pre-stimulus alpha power with a change in performance, the change in the two behavioural indices is correlated with each other. The change in reaction time is larger than the change in accuracy across response-deadlines. This is probably due to the overall high accuracy in the task. Most participants could do the task very well, even under high time pressure (and the correlation takes only validly cued targets into account). The correlation between the change in accuracy and reaction time was significantly positive for participant with low baseline power \( \rho = 0.741, p = .0002 \) but there was only a
significant trend for participants with high baseline power ($\rho = 0.525, p = .054$). Arguably this could be heavily influenced by the single high baseline power participant that showed the largest change in accuracy. Most of the other high baseline participants do not show a large change in accuracy across response-deadline conditions.

The positive correlation between the change in accuracy and reaction time for the low baseline group, could indicate that those participants were able maintain a similar balance between both response requirements across blocks. Participants who showed a large change in accuracy across blocks also showed a large change in reaction time and vice versa. We think that this further supports our suggestion that participants with low alpha power are able to adapt their behaviour more in response to the task requirements. It is hard to determine what ‘superior performance’ that is usually associated with low alpha power would be in the current task. Control over the conflicting requirements of responding fast or accurately could be superior performance and show adaptability to task requirements. Participants with higher power at baseline show a similar change in reaction time across block as participants with low baseline. However this change does not correlate as strongly with their change in accuracy.
Figure 3.7: Relationship between the change in accuracy and the change in reaction time across response-deadlines. Data is shown separately for participants with low (blue) and high (red) baseline power. Negative values on the x-axis mean that accuracy decreased from the slow to the fast blocks. Negative values on the y-axis mean that responses were faster in the fast compared to the slow block.
Chapter 4: Don’t get too excited: High Cortical Excitability is Related to Fast but Incorrect Responses in Visual Discrimination and Selective Attention

4.1 Chapter Prologue

In this chapter we combined a visual discrimination and selective attention task to investigate whether the behavioural effect of fluctuations in alpha power is comparable under the experimental settings that were used in Chapter 2 and 3 respectively. It seems to be generally assumed that decreases in posterior alpha power improve sensory performance and that the lateralisation seen in response to visuospatial cues is in fact indexing a mechanism that takes control over these spontaneous fluctuations of alpha power to support the increase in performance at attended locations. We have shown in Chapter 2 and 3 that this interpretation of the role of alpha power in cortical processing is probably too simplistic. The behavioural consequences of fluctuations in alpha power are more complex than a general ‘improvement’ and to depend on a variety of task settings: In Chapter 2 it was shown that on a single-trial level alpha power was mainly related to a change in response criterion. Depending on the situation a more liberal response criterion under low power can be interpreted as either an increase or decrease in performance. In Chapter 3 low alpha power was associated with a better ability to adapt to task requirements. Results in Chapter 3 furthermore suggest that the cue-related lateralisation might index a mechanism that is not related to the behavioural benefit seen at cued locations. Performance seemed to be influenced by the general level of alpha power over bilateral posterior cortex.

Given these and other recent reports that have started to reveal some of the complexities of the relationship between alpha power modulations and behavioural performance, we wanted to directly compare the behavioural consequences of spontaneous
(i.e. in detection and discrimination tasks) and cue-evoked (i.e. in selection attention tasks) fluctuations in alpha power. Although the proposed role of alpha power for sensory perception seems to be consistent under both task settings (i.e. lower alpha power leads to superior performance), performance in detection and selective attention task does not have to be necessarily related to the same underlying mechanisms. We found it very surprising that a common mechanism and behavioural correlate for alpha power fluctuations seems to be willingly accepted across the field, as is has not, to our knowledge, been tested directly yet.

The analysis methods used in this chapter are similar to the ones described in Chapter 2 and 3. The EEG was recorded using the new version of the Netstation amplifier (Net Amps 400 series). Furthermore we investigate the change in alpha power in response to the visuospatial cue by hemisphere. We found a general difference in pre-stimulus power between hemispheres in Chapter 2. The behavioural effect of pre-stimulus alpha power was however similar across both hemispheres, and most analyses in Chapter 2 looked at alpha power averaged across hemispheres. Alpha power was also averaged across hemispheres in Chapter 3, following the literature that often reports differences between the ipsilateral and contralateral hemisphere and ignores the actual stimulus location. However, hemispheric differences are often reported in the attentional literature and we therefore decided to incorporate hemispheres as a factor in this chapter’s analysis.

4.2 Abstract

A similar role for decreases in alpha power has been inferred from both sensory detection and selective attention tasks. Recent studies show that perceptual performance is increased when pre-stimulus alpha power is low. These studies usually assume that alpha power is spontaneously fluctuating and that these fluctuations might help to explain the commonly observed variability in perception. On the other hand, studies focusing on selective attention suggest that these fluctuations can be brought under top-down control. In
response to visuospatial cues, alpha power is found to be lower over the side of the head contralateral to the anticipated target location and higher over the ipsilateral side. It is assumed that this lateralisation supports the facilitation of performance at the cued location and inhibits distracting information. However whether spontaneous and cue-related fluctuations of alpha power actually have similar behavioural consequences has not been tested yet.

We recorded EEG while 22 participants performed a visual discrimination task. Prior to the target presentation participants either received a spatial cue that informed them where the target would appear, or a neutral cue that indicated that the target was equally likely to appear at the central or at one of the two peripheral target locations. Participants responded faster and more accurately at the central compared to the peripheral locations and when they received a spatial compared to a neutral cue. The general alpha power modulation was similar in both cueing conditions and the lateralisation of alpha power in response to the spatial cue was only shown over the left hemisphere. On a single-trial level fast responses were preceded by relatively low alpha power under both cueing conditions, supporting the suggestion of similar behavioural consequences of cue-related and spontaneous fluctuations of alpha power. Importantly a fast response was more likely to be incorrect in this task, showing that lower alpha power is not necessarily beneficial for all aspects of behavioural performance.

4.3 Introduction

Over the last 15 years or so, oscillations in the alpha frequency band (~8-12Hz) have become the focus of numerous investigations on the variability in sensory perception (see e.g. Foxe & Snyder, 2011; Mathewson et al., 2011; VanRullen et al., 2011 for recent reviews). Our ability to perceive and respond to the plethora of sensory information in our environments varies from moment to moment (Ashby & Lee, 1993). Often the variability seen in response to identical stimuli (especially near perceptual threshold) is downplayed as a
consequence of perceptual noise. However recent research has been able to relate at least some of this variability to spontaneous fluctuations in alpha power at the time of stimulus presentation. Lower alpha power is usually related to better performance (Busch et al., 2009; Ergenoglu et al., 2004; Hanslmayr, Aslan, et al., 2007; Mathewson et al., 2014; Mathewson et al., 2009; Roberts et al., 2014; van Dijk et al., 2008) and decreases in alpha power presumably reflect cortical activation and interaction with the environment during task processing and sensory stimulation (e.g. Berger, 1929; Hanslmayr et al., 2011; Klimesch, 1999; Klimesch et al., 1997; Pfurtscheller, 1992, 2001; Pfurtscheller & Lopes Da Silva, 1999; Sauseng, Klimesch, Doppelmayr, et al., 2005).

On the other hand, it is well established that we can, at least to a certain extent, use processes such as selective attention to influence the way we perceive sensory stimuli. Selective attention is commonly assumed to play a crucial role in enabling our interactions with the environment by selecting certain information for further and more detailed processing and suppressing distracting information (e.g. Broadbent, 1958; Buschman & Miller, 2010; Carrasco, 2011; Treue, 2001). With regard to our discussion here, it has been shown that both the neuronal and behavioural responses to stimuli are enhanced if they are attended to compared to when attention is focused elsewhere (e.g. Desimone & Duncan, 1995; Posner et al., 1980). In a sense, selective attention is therefore another mechanism that leads to the variability in perception of identical stimuli. Processing at the cued locations has been shown to be ‘biased’ or enhanced even before the target appears (e.g. Kastner et al., 1999; Luck et al., 1997). Recent studies found that this orienting of attention might be indexed by a cue-related lateralisation of alpha power over posterior cortex. In preparation for the target, alpha power is usually shown to be lower over the side of the head contralateral to the cue (e.g. Kelly et al., 2006; Rihs et al., 2009; Sauseng, Klimesch, Stadler, et al., 2005; Thut et al., 2006; Trenner et al., 2008; Worden et al., 2000; Yamagishi et al., 2005). This
lateralisation has been related to the increase of performance at cued locations (Haegens, Händel et al., 2011; Händel et al., 2010; van Ede, de Lange et al., 2012; van Ede, Koster et al., 2012). It is a common assumption that both spontaneous and cue-related decreases in alpha power lead to superior performance in visual tasks. Selective attention could thus operate by taking control over the spontaneous fluctuations of alpha power and decrease power contralateral to cued locations to increase performance. Quite surprising though, this has, at least to our knowledge, not yet been tested and studies seem to be divided into either focusing on the role of alpha frequency oscillations in ‘stimulus detection’ or ‘selective attention’. A first hint towards a common neural mechanism comes from a recent study by Mathewson and colleagues (2014). Using optical imaging in a detection task they localised the generator for the behaviourally relevant fluctuations of alpha power to the cuneus region. Importantly this generator was shown to be influenced by regions of the dorsal attention network, which could indicate a common generator for cue-related and spontaneous fluctuations in alpha power. On the other hand recent studies on both detection and selective attention show that the relationship between alpha power fluctuations and behavioural performance might be much more complex than suggested at first sight. However there are many differences in detection and selective attention designs and performance does not have to be necessarily influenced by a common mechanism.

Decreases in alpha power have been related to a heightened state of cortical excitability and a focus on the external sensory environment since their discovery in the early 20th century (Berger, 1929; Bishop, 1933; Hanslmayr et al., 2011; Lindsey, 1952). Although most studies focusing on spontaneous fluctuations of alpha power show superior performance when alpha power is low, there are also conflicting results (especially when using somatosensory stimuli) arguing that either moderate or high alpha power is related to an
increase in behavioural performance (e.g. Babiloni, Vecchio, Bultrini, Luca Romani, & Rossini, 2006; Lange et al., 2012; Linkenkaer-Hansen et al., 2004; Rajagovindan & Ding, 2011; Zhang & Ding, 2010). Likewise more recent reports argue that the changes in performance seen under lower alpha power in detection tasks are not due to modulations of the sensory percept or the processing of the input as such, but rather that alpha power affects a ‘decisional’ stage (see Chapter 2 and Chaumon & Busch, 2014; Grent-’t-Jong et al., 2011; Lange et al., 2013). For example, we show in Chapter 2 that decreases in alpha power are related to a more liberal response criterion that leads to both more hits and false alarms in a signal detection task. A modulation of response criterion is orthogonal to performance, as both a more liberal and a more conservative criterion can be interpreted as superior performance, depending on whether the emphasis lies on not missing any targets (a liberal criterion that leads to both more hits and false alarms would be ‘superior’ here) or not misclassifying noise as a target (a conservative criterion that limits false alarms but increase misses would be ‘superior’ in this case).

Although the alpha lateralisation following a spatial cue is well established there are considerable discrepancies as to how it is related to performance or to certain aspects of performance (most notably accuracy and reaction time). The lateralisation is interpreted as a manifestation of the spatial bias that is responsible for the higher sensitivity for stimuli at cued locations and to be correlated to the associated behavioural benefit (Foxe & Snyder, 2011; Kastner et al., 1999; Posner et al., 1980; Thut et al., 2006; van Ede, Koster, et al., 2012). Whereas some studies indeed show that the lateralisation of alpha predicts the superior performance at cued location in both accuracy and response time (Haegens, Händel, et al., 2011; Kelly et al., 2006), others show effects only in response time and not accuracy (Thut et al., 2006; Trenner et al., 2008). In some studies, the behavioural benefit at cued locations cannot be related to the alpha power lateralisation (van Ede et al., 2014), or at least not if the
cue reliability is relatively low (60-75% see Dombrowe & Hilgetag, 2014; Gould et al., 2011). Our results in Chapter 3 could even suggest that the lateralisation might index a mechanism that although related to the orienting if attention, is not behaviourally relevant. In accordance with earlier results (Rihs et al., 2007) we show that only a subset of participants - those with relatively high power at baseline - show the alpha lateralisation. However the behavioural benefit of the cue is shown regardless of the lateralisation. Together with Dombrowe and Hilgetag (2014) we argue that the general decrease in alpha power is related to behavioural performance (albeit not necessarily in a straight forward manner) but that the lateralisation is a manifestation of some other mechanism.

The motivation of the current study is thus two-fold. Firstly we wanted to directly compare the behavioural consequences of spontaneous and cue-related fluctuations in pre-stimulus alpha power. Secondly we wanted to take the revealed complexities of the relationship between alpha power and behavioural performance into account and carefully investigate the behavioural consequences of both the fluctuations in alpha power and its lateralisation (e.g. accuracy and reaction time as well as central and peripheral target locations). Participants performed a visual discrimination task under two different cueing conditions: Either the cue indicated at which of the three possible locations the target would appear (spatial cue) or the cue was uninformative as to the target location (neutral cue). We hypothesise that participants would be faster and more accurate with a spatial cue, and that this effect would be especially pronounced at the peripheral locations. We expect to find the well-established lateralisation of alpha power over the left and right occipito-parietal cortex for spatial cues to the peripheral locations. Most importantly we hypothesise that although alpha might be modulated differentially in response to the cues, the relationship between alpha power and behaviour will be similar. We expect that lower alpha power will be
beneficial for performance regardless of whether it is low due to spontaneous fluctuations or due to a decrease in response to an attentional cue.

4.4 Methods

4.4.1 Participants

Twenty-five students from The University of Auckland participated in this study and received NZD 20 for their participation. Three participants were excluded because of excessive noise in the EEG data (see Results). Data from the remaining 22 participants were analysed (M = 22.22 years, S.D. = 3.74 years, 5 males). All participants reported normal or corrected-to-normal vision and 19 were right-handed. Participants provided written informed consent and all research protocols were approved by The University of Auckland Human Participants Ethics Committee.

4.4.2 Stimulation and Procedure

Participants were seated in an electrically-shielded darkened booth. Experimental stimuli were presented on a 21- inch LCD (60 Hz refresh rate) monitor using E-Prime 2.0 Professional presentation software (Psychology Software Tools Inc., Pittsburgh). The monitor was positioned at 57 cm in front of the participant and the viewing distance was maintained through the use of a chinrest.

Participants completed 18 blocks of a visual discrimination task. Three coloured circles with a radius of 2° visual angle (blurred with a Gaussian kernel of 56.4 pixel radius) served as placeholders and were presented at the central, left and right potential target location throughout the trial. The central circle was always white, one of the peripheral circles was blue and the other one was green. The location of the green and blue circle changed half-way through the experiment and their initial position was alternated between participants (half the participants started with green on the left and the other half started with
Each of the circles had a central black dot. Participants were asked to fixate on the dot in the central white circle throughout the whole trial. The trials started with the presentation of the fixation array (the three coloured circles). After 750 ms the central fixation dot changed its colour and doubled its size (size from 0.2 to 0.4° visual angle) for 300 ms, which was the cue event. The central dot could either change to grey, blue, green, or stay black (but still double in size). A change to grey indicated that the target array would appear at the central location and a change to blue or green indicated that the target array would appear on top of the circle in that colour (to the left or right of fixation). Taken together these cues will be referred to as spatial cues as they predicted the location of target (instructional cues, 100% valid). If the cue stayed black, it indicated that the target was equally likely to appear at any of the three locations. This will be referred to as a neutral cue as it did not give any information with regard to the upcoming target location. Spatial cues occurred in half of the trials, neutral cues in the remaining half.

Participants were instructed to covertly orient their attention according to the spatial cues in the following cue-target interval. The length of the cue-target interval varied between 1000, 1083 and 1166 ms. Each interval length was presented with equal probability and was assigned randomly in each trial. Next the target appeared for 100 ms. The target consisted of 4 objects aligned to the edges of a non-visible square. Three of the objects were outlines of squares and one was a modified version of a ‘Landolt c’ that is often used to test visual acuity. This object was the outline of a square with a small opening (0.1° of visual angle) to either the left or the right side. The participant had to indicate via button press on a standard keyboard whether the opening appeared on the left or on the right side (index fingers of left and right hand for opening on the left and right side respectively). The target was equally likely to appear at any of the four possible locations within the square and was opened to the left and to the right on half of the trials. Participants had up to 1000 ms to respond and the
inter-trial interval lasted 1000 ms after their response (see Figure 4.1 for a depiction of an experiment trial). A warning to respond faster was displayed in the inter-trial interval if they did not respond within 1000 ms. Participants also received feedback on their performance (%corr) twice during each block. Apart from allowing them to monitor their performance, this feedback was also included to give them a chance to blink. The feedback display was shown for 5 s. Overall participants completed 864 trials in this task. 288 targets were presented per location, 144 of which were proceeded by a spatial and 144 of which were proceeded by a neutral cue.

![Figure 4.1: Experimental task. The peripheral placeholders were positioned at 2° below and 3.5° to the left and right of fixation. The target spanned 0.5° visual angle. Participants had to indicate via button press whether the gap in the target was on the left or right. Shown here is a spatial cue towards the left peripheral location.](image)

Participants received both verbal and written instructions and performed 72 practice trials (1 1/2 blocks) before the start of the experiment. During the instructions and throughout the experiment they were especially instructed to not move their eyes but to covertly shift their attention to either the left or the right placeholder when they received a spatial cue to the periphery. Participants were informed that the left and right placeholder would change their positions half-way through the experiment. Trials in which participants failed to respond (on average 0.4 %, range 0 – 24 trials) were excluded from further analysis. The experiment took approximately 75 – 90 min, depending on the duration of the self-paced breaks. Due to technical issues during the recording, one participant received 1189 trials and another participant received 829 trials. Their results did not appear to be affected by the difference in experimental duration and were therefore kept in the analysis. All the other participants
completed 864 trials. In addition to the ongoing EEG recording (described below) we recorded reaction times and accuracy for subsequent behavioural analysis.

### 4.4.3 Electrophysiological Recording and Pre-Processing

The electroencephalogram (EEG) was recorded using a 128-sensor Geodesic Sensor Net and Net Amps 400 amplifiers (Electrical Geodesics Inc., EGI, Eugene, Oregon, USA). It was digitised at 250 Hz and acquired with respect to the vertex electrode. Individual sensor impedance was kept below 40 kΩ and measured both prior and half way through the experiment. Offline the data was analysed using the EEGLab toolbox (Delorme & Makeig, 2004) and custom-written scripts for Matlab (The Math Works Inc., Natick, Massachusetts). Continuous EEG was first digitally high-pass filtered at 0.1 Hz using a finite impulse response filter. Afterwards the trigger timestamps were shifted to account for both the delay introduced by the anti-aliasing filter of the EGI recording software and the delay in the display of the visual stimuli.

The continuous EEG was segmented into 3250 ms segments, starting 1000 ms before cue presentation to 2250 ms after. Each segment contained the presentation of the fixation, the cue and target display as well as parts of the response interval. Segments were first visually inspected for artefacts. Segments containing blinks immediately before or after stimulus presentation were discarded, as well as segments containing noise (e.g. non-stereotypic artefacts and muscle activity). On average 746 trials were accepted per participant (85%, range 635 to 842). Each condition (per cue and target location) had 124 trials on average (range 98 to 143). There were no significant differences in the number of trials accepted in the different conditions ($F(5,105) = 0.873, p = 0.502$). Three participants were excluded because more than 30% of trials were rejected for them. After artefact rejection, data were decomposed using an independent component analysis (ICA) implemented in EEGLab. Components that were identified as relating to eye blinks were not included into the
remixing of the data (1-2 components per participant). Channels containing excessive noise were discarded prior to the artefact rejection and interpolated after the ICA (using EEGLab’s spherical-spline interpolation). Data were re-referenced to the nasion electrode and analysis focused on three electrode clusters over the occipito-parietal cortex (see Figure 4.3) averaging across six electrodes each. The left electrode cluster included electrode positions P7, P07 and P3, the central cluster was positioned slightly above O1 to O2 and included Pz and the right electrode cluster included electrode positions P08, P8 and P4 of the international 10-20 system. These electrodes were chosen based on the scalp distribution of alpha power across condition and previous studies focusing their analysis on alpha power on occipito-parietal electrodes (e.g. Rihs et al., 2007, 2009; Thut et al., 2006).

### 4.4.4 EEG Data Analysis

**Individual alpha frequency bands.** We adjusted the frequency band used for analysis to account for individual differences in the alpha band (e.g. Başar, 2012; Haegens et al., 2014; Klimesch, 1999; Pfurtscheller & Lopes Da Silva, 1999). The individual alpha frequency (IAF) was defined as the frequency with the maximal power in the 7-14 Hz frequency band (Gould et al., 2011; Thut et al., 2006) determined by a Power Spectral Density estimate via Welch’s method (using the spectopo function implemented in EEGLab) and the alpha band was chosen to encompass +/- 2 Hz around the IAF. We determined the IAF on the whole length of each epoch regardless of condition. The peak frequency was averaged across all 18 electrodes chosen for analysis. The resulting mean IAF was 9.4 Hz (SE = 0.33). The average alpha frequency band (7.4 Hz to 11.4 Hz) is close to the frequency bands chosen in other studies (e.g. Gould et al. 2011 7.9 – 11.8 Hz, Thut et al. 2006 7.8 – 13.8 Hz, Worden et al. 2000 8-14 Hz). Power averaged in this IAF band will be used in all following analysis and called alpha power.
**Time-frequency analysis.** Single-trial spectral power was estimated using a modified Morlet wavelet transformation (Delorme & Makeig, 2004). The length of the wavelets varied from 3 cycles at 4 Hz to 13 cycles at 60 Hz. This analysis resulted in estimates for 400 time points (from 581 ms prior to cue onset to 1829 ms afterwards) and 28 log-spaced frequencies. Analysis focused on the alpha band, which was individually determined as described above. The squared absolute value was taken for each estimate (i.e. power). Single-trial power was then averaged based on condition, resulting in six averages per electrode cluster, and dB baseline corrected to a 200 ms pre-cue time-window (-450 to -250 ms) during the presentation of the fixation cross served as the baseline period. Analysis focused on a 500 ms time window spanning 600 to 1100 ms after cue presentation. The earliest target presentation was at 1300 ms after the cue. The time window for analysis was chosen to be close to the earliest possible target presentation while limiting the effect of target related activity in the pre-target estimates. Alpha power within this pre-target time-window was compared between conditions to investigate whether the different cues (spatial and neutral) as well as the target locations (central, left, right) influenced the alpha power modulation. Additionally we calculated a lateralisation index (Thut et al., 2006) for alpha power in the left and right spatial cueing conditions. This analysis only included the left and right electrode clusters.

The index is calculated as:

\[
\frac{\text{alpha power right cluster} - \text{alpha power left cluster}}{\text{alpha power right cluster} + \text{alpha power left cluster}}/2
\]

The index is positive if there is more power over the right compared to the left hemisphere and negative if there is more power over the left compared to the right hemisphere (Thut et al., 2006). The index is expected to be positive in response to cues to the right location and negative in response to left cues. We used the non-baseline corrected alpha power values to calculate the index.
4.4.5 Brain Behaviour Relationship

Firstly we wanted to investigate whether the general alpha power level affected behaviour in our task. We therefore used Spearman rank correlations to investigate the relationship between alpha power at baseline and in the pre-target interval (in all 3 clusters) and performance (accuracy and response time). We then correlated the lateralisation index with performance in the left and right spatial cue condition. We next focused on single-trial power to investigate behavioural effects of modulations of alpha power within a participant. As our behavioural analysis revealed a speed-accuracy trade-off showing that participants were more accurate in slow trials (see Results), we sorted the single-trial power into two bins based on a median split of reaction time per condition for the left and right electrode cluster. We then compared the averaged and dB baseline corrected power values between bins.

4.4.6 Statistical Analysis

Behavioural analysis. We analysed data separately for the central and peripheral target locations. We compared accuracy and reaction time at the central location between cue types, using Bonferroni corrected paired-sample t-tests. For the peripheral target locations we conducted a 2 x 2 repeated-measures ANOVA with the factors Cue (neutral, spatial) and Target location (left, right) and investigated whether accuracy and reaction time were influenced by our experimental manipulations. These were followed up by planned comparisons using Bonferroni corrected paired-sample t-tests. Additionally, we sorted data based on reaction time and compared accuracy across bins to assess whether there was a speed-accuracy trade-off. We conducted a 2 x 2 repeated-measures ANOVA with the factor Cue (neutral, spatial) and Reaction time bin (slow, fast) for targets at the central location and a 2 x 2 x 2 repeated-measures ANOVA with the factors Cue (neutral, spatial), Target location (left, right) and Reaction time bin (slow, fast) for peripheral targets. We followed this analysis
up with planned comparisons, using Bonferroni corrected paired-sample t-tests to investigate under which condition the reaction time bin significantly influenced accuracy.

**Power modulations.** We conducted a 2 x 3 repeated-measures ANOVA with the factors Cue (neutral, spatial) and Cluster (central, left, right) to investigate whether alpha power was modulated differentially between cueing conditions. We also compared the single-trial variance between cueing conditions, using a 2 x 3 repeated-measures ANOVA with the factors Cue (neutral, spatial) and Cluster (central, left, right) to investigate differences in the standard error of the mean (SEM) between conditions. We then focused on the left and right spatial cues and conducted a 2 x 2 repeated-measures ANOVA with the factors Hemisphere (left, right) and Target location (left, right) to test for a lateralisation of alpha power. We followed these up with planned comparisons between alpha power in the left and right spatial cue condition per hemisphere. We furthermore calculated the above described lateralisation index and used a paired t-test to compare the index between the left and right spatial cue condition.

**Brain Behaviour Relationship.** We used non-parametric Spearman rank correlations to assess the relationship between baseline and pre-target power (per cluster) and performance, as well as the lateralisation index and performance in the left and right spatial cue condition. We then focused on differences in alpha power preceding slow and fast trials (based on a median split of reaction time per participant and condition). For the central target location we conducted a 2 x 2 x 2 repeated-measures ANOVA with the factors Hemisphere, Cue, and Reaction time. For the peripheral target locations we conducted a 2 x 2 x 2 x 2 repeated-measures ANOVA with the factors Hemisphere (left, right), Cue (neutral, spatial), Target location (left, right) and Reaction time (slow, fast). These were followed up with 2 x 2 x 2 repeated-measures ANOVA with the factors Cue, Target location and Reaction time for each hemisphere.
4.5 Results

4.5.1 Behavioural Results

As can be seen in Figure 4.2, participants responded faster and more accurately at the central location. Because of this well-known behavioural benefit for the stimuli presented at the foveal position, data was analysed separately for central and the peripheral target locations. Participants responded faster when they received a spatial compared to a neutral cue at the central location ($t(21) = 7.449, p_{corr} < 0.001$), but there was no significant difference for accuracy. At the peripheral locations, we conducted a 2 x 2 repeated-measures ANOVA with the factors Cue (neutral, spatial) and Target location (left, right) to assess how accuracy and reaction times were affected by our experimental manipulation. The results show a significant main effect for Cue ($F(1, 21) = 7.489, p = .012$) and a Cue x Target location interaction ($F(1, 21) = 11.248, p = .003$) for accuracy. There was no significant effect for Target location, implicating that participants performed equally well for targets presented at the left and right peripheral location but that they were better for the spatial compared to the neutral cues. For reaction time there was a significant main effect for Cue ($F(1, 21) = 20.121, p < .001$), reflecting that they were faster for the spatial cues. Planned comparisons showed that participants responded more accurately with the spatial cue only at the left location (left: $t(21) = -3.815, p_{corr} = 0.004$; right: $t(21) = -1.021, p = 0.319$), but were significantly faster with the spatial cue at both peripheral locations (left: $t(21) = 4.938, p_{corr} < 0.001$; right: $t(21) = 4.883, p_{corr} < 0.001$).

We furthermore tested for a speed-accuracy trade-off in this task. Per condition, we sorted trials into two reaction time bins based on a median split and compared accuracy between them. There was no significant difference at the central location between reaction time bins. At the peripheral locations the repeated-measures ANOVA with the factors Cue, Target location and Reaction time showed a significant effect for Response time ($F(1,21) =$...
17.286, p < 0.001) (in addition to the above reported effects of Cue and the Cue x Target location interaction). As can be seen in Figure 4.2 participants were more accurate if they responded slowly at the peripheral locations. Planned comparisons confirmed that participants responded more accurately in the slow compared to the fast bin at the left location (neutral cue: \( t(21) = 3.163, p_{corr} = 0.02 \); spatial cue: \( t(21) = 5.026, p < 0.001 \)). After Bonferroni correction for multiple comparisons there was only a trend for a difference at the right location with a neutral cue (\( t(21) = 2.513, p_{corr} = 0.08 \)).

![Figure 4.2: Behavioural performance across target locations and cueing conditions. Participants received no information as to where the target would appear in the neutral cueing condition, whereas the cue was 100% valid in the spatial cueing conditions. The dotted brackets indicate significant main effects for cue validity in a) and reaction time bin in b). The solid brackets indicate significant differences in planned comparisons. a) Bars represent accuracy, lines reaction time. Participants responded faster at all locations and more accurately at the peripheral locations with spatial cues. b) Speed-accuracy trade-off across target locations and cueing conditions. Data was sorted based on a median split of reaction time. Participants were more accurate when they responded more slowly for targets presented in the periphery. *p < 0.05, **p < 0.001. Error bars represent SEM.](image)

**4.5.2 Electrophysiology**

**Modulation of alpha power.** As can be seen in Figure 4.3 alpha power (individually determined as IAF +/- 2 Hz, average band 7.4 – 11.4 Hz) was strongest over occipito-parietal cortex. Electrode clusters were chosen based on the scalp distributions across all conditions. There is a strong decrease in alpha power before the cue onset (see Figure 4.4). This decrease is most likely due the onset of the fixation display with the three placeholders. Alpha power
starts to increase around the time of the cue onset and is then decreased by the onset of the cue. This initial modulation (decrease, increase, decrease) is similar across all conditions and is not of interest here. We investigated whether the alpha modulation in response to the cue differed between cue conditions and target locations.

![Figure 4.3: Scalp distributions of alpha power. Locations of left, central and right electrode cluster chosen for analysis are indicated at left scalp map. **p < 0.01.](image)

Alpha power level was not modulated differently between cue conditions in general. (2 x 3 repeated-measures ANOVA with the factors Cue (neutral, spatial) and Cluster (central, left, right); no significant main effects or interactions (all $p > 0.3$)). We did however find a difference in the variance of alpha power between conditions. Across cluster there was less variance in the spatial cue (mean SE = 0.1681) compared to the neutral cue conditions (mean SE = 0.1615) (repeated-measures ANOVA with the factors Cue and Cluster, significant main effect for Cue ($F(1, 21) = 7.75, p = .011$)). We then focused on the left and right spatial cue conditions to assess whether our design elicited the well-established alpha power lateralisation following a spatial cue (e.g. Thut et al., 2006; Worden et al., 2000). We conducted a 2 x 2 repeated-measures ANOVA with the factors Hemisphere (left, right) and Target location (left, right). There was a significant effect of Target location ($F(1, 21) = 6.328, p = .02$) and a Hemisphere x Target location interaction ($F(1, 21) = 7.139, p = .014$), indicating that alpha power was in general lower for the right cue condition, but that there was also a lateralisation. We followed these up with planned comparisons to assess the
difference in alpha power between target locations in each hemisphere. Alpha power was significantly lower for the cues indicating a right target location compared to a left target location in the left hemisphere ($t(21) = 3.885, p_{corr} = 0.002$, see Figure 4.3 for scalp distribution and Figure 4.5b) difference across time-frequency spectra). There was no significant difference between indicated target locations in the right cluster ($p > 0.5$).

We also calculated the lateralisation index for alpha power. The index is positive if there is more activity over the right compared to the left cluster and negative, if there is more power over the left compared to the right cluster (Thut et al., 2006). A positive index is therefore expected in the right cue and a negative index is expected in the left cue condition (as alpha has been reported to be higher ipsilateral compared to contralateral to the indicated target location). There was a significant difference in the lateralisation index of alpha power between the left and right cue condition ($t(21) = -2.728, p = 0.013$) (Figure 4.5 c)). In agreement with earlier findings (e.g. Thut et al., 2006), the index is positive for right cues (indicating higher alpha power over the right compared to the left cluster) and negative for
the left cues (indicating higher alpha power over the left compared to the right cluster). Taken together, these results show that alpha power is modulated by our experimental manipulations especially in the left hemisphere. In response to the spatial cues, there is significantly more power for the left compared to the right cues. The cue-related lateralisation of alpha power across hemispheres is further shown by the lateralisation index.

Figure 4.5: Results of time-frequency analysis. 0 ms indicates cue onset, dotted boxes indicate baseline and analysis windows. Frequency window was chosen individually as +/-2 Hz around the IAF. The averaged frequency window across participants is indicated in the figures. a) Power across time and frequencies for all conditions in central electrode cluster. b) Power difference between in left and right cue conditions in left and right clusters. c) Lateralisation index in left and right spatial cue condition *$p < 0.05$, **$p < 0.01$.

4.5.3 Brain Behaviour Relationship

We did not find any significant correlations (all $p > 0.15$) between alpha power (at baseline and in the cue-target interval) and behavioural performance (accuracy and reaction time) across conditions indicating that the general level of alpha power does not influence overall behavioural performance. As reported above, we found a differential lateralisation of alpha power across hemispheres in the left and right spatial cue conditions (indicated by the lateralisation index). We found significant positive correlations between this index and
performance for the left spatial cue (accuracy: \( \rho = .494, p = 0.02 \); reaction time: \( \rho = .472, p = 0.027 \)). A negative index indicates more power over the left compared to the right hemisphere (which is expected in the left-cue condition). The correlations show that participants with the most negative indices (the strongest lateralisation according to the cue) respond the fastest; however they also have the lowest accuracy. This matches the behavioural results, which show a speed-accuracy trade-off especially for targets presented at the left location. There were no significant correlations between the index and performance for the right cue (all \( p > 0.06 \)). There was however a trend for a correlation between the index and reaction time for right cues (\( \rho = .401, p = 0.064 \)). This effect is opposite to what is shown for the left cue, as the stronger lateralisation according to the cue (a higher index in the right cue condition) seems to be related to slower reaction times.

We found a significant difference in performance for slow and fast trials, indicating a speed-accuracy trade-off. We wanted to investigate whether there was also a difference in alpha power between slow and fast trials. We limited this analysis to the left and right electrode cluster as the general pattern of cue-related changes in alpha power in central cluster did not reveal any additional information. For each participant we sorted the single-trial alpha power into slow and fast bins based on a median split of reaction time, as we did for accuracy (see Figure 4.6). We did not find any difference for targets presented at the central location (2 x 2 x 2 repeated-measures ANOVA with the factors Hemisphere, Cue, and Reaction time; all \( p > 0.19 \)). However there was a significant effect of Reaction time at the peripheral locations (2 x 2 x 2 x 2 repeated-measures ANOVA with the factors Hemisphere (left, right), Cue (neutral, spatial), Target location (left, right) and Reaction time (slow, fast); main effect for reaction time (\( F(1, 21) = 5.078, p = 0.035 \))), indicating that there was more power preceding slow compared to fast trials. We furthermore found significant interactions for Hemisphere x Target location (\( F(1, 21) = 7.142, p = 0.014 \)), Hemisphere x Cue x Target
location ($F(1, 21) = 4.963, p = 0.037$) and Hemisphere x Cue x Reaction time ($F(1, 21) = 5.419, p = 0.030$). The Hemisphere x Target and Hemisphere x Cue x Target location interactions are explained by the above described differences in alpha power for left and right spatial cues across hemispheres (less power for the right cues and a lateralisation in response to spatial cues over the left hemisphere).

To investigate the Hemisphere x Cue x Reaction time interaction further we conducted 2 x 2 x 2 repeated-measures ANOVAs with the factors Cue (neutral, spatial), Target location (left, right) and Reaction time (slow, fast) per hemisphere. In the left hemisphere there was a significant main effect for Target location ($F(1, 21) = 5.989, p = 0.023$), indicating the lateralisation in response to the cue and a significant Cue x Target location ($F(1, 21) = 7.692, p = 0.011$) indicating that this lateralisation is only occurring for the spatial cues. There was a trend for a main effect of reaction time ($F(1, 21) = 3.442, p = 0.078$), but there were no interactions. For the right hemisphere there was a significant main effect for Reaction time ($F(1, 21) = 5.671, p = 0.027$) showing that there is more power for the slow compared to the fast trials. There were no other significant main effects or interactions. Together with the behavioural results, this indicates that more alpha power in the cue-target interval leads to a slower but more accurate response.
Figure 4.6: Single-trial alpha power sorted by reaction time (median split). Right part shows significant main effect for reaction time. *$p < .05$. Error bars represent SEM.

4.6 Discussion

We investigated the behavioural consequences of pre-target alpha power in a visual discrimination task. The target location was either chosen randomly or predicted by a spatial cue, to compare the effects of spontaneous and cue-related fluctuations in alpha power. Our behavioural results show that both the manipulation of cue (neutral vs. spatial) and target location (central vs. peripheral) affected performance. Participants were generally faster and more accurate at the central location compared to the periphery. They were furthermore faster for spatially compared to neutrally cued targets at all locations and more accurate at the peripheral locations. This is in line with earlier findings that show that a cue to peripheral locations significantly improves performance compared to a neutral cue (e.g. Posner et al., 1980). The difference in reaction time at the central location strengthens the notion by Minuissi, Rao and Nobre (2002) that attention modulates perceptual processing even at foveal locations. Additionally, we found a significant speed-accuracy trade-off: At the peripheral locations, participants were more accurate when they responded more slowly,
which is a common observation in perceptual decisions (e.g. Bogacz et al., 2010; Chittka et al., 2009; Schouten & Bekker, 1967; Wickelgren, 1977).

We did not find a difference in overall alpha power modulation between cue conditions. As alpha power is often understood as an index of cortical excitability (e.g. Pfurtscheller, 2001; Romei et al., 2008), this might suggest that participants were equally engaged under both cue conditions. However, the spatial cues led to less variation in alpha power between trials, strengthening our suggestion that alpha power varied spontaneously with the neutral cue and was restricted in its fluctuation by the spatial cue. Replicating earlier findings (e.g. Kelly et al., 2006; Rihs et al., 2009; Sauseng, Klimesch, Stadler, et al., 2005; Thut et al., 2006; Trenner et al., 2008; Worden et al., 2000; Yamagishi et al., 2005) we found a lateralisation of alpha power for the spatial cues to the peripheral locations. Over the left hemisphere alpha power was lower for right compared to left cues. This pattern of cue-related alpha modulation is often interpreted as a baseline shift in favour for the attended side (i.e. alpha is decreased contralateral to the cue to improve performance at that side (e.g. Thut et al., 2006; Wyart & Tallon-Baudry, 2009) or to suppress input from the ipsilateral unattended side (Foxe & Snyder, 2011)). We did not however find a lateralisation of alpha power in the right hemisphere.

Hemispheric differences are frequently noted in the attention literature. It seems that the left hemisphere can only attend to the right visual field, whereas the right hemisphere can shift attention to both visual fields (e.g. Corbetta et al., 2000; Mangun et al., 1994; Pisella & Mattingley, 2004). Differences in alpha power modulations between the hemispheres might be due to similar mechanisms and it has been shown before that the lateralisation is primarily happening over the left hemisphere (Horschig, Jensen, van Schouwenburg, Cools, & Bonnefond, 2014). The hemispheric differences are missed when using a lateralisation index (Thut et al., 2006) that averages power across hemispheres. We found a significant difference...
in the lateralisation index between left and right cue conditions. This suggests that alpha power was lower contralateral to the indicated cue location. However the difference in the lateralisation index could also just be due to the lateralisation shown in the left hemisphere. In fact the lateralisation index seems to be close to zero for the left cues (indication of no lateralisation). By close inspection of the time-course of alpha power modulation in Figure 4.4, it could be argued that the only difference is the decreased alpha power in the left cluster for the right cue. Therefore the significant difference in the lateralisation index could be mainly driven by the lateralisation in the left hemisphere. Lateralisation indices are often used in studies investigating cue-related alpha modulations as a correlate of visuospatial attention (Gould et al., 2011; Haegens, Händel, et al., 2011). Our data argues for a closer inspection of hemispheric differences as the lateralisation index might be biased towards processes in only one and not both hemispheres.

No difference in the alpha modulation in response to left and right cues over the right hemisphere might also be due to our task design. It has been suggested that the ipsilateral increase is shown in addition to the contralateral decrease especially if distracting sensory input as to be supressed at unattended locations (Foxe & Snyder, 2011; Händel et al., 2010). Our design did not include such distractors which could explain the lack of a bilaterally driven lateralisation. However a difference in the alpha power modulation in response to left and right cues was shown over the left hemisphere. Regardless of whether or not distractors are needed to show a true lateralisation (i.e. driven by opposed modulation over both hemispheres), our results therefore still argue for hemispheric differences. Future research could investigate whether distractors influence the cue-related modulation of alpha power similarly over both hemispheres.

We were especially interested in the behavioural consequences of alpha power fluctuations. The cue-related lateralisation of alpha power has been related to the improved
performance at attended locations (e.g. Händel et al., 2010; Thut et al., 2006) however there is increasing evidence that the lateralisation might not necessarily be related to the behavioural performance (see Chapter 3 and Dombrowe & Hilgetag, 2014; Gould et al., 2011; Rihs et al., 2007; van Ede et al., 2014). In Chapter 3 we show that although only participants with high alpha power at baseline show the lateralisation, all participants exhibited superior performance at cued locations and thereby question whether the lateralisation is actually related to the behavioural benefit. The data here points toward a similar direction as the lateralisation is only shown over the left hemisphere, although the behavioural cueing effect is shown at both peripheral locations. As visual input gets primarily processed in the contralateral hemisphere (e.g. Tootell et al., 1998), a decreased cueing effect over the left location could be expected, if the lateralisation of alpha was enabling the behavioural benefit and missing over the right hemisphere. However, quite the opposite seems to be true in our data, as the cue-related behavioural benefit seems to be even stronger over the left compare to the right target location. This strengthens our suggestion that the cue-related lateralisation of alpha power is a manifestation of a process that although related to selective attention does not underlie the behavioural benefit.

One might argue that this suggestion contradicts our own findings as we found a significant relationship between alpha lateralisation and targets presented on the left on a between participants level. Those participants who showed the strongest lateralisation in response to the cue were faster and less accurate for targets presented on the left side. This matches the speed-accuracy trade-off shown for behavioural data and could be taken as evidence that cue-related alpha power lateralisation indicates the orienting of attention and is related to the behavioural benefit shown at the cued locations (e.g. Foxe & Snyder, 2011; Gould et al., 2011; Kelly et al., 2006; Thut et al., 2006; Worden et al., 2000). However, as we pointed out, the lateralisation might be primarily driven by the left hemisphere. Our results
suggest that although the association between the lateralisation index and performance could be taken to reflect the orienting of attention, it might be important to investigate effects separately for each hemisphere and to carefully assess whether it is really the lateralisation of alpha power or the general alpha power level that is related to performance. This apparent failure to link the behavioural cueing effect to the cue-related alpha lateralisation has been shown previously (Dombrowe & Hilgetag, 2014).

We found a significant relationship between alpha power and reaction time. On a within participant level we replicated earlier findings by showing that there is lower power preceding fast compared to slow trials (Haegens, Händel, et al., 2011; Kelly et al., 2006; Thut et al., 2006; Trenner et al., 2008). Importantly, this effect was shown for targets presented at both peripheral locations and did not differ between cueing conditions or over hemispheres. This is the first direct evidence that performance is modulated similarly by spontaneous and cue-related changes in alpha power. Under both conditions participants were able to respond faster under low alpha power. Strengthening our earlier claim that the cue-related lateralisation is not driving the behavioural effect in attention task, we show the same effect in both hemispheres regardless of whether it is ipsilateral or contralateral to the target. If at all, the power difference between slow and fast trials seems to be stronger over the right cluster over which we did not find the lateralisation. Unfortunately due to the higher performance at the central location we were not able to compare performance between locations to investigate whether the behavioural influence of alpha power is different for targets presented at the centre, compared to those in the periphery.

Slower responses are associated with both higher alpha power and increased accuracy. The association of higher pre-stimulus alpha power and increased performance might appear to contradict the general consensus that low alpha power is beneficial for sensory performance at first (e.g. Busch et al., 2009; Ergenoglu et al., 2004; Hanslmayr, Aslan, et al.,
We hypothesise that this is can be explained by speed-accuracy trade-off (Chittka et al., 2009; Schouten & Bekker, 1967; Wickelgren, 1977) showing that a faster response is detrimental for performance in our task. In line with a recent claim by Lange and colleagues (Lange et al., 2014; Lange et al., 2013) this indicates that increased cortical excitability, as indexed by a decrease in alpha power, does not necessarily lead to better performance or more veridical perception but that the effect probably depends on the task characteristics. In their recent review Lange and colleagues (2014) argue that one effect of heightened cortical excitability might be a greater susceptibility to heteromodal input. In experimental designs where input from another modality interferes with the relevant input, heightened excitability might therefore be associated with the wrong response. However, it should be noted that in the natural environment, heteromodal stimuli usually might complement rather than contradict each other, suggesting that heightened excitability would not impede with an adequate sensory experience or behavioural response.

In Chapter 2 the effect of heightened excitability was a shift towards a more liberal response criterion in a simple detection task. We showed that decreased alpha power therefore led to both more hits and false alarms during low compared to high power. This change in response criterion cannot be easily labelled as good or bad performance, as this will heavily depend on the situation and whether for example the goal is to report any possible target presentation (in which case a liberal criterion would be beneficial) or false alarm should be limited (and a liberal criterion would lead to poor performance). Depending on the situation this liberal response criterion might or might not be interpreted as increased performance. Similarly there are situations in which fast decisions are favourable even if more likely to be wrong; and others in which a correct response should be favoured over a speeded one. In both cases of a modulation of the response criterion and the speed-accuracy
trade-off shift, alpha power modulations are associated with ‘post-perceptual’ or ‘decisional’ processes (see also Chaumon and Busch (2014)).

Others have shown that intermediate or high levels of alpha power are associated with increased performance (e.g. Babiloni et al., 2006; Lange et al., 2012; Linkenkaer-Hansen et al., 2004; Rajagovindan & Ding, 2011; Zhang & Ding, 2010). The reason for this discrepancy remains unknown; however, our results might suggest that ‘increased performance’ could have different meanings based on the situation (e.g., veridical perception, faster reaction time, more hits or less false alarms) and that the relationship between alpha power and those parameters might depend on specific task requirements. Alpha power might be only associated with certain aspects of performance (e.g., in our case reaction time, but see van Ede and colleagues (2012) for a recent study showing that changes in alpha power might be related more closely to accuracy) and there is some evidence that other aspects, such as increased task difficulty, or delayed responses hinder the observation of a relationship between pre-stimulus alpha power and performance (e.g., Grent-'t-Jong et al., 2011; Lou et al., 2014; van Ede, de Lange, et al., 2012). A more thorough analysis of different aspects of behavioural performance across tasks might help to elucidate the role of pre-stimulus alpha power modulation in perceptual tasks. Variability in reaction times has recently been linked to changes in functional connectivity between regions that are supposed to be involved in attentional control (especially frontal and parietal regions in the attentional network) (Prado et al., 2011). Changes in functional connectivity were interpreted as representing trial-by-trial changes in attention and therefore leading to variability in reaction times. These results show that variability in behavioural measures can be mapped onto relevant variability in neuronal activity in another measure. Future research should investigate whether and if so how modulations in alpha power are related to changes in connectivity.
In conclusion, our results close the apparent gap between studies investigating the effect of alpha power on discrimination or detection performance and the modulation of alpha power in attentional designs. Where the former especially investigate the behavioural consequences of alpha power modulations, the latter usually focus on the alpha power lateralisation as such and the reported behavioural effects are less consistent. Combining both designs in a single study, we were able to show that the behavioural effect of the alpha power fluctuations is similar in both situations. Regardless of whether alpha power was low due to spontaneous fluctuation or due to cue-related changes, the response was faster but less accurate. This strengthens the notion that low alpha power is not in general beneficial for performance, but that it might influence different aspects of behaviour based on task requirements. Furthermore although alpha power fluctuations seem to play a similar role, we did not find evidence for the notion that selective attention operates by lateralising alpha power. Although the variability in alpha power was restricted by the attentional cues (which might suggest that it was under stricter top-down control), we were not able to relate the lateralisation to an enhancement in behaviour. The behavioural effect was shown over both hemisphere and for both target locations, which strongly suggest that the bilateral level of alpha power prior to stimulus presentation influences the behavioural performance, but not a lateralisation.

4.7 Chapter Epilogue

In addition to our analysis presented in this chapter in which we sorted the single-trials based on reaction time and found a significant difference in power, we also sorted the single-trial data based on power and investigated whether there was a difference in accuracy. This analysis is similar to the analysis reported in Chapter 2 and the epilogue of Chapter 3. A 2 x 2 x 2 x 2 repeated-measures ANOVA with the factors Hemisphere, Cue, Location and Power showed a significant Hemisphere x Cue x Location x Power interaction ($F(1,21) =$
4.62, \( p = 0.043 \)). A planned comparison showed that for the spatial cues (averaged across hemispheres) accuracy was higher in trials preceded by high compared to low alpha power (\( t(21) = -2.153, p = 0.043 \)). This strengthens two of our claims. Firstly it shows that low alpha power is indeed associated with lower and not with higher accuracy in this task. Probably due to the speed-accuracy trade-off low pre-stimulus alpha power leads to faster but less accurate responses. Secondly it further argues that the pre-stimulus alpha level determines behaviour and not the lateralisation. As can be seen in Figure 4.7 higher alpha power led to more accurate responses regardless of whether it was measured over the ipsilateral or contralateral hemisphere.

Figure 4.7: Effects of single-trial pre-stimulus alpha power on accuracy. Single-trials were sorted in low and high power bins. Error bars represent SEM.

To supplement the main analysis in the chapter we provide the median reaction times per reaction time bin that were used to sort the single-trial power estimates in Figure 4.7. Figure 4.8 further depicts the large amount of variability seen in reaction times. The median of the bins (so effectively the 25% fastest and slowest trials) differed by over 100 msec. This difference was similar for neural and spatial cues.
The results in this chapter are in line with those in Chapter 2 and 3. Alpha power does not generally enhance performance and the level of pre-stimulus alpha power across both hemispheres is more important for performance than the lateralisation. As we have shown in Chapter 2, the effect of heightened excitability seems to be a shift to a more liberal response criterion, leading to an increase in both hits and false alarms during low compared to high power (less hits and false alarms). Depending on the situation this liberal response criterion might or might not be interpreted as increased performance. This study is probably a situation in which heightened excitability leading to fast responses is detrimental for accurate performance.
Chapter 5: General Discussion – The Good, the Bad, and the Complex

5.1 Summary of Empirical Studies

This thesis reported three empirical studies exploring the relationship between alpha power and psychophysical performance. Low alpha power over posterior cortex is usually assumed to index a state of increased cortical activity and tuning to the environment (e.g. Berger, 1929; Hanslmayr et al., 2011; Romei et al., 2008). Current research suggests that decreased alpha power leads to superior perceptual performance (e.g. Busch et al., 2009; Ergenoglu et al., 2004; Mathewson et al., 2014; Mathewson et al., 2009; Roberts et al., 2014; van Dijk et al., 2008). The research presented here expands these findings by revealing the complexity of the relationship between fluctuations in alpha power and behavioural performance in both sensory-detection and visuospatial selective-attention contexts. Alpha power seems to affect aspects of the behavioural response (such as the response criterion and speed-accuracy trade-off) that are somewhat orthogonal to performance. A decreased level of alpha power leads to a less cautious and faster response, which results in superior or inferior performance depending on the situation.

In the Chapter 2 we focused on the role of alpha oscillations in a backward-masking task. We aimed to replicate and expand a series of studies by Mathewson and colleagues (e.g. 2009, 2014) that showed that pre-stimulus alpha activity can predict detection performance. Their data showed that performance was higher (as indexed by hit rates), when pre-stimulus alpha power was low. Although we replicated these results, we further analysed the data with a signal detection approach that allows the separation of two factors that independently influence the response, namely sensitivity to the target and the response criterion (Macmillan & Creelman, 2005). Our results show that as the hit rate decreased with increasing alpha power, the false alarm rate decreased as well and the response criterion became more
conservative. We argue that this more conservative response criterion can explain the decrease in hit and false alarm rate without a corresponding change in sensitivity. On the other hand a more liberal criterion was associated with low alpha power (i.e. higher state of excitability), which indicates that less sensory activity, or less evidence for stimulus occurrence is needed to report the stimulus as present.

We focused on a visuospatial selective attention task in Chapter 3. It has been consistently shown that alpha power over the occipito-parietal cortex is lateralised in response to attentional cues (e.g. Kelly et al., 2006; Rihs et al., 2009; Sauseng, Klimesch, Stadler, et al., 2005; Thut et al., 2006; Trenner et al., 2008; Worden et al., 2000; Yamagishi et al., 2005). However no clear behavioural correlate of this lateralisation has been established yet. We manipulated the speed-accuracy trade-off via response-deadlines to elucidate the effects of alpha power on accuracy and reaction time in more detail. Performance was affected by both the manipulation of selective attention and response-deadline and we replicated the well-established effect of alpha lateralisation after an attentional cue. As reported previously (Rihs et al., 2009) only a subset of participants - those with high alpha power at baseline - showed a strong alpha lateralisation. Yet, the benefit in performance for validly compared to invalidly cued targets was shown regardless of the lateralisation. This challenges the notion that the alpha lateralisation is indexing the mechanism that is responsible for behavioural benefit of the orienting of attention. On an individual level the amount of change in alpha power was related to the amount of change in accuracy due to the increased time-pressure to respond. This relationship is shown for both hemispheres, which further stresses our argument that alpha power fluctuations – but not the lateralisation - affect behavioural performance. It confirms earlier suggestions of a more complex relationship between alpha power and performance by showing that the amount of change in alpha power
(and not necessarily the absolute level) predicts the change in the behavioural performance
(Gould et al., 2011; Horschig et al., 2014).

In Chapter 4 we combined aspects of the previous two studies to investigate whether
modulations of alpha power have similar effects on performance in both detection and
selective attention tasks. Participants performed a visual discrimination task in which they
were either cued to a specific location (a selective attention task) or received a neutral cue,
which did not convey any information about the location of the upcoming target (a detection
task). Our results show a similar effect of alpha power fluctuations for both tasks. Lower pre-
stimulus alpha power was related to a faster response. This is especially interesting as
behavioural results showed a speed-accuracy trade-off and performance was significantly
better for slow compared to fast trials. In agreement with our previous results in Chapters 2
and 3 this demonstrates that the relationship between alpha power and behavioural
performance is complex and that a decrease in power does not necessarily lead to superior
performance. Following up on the results from Chapter 3 we again showed that the
lateralisation of alpha power does not seem to index a mechanism that is responsible for the
orienting of attention. Although participants showed a clear attentional cueing effect at both
peripheral target locations, alpha power was only lateralisated over the left hemisphere (similar
to Horschig et al., 2014). Low alpha power was associated with faster responses over both
hemispheres and irrespective of whether the target was present ipsi- or contralaterally.

5.2 The Behavioural Consequences of EEG Alpha Power Modulations in Visual
Detection and Selective Attention

The most simplistic interpretation of earlier studies that relate pre-stimulus alpha power
to performance in sensory detection and selective attention (e.g. Busch et al., 2009; Capotosto
et al., 2009; Ergenoglu et al., 2004; Foxe & Snyder, 2011; Gould et al., 2011; Haegens, Händel,
et al., 2011; Hanslmayr, Aslan, et al., 2007; Kelly et al., 2006; Mathewson et al., 2009; Rihs et

al., 2007; Thut et al., 2006; van Dijk et al., 2008; Worden et al., 2000; Wyart & Tallon-Baudry, 2009) is that lower alpha power, and thereby higher excitability, leads to superior performance (Romei et al., 2008) and that the local excitability can be under top-down control (as shown during the lateralisation of alpha power in response to attentional cues) (e.g. Foxe & Snyder, 2011; Haegens, Händel, et al., 2011). We replicated the findings that pre-stimulus alpha power is related to variability in behavioural performance to a great extent. However, by refining both the behavioural measures and increasing the control over the task requirements, the complexity of the relationship between alpha power and performance becomes evident. Our results show that:

1. Lower alpha power is associated with a less cautious and faster response. Alpha power fluctuations modulate the placement of the response criterion and the speed-accuracy trade-off, both factors that are orthogonal to performance and presumably rely on processes that are not just concerned with the processing of sensory input.

2. Alpha power fluctuations play a similar role in both sensory perception and selective attention tasks.

3. The alpha power lateralisation in response to attentional cues does not seem to be related to the behaviourally relevant orienting of attention.

Our results reveal that a decrease in alpha power does not simply index better performance. Despite a decrease in alpha power being associated with an increase in hit rate in Chapter 2, we show that this is most probably due to a change in response criterion. Participants were more willing to report a stimulus (regardless of a stimulus actually appearing) when excitability was higher. In a similar vein lower alpha power predicted faster – but less accurate - responses in Chapter 4. The fast response is probably executed before
enough evidence is gathered to ensure a correct response (e.g. Bogacz et al., 2010) and this could be interpreted as a more liberal and less cautious response.

Successful interactions with the environment presumably rely on the ability to dynamically change the balance between the often opposing demands of making a fast or a correct response or between detecting small changes without reacting to too much noise. Similarly, whether or not lower alpha power indexes superior performance, likely depends on the task context. If superior performance was defined as fast reactions to any potential target stimulus, our results would suggest that heightened excitability increases performance. However if superior performance was defined as making the most correct choice (and to not falsely report noise as stimulus) then heightened excitability would not be beneficial for performance. These results could also be interpreted such that lower excitability is associated with a more cautious interpretation of the sensory input. This would match current models of the speed-accuracy trade-off that assume it takes time to accumulate enough evidence to ensure a correct response. This accumulation is cut short, if there is increasing demand to respond quickly (Bogacz et al., 2010). Alpha power fluctuations could thus influence how much time is spent gathering sensory evidence.

We show in Chapter 3 that there might not be a direct relationship between alpha power modulation and behavioural performance (e.g. accuracy or reaction time) under more demanding task requirements. Individuals, who decrease their alpha power more under increasing time-pressure also show a greater decrease in accuracy from the slow to the fast response conditions. However, a stronger modulation of accuracy due to task requirements does not necessarily have to be interpreted as better performance, which complements our other findings that that the behavioural effects of alpha power fluctuations depend on task requirements and cannot be easily classified as either positive or negative. This could also be interpreted to show that the ability to modulate alpha power in response to the task
requirements is reflected in the adaptability of the behavioural response. The additional analysis in the epilogue to Chapter 3 might suggest that lower alpha power at baseline might support a better ability to balance both accuracy and reaction time during the task.

Our findings are in agreement with other more recent studies on the role of pre-stimulus alpha power on performance in perceptual tasks. Lange and colleagues (Lange et al., 2014; Lange et al., 2013) show that higher cortical excitability does not necessarily lead to a more veridical performance but changes the susceptibility to (in their case multimodal) sensory input. In more excited states, participants’ response to visual stimulation was more likely to be influenced by task-irrelevant tactile stimulation (regardless of whether that increased or decreased performance in the visual task). This higher susceptibility could be interpreted as a more liberal response criterion and maybe even a less cautious response that relies on any (and not necessarily only the task-relevant) input from the environment. Chaumon and Busch (2014) also claim that alpha oscillations do not influence the input to the system (i.e. the sensitivity to visual information) but the visual system’s ‘input/output transformations’. They show that ongoing alpha oscillations influence the response and not the contrast gain in the processing of visual stimuli, especially for those presented above-threshold. This is in line with our other results as we show that modulations of alpha power probably influence the ‘decisional stage’ (i.e. response criterion or speed-accuracy trade-off) that might rely on processing higher up in the cortical hierarchy.

We replicated the well-established lateralisation of alpha power in response to a spatial cue in selective attention tasks in Chapters 3 and 4 (e.g. Foxe & Snyder, 2011; Haegens, Händel, et al., 2011; Kelly et al., 2006; Rihs et al., 2009; Thut et al., 2006; Worden et al., 2000). In response to an attention cue, alpha power is lower contralaterally to the cued side. This lateralisation is often interpreted as the attentional bias, leading to increased performance for attended stimuli and the suppression of distracting information on the
opposite side. Although the bilateral alpha decrease prior to stimulus presentation was shown to affect behaviour, we were not able to establish an additional relationship between the lateralisation and behaviour. We argue that this seriously challenges the notion that the alpha power lateralisation indexes the mechanism underlying the orienting of attention. In Chapter 3 the lateralisation is only shown by participants with relatively high level of power at baseline. However, the benefit for validly compared to invalidly cued targets is shown independent of the lateralisation, which is in agreement with the first report of individual difference in the lateralisation (Rihs et al., 2009). In Chapter 4 the differential modulation in response to left and right cues is only shown over the left hemisphere but the behavioural benefit of the cue is shown bilaterally. Other studies have also failed to establish a relationship between the lateralisation and behavioural attention effect or at least did not show it under all experimental conditions (Capilla et al., 2014; Dombrowe & Hilgetag, 2014; Gould et al., 2011; van Ede et al., 2014). In agreement with Dombrowe and colleagues (2014) we argue that it is the non-lateralised aspect of the modulation of alpha power prior to stimulus presentation that affects its processing. The lateralisation does not appear to be a manifestation of the behaviourally relevant orienting of attention.

Therefore the question of what mechanism the alpha lateralisation is indexing remains to be answered. Decreases in alpha power have also been shown to be related to superior performance in tasks requiring saccadic eye movements (Drewes & VanRullen, 2011; Hamm et al., 2012; Medendorp et al., 2007). Alternatively the lateralisation of alpha power might therefore index mechanisms that suppress saccadic eye movements to the cued locations in covert attention tasks. According to the pre-motor theory of attention, the networks responsible for the deployment of attention, the planning of eye movements, and the anticipatory re-mapping of space, are overlapping (Findlay & Walker, 1999; Medendorp et al., 2007; Posner et al., 1980; Rizzolatti et al., 1987; Smith & Schenk, 2012). The
lateralisation of alpha power might therefore index a mechanism that is related to the suppression of a saccade (to the cued locations) that does not influence the behavioural performance. If the lateralisation was related to such a mechanism, that could explain why numerous studies, including ours, have established that the spatial orienting of attention leads to the lateralisation of alpha power although it does not relate to performance (Capilla et al., 2014; Dombrowe & Hilgetag, 2014; Gould et al., 2011; van Ede et al., 2014).

Our results in Chapter 4 suggest a highly similar relationship between alpha power fluctuations and performance in detection and selective attention tasks. In particular the decrease in power prior to target onset seems to be related to modulations in performance. By combining EEG and event-related optical signals (EROS), Mathewson and colleagues (2014) showed that the alpha suppression that is related to increased detection performance over occipital-parietal cortex can be localised to the cuneus and precuneus regions. Furthermore, they showed that a decrease in alpha activity in the cuneus is preceded by increased activity in the dorsal attention network and decreased activity in the cingulo-opercular network. This is consistent with the notion that the modulation of detection performance is under top-down attentional influence. A similar relationship between alpha power over posterior cortex and fronto-parietal areas, supposedly involved in the top-down control of selective attention (Corbetta & Shulman, 2002), has been shown by Capotosto and colleagues (2009) in a selective attention task. They showed that TMS pulses to the right intraparietal sulcus and frontal eye fields disrupted both the contralateral decrease of alpha power over posterior cortex and the attentional benefit seen in the behaviour. Taken together this suggests that local excitability as indexed by alpha power is controlled by areas higher in the processing hierarchy. Those areas supposedly modulate excitability either spontaneously, or in response to spatial cues. Again this top-down controlled decrease might be – at least to some extent - independent of the lateralisation.
Therefore, these studies start to investigate how fluctuations in alpha power over posterior cortex are related to processing characteristics that operate on a larger scale. Current research indeed suggests a relationship between modulations in alpha power and connectivity between task-relevant brain areas. Oscillations are purportedly important for the organisation of neuronal activity (Chaumon & Busch, 2014; Palva & Palva, 2007; Saalmann, Pinsk, Wang, Li, & Kastner, 2012; von Stein & Sarnthein, 2000) and changes in connectivity are believed to add to the variability seen in perceptual performance (Prado et al., 2011). Taken together this could suggest that the perceptual modulations associated with alpha power are in fact a manifestation of changes in the communication between visual areas including those high in the processing hierarchy (Chaumon & Busch, 2014). It may be that lower alpha power indexes increased or more efficient connectivity between task-relevant areas. In a recent review on the neural correlates of consciousness (Crick & Koch, 1998), Ruhnau and colleagues (2014) argue for a more in-depth investigation of the relationship of alpha power and connectivity. According to their “windows to consciousness’ framework, decreased alpha power, and thereby increases in local excitability, only leads to conscious experience if it is paired with pre-established pathways, meaning connectivity with the relevant areas. Although consciousness is not further discussed here, this further strengthens the suggestion that while alpha power is related to our perception, we are far from understanding the complexities of these interactions and the effects seen in behavioural responses might well depend on processes that are not primarily ‘sensory’. Both sensitive behavioural measures as well as other indices of brain functioning such as connectivity have to be taken into account to understand how alpha power modulations relate to the variability in perception.

5.3 Limitations

There are several limitations to the studies in this thesis, both concerning the experimental designs as well as the analysis techniques. Our studies showed that at least
some of the variability in behavioural performance can be attributed to fluctuations of alpha power. The most general critique of our approach could be that scalp EEG oscillations may not be directly related to neural oscillations and the associations with behaviour therefore do not reveal functionally relevant cortical processes. However as discussed in Chapter 1 there is good evidence that EEG oscillations are related to neural oscillations and that those have a causal influence on cortical processing (e.g. Buzsaki et al., 2012; Buzsáki & Draguhn, 2004). This offers the advantage of being able to relate our results to the rich literature in neural oscillations from other fields in neuroscience (e.g. Cohen, 2014). We argue that our result show how different states of neuronal excitability influence behavioural performance and inform future studies (potentially using more invasive methods) that will enable further elucidation of the underlying processes. For example we suggest that excitability does not influence the sensitivity to input but rather decisional processes that might be localised to areas higher in the processing hierarchy. We also show that the lateralisation of alpha power is not an index of the behaviourally relevant mechanism that leads to the orienting of attention. The search for the neural basis of the orienting of attention should therefore focus on other markers.

We limited our analysis to the relationship between pre-stimulus fluctuations in alpha power and behavioural performance. However as mentioned in Chapter 1 and reported by numerous studies, it is highly likely that other oscillatory parameters apart from power can carry additional information; namely phase, frequency, and coherence both between frequencies and locations, (e.g. Bishop, 1933; Engel, Fries, & Singer, 2001; Hanslmayr et al., 2011; Lakatos et al., 2008; Neuling et al., 2012). There is ample reason to believe that a better understanding of the role of oscillations in cortical processing will lead to a greater understanding of cognitive processing in general (Buzsáki, 2006; Cohen, 2014; Lopes Da Silva, 2013). Of course these investigations should not be limited to the analysis of power. As
will be discussed in the next section of future directions, especially the combination of multiple parameters and particularly the relationship between oscillations and connectivity between distant brain areas promises especially exciting new insights. Different oscillatory parameters might contribute to different aspects of neuronal communication and processing.

Furthermore the focus on oscillations in the alpha frequency band is arbitrary to a certain point. Although there is ample evidence that oscillations in this frequency range affect behavioural performance (e.g. Klimesch, 1999; Mazaheri & Jensen, 2010; von Stein & Sarnthein, 2000), other frequency bands should be taken into account as well. The reason for the importance of alpha oscillations for sensory processing is probably related to the size of the networks and their connections with other task relevant regions (or maybe even especially between the thalamus and sensory areas in the case of alpha) (Gratton, 2014; von Stein & Sarnthein, 2000). Oscillations in the alpha range might therefore be well suited and important for the investigation of sensory and attentional processes. However, the exact frequency borders are often chosen based on historical or practical reasons. Individual variations in the alpha band were taken into account in the analysis by adjusting the frequency band to the individual peak in the 7-14 Hz range. This adjustment might not work in an ideal way for each participant (Haegens et al., 2014) and the selection of +/- 2 Hz around the peak frequency is also somewhat arbitrary, although consistent with previous reports (e.g. Gould et al., 2011; Thut et al., 2006). Across participants our effects appear to be centred on this 8-12 Hz alpha band, but similar modulations are shown for neighbouring frequencies. This queries the importance of the traditional frequency bands subdivisions (Lopes Da Silva, 2013). A greater focus on both individual differences in alpha frequency and their relationship to task requirements should inform the choice of frequency bands for analysis in future research (Haegens et al., 2014; Klimesch, 1999).
Another limitation of the current studies is that we restricted our EEG analysis to the sensor level and did not investigate the source of the alpha modulation. The electrical signal emitted by active neurons gets spatially distorted on its way from the neuronal generator to the scalp. Therefore there is no single mathematical solution for the localisation of the activity once it is recorded on the scalp (the so called inverse problem) (Cohen, 2014). There are several different procedures to estimate the neural generators from scalp recordings; but those were beyond the scope of the present analysis. However, the investigation of the neuronal generators of alpha power modulations could have important theoretical implications. As an example Capilla and colleagues (2014) showed that the ipsilateral and contralateral modulation of alpha power in a selective attention task have different generators, which can then help to understand their behavioural contribution. Furthermore understanding whether the behaviourally relevant alpha modulations originate in primary sensory areas or those higher in the processing hierarchy is important for the further development of theories on the role of alpha oscillations for cortical processing. As pointed out by Ruhnau and colleagues (2014) a source in sensory areas would implicate that the excitability state of the local sensory system is influencing behaviour whereas a source in the parietal cortex could implicate the importance of a more general attentive state. Our results that alpha power modulates the ‘decisional’ stage and the speed-accuracy trade-off would argue for a localisation in higher cortical areas.

An emerging theme throughout this thesis is that the behavioural effect of alpha power modulation crucially depends on the experimental context and task requirements. Nevertheless we changed the experimental task from a masked detection task in Chapter 2, to a masked discrimination task in Chapter 3 and a discrimination task without a mask (but with a more crowded display to increase the difficulty) in Chapter 4. The general finding of a complex relationship between alpha power modulation and behavioural performance that
goes beyond demonstrating that decreases in alpha power are beneficial for performance is shown across tasks. This variation is advantageous as it points out that the effects of alpha power modulations can be generalised to a range of tasks. However, a more systematic choice or modulation of experimental tasks might have helped to clarify the role of alpha power to a greater extent. In particular, the switch from a detection to a discrimination task is not ideal, given that we found an influence of alpha power on response bias in Chapter 2. Performance in a discrimination task is generally less biased than in a detection task. Choosing a task where participants usually demonstrate a bias therefore could have strengthened the behavioural effects. The choice of an unmasked task in Chapter 4 was motivated by the consideration that it is not clear how a change in excitability could explain performance in a masking task. Performance could depend on the relative difference in strength between the target and mask and excitability should affect both. On the other hand masking could also depend on re-entrant information. Based on a current theory a stimulus is successfully masked, if by the time the stimulus information re-enters early visual areas (after processing in later areas), the sensory template there has already been replaced by the mask (e.g. Di Lollo et al., 2000; Ro et al., 2003). We are unable to explain, how excitability could be related to those processes and decided to use a task with a single stimulus display in the later study. While the similarity in the results across tasks is striking, future research should address the choice of task in greater detail and focus on the different influence of alpha power modulation.

We furthermore restricted our analyses to the investigation of variations in pre-stimulus activity. Importantly though the variations in pre-stimulus activity have been shown to affect the activity evoked by the stimulus (e.g. Rajagovindan & Ding, 2011). It can thus be assumed that both pre- and post-stimulus activity affect behavioural performance. Recent studies show that pre-and post-stimulus activity do not sum linearly. Therefore a better
understanding of variability in performance can potentially be reached by taking both pre- and post-stimulus activity as well as their interactions into account (Britz et al., 2014; He, 2013; Wyart & Tallon-Baudry, 2009).

5.4 Future Directions and Applications

The findings from our studies have important implications for future research. Most importantly they reveal the complexity of the relationship between pre-stimulus alpha power fluctuations and behaviour in sensory tasks. This is especially evident in Chapter 2 and 4, in which an increase in alpha power was related to a stricter response criterion and to a slower but more accurate response. This challenges previous notions that an increase in alpha power decreases sensitivity in perceptual tasks (e.g. Mathewson et al., 2009; Romei et al., 2008; Romei et al., 2010). In Chapter 3 we show that the change in alpha power due to increasing time-pressure to respond affects the change in accuracy. Participants, who decrease their alpha power more when they have to respond fast, also show a greater decrease in accuracy for fast compared to slow responses. Our studies therefore show that both a more nuanced behavioural analysis and an increased control over response settings may enhance our understanding of the behavioural effect of alpha power.

Alpha power modulations are related to variability in behaviour across a wide range of tasks. Whereas this is strong evidence for the general importance of alpha power in perception on the one hand, on the other hand it also poses the questions of which mechanisms these fluctuations are actually indexing. As alpha power seems to be an index of cortical excitability, the wide range of behavioural effects is no surprise, but in fact poses the more interesting and important question of how cortical excitability is related to behavioural performance. For example the results in Chapter 2 and 4 could be interpreted as lower excitability leading to a more cautious response (both a stricter response criterion and a slower response). Results in Chapter 3 could be interpreted such that the ability to modulate
alpha power in response to task requirements influences the adaptability of the behavioural response. Together with the recent finding that participants who modulate their alpha power more strongly in response to implicit statistical properties of the task also show a greater adaptability in their behavioural responses (Horschig et al., 2014), this could show how a ‘tuning to the environment’ that is often associated with cortical excitability actually affects performance. Future research should investigate more closely how both explicit and implicit task properties influence alpha power fluctuations and behavioural responses.

As pointed out in the discussion of Chapter 2, one important factor in the experimental design of detection tasks might be an equal amount of target present and target absent trials. Arguably to understand variability in performance, we not only have to understand why we miss stimuli that are presented, but also why we perceive the presentation of noise as a stimulus (i.e. why false alarms occur). We and others argue that the effect of alpha power fluctuations does not seem to be on an ‘input’ level, but more on a ‘decisional stage’ (Chaumon & Busch, 2014). Both the effects of alpha power fluctuations on response criterion and speed-accuracy trade-off suggest a ‘post-perceptual’ processing stage, if performance can be meaningfully divided into such discrete stages. Future research should be designed to further define the aspects of performance that are influenced by alpha power fluctuations.

It is not entirely clear yet how modulations in alpha power affect behaviour in both masked and unmasked tasks, as performance probably depends on very different aspects of the stimulus processing. If successful masking really depends on the re-entrant of information from higher to lower sensory areas (Di Lollo et al., 2000), the investigation of alpha power in this context should be investigated more closely as fluctuations of alpha power might influence the connectivity between distant brain areas (Ruhnau et al., 2014). Therefore the investigation of alpha oscillations might not only help us to understand visual masking but
also the behavioural consequences of modulations of general processing characteristics such as connectivity. As pointed out in Chapter 1 the behavioural relevant alpha power fluctuations in masked and unmasked tasks might also be localised to different generators.

Furthermore we should try and understand more about the task settings that are best suited to investigate the behavioural relevance of alpha power modulations. The task difficulty seems to have profound effects on both the variation of alpha power and the relationship between modulations of alpha power and behaviour (Grent-'t-Jong et al., 2011; Haegens et al., 2012; Roberts et al., 2014). The behavioural effect of fluctuations in alpha power could be concealed by other aspects, if the difficulty gets too high (Capilla et al., 2014; Drewes & VanRullen, 2011; Hanslmayr, Aslan, et al., 2007). Future research could therefore focus on finding the most appropriate level of difficulty, which is likely to differ between participants, and could also depend on a participant’s motivation. In Chapter 3 we tried to disentangle the effects of alpha power on reaction time and accuracy. Although the response-deadline manipulation successfully affected behaviour, it did not modulate alpha levels between participants. Other instructions that modify behaviour more strongly or on a trial-by-trial basis might be more effective in creating these differences (Pastötter et al., 2012).

In Chapter 2 and 3 we found differential effects of alpha power modulations for between and within participant levels. This opens up several opportunities for future research: Firstly there are several findings that suggest oscillatory signatures as trait variables that might help to understand individual differences in information processing (Klimesch et al., 2007; Laufs, 2003). Although individual differences in resting power are far from being understood, resting power seems to be influenced by various factors as for example expertise in a sport (Babiloni et al., 2010), or intelligence (Doppelmayr, Klimesch, Stadler, Pollhuber, & Heine, 2002). A more detailed analysis of how stable individual differences in resting or baseline alpha power are, and how they affect performance might inform models of the role
of alpha power in behaviour. There is currently increased interest in the relationship between cardiovascular fitness and cognitive performance (Hillman, Erickson, & Kramer, 2008). Given that alpha power might be influenced by fitness (or expertise in a sport see Babiloni and colleagues (2010)) and cognitive abilities (Doppelmayr et al., 2002), differences in resting alpha power might help to understand the relationship between fitness and cognitive performance. The resting level influences the way alpha power is modulated during the experimental tasks. In Chapter 3 we show alpha lateralisation in response to an attentional cue, but only for participants with high alpha power at baseline. Future research should not only focus on understanding individual differences in alpha power at rest but also how these relate to task-induced decreases and behavioural performance. Variability in performance does not only depend on differences in pre-stimulus power but also on the post-stimulus activity. The relationship between pre- and post-stimulus activation is not linear and might provide important insights into trial-by-trial variability in performance (Britz et al., 2014; He, 2013; Wyart & Tallon-Baudry, 2009).

As already highlighted in the previous section, our understanding of variability in perceptual performance from trial to trial is likely to benefit immensely from a more comprehensive analysis of multiple oscillatory signatures. The relationship between alpha oscillations and connectivity between different brain areas is especially promising. Ruhnau and colleagues (2014) even suggest that the connectivity states might be more important to determine the fate of sensory input than the excitability state. However it might well be that alpha power modulation also indexes changes in connectivity (given that they are supposedly generated by cortico-thalamic and cortico-cortical connections (von Stein & Sarnthein, 2000)) in addition to modulations in excitability. Furthermore there are several studies that suggest that either in addition or independent of power modulations, the pre-stimulus phase is crucially involved in determining the perceptual fate of a stimulus (Busch et al., 2009; Busch
There are numerous potential applications for this research. Understanding the mechanisms that lead to variability in performance might help to inform ways to increase performance or to design environments in a way that favour beneficial performance. There is also mounting evidence that certain brain pathologies, such as Parkinson’s, schizophrenia, autism, and ADHD are characterised by abnormal oscillatory signatures (for recent reviews see Calderone, Lakatos, Butler, & Castellanos, 2014; Uhlhaas & Singer, 2006). As pointed out by Calderone and colleagues (2014), the attentional deficits seen in patients suffering from schizophrenia, dyslexia, ADHD might stem from a deficit in the ability to entrain intrinsic oscillations to those naturally occurring in the environment. Neuro-feedback training that focuses on training patients to increase entrainment could thereby offer new treatment opportunities to improve functionality (Calderone et al., 2014).

5.5 Conclusion

Fluctuations in alpha power influence performance in perceptual tasks. The studies presented here argue that this relationship is more complex than suggested by earlier research and that a more in-depth analysis of the behavioural performance as well as a stricter control of experimental manipulations is needed to understand the behavioural consequences of changes in alpha power. A decrease in alpha power seems to index an increase in cortical excitability and a greater tuning to the environment. How this relates to performance seems to primarily depend on the task at hand. Increased excitability has been shown to lead to faster responses with a more liberal criterion, but those responses are not necessarily more correct. Additionally we show that although related to the orienting of attention, the lateralisation of alpha power following an attentional cue does not index the behaviourally relevant aspects of the attentional shift.
Generally speaking these results indicate that the brain state prior to stimulus presentation contributes to the variability in perception, even if the stimulus itself does not change. Therefore they do not only shed light on one of the oldest problems in experimental psychology, but also reveal how variability in cortical activity affects the processing of sensory stimuli. Fluctuations in alpha power affect the behavioural response in visual detection and selective attention tasks but not the early perceptual representation of the visual stimuli.
PARTICIPANT INFORMATION SHEET

Project title:
The role of alpha oscillations in visual processing

About the Researcher:
My name is Katharina Limbach and I am working towards a PhD in Psychology at the University of Auckland under the supervision of Associate Professor Paul M. Corballis. I would like to invite you to participate in my research project at the University of Auckland. It is important to read this document carefully so that you can make an informed decision about whether you would like to participate.

Research Background
The goal of these experiments is to investigate the brain mechanisms of visual perception and attention in healthy adults. Your results will help us understand more about how the brain processes perceptual information. I am especially interested in variations of perceptual performance and how perceptual performance can be predicted and modulated.

Procedure
During the experiment you will make simple judgments about stimuli presented on a computer monitor. Your responses will be in the form of button presses using the computer keyboard or a button box. You will be given specific instructions at the start of each task. In addition, your brain waves will be measured during the task using an electroencephalogram (EEG). Therefore electrodes will be placed on the surface of your scalp by means of an elastic ‘cap’. The electrodes are encased in sponges, which are soaked in an electrolyte solution (consisting of shampoo, salt, and water). The total duration of the experiment, including preparation time, will be about two hours. You will be given brief rest breaks every few minutes during the experiment. Please ask the experimenter any questions that may arise while you are doing the task(s).

Some tasks may involve flickering stimuli. Flickering stimuli can occasionally lead to epileptic responses or migrainous symptoms (such as nausea and headaches) especially in individuals with a history of these diseases. However, our study is designed in a way that minimizes the risk for these effects. There are no other known risks involved with this project beyond those encountered in everyday life. The electrodes and the device used to record your brain waves are electrically isolated so there is no possibility of shock in the unlikely event of an electrical fault in the equipment. The electrode cap is disinfected after each use to prevent the possibility of biological contamination. However, should you feel any discomfort during the experiment, please inform the experimenter immediately. You can choose to stop participation at any time and the experimenter will be with you all the time.

Benefits
There is no direct benefit to you by participating in this study, however; your participation will help us to gain a better understanding of the relationships between brain activity, perceptual and attentional phenomena.

For your time, you will be compensated with a $20 Westfield voucher. If you decide to leave the study early, you will be compensated for the time you participated. You can also request a copy of the final published report of this study.

**Anonymity and Confidentiality**

Participation in this study is entirely voluntary, and if you choose to participate, you can change your mind at any time without giving a reason. After your participation is completed, you will still have the right to request that your data be withdrawn from the study for up to one month. You will be given a copy of this document to keep. The anonymity of the data you provide will be preserved and any information that identifies you as a participant will be used confidentially. Your name will only appear on the attached Consent Form, which will be coded with an identification number that will be used throughout the study. If the information you provide is reported or published, this will be done in a way that does not identify you as its source.

Access to consent forms and data will be restricted to the researchers directly involved in this project and will be stored in a locked cabinet on university premises. All data will be kept for a minimum period of six years to allow for publication and future re-analysis. Consent forms and other potentially identifying data will be destroyed after six years.

If you would like to participate in this research project, please contact me (Katharina Limbach) via email. If you any have questions or concerns about the project, please contact one of the following:

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For any queries regarding ethical concerns you may contact the Chair, The University of Auckland Human Participants Ethics Committee, The University of Auckland, Office of the Vice Chancellor, Private Bag 92019, Auckland 1142. Telephone 09 373-7599 extn. 83711.

Funding for this project is provided by the Department of Psychology

**APPROVED BY THE UNIVERSITY OF AUCKLAND HUMAN PARTICIPANTS ETHICS COMMITTEE ON 5.12.2011 for 3 years, Reference Number 2011/7525**
CONSENT FORM

THIS CONSENT FORM WILL BE HELD FOR A PERIOD OF SIX YEARS

Project title: The role of alpha oscillations in visual processing
Researchers: Katharina Limbach, Associate Professor Paul M. Corballis

I have read and understood the accompanying Participant Information Sheet, which explains this research project and my role as a participant. I have had an opportunity to ask questions and have had them answered satisfactorily.

In particular I understand that:

• I have the right to stop participation at any time without having to give a reason.
• Whether or not I participate will not affect my relationship with the researchers.
• For one month after my participation I will still have the right to request that my data be withdrawn from the study.
• My name will appear only on this form. The data from this research will be stored anonymously, coded by number.
• All data will be kept for a minimum period of six years to allow for publication and future re-analysis, after which it will be securely and confidentially disposed
• Research publications and presentations from this study will not contain any information that could identify me.
• I will receive a $20 Westfield voucher in compensation for my time

I voluntarily agree to take part in this research.

Signed: ___________________________
(Researcher Use Only)
Name: ___________________________
Participant Number: (please print)
Date: ___________________________

Approved By The University of Auckland Human Participants Ethics Committee On 5.12.2011 For 3 Years Until 5.12.2014. Reference Number 2011/7525
Demographic Questionnaire

Please complete the questionnaire by answering all questions. This is entirely voluntary and the information will be treated confidentially.

Date: ________________

1. Sex:  □ Female  □ Male

2. Age:  ____________

3. Vision:
   a. Do you have corrective eyewear?  □ Yes  □ No
   b. If so, what type of corrective eyewear are you wearing right now?
      □ Glasses  □ Contact Lenses  □ Nothing
   c. What best describes your vision?
      □ Nearsighted: nearby objects can be seen clearly, but distant objects are blurry
      □ Farsighted: distant objects can be seen clearly, but nearby objects are blurry
      □ I’m not sure

4. Do you have any history of epilepsy?  □ Yes  □ No

5. Do you have any history of migraine?  □ Yes  □ No

------------------------------------------------------------------Experimenter------------------------------------------------------------------

Experiment:  _________________  Version:  _________________
Participant #:  _______________
Edinburgh Handedness Inventory

Please indicate your preferences in the use of hands in the following activities by putting + in the appropriate column.

Where the preference is so strong that you would never try to use their other hand unless absolutely forced to, put ++.

If in any case you are really indifferent, put + in both columns.

Some of the activities require both hands. In these cases, the part of the task, or object, for which hand preference is wanted is indicated in brackets.

Please try to answer all questions, and only leave a blank if you have no experience at all of the object or task.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Left</th>
<th>Right</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.   writing</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.   drawing</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3.   throwing</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4.   scissors</td>
<td></td>
<td></td>
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<tr>
<td>5.   toothbrush</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6.   knife (without fork)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7.   spoon</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8.   broom (upper hand)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9.   striking match (match)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10. opening box (lid)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

i. which foot do you prefer to kick with?
ii. which eye do you use when using only one?

Experimenter:

Please leave these spaces blank

<table>
<thead>
<tr>
<th>L.Q.</th>
<th>L.S.</th>
<th>decile</th>
</tr>
</thead>
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Participant #:


Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex, 1*(1), 1-47. doi:10.1093/cercor/1.1.1


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