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Success Comes in Waves: The role of neuronal oscillations in the modulation of visuospatial attention, perception and cortical excitability

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Chapter 1: General Introduction

The overall aim of this thesis is to contribute to investigations into the role that neuronal oscillations play in the top-down control of visuospatial attention, perception and more generally, cortical excitability. In the achievement of this, a range of studies have been conducted, attempting to both replicate current findings within the literature, as well as contribute new knowledge through the implementation of carefully designed studies. Open-science methods have also been adopted within this thesis, where secondary data has been utilised to conduct novel analyses that offer new insights into existing research findings. Prior to examining these though, it is first critical that several topics are outlined and explored so that a comprehensive understanding of the relevant background can be achieved; creating an important foundation of knowledge that the progression of this thesis relies upon. This general introduction chapter will aim to provide this, with an overview of neuronal oscillations, covering the history of their initial discovery to their use as an informative neural signal in modern research. It will then proceed to highlight important neuroimaging techniques that are cited in subsequent chapters, where all have been applied in the experimental studies that make up this thesis, to record or induce oscillations within the cortex.

1.1 A brief history of neuronal oscillations

From a time that can be traced back to ancient Egypt, to a time still ongoing now, one of our primary research objectives has been to uncover and detail how the brain works (Wickens, 2014). Nowadays, we refer to this practice as neuroscientific research, with the field continuously growing to provide revisions and updates to our knowledge, as well as revealing novel findings that enable us to better understand how our brain functions (Banich, 2018). In time, we have also become exceedingly better at neuroscientific investigations, creating and developing a multitude of techniques that have enabled us to achieve large-scale and non-invasive explorations of the cortex. With this, research has been able to determine that electrical activity is at the forefront of our cognitive functions, with electrical connections inside the brain being used for communication across and within regions (Caton, 1875, 1877; Borroto-Escuela et al., 2024), enabling a vast range of functions from speech to movement, to being able to perceive an object in front of you.

When this electrical activity is examined, neuronal oscillations are one predominant feature that can be seen, typically defined as activity that demonstrates rhythmic fluctuations observable in both electrical and

magnetic neural field recordings (Buzsáki & Draguhn, 2004; Thut et al., 2012; Cole & Voytek, 2017). These oscillations are ever present in the cortex and can be generated spontaneously or in response to either internal or external stimuli (Linkenkaer-Hansen et al., 2001; Samaha et al., 2020). Also known more commonly as brain waves, oscillations show a fluctuation that is distinct in periodicity and cyclic nature, enabling them to be categorised into meaningful canonical frequency bands: Delta (0.5-4 Hz), Theta (4-8 Hz), Alpha (8-12 Hz), Beta (12-30 Hz) or Gamma (30-80 Hz) waves (see Figure 1.1, Jia & Kohn, 2011). For example, one of the first and most prominent oscillations to be recorded was alpha-band activity, which presents itself as a rhythm that maintains a frequency of between 8-12 Hz (8-12 cycles per second). This was recorded by Hans Berger in 1929 and so the alpha wave is synonymous with its alternative name of the 'Berger wave' (Proekt, 2018; İnce et al., 2021). This discovery changed the way we viewed the brain, as Berger was able to observe neural activity changes of alpha during different behaviours and states, such as relaxation (Berger, 1929; Columbus, 2008). For example, he determined that when individuals closed their eyes, there was a clear increase of alpha rhythms, resulting in the popular (but outdated) view that these oscillations may reflect a type of 'default' state within the cortex (Hohaia et al., 2022). Following his discovery, Berger replicated this findings hundreds of times, with his most amenable subjects being both himself and his son (Millett, 2001), providing hallmark evidence for the electrophysiological basis of cognitive functioning.

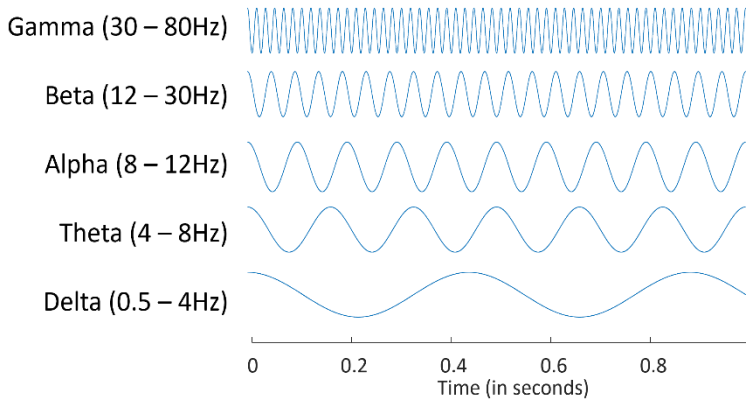


***Figure* 1.1**: Simulated oscillatory signals to illustrate the canonical frequency bands seen in neural signals, ranging from the fastest frequency of Gamma (30-80 Hz, top), to Beta (12-30 Hz), Alpha (8-12 Hz), Theta (4-8 Hz) and finally the slowest, Delta (0.5-4 Hz, bottom)

1.1.1 Oscillatory Phase

Beyond frequency, when defining oscillations, it is important to consider their two other features of phase and power. Firstly, phase is a feature that reflects the position of the oscillatory cycle at any given time (Ward, 2003), which many express in terms of phase angles (see Figure 1.2, below). The phase of a cycle can also be expressed in basic terms such as '*peak'*, referring to the highest point of the cycle and '*trough'*, the lowest point. Evidence has shown that the phase of an oscillation is important to consider when evaluating the role of neuronal oscillations, as they have been found to play a key part in the fluctuation of cortical excitability, including network excitability (Bishop, 1933; Buzsáki & Draguhn, 2004; Busch et al., 2009; Bergmann et al., 2019). In basic terms, this refers to the degree of activity both within regions of the cortex, as well as across them. There is compelling evidence to suggest that oscillatory phase is able to influence excitability through the correlative relationship it has with neuronal firing rates, where certain phase angles can rhythmically inhibit neuronal firing (Haegens et al., 2011; Ng et al., 2013). Specifically, it has been shown that alpha peak phases are able to reduce firing rates observed within the cortex and thus decrease cognitive processing abilities at these times (Haegens et al., 2011). This is particularly important for uncovering how oscillations may modulate behaviour, where the phase of alpha oscillations create what some term as "windows of excitability". An example of this can be seen when examining visual perception, where the success of visual processing will depend on the time at which a visual stimulus arrives at the cortex and whether oscillatory phase is in a position to promote neuronal excitability and consequently improve perception, or not (Dugué et al., 2011; Mathewson et al., 2009; Schroeder & Lakatos, 2009). One such study that has investigated this has presented empirical evidence to suggest that if alpha phase is positioned between troughs to rising phases, performance in a visual detection task is significantly improved than compared to when the phase is at an opposite position of peak to falling phase (Mathewson et al., 2009). This relationship has been referenced within the literature numerous times, acting as a foundation for theories such as the pulsed inhibition hypothesis (Mathewson et al., 2011). This proposes that alpha oscillations can cyclically inhibit cognitive processes based on their phasic behaviours, often in an effort to allocate limited neural resources to those that are perhaps considered more important for a task at hand. However, despite its popularity, it should be noted that newer research is beginning to question these theories and has suggested that perhaps alpha phase reflects periodic facilitation of excitability, rather than inhibition (Bergmann et al., 2019). Additionally, there is an ever-increasing number of studies presenting null evidence of this effect (see Keitel et al., 2022), creating a debate within the field as to

the true role of neuronal phase in modulating certain cognitive processes; something that will be explored in depth within the following chapters. Such conflicting evidence has in fact motivated three out of four of our experimental chapters, with Chapter 2 investigating the role of oscillatory phase in modulating global levels of cortical excitability, Chapter 3 then expanding on this by determining the role of phase in visual perception and Chapter 4 concluding with a study of phase in the complex process of visuospatial attention. Each has been conducted purposefully to address the conflicting evidence currently dominating their respective fields, the main focus here being the role of oscillatory phase.

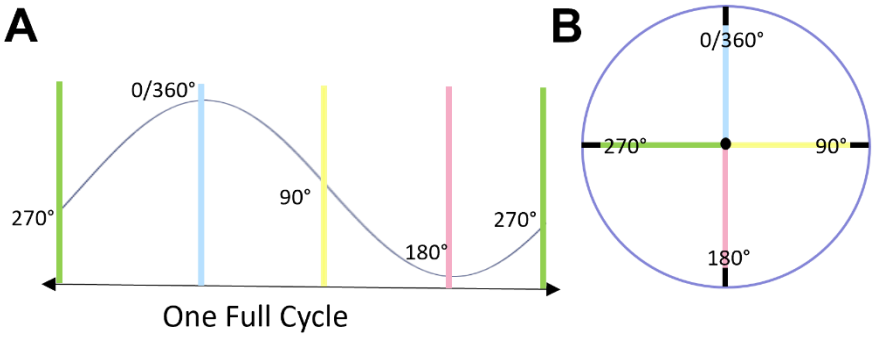


***Figure* 1.2**: An exemplar illustration of an oscillatory cycle with phase measurements represented in degrees. Here, one full cycle of an oscillation is shown (A) with phase angles highlighted and labelled, their position indicated with shaded colour bars. In an alternative depiction of this, a circular plot (B) demonstrates the cyclic nature of oscillations. Shaded colours across the two figures correspond to one another.

At this point, it is vital to emphasise how the mentioned oscillatory phase-excitability relationship has been found to extend beyond just alpha-band activity, with research proposing that the phase of both low- and high-frequency bands are also able to influence neuronal excitability throughout the cortex (Schroeder & Lakatos, 2009). For example, it has been evidenced that the phase of oscillations such as those within the gamma- and beta-band, demonstrate an ability to 'lock' single-unit neuronal spiking activity to their cyclic fluctuations (Womelsdorf et al., 2006; Haegens et al., 2017, respectively). Further, it has similarly been proposed that the phase of theta oscillations can influence the firing rate of individual neurons, with popular examples of this coming from studies of rat movement behaviours and how they learn spatial maps, as observed within the cortex (Jones & Wilson, 2005; O'Keefe & Recce, 1993). The broad range of frequencies being identified here seeks to emphasise not only the general importance of phase in modulating a variety of cognitive processes, but it also highlights a need for studies to consider these measures and their corresponding frequencies within investigations.

From the current literature, it is well established that neural phase is important in defining how our brain operates mechanistically, even whilst it may yet be unclear what the true role of phase in cortical excitability may be (i.e., facilitation, inhibition, or both). Despite this though, neural phase is not always included within empirical analyses, resulting in missed opportunities to further our knowledge. When it is included, debates have often emerged from the appearance of several contradictory and null results, some of which are explored in depth within Chapter 2 and 3 specifically. Beyond this, many current studies look at only alpha band oscillations due to their popularity, again likely resulting in missed knowledge as we know a range of frequencies may be implicated in this phase-excitability effect. With this in mind, the first three studies presented within this thesis have each implemented analyses that focus on uncovering the role of phasic behaviours, not restricting searches to just one oscillatory band and thus minimising the risk of missing important findings.

When conducting research within the field of cognitive neuroscience, often the primary aim of our studies is to determine how certain cognitive processes are achieved, controlled, manipulated, and so on. To do so, we must first acknowledge how such processes often occur as a result of activity across multiple brain regions, due to widespread neural networks that sometimes cover large sections of the cortex (Sauseng & Klimesch, 2008). Whilst it is true that there are localised regions specialised for certain functions, e.g., the occipital cortex is specialised for visual processing, it is likely that neural activity from beyond this region will also contribute to processes in some capacity (O'Sullivan, 2024), an idea that is illustrated by the visual system being traditionally viewed as a hierarchy of cortical areas (Hochstein & Ahissar, 2002). With this in mind, it becomes important to consider how cortical communication is achieved, so that we can better understand the neural mechanisms behind this behaviour and also guide our knowledge of how we may manipulate these signals to enhance cortical communication and thus cognitive abilities. As such, we must turn our attention towards oscillatory phase measures once again, as research has shown that coherence of this feature, amongst others, may play a role in connectivity and communication between cortical regions (for a review, see Bowyer, 2016). This has been eloquently termed the communication through coherence theory (CTC), first proposed by Fries (2005, 2015), who determined that as oscillations create periodic windows of excitability. When there are two coherently oscillating signals, these will have identically timed open periods that create opportunities for the transfer of neural signals and thus communication between these groups (i.e., when windows are open). This is

in line with additional evidence presenting how patterns of phase coherence define the path of information flow (Palmigiano et al., 2017), creating an insight into how signals propagate across the cortex based on phasic behaviours; the understanding of which is considered a central goal of neuroscience (Seguin et al., 2023). Importantly, investigations into the CTC hypothesis have mainly found evidence attributing this to oscillations in the gamma and beta bands (Bastos et al., 2015), but again, there is additional research to suggest that this effect extends into multiple frequencies. As an example of this, it has been demonstrated that when integrating visual and sensory touch information during a task, there is a strong alpha phase coupling between visual and somatosensory regions of the brain (Hummel & Gerloff, 2005). For this, Chapter 3 offers an interesting insight into how phasic behaviours may operate on a global scale, with the phase of oscillations within the visual cortex influencing the excitability of the motor cortex, perhaps through mechanisms of cortical communication.

Phase coherence has also been evidenced to reflect the connectivity between cortical regions (Sauseng & Klimesch, 2008; Marzetti et al., 2019) and so offers an additional insight into how the brain functions as an integrated system. To define this clearly, coherence is a measure of how correlated two oscillatory phases are with one another (Conway et al., 1995) and can be calculated using phase locking values (PLV; Hurtado et al., 2004; Lachaux et al., 1999; Tass et al., 1998) and numerous other empirical methods, such as pairwise phase consistency (PPC; see, Vinck et al., 2010). To achieve these calculations, formulas can be followed for each, with the following equation (1) outlining how to attain phase locking values:

$$(1)\ PLV_t = \frac{1}{N}\left|\sum_{n=1}^{N}\exp\big(j\theta(t,n)\big)\right|$$

where $j\theta(t,n)$ is the phase difference $\phi_1(t,n) - \phi_2(t,n)$ of signal j. Here, t refers to each time and n the trial (Lachaux et al., 1999). Similarly, phase consistency measures can be attained using the following formula (2):

$$(2)\ PPC = \frac{2}{N(N-1)}\sum_{j=1}^{N-1}\sum_{k=(j+1)}^{N} f\big(\theta_j,\theta_k\big)$$

where the value N refers to trials again, j and k are representative of the two compared signals, whilst function f is the computed dot product between two unit vectors, defined by:

$$(2.1)\ f\big(\theta_j,\theta_k\big) = \cos(\theta_j)\cos(\theta_k) + \sin(\theta_j)\sin(\theta_k).$$

1.1.2 Oscillatory Power

Moving on from phase, the power of an oscillation is another important measure, here referring to the strength or amplitude of neural activity, typically measured in microvolts (μV; Jensen et al., 2019; for a depiction of oscillatory power, see Figure 1.3). It is important to acknowledge the distinction between the phase and amplitude of an oscillation, as these are frequently used within research as both separate and complementary measures (Ding & Simon, 2013). On its own, the strength of an oscillation has important implications for numerous cognitive processes and can be used to also predict behaviour (Donoghue et al., 2020). For example, going back to the alpha led theory of inhibition, research has evidenced that higher alpha power is associated with reduced neuronal excitability and regional activity, separate to any additional influence of phase (Iemi et al., 2017; Samaha et al., 2020; Sauseng et al., 2009). In illustration of this, when examining the role of alpha power within the visual cortex, studies have suggested that power here is inversely related to regional excitability, where high alpha power is able to inhibit neuronal firing activity (Ergenoglu et al., 2004; Rahn & Basar, 1993; Romei, Rihs, et al., 2008). When utilising this knowledge in practice, this inverse relationship can predict behaviour, as research has been able to determine power signatures of certain cognitive processes, such as how lateralised increases of alpha power within the occipital cortex are linked to the inhibition of visual processing for stimuli in the contralateral hemifield; illustrative of individuals shifting their attention (Kelly et al., 2006; Thut et al., 2006; Worden et al., 2000). Importantly also, power measures have been suggested as a potential biomarker for certain neurological disorders, such as beta power changes being predictive of Parkinson's progression (Boon et al., 2019; Little & Brown, 2014). Such a discovery emphasises the functional importance of oscillatory amplitude in healthy cognition, and creates an opportunity for the development of potential diagnostic methods to draw on these findings (Karekal et al., 2022). Whilst this disease related research is not yet considered robust (Shirahige et al., 2020), it works to highlight the involvement of oscillatory power in modulating cognitive processes and by better understanding these mechanism, it offers a potential insight into how we can manipulate such neural activity to improve our cognition and perhaps even alleviate clinical symptoms.

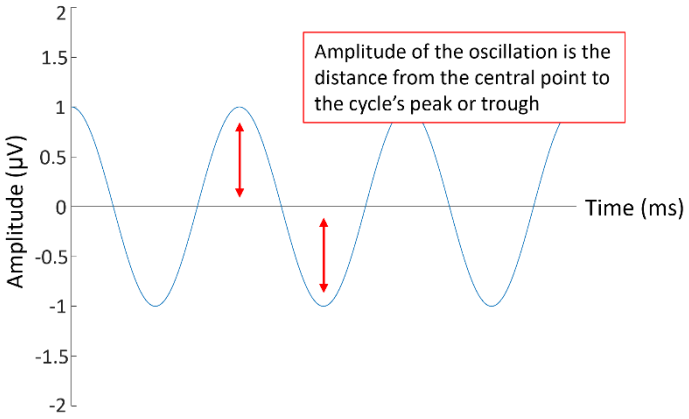


***Figure* 1.3**: Depiction of oscillatory amplitude (power), where the red arrows are indicative of power measures for this signal. The arrows highlight how amplitude measures are taken from the central amplitude line to the peak or trough of a single cycle.

1.1.3 Oscillatory Phase and Power Interactions

Moving on to examine the interplay between these oscillatory features, as complimentary measures, it has been determined that phase and amplitude interact to form a coupling (PAC) mechanism that also influences cognitive processes. This is achieved when the amplitude of a fast signal is modulated by the phase of a slow signal (Buzsáki & Draguhn, 2004; Chrobak & Buzsáki, 1998; Cohen et al., 2008; see Figure 1.4, below), a behaviour that is often referred to as "nesting" (Lakatos et al., 2005). For example, this is most often demonstrated with the modulation of gamma-band amplitude by the phase of theta-band frequencies (Tort et al., 2010). These cross-frequency relationships are important to acknowledge, as evidence has frequently shown that PAC is essential for routing the flow of information in the cortex and encoding this information effectively (Buzsáki & Draguhn, 2004; Colgin et al., 2009; Qin et al., 2021; Wang et al., 2021), working to temporally align processes that are related to low or high oscillatory amplitudes (Siegel et al., 2012; Von Nicolai et al., 2014). In other terms, this has been referred to as a mechanism of neural integration and has been demonstrated to influence behavioural outcomes, such as subserving signal detection through the successful discrimination of visual targets based on PAC strength between gamma amplitude and delta phase (Händel & Haarmeier, 2009).

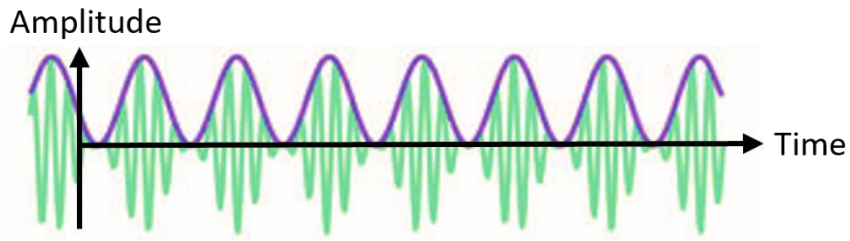


***Figure* 1.4**: An illustration of phase-amplitude coupling (PAC), where the amplitude of a fast oscillation (blue trace) is modulated by the phase of the slow oscillation (green trace).

In review of the outlined evidence detailing some general influencing features of neuronal oscillations, it is clear that the discovery and continual analysis of this rhythmic activity has enabled a deeper understanding of specific mechanisms in the brain. The use of such neural signals has become both popular and prominent in modern research, with a notable resurgence of interest over the last two decades (Buzsáki & Draguhn, 2004; Donoghue et al., 2022; Shackman et al., 2010). Moving beyond simply being able to record and analyse them, developments have meant that researchers are now able to induce neuronal oscillations in specific cortical regions using several techniques (e.g., stimulation methods, see Chapter 1.2.2 Transcranial Magnetic Stimulation; Thut et al., 2011). This has meant that not only have oscillations been able to offer us correlational evidence through their recording, but they can also aid the collection of causal evidence with manipulation methods, adding a vital line of argument to their importance in the brain. This is something that will be explored in more detail in subsequent chapters, with Chapter 5 specifically designed to add a level of causality to our investigations. For now though, it would be most appropriate to conclude that despite research in this area being conducted for nearly a century already, with the addition of technological and analytical advances continually, there is still a lot that we do not know about how oscillations can influence cortical functioning and behaviour (Donoghue et al., 2022). It is therefore pivotal that research into oscillations continues so that we can work towards a clearer understanding of these rhythmic signals and the vital role that they play in everyday life, utilising validated methods that achieve robust conclusions and resolve the currently ongoing debates. As a whole, this thesis aims to contribute to such aims, utilising neuroimaging techniques that have enabled an in depth and meaningful exploration of how our brains may function. Such techniques will be introduced and evaluated in the following paragraphs.

1.2 An overview of relevant neuroimaging techniques

1.2.1 Electroencephalography (EEG)

In 1875, the scientist Richard Caton made perhaps one of the most significant discoveries in neuroscience, providing evidence for the electrical properties of the brain (Caton, 1875). He was able to show that when placing electrodes on the exposed brains of rabbits, a galvanometer indicated the existence of electrical currents that varied depending on their behaviour at the time. He detailed in a later report that these variations were associated with sleep, wakefulness, anaesthesia and death (i.e., the absence of activity), and that they could be conveniently recorded from the scalp rather than the surface of the brain (Caton, 1877). By demonstrating the existence of electrical currents within the cortex, this provided a unique and pioneering insight into how the brain works, creating an opportunity for the development of techniques that would enable these electrical recordings in humans.

However, despite this early discovery, it was not until 1929 that the first electrical neural recordings, using human subjects, were published (Berger, 1929). It was during this time that Hans Berger used electrodes placed on the scalp of his son to replicate the findings from previous animal studies, demonstrating the electrical features of the human cortex. He subsequently named this technique: electroencephalography (EEG), something that is now a popular non-invasive neuroimaging technique in both clinical and research populations (Weiss et al., 2023). By its definition, this is a method that we use to record the electrical signals of the brain to determine activity across the cortex.

As previously alluded to, EEG works by placing electrodes on the scalp surface and recording electrical potentials from the neurons located underneath. In very simple terms, neurons are cells in the brain that use electrical and chemical signals to communicate both within and across the cortex (Lovinger, 2008; Zhang, 2019). Action potentials are key to this transmission, defined as a rapid change of voltage potential across the membrane of the neuron, reaching a certain threshold to induce a ‘spike’ in activity (Hodgkin & Huxley, 1939; Barnett & Larkman, 2007; Zhang, 2019). This threshold is only reached when there is an influx of sodium ions flowing into the neuron, causing depolarisation followed by repolarisation, once potassium ions subsequently move out; the neuron’s membrane potential must reach -50 mV for this to occur. Once an action potential is created, this then propagates along the axon of the neuron towards the axon terminals. It is here that this electrical signal (a.k.a., action potential) is converted into a chemical message so that it can travel across a synaptic gap to reach neighbouring neurons. Upon arrival, this whole process starts again. It is this transmission

of signal and connection between neurons which enables rapid and integrated communication both within and between cortical regions.

It is important to acknowledge however, that whilst it is well known that EEG records electrical potentials, what many tend to forget is that these electrical signals are the summed *post*-synaptic activity of pyramidal cells, of which are synchronously active at any one time (Hallez et al., 2007). It is these pyramidal neurons specifically that are suggested to be the generators of EEG signals, as they are organised in such a way, normal to the cortical surface, that means they amplify each other's extracellular potentials (Hallez et al., 2007). This is particularly important as the human head has many layers (e.g., scalp, skull, brain, etc.) and contains additional noise, so in order to break through such barriers, recordable signals come from large populations of neurons creating summed activity that can be recorded at EEG electrodes (Sanei & Chambers, 2013).

Once a signal has been obtained, the EEG recording can be transformed into meaningful patterns of activity through brain wave analysis. This can be achieved through the application of Fourier Transform methods, which is a technique that is used to identify sinusoidal components (i.e., oscillations) in a neural time series (Bloomfield, 2000; Semmlow, 2012). In result of this transformation, the frequency spectrum of the EEG signal will be revealed for use in further analysis and interpretation. However, it is worth noting that recent advances in our understanding of oscillations have determined that not all oscillatory rhythms may actually be rhythmic (Jones, 2016) or sinusoidal (Cole & Voytek, 2017). Whilst this delves into a topic well beyond what this thesis aims to address, it is something worth considering when interpreting EEG findings more generally. For the purposes of this chapter though, the content here will work on the assumption that oscillations do exhibit rhythmic tendencies.

Whilst EEG is known as a reliable and effective technique for obtaining a non-invasive measure of neural activity (McEvoy et al., 2000; Suarez-Revelo et al., 2015), it does not come without its limitations. Firstly, one of the most important limitations to consider, is that EEG has poor spatial resolution capabilities (5-9 cm; Babiloni et al., 2009). This means that the EEG electrodes are not able to pick up signals from specific locations of the brain. Instead, recordings suffer from volume conduction effects, meaning that the resulting signal is blurred because it travels through disruptive layers (e.g., the skull) to reach receiving EEG electrodes (Myslobodsky et al., 1991; Nunez & Srinivasan, 2006). As consequence, the recording at each electrode is a mixture of underlying brain sources, highlighting the caution needed when interpretating signal localisation

(Michel & Brunet, 2019). Despite this, EEG has been documented to have an excellent temporal resolution in the millisecond range, meaning that the timeline of neural events can be mapped out with relative precision (Handy, 2005).

1.2.2 Transcranial Magnetic Stimulation (TMS)

Besides the ability to record electrical activity of the cortex, we are also able to manipulate it using a multitude of techniques, from stimulation methods to the application of periodic visual stimuli that results in steady-state evoked potentials (SSEPs; Herrmann, 2001; Norcia et al., 2015; Polanía et al., 2018), e.g., a presented 10 Hz visual flicker induces a related 10 Hz SSEP in the occipital cortex, as first demonstrated by Adrian and Matthews (1934). Here, focus will remain on the former of these techniques, exploring the application of transcranial magnetic stimulation (TMS) to investigate brain function and cognitive processes.

TMS is a non-invasive method of brain stimulation (NIBS), used widely to study cortical functioning through the activation of neuronal populations within the cortex (beneath the stimulation site), aiding in the establishment of causality between the induced neuronal activity and resulting cognitive/behavioural processes (Klomjai et al., 2015; Ziemann, 2017). In basic terms, if the stimulation of area A leads to a reduction of behaviour B, then a cause-and-effect relationship is assumed. The results of this can also be utilised in the investigation of which cortical regions are responsible for which behaviours/cognitions, a process known as cortical mapping, where a behaviour observed following the stimulation of a specific brain region can therefore be attributed to its localised activity (for a review on the causal mapping of brain function, see Siddiqi et al., 2022). This technique was first demonstrated by Anthony Barker in 1985, whereby he successfully stimulated the motor cortex using such techniques, resulting in movement of the contralateral hand, leg or even finger; the choice of which being dependent on the exact location of stimulation (Barker et al., 1985). Since this, the popularity of TMS has continued to grow, particularly within the cognitive neuroscience community (Ziemann, 2017), where, to date, more than 3 million scientific papers have been published utilising this method of NIBS (Google Scholar, 2024).

With the rising prevalence of TMS in modern research, it is important to understand how TMS works so that accurate interpretations of such research and their outcomes can be made (Walsh & Pascual-Leone, 2003). First and foremost, TMS works as a device, whereby an electrical current is sent through a wired coil to produce a magnetic field, as per the laws of electromagnetic induction (Rotenberg et al., 2014). This

magnetic field can then pass through the skull and stimulate brain regions that are located underneath (Barker, 1991; Kobayashi & Pascual-Leone, 2003). However, this only occurs if the magnetic field is strong enough to cause the depolarisation of neurons and create an action potential (Nevler & Ash, 2015; Siebner et al., 2022). If this is indeed the case, these action potentials then propagate along the neuron and trans-synaptically to neighbouring neurons, resulting in either inhibitory or excitatory communication both within and across the stimulated cortex (Fletcher, 2011).

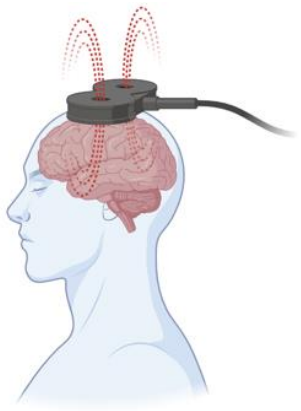


***Figure* 1.5**: An example of how a TMS figure-of-eight coil may be placed on the head of a participant, with the red dashed signal depicting a generated magnetic field which passes through the cortex and stimulates underlying brain regions.

When delivering TMS, a coil is placed on the scalp of the participants head (see Figure 1.5, above), the positioning of which will determine the subsequent stimulation site. Most often, researchers choose to utilise a figure-of-eight coil for this technique which is specially constructed to achieve a high spatial focality of stimulation at the centre point of where the two coils meet (see Figure 1.6, below; Cohen et al., 1990; León Ruiz et al., 2022; Ueno & Sekino, 2021). This can be used to selectively activate or inhibit small cortical structures near the surface of the cortex, often with the aim of determining their function (Bolognini & Ro, 2010). For example, one of the earliest applications of TMS was used to stimulate the left inferior frontal cortex, with researchers finding that this would induce speech arrest in participants (Pascual-Leone et al., 1991). From this, researchers were able to determine that the stimulation created a 'temporary lesion' in the activity of Broca's area, highlighting that such a region was essential for speech production (Epstein et al., 1999); a conclusion that was arguably only possible because stimulation techniques are able to establish causality. Nowadays the term 'lesion' is considered outdated as newer information has been able to establish

that TMS can improve performance (Luber & Lisanby, 2014) rather than simply impair it, making 'lesion' a misleading description.

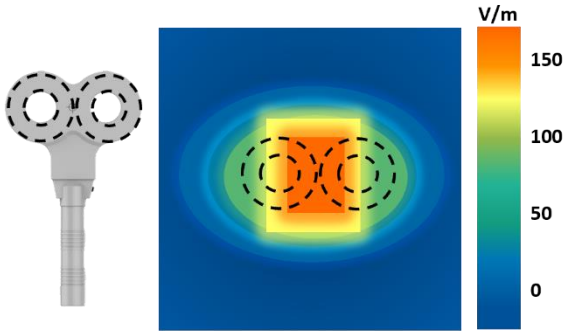


***Figure* 1.6**: A simulated illustration of the distribution of electrical fields that are induced by a standard figure-of-eight coil. The black bashed lines depict the shape of the coil, whilst the colour bar is indicative of the E-field generated during stimulation (red = strong, blue = weak)

There are two popular protocols that can be applied when utilising TMS methods, namely single pulse TMS (spTMS) and repetitive TMS (rTMS). These are useful for different reasons, performing different roles in both research and clinical applications. Firstly, spTMS consists of one pulse delivered to a targeted area of the cortex (Thut & Pascual-Leone, 2010), inducing a short change in neural activity. This type of stimulation is often delivered to the motor cortex, as was originally demonstrated by Barker (1985), inducing motor evoked potentials (MEPs) that can be recorded from muscles contralateral to the stimulation site (Kobayashi & Pascual-Leone, 2003, see Figure 1.7). This muscle is often the first dorsal interosseus hand muscle (FDI) and resulting activity here allows the establishment of motor thresholds (Groppa et al., 2012). These are thresholds that reflect the lowest stimulation intensity needed to evoke MEPs, exhibiting the strength of neural excitability at the stimulated region (Ah Sen et al., 2017; Bestmann & Krakauer, 2015). For example, a large MEP amplitude suggests that the motor cortex is highly excitable at the time of stimulation, and so neurons demonstrate an increased response. In experimental studies, by quantifying participants' unique motor thresholds (MTs), these can then be used to dictate the intensity of the delivered pulses during subsequent experiments, which is essential as research has shown that threshold levels may be driven by individual differences such as skull thickness (Stokes et al., 2007), grey matter volume, and other anatomical and/or functional individual differences (Rosso et al., 2017). It is therefore standard to use an individual's resting MT (rMT) to control the 'dosage' of TMS stimulation, so that the intensity is normalised across participants; based on their physiological variability (Herbsman et al., 2009). Clinically, spTMS has also been used with stroke

patients to identify the presence or absence of MEPs in order to assess the functional integrity of the corticospinal tract (CST; Albuquerque et al., 2023; Hordacre et al., 2021; Stinear et al., 2006). This enables clinicians to determine the degree of post-stroke motor function recovery that could be possible in these individuals (Smith & Stinear, 2016). If there is a clear MEP after stimulation, this suggests that the CST is intact, and motor function is likely to recover with the correct treatment and therapy.

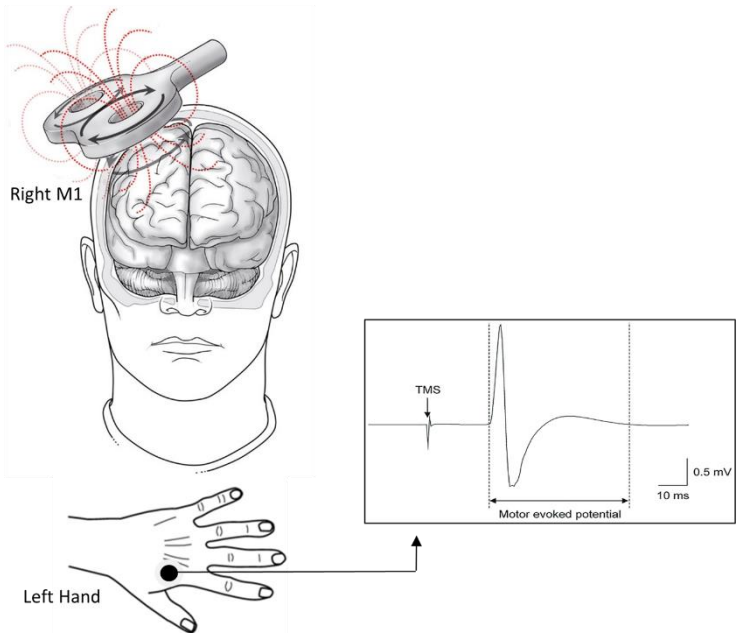


***Figure* 1.7**: When transcranial magnetic stimulation (TMS) is delivered to the motor area, this causes a motor evoked potential (MEP) in a contralateral muscle. The muscle that is activated is dependent on the location of stimulation. In this case, the figure demonstrates how targeting the right M1 region causes an MEP in the left-hand muscle.

In contrast, repetitive TMS (rTMS) is a stimulation technique that delivers multiple magnetic pulses to the cortex in quick succession of one another (Klomjai et al., 2015). This technique is most often utilised to induce lasting changes of excitability at the stimulation site (Chen & Seitz, 2001; Siebner & Rothwell, 2003), with research finding that high frequency rTMS results in the facilitation of cortical excitability (Chen & Seitz, 2001; Fitzgerald et al., 2006). Such protocols have also been proposed to entrain neural activity to the pattern of delivered pulses (Thut, Schyns, et al., 2011). Here, entrainment is defined as the alignment of oscillations to an external rhythm, where alignment occurs due to the application of this exogenous source (Lakatos et al., 2019; Obleser & Kayser, 2019). For example, rTMS can be used to stimulate the left intraparietal sulcus (IPS) at 5 Hz, causing an increase in parietal theta oscillations, and subsequently an increase in working memory

performance (Albouy et al., 2017). Such an example is important as it highlights not only the ability of rTMS to entrain oscillatory rhythms in the cortex, but it also emphasises its major advantage of being able to establish causality, i.e., increasing theta rhythms causes memory performance to increase.

Prior to moving past the topic of entrainment though, it should be emphasised that there is still a debate surrounding this process, encompassing whether we are defining it accurately in order to appropriately interpret entrainment and its consequences (Bánki et al., 2022; Duecker et al., 2024; Keitel et al., 2014; Zoefel et al., 2018). Some researchers have suggested opposing arguments whereby rather than achieving oscillatory entrainment through rhythmic stimulation, instead we are eliciting a series of evoked potentials that follow the applied rhythmic pattern, also known as stimulus or frequency tracking (Capilla et al., 2011). If this is true and we are not able to entrain oscillations using rhythmic stimulation, then deciphering the causal impact of oscillations on cognition becomes challenging. Although, instead of these arguments being pitted against one another, where only one must be true, perhaps they rather reflect distinct neural manipulation methods, and we should re-label and separate 'narrow' from 'broad' entrainment processes (Obleser & Kayser, 2019). Here, the former can be viewed as where an oscillation is changed through the application of an external source (i.e., rhythmic stimulation) and the latter is instead the evoked appearance of neural responses that temporarily align with oscillations. As of current, to gain a better understanding of this, research must continue so that our methods for investigating neural functioning are validated and results can be accurately interpreted. Both sides of the debate have support from a number of studies, with those stating their unequivocal support for entrainment (e.g., Doelling et al., 2019; Notbohm et al., 2016) and others rejecting the possibility of this within their results (e.g., Capilla et al., 2011). Without further research, the concluding remarks of this debate are currently beyond reach. Regrettably, due to a lack of resources within our own investigations, we were not able to decipher whether our TMS protocol entrained oscillations in either sense, a limitation attributable to our lack of concurrent EEG recordings; something which will be explored further in Chapter 5.

Regardless, in encouragement for the use of rTMS, such techniques have been evidenced to induce changes in brain activity that last significantly longer than those seen from spTMS, stretching beyond the stimulation period (Klomjai et al., 2015). This occurs because each pulses' effects temporally summate together and induce a much larger change of neural activity, than compared to spTMS protocols (Anand & Hotson, 2002). Taking advantage of this long-term effect, rTMS has been applied in clinical settings, where such protocols are adopted in an attempt to treat both neurological and psychiatric disorders (Lefaucheur et al.,

2014, 2020; McClintock et al., 2018). One such instance of this is the use of rTMS in stroke patients, where stimulation is applied to the motor cortex to increase the excitability of this region and thus promote physical rehabilitation (Smith & Stinear, 2016).

On a final note though, despite the popularity of TMS being routed in its causality establishing abilities, it should be noted that there are often confounds in all facets of research which make it difficult to reliably determine causal relationships, even in circumstances of brain stimulation (Bergmann & Hartwigsen, 2021). For example, despite the high focality of TMS, an induced electric field (E-field) from the stimulation may produce neuronal activity in non-targeted regions that were not 'aimed for' (Bergmann & Hartwigsen, 2021). This, therefore, makes it difficult to determine whether the induced effect was due to the stimulation of the targeted region, or instead due to stimulation consequences within the cortex. However, there are a growing number of methods that can be adopted to mitigate this limitation (see Bergmann & Hartwigsen, 2021) and so this point simply seeks to advise caution in the interpretation of TMS results.

1.3 Utilising neuroimaging techniques within this Thesis

With the outlined techniques of EEG and TMS, a multitude of possibilities and new avenues have become available to aid further investigations into cognitive neuroscience. Within this thesis, I will describe and discuss how these neuroimaging techniques, and others, have been utilised to explore the role of neuronal oscillations in visual perception and visuospatial attention, alongside their more general role in cortical excitability. These investigations have predominantly been conducted with the aim of furthering our understanding of how oscillations shape our cognitive processes. However, the second study to be reported within this thesis (Chapter 3) should be highlighted for its importance in contributing to the efforts being made in alleviating the replication crisis that is becoming more and more apparent in all fields of research, but especially in cognitive neuroscience (Huber et al., 2019). With the inclusion of this, we have not explicitly aimed to add any new knowledge to the literature, but instead to improve the reliability of the current research that is guiding our understanding of the underlying mechanisms within visual processes.

As a whole, this thesis is organised in such a way that enables a comprehensive understanding of the existing literature and how our research has been shaped to bridge gaps in our knowledge, particularly surrounding the role that neuronal oscillations play in the top-down control of visuospatial attention, perception and more generally, cortical excitability. To achieve this, the following chapter will first explore how important and fundamental oscillations may be for the normal functioning of the cortex, outlining our use of

secondary data to explore whether occipital neural phase can influence motor cortex excitability, a global mechanism that is significantly underexplored within the field, as of current. Next, we will introduce our replication attempts that have been previously mentioned, helping to create an insight into how the literature has been contradictory and ultimately leaving more open questions than answers. This chapter will focus on visual perception solely, which is an important process to initially explore without the added complexities of attentional mechanisms, which will come up in succeeding chapters. By developing this first, this creates a foundation of knowledge for the subsequent topics presented within this thesis. Next, we will progress onto what is perhaps considered to be our main investigation, where we have utilised EEG recordings to explore how oscillations can be modulated by shifting our visuospatial attention based on cues, and how this in turn modulates visual perception. Using the knowledge gained from this, a stimulation study was then designed to support our EEG investigation and provide an in-depth examination of whether the relationship between oscillations and perception could be evaluated as causal in nature; something that is essential for a complete understanding of oscillatory roles. These chapters importantly address the role of oscillations in modulating cognitive processes and as such, measurable performance. By exploring each of these topics, we hope to emphasise the broad role of oscillations within the cortex, promoting continuously their importance and their need to be studied further.

Chapter 2: Occipital Alpha Phase Influences Motor Cortex Excitability, a TMS-EEG Study

2.1 Introduction

When first considering the brain and how it functions more generally, it is important to acknowledge the role that cortical excitability plays in all cognitive processes (Badawy et al., 2012). To ensure understanding, cortical excitability has been defined as the strength of neural activity in response to a given stimulation or stimulus (Ly et al., 2016). During high cortical excitability, neural activity is also high, and so information can be efficiently carried within and between brain regions (Thut et al., 2012). This plays an essential part in aiding cortical communication and thus enabling important behaviours, such as orienting the focus of attention (Rosanova et al., 2011).

One method used to probe the level of cortical excitability within the brain, is by using TMS in combination with EEG (Rogasch & Fitzgerald, 2013). This technique has been praised for its ability to acquire cortical excitability information directly from the cortex, with high temporal resolution, revealing the causal connectivity between cortical areas (Hallett et al., 2017; Saari et al., 2018). For example, TMS can be used to activate area A and if area B then becomes active, it can be assumed that area A might cause an increase (or decrease) in the activity of area B through excitatory (or inhibitory) connections between the two areas (Hallett et al., 2017). Concurrent EEG can thus be used to uncover the neural signature that characterises the influences that one region may have upon another, enabling us to build a detailed understanding of how the brain functions. So, in general, by stimulating the cortex and measuring the level of evoked activity, this will produce an indication of cortical excitability levels.

Within the current literature, in an attempt to measure cortical excitability (both with or without neural recording methods), it is often standard for studies to stimulate the motor region of the brain (Fitzgerald et al., 2006). By stimulating this site with TMS, motor evoked potentials (MEPs) are produced in the participant's muscles contralateral to the stimulated hemisphere, commonly a hand muscle (e.g., the first dorsal interosseous: FDI). Although MEPs are generated by the activation of the cortico-spinal tract, they are considered to be an effective proxy of cortical excitability (Cortese et al., 2017), with the minimum amount of stimulation required to elicit these MEPs being known as the resting motor threshold (rMT). If an individual has a low MT, this suggests that they may have high levels of cortical excitability (Cortese et al., 2017). However,

threshold levels are also driven by individual differences such as skull thickness (Stokes et al., 2007), grey matter volume, and other anatomical and functional individual differences (Rosso et al., 2017). To account for these during stimulation studies, it is standard to use an individual's rMT to control the 'dosage' of TMS stimulation, so that the intensity is normalised across participants; based on their physiological variability (Herbsman et al., 2009).

Whilst many studies and explorations have established that the application of TMS can measure cortical excitability and inhibition levels (Fitzgerald et al., 2006), the literature is somewhat lacking when considering the role that oscillations play in cortical excitability (Romei, Brodbeck, et al., 2008; Romei, Rihs, et al., 2008; Schutter & Hortensius, 2011). However, the popularity of this research is now growing and studies are beginning to emphasise the importance of oscillatory activity in all facets of cognition, including cortical excitability (Bergmann et al., 2012). It is therefore starting to be documented that there is a functional relationship between the two (Sauseng et al., 2009; Tamura et al., 2005), with research highlighting the importance of alpha oscillations in particular (Palva & Palva, 2011; Romei, Rihs, et al., 2008; Sauseng et al., 2009). For example, studies have proposed that even at rest, alpha power can determine the magnitude of cortical excitability (Mäki & Ilmoniemi, 2010; Sauseng et al., 2009), as measured by the amplitude of TMS induced MEPs. Specifically, the higher the alpha power, the lower the excitation level in the cortex and thus the smaller the amplitude of subsequent MEPs (Sauseng et al., 2009). This inverse relationship between alpha and excitability can be explained by the inhibitory role that alpha oscillations have long been evidenced to play in the cortex (Bergmann et al., 2012; Jensen & Mazaheri, 2010; Klimesch et al., 2007; but see Foster & Awh, 2019). Specifically, it appears that during increased (occipital) alpha power, alpha troughs cause the inhibition of processing, reduction of excitability levels and impairment of visual detection abilities (Mathewson et al., 2011). In contrast, when (occipital) alpha power is low, cortical excitability is high enough (regardless of phase) to maintain processing capabilities and increase detection abilities (Mathewson et al., 2011). For an illustration of this, see Figure 2.1 (below). Further evidence in support of this has found that by using TMS-EEG, low alpha power at the time of stimulation reliably results in increased cortical excitability measures, and vice versa (for review, see Thut & Miniussi, 2009), highlighting the potential *causal* role that alpha plays in modulating the excitability of the cortex. Importantly, during periods of decreased alpha, there are notably increased effects of

TMS in both the visual and motor cortex (Romei, Rihs, et al., 2008; Sauseng et al., 2009), suggesting that these regions are most susceptible to the modulatory effects of alpha-band oscillations.

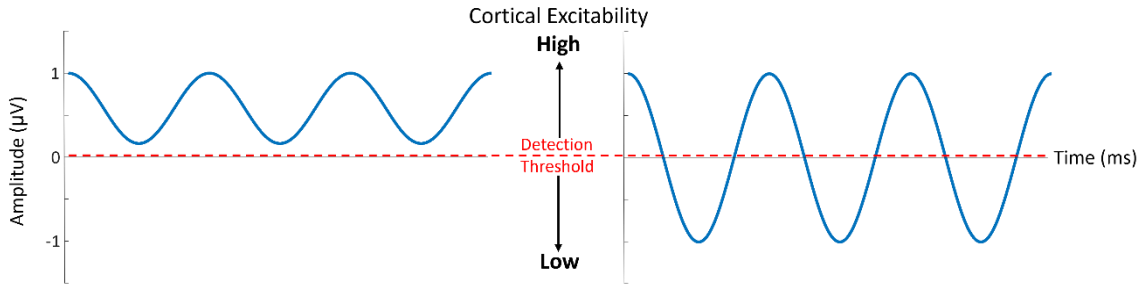


***Figure* 2.1**: Simulated example of how alpha power and phase measures may influence cortical excitability and result in modulated perception. In the first panel, when alpha power is low, cortical excitability remains consistently high and there is no influence of phase effects. This means that detection is equally likely at all parts of the cycle (alpha remains above the detection threshold; red dashed line). In comparison, when alpha power is high, cortical excitability fluctuates along the phase of alpha, with peaks representing high excitability and troughs low. This in turn means that perceptual detection fluctuates in line with this cyclic pattern. Illustration inspired by Mathewson et al., (2011)

However, it should also be noted that there is contradicting evidence within the literature, where cortical excitability is increased (facilitated) during periods where alpha phase is at a *trough* and alpha power is high (Bergmann et al., 2019). Within this study, Bergmann et al., (2019) utilised both single- and paired-pulse TMS protocols to stimulate the motor region at five timed conditions and either during low alpha power, at random phases, or high alpha power when phase angles were at their peak (0°), falling phase (90°), trough (180°) or rising phase (270°). Resulting MEP measurements revealed that amplitudes following stimulation during high-power alpha windows, at troughs and rising phases, was significantly increased relative to when stimulation was delivered at peaks and rising phases (high-power) or during low-powered trials more generally. Further, Bergmann's study found no evidence to corroborate theories of a phasic suppression of cortical excitability within their results, instead suggesting that the evidence was in favour of facilitation, emphasising the need for research to explore whether alpha is in fact inhibitory. They therefore move towards a 'pulsed-facilitation' hypothesis of cortical excitability rather than the more traditional 'pulsed-inhibition', with the latter term coined by Mathewson et al., (2011).

There are also results that contradict both sides of this debate and suggest instead that alpha oscillations have no relationship with corticospinal excitability. In fact, many studies find no MEP modulation based on alpha-power measures (for a review see Madsen et al., 2019). Instead, these studies often find an

effect of beta, where beta power and/or phase modulate MEPs and therefore excitability (Berger et al., 2014; Lepage et al., 2008; Schulz et al., 2014; van Elswijk et al., 2010). In an example of this, one study found evidence that MEP amplitude could be modelled by theta and beta oscillations in the left and right M1, contributing to local levels of cortical excitability (Schutter & Hortensius, 2011). Similarly, another study demonstrated that there is a clear dependency of TMS-induced MEPs on the state of pre-stimulation beta phase and power fluctuations, at approximately 18 Hz (Keil et al., 2014). With this latter study in particular, Keil et al., (2014) examined the correlations between oscillations and MEP amplitudes during wakefulness, where participants were asked to sit comfortably but fixate on a centrally presented cross. Whilst their results have been attributed to reflect beta oscillations modulating the excitability of the local motor cortex, it could also be argued that this significant effect may reflect a state of attentiveness influencing our brain state instead. This is based on the task instructions requiring participants to attend to a fixation. Such suggestions are reinforced by the fact that such beta effects were observed most strongly in parietal regions (Engel & Fries, 2010).

Moreover, when considering all the evidence and evaluating how we can progress our knowledge, it is important to note that much of the current research has focused on the oscillatory activity at the stimulation site. This includes the aforementioned study by Sauseng et al., (2009) who found that alpha power effects were localised over the motor area, where stimulation was applied. They concluded that motor cortical excitability is therefore modulated by local alpha power changes only. However, they note that this finding could simply be a result of limited resources, as they only recorded EEG from 29 channels, meaning that despite looking across a large area of the scalp, they perhaps missed evidence regarding the global effects that alpha-band activity may have on excitability. Nonetheless, there is yet more contrasting research here, where some studies, such as Mäki and Ilmoniemi (2010), present evidence to suggest that excitability levels can be influenced by global mechanisms of neural oscillations. Specifically, they found that there was a significant difference in occipital midrange-beta phase when comparing trials that result in either small or large-amplitude MEPs (indexing cortical excitability). This presents the notion that the excitability of neurons in the motor cortex appear to be modulated by input from occipital areas, or perhaps that this excitability is related to activity of occipital areas through a shared modulator (Mäki & Ilmoniemi, 2010). This theory is based on previous research showing that visuomotor tasks are often associated with changes in occipital beta oscillations and a beta phase coupling between visual and motor areas (Kilner et al., 2004). However, when looking at oscillation amplitude,

interestingly the study by Mäki and Ilmoniemi, (2010) only found a significant dependency between MEPs and beta power within the left Rolandic region (i.e., the stimulation site). This suggests that whilst beta amplitudes may modulate localised brain states, their phasic behaviours have effects that reach beyond their locality and thus modulate excitability on a global scale. Such extended phase effects have been additionally found in studies stimulating the frontal-eye-fields (FEFs), which was found to cause a phase reset of beta activity and also modulate the excitability of the V5 area (Veniero et al., 2021). This works to reinforce the theory that oscillatory phase may exhibit global excitability effects instead of just local, albeit between frontal-occipital regions in this latter example.

Whilst the literature evidencing the ability of oscillations to globally modulate cortical excitability is relatively sparse, it can be seen even within one of the first studies to investigate the neural activity accompanying motor behaviours (Bates, 1951). Here, it was found that alpha oscillations within parieto-occipital regions synchronised with voluntary motor movement (Bates, 1951), offering a different approach to investigating this topic. Specifically, the study noted how self-initiated movement occurred at the same point in the phase of an occipital alpha cycle, highlighting the importance of occipital alpha phase in modulating motor behaviours. However, due to the lack of technological advancements at the time, the EEG recordings supporting this suggestion were made with moving paper and an ink-pen (see Figure 2.2, below). It should therefore be expected that this method would result in a delay between neural activity and recording, suggesting that the findings may not reflect accurate temporal information. Although, research has continued to build on this finding by using more modern and reliable techniques. One such study used a closed-loop TMS-EEG study to stimulate the M1 area during different occipital (O1) alpha phases (phase 0, 90, 180 and 270°; Ding et al., 2023). Their results found that occipital alpha phase has a significant modulation effect on neural network and cortical connectivity, which was therefore perceived as the ability of alpha phase to facilitate cortical excitability (Ding et al., 2023). However, this study included no direct measure of brain state (i.e., MEPs or TMS evoked potentials) and therefore the extent to which cortical excitability is influenced can only be speculated upon.

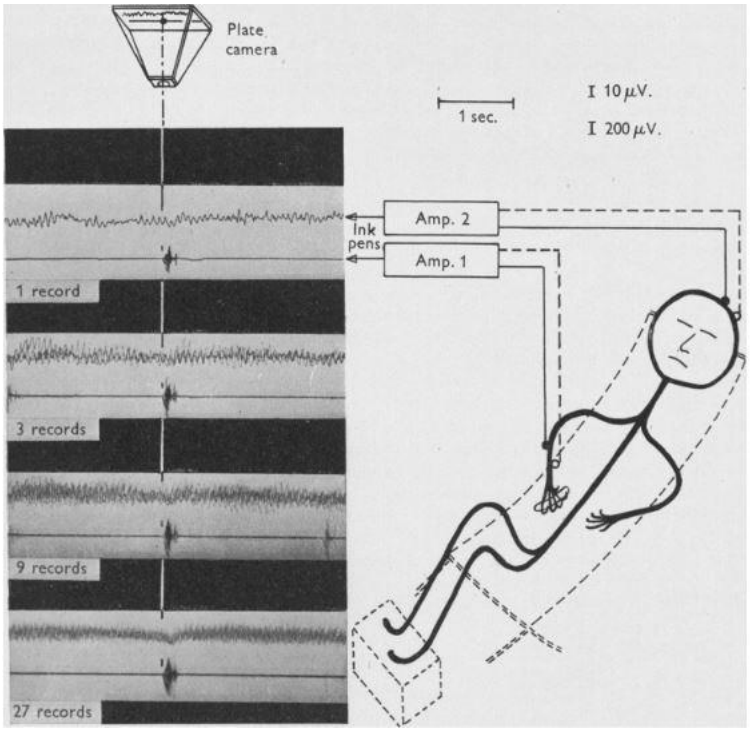


***Figure* 2.2**: Recording setup (left panel) and superimposed EEG traces (right) in the study by Bates (1951) investigating the neural activity that precedes voluntary motor movements. Participants were asked to lie in a comfortable position and make successive grips on a cardboard tube that they were holding in their hand. During this, neural recordings were taken from the motor region contralateral to the hand making grips, and the occipital region. Due to early restrictions on techniques, EEG recordings were output as a pencil trace. Figure obtained from original paper.

When considering the links between this proposed 'global' occipito-parietal alpha phase relationship with cognition, it is feasible to theorise that this may exist as our motor behaviours are typically influenced by what we observe within our environment. As humans, we are readily able to respond to objects within our visual field, and so there clearly exists a mechanism which enables the information transfer required for appropriate motor responses to be made. Previous research has indeed suggested that this may be achieved by gating the flow of information between occipito-parietal regions via the phase of alpha oscillations (Babiloni et al., 2014; Hussain et al., 2019; Jensen & Mazaheri, 2010; Zhigalov & Jensen, 2020). This suggestion is reinforced also by two previous studies who looked to determine whether the excitability of the motor cortex could be influenced by conditions of either eyes open or closed, and therefore based on visual input (Chen & Huang, 2018; Leon-Sarmiento et al., 2005). Both studies determined that there were differences in motor excitability levels between conditions, perhaps suggesting that visual input may modulate occipital alpha, thus resulting in the adjustment of motor excitability in response. However, neither of these latter studies included

neuroimaging techniques, meaning that this proposal is currently mere speculation as to the ongoing processes achieving such excitability changes. In light of this limitation and with the knowledge that the current literature does not provide us with enough evidence to determine how oscillations may impact cortical excitability, the aim of the current study is to determine whether the phase of occipital alpha oscillations are able to modulate cortical excitability. Whilst we will explore a wide range of frequencies, focus is on alpha-band oscillations in particular, as we believe that these are the strongest candidate for observing modulation effects based on their ongoing presence at rest; a condition that the participants are encouraged to present for the duration of the study. Further, as the study by Bates (1951) inspired this investigation and the majority of the limited literature acknowledges alpha as a driver in excitability changes, it seems most appropriate to spotlight this oscillatory band.

Therefore, we hypothesised that the phase of occipital alpha would likely exhibit the strongest relationship with motor excitability. Specifically, we expected to see both power and phase effects of alpha-band oscillations, with an inverse relationship being present between alpha power and excitability, but the phasic relationship being more difficult to predict due to contradictions amongst the literature. To explore this aim, we acquired open-source data from a TMS study whose investigative aims extend beyond what we require, but offer two signals to reach our current aim: pre-stimulation neural activity and TMS induced MEP measurements. By comparing the neural activity observed prior to high and low MEP amplitudes (representing high and low excitability, respectively), we hope to illuminate towards the *global* mechanisms that may contribute to motor cortex excitability. Importantly though, as the current evidence base surrounding this topic is limited and unclear, we believe that any additional insights into this neural-excitability relationship will offer an important milestone in field knowledge progression.

2.2 Materials and Methods

The data used in this study were obtained from the OpenNeuro Repository (doi: 10.18112/openneuro.ds004024.v1.0.1). This dataset was originally collected by Hernandez Pavon et al., (2022) and is publicly available under license CC0.

2.2.1 Subjects

All participants were healthy (no neurological, psychiatric or another medical condition that could alter brain function), aged 18-85 years, right-handed and had normal-to-corrected vision and hearing. Due to

the nature of the study, participants were not recruited if they did not meet the standard criteria for TMS and MRI studies (Rossi et al., 2009). This study was approved by the Northwestern University Institutional Review Board and was conducted in accordance with the Declaration of Helsinki. Fourteen participants were recruited and gave their informed consent prior to commencement of the study. After completing the study, two participants were removed due to technical issues with the EEG equipment, one due to excessive muscle artifacts and another due to a small number of trials following data cleaning. Thus, the final sample was made up of 10 participants (7 females; aged 19- 47 years).

2.2.2 Experimental Design

For the purposes of this study, we will only consider one aspect of the original task (as reported in Hernandez-Pavon et al., 2022), focusing only on EEG recordings acquired before any experimental manipulation (see below for details). During the study, single-pulse TMS (spTMS) was delivered to the left and right M1 (during separate runs). As a direct index of cortical excitability, resulting MEPs were recorded from the contralateral first dorsal interosseous (FDI) hand muscle and correlated with concurrent EEG recordings. To ensure the correct brain regions were targeted by TMS, MRI recordings were also obtained (for neuronavigational purposes).

2.3 Data Acquisition

2.3.1 Structural MRI Recordings

For each participant, high-resolution 3D T1-weighted images were acquired using a 3T Siemens Prisma Scanner with a 64-channel receiver array (Siemens, Erlangen, Germany). Such images were obtained using a Multi-Echo Magnetization-Prepared Rapid Acquisition Gradient Echo Sequence (T1/TR/TE1/TE2/TE3/TE4/α = 1190/2400/1.87/3.75/5.63/7.51 ms/7°, sagittal slice orientation = 0.8mm or 1.0mm isotropic resolution).

2.3.2 TMS Application and Parameters

TMS was delivered using a MagPro X100 with MagOption stimulator and a C-B60 figure-of-eight coil (MagVenture, Farum, Denmark), using a biphasic pulse. To ensure the M1 was accurately targeted with TMS, a neuronavigational system (Localite, St Augustin, Germany) was used to locate this region using participants unique MRI (see above). During TMS delivery, participants were instructed to wear earplugs, and their resting motor threshold (rMT) was determined by finding the lowest TMS intensity that evoked a subsequent MEP with an amplitude larger than 50 μV peak-to-peak in at least five of ten consecutive trials (Rossini et al., 1994).

During a baseline block, participants received 80 pulses at 120% rMT to the left and right M1, on separate runs. When the experiment commenced, participants were instructed to blink as little as possible and focus on a central fixation cross presented in front of them (see Figure 2.3, below). This ensured that participants remained focused throughout the experiment. In the original experiment, the baseline block was followed by three different types of cortico-cortical paired associative stimulation (ccPAS), a protocol used to induce short lasting plastic changes to targeted connections. These blocks were not used in the current analysis. As each participant underwent 3 sessions on different days, we merged all baseline blocks to acquire a total maximum of 480 trials per participant (80 baseline trials per condition x two stimulation sites), at a stimulation intensity of 120%. However, not all participants completed each condition due to availability restraints. As a result, for the 120% stimulation intensity condition, five participants completed all three baseline sessions, four completed two sessions and one individual completed a single session.

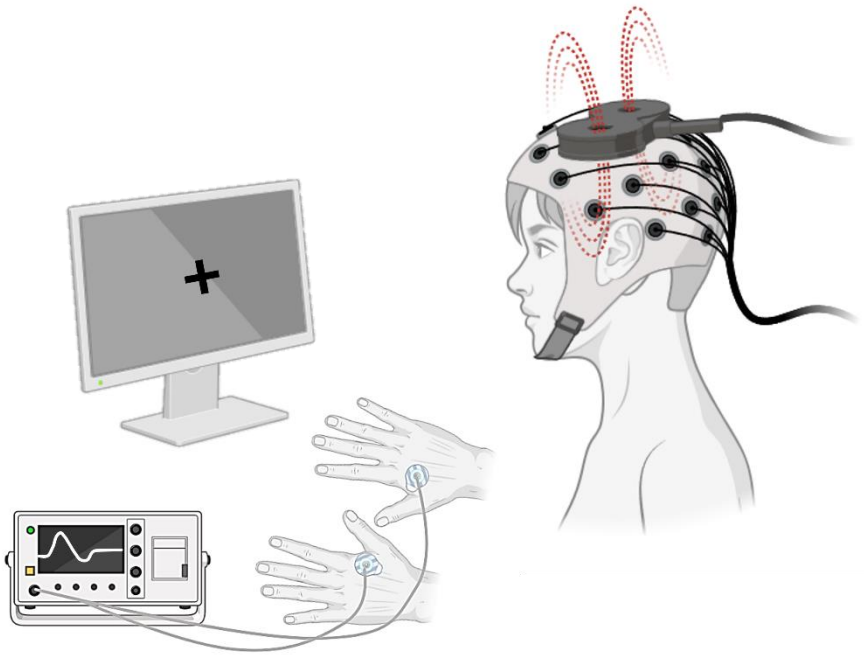


***Figure* 2.3**: Schematic representation of experimental set-up. Participants were tasked with focusing on a centrally presented fixation cross. Throughout the experiment, TMS pulses were delivered to either the right or left M1, with motor evoked potentials recorded from the contralateral hand. EEG was concurrently collected from the whole cortex using a 64-channel overlay.

To minimise TMS-EEG artifacts, cables from each EEG electrode were positioned to an orientation pointing away from the coil and perpendicular to the coil windings (Sekiguchi et al., 2011). In addition, the EEG cap was covered with plastic wrap to reduce electrode and wire movement. Specialised TMS-optimised pellet

electrodes (EasyCap GmbH, Herrsching, Germany) were also used, with researchers constantly monitoring the online EEG recordings so that any issues could be identified and resolved immediately; ensuring the minimisation of any TMS induced artifacts.

2.3.3 EEG Recordings

To reduce the effect of interfering electromagnetic fields, EEG recordings were conducted inside a two-layer electrically shielded room (Gaven Industries Inc, Saxonburg, PA). EEG data was acquired with a TMS-compatible 64-channel system (NeurOne Tesla, Bittium, Kuopio, Finland) and digitised to a sampling rate of 20 kHz. Five additional external electrodes were also used, placed at the right mastoid for reference purposes, the lateral canthus of each eye to record horizontal eye movements, and above and below the right eye to record vertical eye movements (electrooculogram; EOG). Electrode impedance was kept below 5 kΩ.

After EEG set-up, each scalp electrode, three fiduciary points (nasion and two preauricular points), and ~120 additional scalp surface points were recorded with the TMS navigation system (Localite, Bonn, Germany).

2.3.3 Motor Evoked Potentials Recordings

MEPs were recorded from the FDI muscle contralateral to the stimulation site (e.g., right M1 stimulation = left hand MEP). This data was recorded with a Bittium amplifier (Kuopio, Finland), alongside concurrent EEG.

2.4 Data Analysis

2.4.1 EEG Data Analysis

EEG recordings were pre-processed and analysed offline using custom MATLAB scripts (The Mathworks, Inc, Natick, MA) and FieldTrip (2021 release, https://www.ru.nl/neuroimaging/fieldtrip; Oostenveld et al., 2011).

Preparatory Data Steps

For each participant (N = 10), available data for both stimulation sites (right and left M1) were combined to create a single dataset per participant (left and right M1 stimulation combined). Epochs were then defined by TMS onset, resulting in a maximum of 480 trials per participant. Initially, epochs ranged from -4000 to 0ms pre-stimulation (TMS onset = time 0) as this was the full extent of the available pre-stimulation signal. This was then zero-padded to 5 seconds (to avoid filter artifacts), band-pass (1-48 Hz) and two-pass reverse filtered (Gross, 2014), then demeaned to achieve baseline correction. Data was also resampled to 256 Hz.

The resulting EEG signal was re-referenced to the average of all channels (excluding EMG and EOG). Artifact rejection was then carried out on each trial individually, where we removed those that contained TMS-related artifacts. Bad channels were also identified and interpolated (on average, 0.3 channels removed from each participants dataset). Independent component analysis (ICA) was then conducted, using the *runica* method in FieldTrip, however we limited the output to 20 components (via PCA reduction). The produced components topographies, time courses and average activities were then plotted and visually inspected to assess whether they represented blinks, saccades, heartbeat signals, and/or movement artifacts. On average, 5 components were removed for each participant. Finally, variance and standard deviation of each trial and channel was plotted to ensure they were artifact-free. If trials presented as extreme outliers at this step, these were removed.

Clean EEG data was then matched with clean EMG data (see below), where only trials that were present after both artifact rejections (EEG and EMG) were kept, resulting in an average of 335.7 trials per participant (*SD* = 115.27, range = 144 - 464 trials).

2.4.2 Motor Evoked Potentials Analysis

Motor evoked potentials were recorded in the data as electromyography (EMG) recordings. These EMG recordings were pre-processed similarly to the EEG recordings, with the data being epoched based on the time of the TMS stimulation (TMS = time 0). For this measure, epochs stretched to 1000ms pre-stimulation and 1000ms post-stimulation as we were interested in the MEP that resulted from stimulation, typically not lasting longer than 20ms (Hernandez-Pavon et al., 2022). EMG signals were demeaned to achieve baseline correction and high pass filtered (0.1 Hz). This data was then resampled to 5000 Hz. EMG data was visually inspected for artifact rejection purposes, removing any trials where there was significant muscle contraction prior to the TMS stimulation, as this may confound subsequent measurements of MEP amplitude.

MEPs for each trial were then categorised into high or low amplitude for each participant individually. To achieve this, MEP amplitudes were calculated by measuring peak-to-peak and calculating the median observed amplitude, using this to categorise high versus low MEPs (Biabani et al., 2021). Those that surpassed the calculated median were thus considered to represent ‘high excitability’ conditions, whilst the lower amplitudes were ‘low excitability’.

2.4.3 EEG Data Analysis: II

Irregular Resampling Auto-spectral Analysis

For each participant, to ensure that our subsequent analyses were accurately investigating oscillatory activity, irregular-resampling auto-spectral analysis (IRASA; Wen & Liu, 2016) was used to separate true oscillatory signals from concurrent power-spectral 1/*f* modulations. This was conducted on a single-trial level for each participant separately, then averaged across both (participants and trials) to provide an overview of EEG spectra. Importantly, this was limited to occipito-parietal electrodes (O1, Oz, O2, PO3, POz, PO4, PO7 and PO8), for frequencies between 5 and 75 Hz.

Phase Opposition Sum

To evaluate the effect of phase on MEPs amplitude, we used the Phase Opposition Sum (POS) to compared the signals of trials containing high versus low MEP amplitude (VanRullen, 2016a). Here, EEG epochs were redefined to -1000 to -10ms pre-stimulation as we were only interested in exploring neural activity immediately prior to stimulation and did not want to include any evoked potentials by choosing an end time of pulse onset (i.e., time 0). A copy of this epoch was then flipped along the time axes, with the real and mirrored signals concatenated so that any post-event/stimulation-evoked activity was removed from neural data. Spectra estimations were then extracted for frequencies of 4-25 Hz, chosen on the basis that we have hypothesised effects within the alpha-band. To this aim, the signal was band-pass filtered (two-pass reverse) between a range of [*fc – hw, fc + hw*], where *fc* is the centre frequency and *hw* is frequency width, set to 0.3 times the centre frequency, determining spectral smoothing. A Hilbert Transform was then applied to this filtered data, from which phase measures were extracted using the following formula:

$$\theta(n, f, t) = tan^{-1}\left(\frac{\mathrm{Im}(n, f, t)}{\mathrm{Re}(n, f, t)}\right)$$

where *n* is the trial number, *f* is the centre frequency, *t* is the time point, and *Im* is the imaginary part of the complex value from Hilbert transformation, whilst *Re* is the real value. Remaining flipped data was then discarded for further analysis.

POS calculations were then implemented to assess occipital phase differences between trials reflecting either high or low (motor) cortex excitability states. Each participants' dataset was therefore split into

low or high amplitude MEP trials (see 'Motor Evoked Potentials' below for details) and phase opposition measures were calculated for both conditions following VanRullen's (2016) method:

$$POS = ITC_A + ITC_B - 2ITC_{All}$$

where ITC is the inter-trial phase coherence of A, high MEP amplitude and B, low MEP amplitude, with the two conditions together being represented as All. Following traditional calculations, each ITC is calculated via the following equations:

$$\boldsymbol{ITC_{All}} = \left| \sum_{[\boldsymbol{i=1:n}]} \boldsymbol{\omega_i}/|\boldsymbol{\omega_i}| \right| / \boldsymbol{n_{All}}$$

$$\boldsymbol{ITC_A} = \left| \sum_{[\boldsymbol{i \in group_A}]} \boldsymbol{\omega_i}/|\boldsymbol{\omega_i}| \right| / \boldsymbol{n_A}$$

$$\boldsymbol{ITC_B} = \left| \sum_{[\boldsymbol{i \in group_B}]} \boldsymbol{\omega_i}/|\boldsymbol{\omega_i}| \right| / \boldsymbol{n_B}$$

Here, the use of these assumes that $\boldsymbol{\omega_i}$ is a complex number representing the analytic signal for trial i. Oscillatory amplitude and phase are then represented by $|\boldsymbol{\omega_i}|$ and $\boldsymbol{angle}(\boldsymbol{\omega_i})$, respectively (Lachaux et al., 1999; Tallon-Baudry et al., 1996). As before, A and B subscripts represent the two MEP amplitude conditions, with their combination being All. As we were most interested in how phasic behaviours at the occipital region could influence motor cortex excitability, POS analysis was conducted for channels O1, Oz, O2, PO3, POz, PO4, PO7 and PO8 only. Statistical significance was then calculated for each participant, time, channel and frequency of interest following a permutation whereby trial assignment to condition *A* and *B* was randomly shuffled 1000 times (VanRullen, 2016a). For each of these, the final calculated *p*-value was the proportion of permutations that yielded a higher measure than in the original dataset. In the first instance we determined that it was especially important to review POS at the individual participant-level to evaluate differences across participants, assessing whether averaged analyses were masking variation in oscillatory behaviours (Donoghue et al., 2022). Thus, POS *p*-values for each channel were combined, using a method first outlined by Fisher, (1932). Here, *p*-values are combined in the log domain using the following equation:

$$P_{Combined} = -2 \sum_{n=1}^{N} \log (p_n)$$

where p_n represents the *p*-value of channel n, with the final combination of *p*-values calculated under the null hypothesis with a Chi-squared distribution with $2N$ degrees of freedom. Importantly, POS analysis already corrects for time and frequency multiple comparisons itself, so this did not need to be considered within our analysis.

When looking to determine any effects at the group-level, we took these averaged channel *p*-values (see above) and combined them again at the participant level using a method that takes into account independent variables, developed by Stouffer et al., (1949) and also applied by VanRullen (2016). Here, we took the inverse normal cumulative distribution function of each individual participants' *p*-values and transformed them into equivalent z-scores. These z-scores could then be combined with ease as they are evaluated in standard deviation terms, meaning that individual variability is accounted for. These were then converted back into probability *p*-values using the normal cumulative function. The following equation details this procedure:

$$P_{Combined} = 1 - \Phi(\frac{\sum_{[i=1:N]} \Phi^{-1}(1 - p_i)}{\sqrt{N}})$$

Here, both normal and inverse normal cumulative function are represented by Φ and Φ^{-1}, respectively. N, P and i are then the number of participants, the *p*-value and trial number, correspondingly.

Pre-stimulation Power Differences

Next, we investigated power effects on MEP amplitude. In this case, the single-participant output of the Hilbert transform was used to extract the power using the following formula:

$$pow(n, f, t) = \left| \left(\frac{\mathrm{Im}(n, f, t)}{\mathrm{Re}(n, f, t)} \right) \right|^2$$

where the parameters are the same as before: *n* is the trial number, *f* is the centre frequency, *t* is the time point, and *Im* is the imaginary part of the complex value from Hilbert transformation, whilst *Re* is the real value. Remaining flipped data was similarly discarded for further analysis.

The pre-stimulation power measures for conditions of high and low MEP amplitude were then calculated and compared using a cluster-based permutation analysis (2500 permutations, cluster statistic = *maxsum*). This was performed as a paired samples *t*-test where we averaged power for each condition (high vs.

low MEP amplitude) over pre-stimulation epochs of -500 to -20ms and across the average of occipital channels only (PO7, PO3, POz, PO4, PO8, O1, Oz and O2) as we are solely interested in activity at this region. Additionally, as we were primarily focused on effects within the alpha-band, as per our hypothesis, this cluster was implemented between the frequencies of 8-12 Hz. When reviewing our obtained results from previous POS analysis though, we deemed it necessary to further extend this power investigation and conduct an additional cluster analysis between the frequencies of 13-25 Hz (otherwise identical).

Scalp Current Density Check

Once results have been obtained, we wanted to ensure the oscillatory activity found to have a significant effect was originating from the occipital cortex. To achieve this, EEG epochs were converted to scalp current densities via a spherical spline method (Ferree, 2006; Kayser & Tenke, 2015), using *ft_scalpcurrentdensity* function in MATLAB, FieldTrip. While scalp current density might not be as accurate as source analysis, it offers a useful approximation by reducing the effects of volume conduction. This makes it a valuable method for providing insights into the general location of neural activity. Pre-target epochs of between -500ms to -10ms were then demeaned and detrended, before bandpass filtering between either 8-12 Hz (alpha) or 13-25 Hz (beta). These frequencies were chosen based on significant results acquired in the previous POS analyses. In a final step, this data underwent a Hilbert Transform to obtain final power measures for both frequency bands (see formula above). Topographies could then be plotted to reveal estimates of current flow at the scalp level.

2.5 Results

The main aim of this study was to explore whether occipital alpha phase and/or power influenced motor cortex excitability, as indexed by MEP amplitude.

Irregular Resampling Auto-spectral Analysis

As an initial check to confirm that subsequent analyses would be validly investigating alpha band oscillations in the occipital cortex, we applied IRASA to separate oscillatory signals from aperiodic components. From this, we could clearly determine that alpha band oscillations peaked above fractal components between the frequencies of 8-12.5 Hz (see Figure 2.4, below).

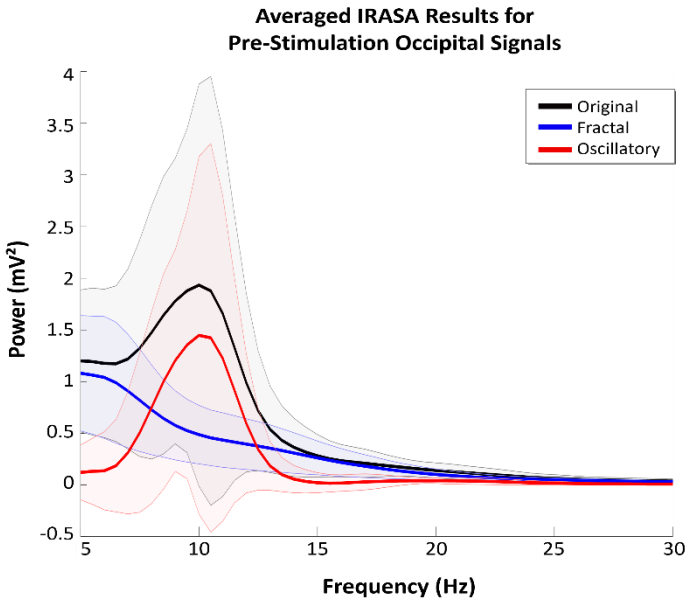


***Figure* 2.4**: IRASA results for the EEG signal recorded over occipital channels, prior to the onset of stimulation (i.e., TMS pulses). This has been calculated at the group level, with the oscillatory signal (red) demonstrating higher power over fractal components (blue) between alpha frequencies of 8-12.5 Hz, both extracted from the original data (black).

Phase Opposition Sum

POS was then calculated for each participant, using collapsed stimulation data (right and left stimulation). This analysis aimed to determine whether there were any phase differences in pre-stimulation activity that evoked large versus small MEP amplitudes. This was conducted first at an individual level (see Figure 2.5, below) and then a group level (see Figure 2.6, below). When examining the individual phase opposition results, it is apparent that there are individual variations across both time and frequency. Based on these outputs, it is difficult to determine patterns where phase effects may lie, encouraging us to look to group averages to make interpretations. However, even despite difference at the individual level, it remains clear that all participants exhibit significant clusters of phase opposition, preliminarily suggesting that the phase of occipital oscillations do have an effect on MEP amplitude.

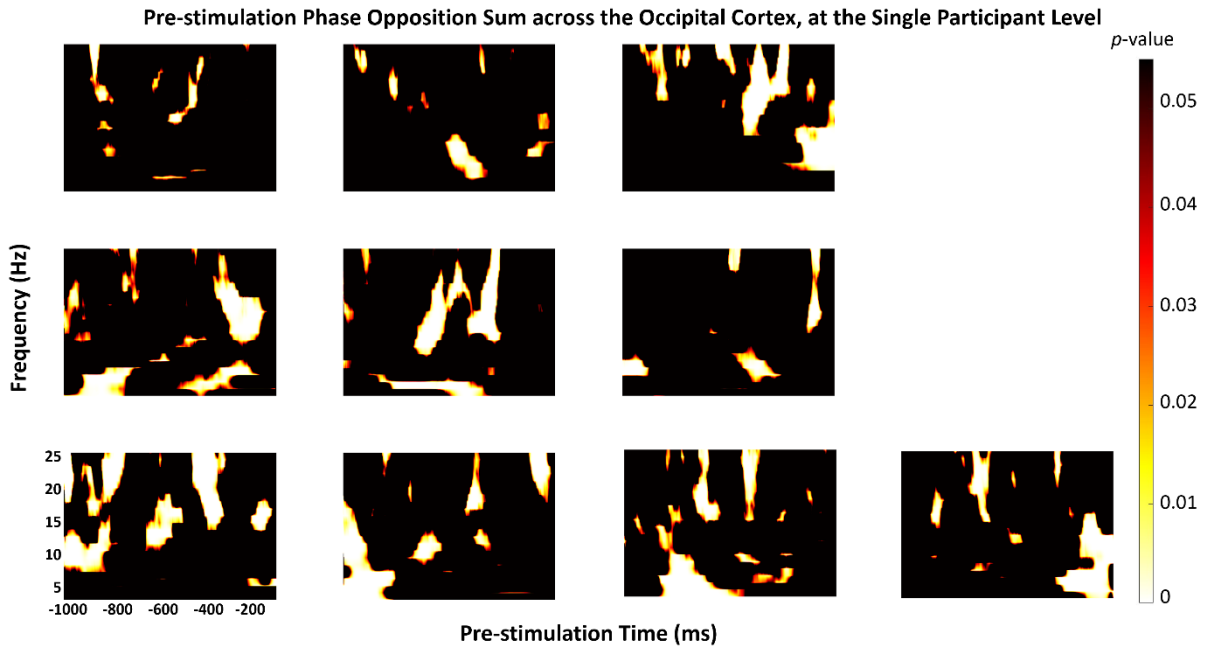


***Figure* 2.5**: Phase opposition sum at the single-participant level acquired from pre-stimulation data, when comparing high and low MEP amplitude trials. Each panel represents an individual participant. All significant *p*-values are highlighted in non-black colours ($p < .001$ = white). This is plotted as an average of phase opposition sums across the occipital cortex (POz, Oz, PO8, PO7, PO4, PO3, O2 and O1).

When looking at the POS across occipital electrodes at the group-level (see Figure 2.6, below), we found a significant phase opposition at around 100ms before the TMS pulse in the alpha band (~ 7-12 Hz). Besides this, there were additionally clusters of significance present within the beta-band (~ 13-25 Hz), but as we did not find a significant presence of oscillatory beta in our IRASA results, this latter finding should not be viewed with too much curiosity.

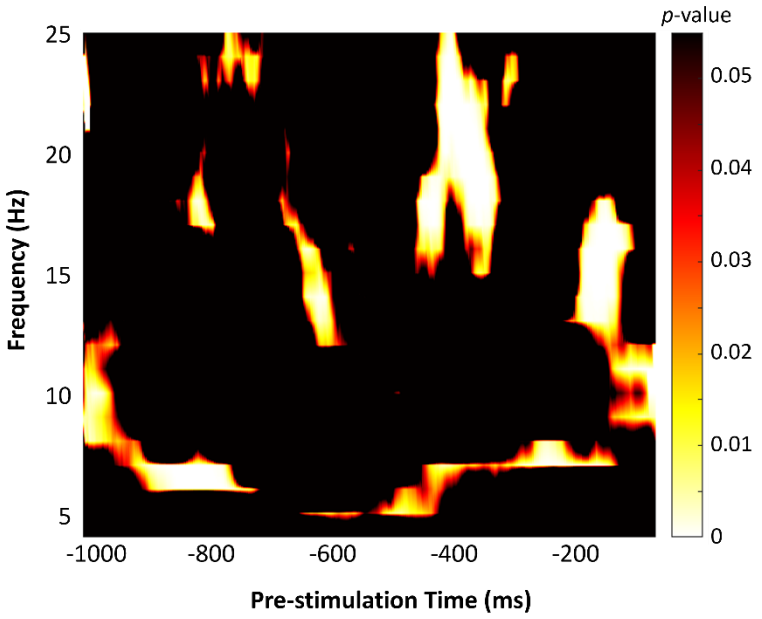


***Figure* 2.6**: Phase opposition sum at the group level, exploring the phase difference present at pre-stimulation time points, between high and low MEP amplitude trials. All significant *p*-values are highlighted in non-black colours ($p < .001$ = white). This is plotted as an average of phase opposition sums across the occipital cortex (POz, Oz, PO8, PO7, PO4, PO3, O2 and O1).

Pre-stimulation Power Differences

To evaluate possible effects of power, time frequency representations were calculated for both high and low MEP amplitude trials, at a single-participant level (see Figure 2.7, below). These were then compared against one another and input into a group-level cluster analysis to reveal that there was a significant difference between the two conditions in the alpha band (1 negative cluster: $t = -20.16$, $p = .032$). Specifically, it appears that pre-stimulation occipital alpha power is significantly reduced for high MEP amplitude trials than compared to low (see Figure 2.8, below). In contrast, there was no significant power difference observable within the beta-band (2 negative clusters: $t = -7.3$, $p = .13$ and $t = -2.38$, $p = .18$).

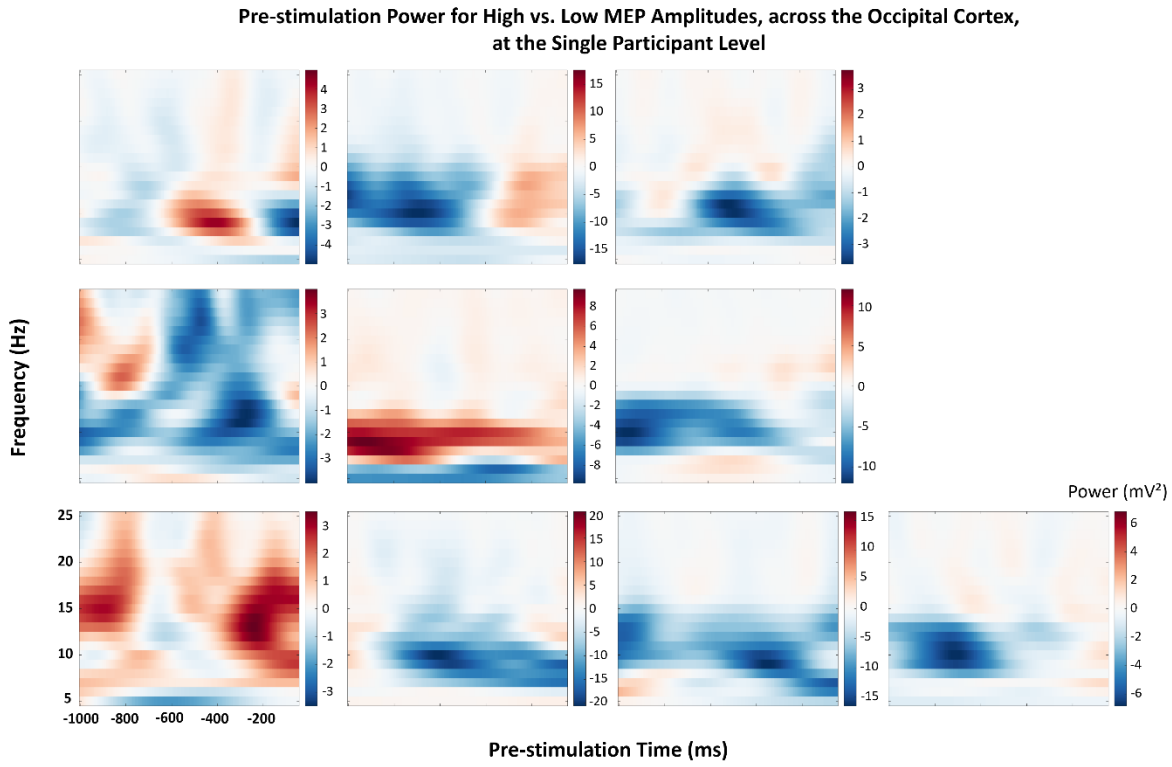


***Figure* 2.7**: Difference in alpha power between high vs low MEPs trials. Each figure represents pre-stimulation power from a single participant, observed across occipital channels (POz, Oz, PO8, PO7, PO4, PO3, O1 and O2). Blue colours on both figures are indicative of decreases in power, whilst red represents increases.

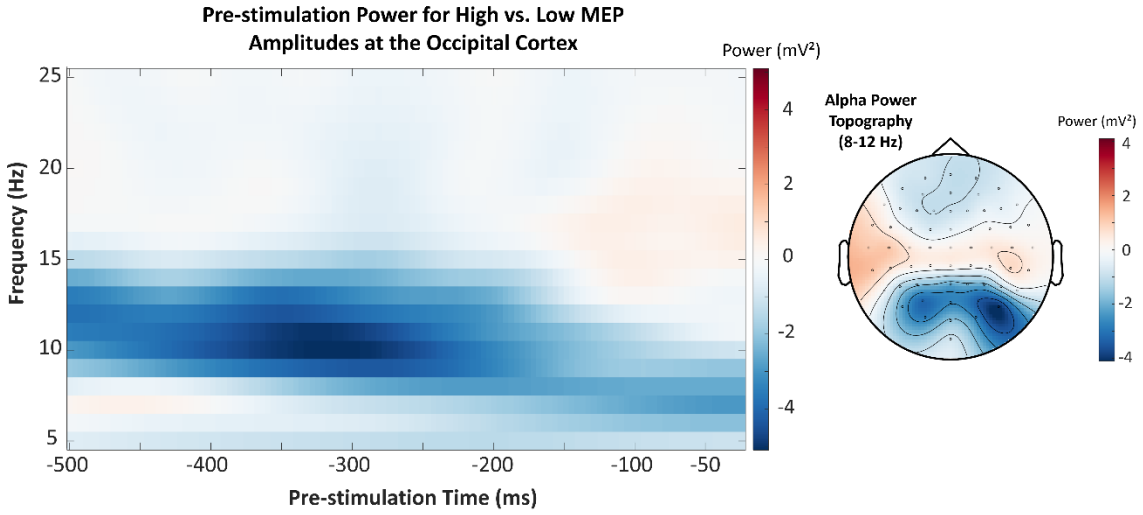


***Figure* 2.8**: Difference in alpha power between high vs low MEPs trials. Both figures represent the average power observed across participants and occipital channels (POz, Oz, PO8, PO7, PO4, PO3, O1 and O2), with the left figure showing power across pre-stimulation time. The topography plotted on the right show alpha-band differences (8-12 Hz) across the whole pre-stimulation time window (-500 to -20ms). Blue colours on both figures are indicative of decreases in power, whilst red represents increases.

Scalp Current Density Check

In a final step, to ensure our observed effects were localised to the occipital cortex, current source density was computed to obtain a more accurate topographical representation of both alpha (8–12 Hz) and beta (13–25 Hz) frequency band activity. As shown in Figure 2.9A, alpha-band power was predominately limited to occipital sites. Whilst in comparison, beta-band power appeared to be mainly located over the frontal channels of F5 and F6, with minimal presence over occipital sites (see Figure 2.9B). Note that the occipital beta seemingly present within Figure 2.9B is likely an effect of the spectral smoothing (+/-3 Hz).

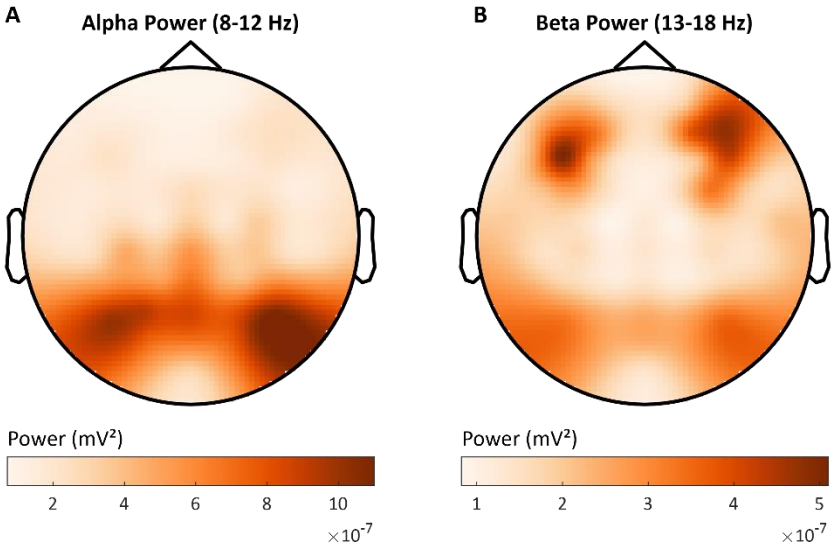


***Figure* 2.9**: Topographical distribution of EEG scalp current for alpha (A) and beta (B) power at pre-stimulation times (-500ms to -10ms). Higher current densities of power are observed over occipital sites for alpha, and over frontal sites for beta, illustrated with orange and red colours.

2.6 Discussion

This study aimed to determine how neural oscillations modulate cortical excitability, specifically investigating whether occipital alpha power and/or phase influences excitability of the motor cortex, as indexed by MEP amplitude.

When examining possible effects of power, our results support our original hypothesis and suggest that occipital alpha power does indeed have a significant effect on motor cortex excitability. Here, we found that power is significantly reduced during pre-stimulation periods for high amplitude MEP trials compared to low, supporting our original hypothesis. This reinforces the empirical evidence of previous investigations,

where the literature has frequently commented on the link between alpha and cortical excitability, finding that alpha power has an inverse relationship with excitability levels (Sauseng et al., 2009; Thut & Miniussi, 2009). Such findings complement what we already know about the general role of alpha oscillations, where decreases in alpha power have been attributed to both facilitatory (Bergmann et al., 2019) and non-inhibitory behaviours (Mathewson et al., 2011). It is important to note the distinction between these two types of mechanisms, where the literature is currently unclear on whether alpha oscillations work to enhance processing abilities via decreases in power, or inhibit processes through increases in power, or perhaps even both. Regardless of the precise mechanisms, our results go to show that decreases in alpha power can be linked with higher cortical excitability, reinforcing the notion of their modulatory effects.

In terms of our observed *global* relationship between alpha power in the occipital cortex and excitability in the motor, the literature supporting this is sparser. To our knowledge, there is no other study that has clearly determine such effects, instead only offering evidence for *local* modulation of excitability via oscillatory alpha power (e.g., Bergmann et al., 2019; Keil et al., 2014; Sauseng et al., 2009). Whilst this may currently be the case though, there has been some indirect investigations of such effects, where motor cortex excitability changes have been examined and found between eyes open and closed conditions (Chen & Huang, 2018; Leon-Sarmiento et al., 2005). Whilst these investigations did not record oscillatory activity and so cannot attest to the role of alpha oscillations, they did indeed find differences in MEP amplitude when comparing trials where participants had their eyes closed or open. This may suggest that changes in occipital alpha (influenced by visual input), may modulate motor cortex excitability (Ogata et al., 2019), thus supporting our current findings. Though, it is crucial to note that of the two studies that explored this effect, both reported contradicting results, with Chen and Huang (2018) finding that MEP amplitude was increased during eyes open conditions, whilst Leon-Sarmiento et al., (2005) found that MEP amplitude increased during eyes closed. As there is minimal research here, we cannot conclude which direction of findings is reliable. Additionally, without the support of EEG recordings, we cannot say for sure whether these studies would provide support to our conclusions, stressing the need for more studies to evaluate the occipital EEG-MEP relationship before clear deductions can be made.

Our results also indicate a significant effect of occipital alpha and beta phase in modulating the excitability of the motor cortex, as shown by a significant phase opposition at these frequencies when

comparing the pre-stimulation EEG signals for high versus low MEP amplitude trials. This ultimately suggests that the phasic position of occipital frequencies between 5-25 Hz can determine fluctuations in motor cortex excitability, indicating again the global modulatory mechanisms of neural oscillations. Specifically, at time points closest to the onset of the TMS pulse (~ 100 to 10ms pre-stimulation), it appears that there is a significant phase opposition between 9-12 Hz, supporting our initial hypothesis that there is an effect of alpha phase on establishing cortical excitability. Importantly, this finding is in line with the 'original' study by Bates (1951) who determined that the onset of hand movements was time-locked to certain phases of alpha activity in the occipital cortex. Such findings reinforce the notion of an occipito-motor connection within the brain, as well as strengthening the suggestion that alpha oscillations have a global ability to modulate excitability of networked regions within the cortex. Alongside this, whilst they did not find global effects, our emphasis on the role of alpha oscillations is further supported by previous research from Mathewson et al., (2011) and Bergmann et al., (2019) who both proposed an effect of alpha phase on measures of cortical excitability whereby brain state fluctuated along the alpha rhythm.

When moving to assess the proposed role of beta phase presented here, there is one other study to our knowledge that has similarly evidenced how MEP amplitudes are related to the phase of occipital beta-band oscillations (Mäki & Ilmoniemi, 2010), matching our current results. Such beta effects have been proposed to result from visuomotor processing, where beta oscillations are frequently noted as responsible for motor functions (Engel & Fries, 2010; Khanna & Carmena, 2015), as well as being especially present within the motor region of the brain (Jasper & Penfield, 1949; Morillon et al., 2019). However, whilst we do find this beta-band effect within our POS analysis, it is important to emphasise that our IRASA results highlight a lack of beta oscillations present within our obtained EEG recordings. Instead, only alpha oscillations peak above fractal components, meaning that we cannot accurately state that our findings found any significant effects within the beta-band, for power or phase. Furthermore, when looking at the scalp current density topographies, we found no clear indication for occipital activity in the beta band. Instead, beta was most prominent in frontal channels F5 and F6, perhaps suggesting that there is a closer link with this neural behaviour and the inhibitory control of motor movements (Picazio et al., 2014). It is therefore likely that our lack of beta effects are simply a result of reduced activity within the occipital cortex, which is to be expected when considering that participants did not have to engage in any cognitive task (Engel & Fries, 2010; Schilberg et al., 2021). When at

rest, alpha oscillations have frequently been noted as prevalent within the occipital cortex (Pfurtscheller & Lopes Da Silva, 1999; Romei, Brodbeck, et al., 2008; Webster & Ro, 2020). On the other hand, during cognitive tasks such as engaging endogenous top-down processes, beta oscillations have been shown to boost within occipital regions (for a review, see Engel & Fries, 2010). This perhaps suggests that whilst beta activity is important for modulating processes required for cognitive tasks, alpha is more apparent as an ongoing modulator; a point that we hope will also be emphasised across succeeding chapters within this thesis. As this investigation only required participants to fixate on a central target but otherwise rest comfortably, perhaps this is why we have found primary effects associated with alpha-band oscillations, rather than beta.

When viewing our results alongside previous literature, it is interesting to first consider why there is such limited research examining the global effects of oscillations on cortical excitability. When addressing why this may be, perhaps it is simply due to these studies solely focusing on local effects by recording EEG from the stimulation site and therefore not considering the possibility of global effects (e.g., Bergmann et al., 2019, focused only on four channels – CP1, CP5, FC1 and FC5). We can see this with the popular study by Sauseng et al., (2009) who stated that there was no evidence to support global modulations, but this could feasibly be attributed to limited EEG recordings they acquired from the occipital region. We believe that whilst our results may present new evidence, they are not so far removed from our understanding of how alpha oscillations may influence cognition.

Firstly, we know from previous research that the occipital and motor cortices are functionally connected through large-scale brain networks, such as sensorimotor integration pathways (Cheyne, 2013). It is therefore possible that our findings may reflect the role of pre-target alpha rhythms in gating the flow of information using these, connecting occipito-parietal regions of the brain (Babiloni et al., 2014; Hussain et al., 2019; Jensen & Mazaheri, 2010; Zhigalov & Jensen, 2020). Conceivably, such connections make it possible to transmit essential information signals that enable us to perform normal integration behaviours (Romei et al., 2010). This is particularly true when considering our observed alpha phase effects, where previous studies have found that gating behaviours can be achieved via phasic mechanisms that result in fluctuations of excitability levels (Busch & VanRullen, 2010; Hanslmayr et al., 2013; Keil et al., 2014). Perhaps here we could also consider whether there is the existence of phase coherence between the two regions, creating windows of excitability that promote communication from one region of the brain to another (Bowyer, 2016). Such extensions should

consider this possibility and extend our implemented analyses to evaluate this potential. Additionally, it is important to highlight that in a general sense, the literature has already established that higher occipital alpha power may indicate a greater inhibitory state that therefore reduces excitability across interconnected regions (Klimesch et al., 2007; Zumer et al., 2014), i.e., via thalamic-cortical modulation. Our resulting data seeks to reinforce such findings, where we have observed that pre-stimulation alpha power is higher prior to low excitability indexes, than compared to high.

Overall, we have proposed that occipital alpha oscillations are able to modulate motor cortex excitability. This is a vital contribution to the literature as it reflects the network of integration between sensory and motor information in the cortex. By exploring how this occurs via mechanism of oscillations, we are one step closer to understanding how the cortex functions. However, there is still extensive amounts of information that we do not yet know. For example, whilst it may be the case that the aforementioned interpretation of our results holds true (i.e., alpha phase enables regional communication and power inhibits neural excitability), it could equally be possible that our results reflect alternative explanations. Much like the studies seeking to determine whether MEPs varied depending on visual input differences (Chen & Huang, 2018; Leon-Sarmiento et al., 2005), perhaps our results reflect occipital alpha regulating visual information processing and therefore modulating motor readiness (Klimesch et al., 2011). This would be particularly important for tasks that require visuomotor coordination. When occipital alpha is therefore high, this could result in the reduction of visual processing and thus the lowered influence of sensory input on motor excitability. Without additional investigations though, it is difficult to determine which of these theories may reflect our current findings, instead prompting further explorations into this topic so that the field can work towards a comprehensive answer.

Further, alongside contributing to the literature, we also believe that these results are especially important when considering the application of closed-loop (or EEG-guided) TMS protocols within neuroscientific research, a technique that uses real-time neural data to determine when TMS pulses should be delivered, arguably in an attempt to control for the differential effects that can be observed across participants when stimulating different brain states (for further details, see Zrenner & Ziemann, 2024). The theory behind this is sensible as it has been well-established that brain state is crucial in defining the outcome of cortical stimulation (Bergmann, 2018; Sack et al., 2024; Silvanto et al., 2018), but optimal phase delivery is often

determined based on recordings from the stimulation site. This is a challenging technique for a number of reasons, including how the EEG signal can become contaminated with TMS evoked potentials (TEPs), especially when delivering pulses in quick succession (Ilmoniemi & Kičić, 2010; Shirinpour et al., 2020). Additionally, we know that often alpha activity is not typically maximal at the motor cortex as this is not its 'natural' frequency (Hannah et al., 2022; Rosanova et al., 2009), making it difficult to read these brain waves for subsequent targeting. With our results, we are thus proposing that as we have presented evidence of occipital alpha modulating motor cortex excitability, it would be easier and more appropriate to use neural recordings within visual regions, to define stimulation delivery times. It is here that alpha oscillations are most prominent, especially during visual tasks and at rest (Pfurtscheller & Lopes Da Silva, 1999; Romei, Brodbeck, et al., 2008; Webster & Ro, 2020), and so phase angles could be identified and targeted in a more reliable manner.

It is important to also acknowledge that whilst this current investigation offers an insight into oscillatory effects of excitability, our findings are limited by a small sample size of only 10 participants. This likely means that there is a risk our study is underpowered and not robust enough to offer generalisable results. However, the simplicity of this investigation offers promising potential for these results to be extended by simply accruing more open-source data that has collected both EEG recordings from the occipital cortex and MEP amplitude following spTMS; regardless of study aims or subsequent task paradigms. By achieving this, our current findings could be scrutinised to determine whether they are replicable and ultimately lead to increased knowledge surrounding the global mechanisms of neural oscillations in defining activity of the cortex.

2.7 Conclusion

In summary, we have determined that both alpha power and phase in the occipital cortex can influence excitability of the motor cortex, as indexed by MEP amplitude. This supports some of the available literature that explores this topic, accentuating the importance of alpha oscillations in establishing fluctuating brain states that define subsequent cognitive processes (i.e., making a voluntary movement). However, it also reveals new evidence emphasising the global role that this oscillatory band has within the cortex, a finding we believe to be essential to the improved application of TMS-EEG protocols, perhaps even for clinical purposes.

Chapter 3: Investigating the Role of Alpha Phase on Visual Perception, a #EEGManyLabs Project

3.1 Introduction

One of the current (and historical) questions within cognitive neuroscience research, surrounds our desire to understand how we can perceive and process visual information that we encounter within our environment (VanRullen et al., 2014; Wade & Swanston, 2013). Specifically, within this wide research scope, narrower aims have attempted to address why humans are not reliable in their perception of visual objects, being able to detect something at one point in time and then not the next, despite identical conditions (Dugué et al., 2011). Imagine you are looking outside the window on a stormy day, when suddenly there's two flashes of lightning in the distance. You saw the first one but completely missed the second, even though you were watching very closely and not blinking throughout. How is that possible? This is something that has puzzled many, with a vast number of study paradigms and neuroimaging techniques being implemented in the investigations aiming to uncover the answer to this unstable perceptual experience (Dugué et al., 2011; Mathewson et al., 2009). From these searches, the predominant line of research now focuses on how neural oscillations may play an important role in visual perception (VanRullen, 2016b); an idea that will be addressed throughout this chapter. In reflection, this is quite a broad statement, but it is perhaps most appropriate, as delving into the literature reveals how there is arguably no complete understanding of the role that oscillations play in perceptual processes, despite being a key focus within the field. Instead, new research is seeming to offer more and more contradictions to what has formerly been proposed, alongside null results, bringing into question the reliability of research that has previously guided our knowledge. Such conflicts and the remaining open questions of this topic will be outlined and discussed in depth throughout the progression of this chapter.

Historically, there have been many theories that have aimed to reveal insights into how visual perception is achieved and controlled, with consistent focus being on neuronal activity across the cortex (Pollen, 1999; Taylor & Thut, 2012). When first looking amongst the earliest research, this has traditionally been limited to only examine the impact of a stimulus on perceptually relevant neural activity (i.e., post-stimulus activity; Busch et al., 2009). This choice has been motivated by the initial desire to understand the *process* of visual perception, and so it has logically been presumed that focus should be on how our neural signals change in response to stimuli, marking the start of visual perception by its definition. In the pursuit of

this, it has meant that event-related potentials (ERPs) have been adopted as a measure to uncover the empirical signature of this neural reaction, defined as the change in neuronal activity that can be attributed to the onset of stimuli or a reflection of cognitive processes (Luck, 2014). For visual stimuli, these are most commonly referred to as visually evoked potentials (VEPs) and through many years of recordings, it has been established that there are three common markers that characterise a healthy VEP: N1, defined by a negative component at around 70ms after stimulus onset; P1, showing a positive component at around 100ms post-stimulus; and N2, a final negative component at around 140ms (Creel, 1995; Tobimatsu & Celesia, 2006; see Figure 3.1, below, for a representation of this). This pattern of events highlights fluctuating neuronal excitability in response to a visual stimulus, uncovering how our brain responds to our visual environment and how it may reflect perceptual processes. However, focus on this measure has meant that we have not been able to investigate the *impact* of neuronal activity on the perception of a visual stimulus (i.e., via pre-target activity), meaning that our knowledge was only able to extend so far. Fortunately, the need for such investigations has become markedly apparent within the field, with more and more of this research now beginning to suggest that oscillations may indeed modulate our perceptual processes (e.g., VanRullen, 2016; Ward, 2003; for a review, see Kienitz et al., 2022; Keitel et al., 2022).

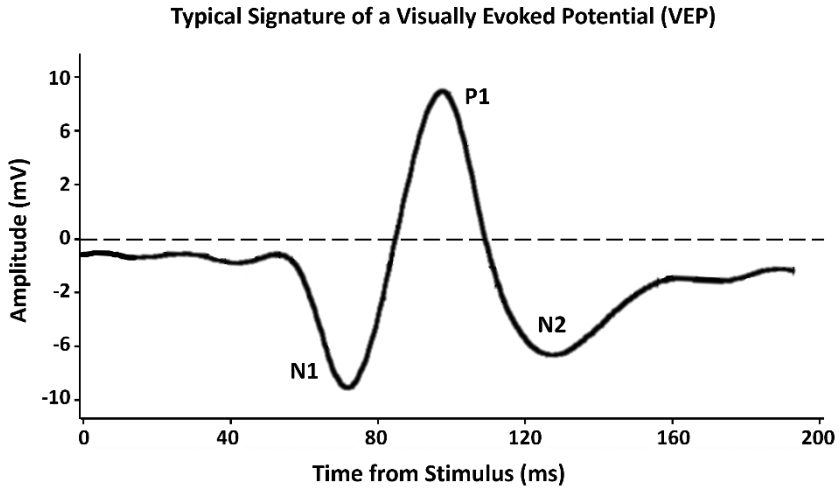


***Figure* 3.1**: Example of a typical visually evoked potential (VEP), measured from stimulus onset (time = zero). This signature is characterised by a negative component at ~70ms post- stimulus (N1), then a positive component at ~100ms post-stimulus (P1) and a final negative component at ~140ms (N2)

To achieve such investigations, studies have shifted toward examining pre-target activity, using it to inform theories on how visual perception can be influenced before stimulus onset and, consequently, before perception even begins. As a result, studies have focused on the cyclic nature of neuronal behaviour, investigating whether oscillatory activity could help us to understand why our perceptual abilities also fluctuate over time (Brascamp et al., 2018; Dugué et al., 2011; Samaha & Romei, 2024). Specifically, the bulk of research here has suggested that alpha oscillations are responsible for influencing our visual perception abilities, modulating this process via a number of their features, such as alpha fluctuation speed, amplitude and phase (Clayton et al., 2018; Lange et al., 2014; Samaha & Romei, 2024). Whilst these findings have only gained extensive attention within the last two decades or so, it is important to emphasise how long this research has been ongoing, with one of the first studies to investigate this being conducted in 1977 by Coffin and Ganz. Within their study, EEG recordings were taken from a single site of the occipital pole (Oz channel in 10-20 EEG systems) whilst participants performed a visual perception task of identifying whether two flashes were presented during a single trial. Importantly, the time between these two flashes was kept constant throughout the experiment, meaning that if perception was stable over time, task performance should also be stable. Upon reviewing their results and correlating their single-channel EEG spectra with task performance, it was found that participants were able to perceive both flashes most often when their occipital alpha frequencies were cycling at a faster rate. From this, Coffin and Ganz (1977) were among the first to conclude that alpha frequencies play a crucial role in influencing the temporal sensitivity of visual processing. Since then, this study has been replicated by many, including Samaha and Postle (2015), who adopted the two-flash paradigm to similarly find that pre-target alpha frequencies can significantly predict visual perception accuracy. When alpha oscillations were cycling at a faster rate (~ 11 Hz), this resulted in a significantly increased likelihood of perceiving two target flashes, than compared to when alpha oscillations were slower (~ 9.5 Hz). This works to emphasise the modulatory role of alpha oscillations in the context of visual perception. These findings also perhaps signify a process of discrete perception, whereby perception can occur in ‘snapshots’ rather than being a continuous process (VanRullen, 2016b). Here, the term ‘snapshot’ can be viewed as representing one alpha cycle. Thus, based on this theory, the matching results from both studies (Coffin & Ganz, 1977; Samaha & Postle, 2015) can be explained by the idea that when two flashes fall into one of these snapshots, they are then perceived as a single stimulus and processed as such. In contrast, when each flash falls into a separate

snapshot, which is more likely to occur if alpha is cycling at a faster rate, then this leads to the perception of two singular flashes.

Whilst there is evidence to suggest that ongoing alpha-band activity is important to perceptual abilities, to achieve a comprehensive understanding of how they may modulate cognitive processes, we must assess how power and phase may individually (and sometimes in combination) influence the processing of stimuli; like the lightening flash that we sometimes miss. When looking at the former first, numerous studies have found a significant negative relationship between alpha power and visual perception (Brüers & VanRullen, 2018; Busch et al., 2009; Mathewson et al., 2009; Romei, Brodbeck, et al., 2008; Van Dijk et al., 2008). To illustrate this, Ergenoglu et al., (2004) recorded EEG from 12 participants performing a visual detection task. When analysing the difference between trials which resulted in either detected or undetected targets, they found that lower pre-target alpha power at parietal and occipital electrodes correlated with an improved target detection performance. It is believed that such facilitated perception of visual stimuli is achieved via conditions of decreased alpha power reflecting a state of enhanced neural excitability (Baumgarten et al., 2016; Ergenoglu et al., 2004; Harvey et al., 2013; Jensen & Mazaheri, 2010; Roberts et al., 2014; Romei, Brodbeck, et al., 2008; Van Dijk et al., 2008; Van Kerkoerle et al., 2014); see previous Chapter for further insight into this relationship. Lange et al., (2013) investigated this with a single task designed to test perception using both the double-flash illusion and fusion effect, alongside concurrent magnetoencephalography (MEG). Here, the double-flash illusion is a multisensory perception task, where a single visual stimulus is paired with two tactile stimuli, resulting in individuals often perceiving there to be two visual stimuli (Lange et al., 2011; Violentyev et al., 2005). The fusion effect is the opposite of this, where two visual stimuli are paired with none or one tactile stimulus, resulting in individuals often perceiving there to be one visual stimulus only (McCormick & Mamassian, 2008). Upon reviewing their results, there was a significant pre-target decrease of occipital alpha power during trials where participants did not experience the fusion effect, suggesting improved perception. However, alpha power decrease was significant also during trials where participants perceived the double-flash illusion, suggesting reduced performance. Thus, they use such findings to suggest that a reduction in alpha power enhances occipital excitability levels, meaning that this region became more sensitive to visual input, accounting for why two flashes were perceived during both the fusion effect and double-flash illusion tests, regardless of whether both were presented or not. Romei et al., (2008) further used TMS to examine the

excitability of the visual cortex by inducing phosphenes; their quantity used as a marker of excitability (Silvanto, 2013; Walsh & Pascual-Leone, 2003). Whilst concurrently recording EEG and after delivering spTMS, participants were simply asked to report whether they had perceived phosphenes. Results revealed that phosphenes were more likely to be reported when pre-target alpha power was reduced, highlighting again the link between ongoing alpha power and cortical excitability. Alongside the previous chapter (Chapter 2), this chapter will also seek to determine the role of alpha oscillations in excitability, here by using indexes of the aforementioned ERPs.

When continuing to investigate the role of alpha power on visual perception, there are a growing number of contradictions within the literature, where some studies suggest that the evidence is not as clear cut as previously noted. One of such studies was conducted by Benwell et al., (2022) who investigated this relationship on a single-trial level, designing a multi-alternative forced choice task, where participants had 19 responses to choose from per trial (19AFC). Unlike most studies in this field opting for flash stimuli, this study presented participants with a consonant letter during each trial, of which had a complete appearance time of between 10-50ms. This was then followed by a patterned mask, consisting of all consonant letters overlayed onto one another. To assess objective perception, participants were asked to identify the presented target by pressing the corresponding letter on a keyboard and rating the clarity of their perceptual experience as either: no experience, brief glimpse, almost clear experience or clear experience. This additional question was included as previous experiments found evidence that alpha may modulate perceptual awareness on a subjective level (Benwell et al., 2017). When analysing results from this newer study, interestingly it was found that pre-target alpha power did not significantly predict discrimination accuracy, going against an abundance of the previously noted research. Instead, a negative relationship was found between alpha power and visual *awareness*, suggesting that alpha power modulates perceptual experience rather than performance. Although, it should be noted that in both their initial 2017 and newer 2022 study, whilst the relationship between neuronal power and subjective awareness was found most strongly within the alpha band, the significant frequencies resulting from their analyses ranged from 3-31 Hz. Further, this significant effect was also extended across much of the scalp, with both the frequency range and topographical distribution suggesting that this modulatory behaviour was more reflective of excitability changes, rather than a functionally relevant mechanism of perception within the visual cortex. In a similar outlay of results, studies have also found that

rather than modulating perception accuracy, higher alpha power instead increases an individual's decision criterion, making them more likely to respond 'no' to whether they perceived the target during visual perception tasks (Iemi & Busch, 2018; Kloosterman et al., 2019; Limbach & Corballis, 2016; Samaha et al., 2017, 2022).

When moving onto alpha phase, this is where the current evidence base becomes increasingly unclear and muddied. From the literature that is available, we can begin to build a picture that reveals how the phase of ongoing alpha oscillations can perhaps modulate visual perception by creating fluctuating 'windows of excitability', a.k.a., discrete perception. This has also been known as the rhythmic sampling theory, whereby our perceptual processes (amongst other cognitions) are directed by the discrete sampling of our environment during such 'windows' (Keitel et al., 2022; VanRullen, 2016b). Evidence for this has come from a number of studies, including Busch et al., (2009) who found that there was a significant alpha-phase difference between the neural signals of performance hits vs. misses. Based on this information, alpha phase could therefore be defined/classified as either 'optimal' for perception, or not. These results were thus interpreted as evidence of how our visual perception abilities fluctuate along the phase of oscillations, following the rhythmic waxing and waning of their profiles. Similarly, such results are reinforced in a TMS-EEG study, where Dugué et al., (2011) applied a single TMS pulse over the occipital cortex to induce phosphenes, the appearance (or not) of which participants were tasked with reporting. When reviewing results, alpha phase differences in phosphene-present versus phosphene-absent trials were observed up to 400ms pre-target, again working to highlight the modulatory effects of alpha phase in our perceptual abilities but importantly also offering causal evidence of such.

Amongst this literature, one of the key studies that has influenced our understanding of such alpha phase effects was conducted by Mathewson et al., in 2009. Whilst this was not the first study to explore how the features of neuronal oscillations predict visual perception, it is considered to be one of the most influential within the field, cited over 1000 times to date (Google Scholar, 2024). This research utilised a visual detection task whilst recording EEG to uncover whether there is an optimal oscillatory behaviour that results in the successful perception of a centrally presented visual target. In line with previous studies, when pre-target occipital alpha power was reduced, this was associated with an increase in detected targets (hit). Further, when examining phase effects, the perception of the target was indeed found to be modulated by the phase of

occipital alpha, but this effect was only seen for high-power alpha trials, where participants were more likely to perceive a target if it was presented during an 'optimal' phase (i.e., peak phase of 225-45°). Importantly, the results from Mathewson et al., (2009) formed the basis of the pulsed inhibition theory, which proposes that within the alpha cycle there are alternating windows of inhibition and excitation. Specifically, they provide evidence to suggest that the modulation of perception is achieved via one of two routes, either: the reduction of ongoing alpha power resulting in increases of excitability, or the fluctuations of alpha phase when power is high, resulting in fluctuating periods of inhibited perceptual processing (Mathewson et al., 2011). This is reinforced further in additional analyses by Mathewson et al., (2009), revealing that when ongoing pre-target alpha oscillations met the two conditions of high power and optimal phase, this increased the magnitude of post-stimulus evoked potentials (e.g., N1, P1, P2 and P3) and thus suggests increased visual processing. However, it is essential to also acknowledge a potential flaw in the task design chosen by Mathewson et al. (2009), where there was a fixed delay between the start of each trial and the onset of the target (400ms). This choice meant that participants were able to temporally predict the onset of the target, which potentially modulated pre-target activity in itself, including phase measures, thus biasing empirical results to be positive. This is important to consider when interpreting the results from this popular study, particularly as research following this has offered contradictions in findings when accounting for such limitations (Ruzzoli et al., 2019).

In a review by Keitel et al., (2022) the extent of these contradictions was plainly revealed, highlighting that of 23 studies that investigated the effects of oscillatory phase on cognition, only 11 offered empirical evidence in support of such processes. The remaining 12 returned inconclusive or null findings. In an example of this, the aforementioned study by Ruzzoli et al., (2019) utilised a design similar to that from Mathewson et al., (2009), but modified the task to include a jittered interval between the fixation and target onset; accounting for a limitation in the original study and reducing expectation effects. In their results, although there was evidence for the contribution of alpha power in visual perception (i.e., decreases prior to detected targets), there was no evidence to suggest that alpha phase modulated visual perception, contradicting Mathewson et al., (2009). Perhaps this could easily be attributed to the change in task design, but it is also true that Ruzzoli et al.'s null results may have been observed due to the use of a strict participant inclusion criterion (e.g., FA rate < 15%), excluding participants if their performance did not accurately reflect minimal guesses. Although, even without these changes, Benwell et al., (2017) similarly investigated the influence of alpha phase

on visual perception and reached the same conclusion of null evidence to support such suggestions. Similarly, in an alternative study that investigated not just visual perception but discrimination also, Michail et al., (2022) likewise found null evidence of an occipital alpha phase effect on measures of perception accuracy, response speed, decision criterion nor perceptual sensitivity. To note though, this study was modified to present salient targets for a longer duration than previously investigated (i.e., until participants make a choice). It is therefore possible that the absence of phase effects observed here could be a direct result of this change, as perception of the target would not solely rely on neural phase at target onset.

Through reviewing the literature, it is clear that whilst the evidence proposed by Mathewson et al., (2009) has been significant in its contributions to the field, it has become important to verify the accuracy and reliability of their findings. The need for this encompasses a greater issue within the field of cognitive neuroscience as a whole, where we are in the midst of a replication crisis (Huber et al., 2019). Whilst low replicability of our studies could be due to neuroimaging data being noisy and varying across participants, it is also true that this research is often afflicted by small sample sizes, ultimately leading to the low statistical power of investigations and thus unreliable results (Button et al., 2013; Huber et al., 2019; Ruzzoli et al., 2019; Szucs & Ioannidis, 2021). For example, Mathewson et al.'s study only included a total of eleven subjects, which is a relatively small sample size for electrophysiology investigations, likely meaning that this is not a well powered investigation for the design (based on estimation by Ruzzoli et al., 2019). In response to this, as a field, we must strive to improve our investigations and attribute a greater weight to studies that offer reliability over 'storytelling' (proposed by Huber et al., 2019). This is something that the #EEGManyLabs Initiative has been launched to do, investigating the replicability of 20 influential EEG experiments in a large-scale effort to progress our knowledge (Pavlov et al., 2021). To achieve this, multiple laboratories across the global are recruited into a single investigation, whereby they are tasked with replicating the same experiment (one of the chosen 20 EEG experiments) and pooling their data to eventually construct a meta-analysis that determines the reliability of important findings, i.e., whether alpha phase modulates visual perception. By doing so, not only will investigations become substantially higher in their statistical power, but each dataset will be collated to produce an open access database that can be used to aid and inform future practices; something that is essential to continual growth of neuroscience research that we can be confident in.

As one of the leading replication labs for one of these #EEGManyLabs projects, we aimed to conduct a replication of Mathewson et al.'s (2009) experiment, alongside another nine labs dispersed around the globe. The replication of this particular study was decided upon by means of a voting system, where members of the #EEGManyLab community determined that Mathewson's study was one of the most influential and worthy of replication. Such decision processes and #EEGManyLabs procedures are outlined further in Pavlov et al., (2021). Our investigation is also outlined in depth within our registered report, which has been peer-reviewed and recommended by PCI Registered Reports (Ruzzoli et al., 2023). The report can be accessed here: https://osf.io/3dhpx. For the purpose of this thesis though, the remaining sections of this chapter will outline the procedures conducted in our Nottingham lab only, excluding the eventual meta-analysis details as these are not yet available. Despite this focus, all participating labs will be utilising the same task presentation and data analysis scripts. Differences will only arise in the language of task instructions, choice of EEG amplifier and the number of recording EEG electrodes (range = 32 – 64 electrodes, M = 53.67). We therefore hope that the findings presented here will not be so far removed from the overall meta-analysis results, although at current we cannot knowingly determine whether this is indeed the case.

Whilst conducting this experiment, alongside other members of our Nottingham team, I was primarily responsible for the recruitment of participants, data collection, data analysis and reporting of results. During such investigations, we predominantly aimed to replicate three of the results reported in the original paper. First, we tested whether visual perception performance depends on alpha phase, but only when alpha power is high – in line with the pulsed inhibition hypothesis. If this proves true, then support will be given (in part) to the findings of Mathewson et al., (2009), reinforcing the idea that visual perception is a cyclic process and follows pulsed inhibition. Second, we tested whether detection rate is associated with separated (ideally, opposite) phase angles, without any power or phase binning methods (via a Hotelling test). Finally, we wanted to test if alpha phase at the onset of a visual stimulus influences electrophysiological correlates of stimulus processing, as represented by the observed N1 amplitude and latency.

It should be pointed out that these three results only make up one of the two hypotheses presented as the #EEGManyLabs multi-site aims. The second hypothesis surrounds the influence of temporal expectedness on our perceptual processes. However, this will be evaluated in a future study, which is beyond the scope of our current lab investigations. Importantly also, the results section and discussion of this chapter

are based on the data from our Nottingham lab alone, with analysis being conducted independently from any other lab. As an additional note, the original Mathewson study will also be contextually addressed further in the following chapter (Chapter 4).

3.2 Materials and Methods

3.2.1 Subjects

Prior to conducting this study, it was estimated that we would need a total of 35 participants to reach a sample size that enabled suitable statistical power of our investigations. This was calculated using effect sizes obtained from Mathewson et al., (2009), where we considered half of the computed effect size from the original statistics and utilised G*Power software (version 3.1.94; Faul et al., 2009) to determine the number of participants required to replicate this effect at 90% power and $p < .02$.

A total of 71 healthy (no neurological, psychiatric or other medical condition that could alter brain functioning) participants were recruited for the current study (44 females, 27 males), all of whom had normal-to-corrected vision. Ages ranged between 19 – 29 years ($M = 23.64$, $SD = 2.41$) and all besides four participants reported being right-handed. Participants were not excluded based on their preferred handedness. Following an initial test of performance using a staircase procedure, 17 participants were excluded from continuing onto the main task as their performance did not meet desired performance criteria (see staircase details, below). Following this, of the remaining 54 participants that completed the main task, a further 18 participants were excluded, again due to their performance not meeting threshold criteria (eight participants = high accuracy, one participant = low accuracy, nine participants = high false alarm rates). One additional participant was removed due to insufficient EEG data quality. This decision was made due to a poor scalp-to-reference electrode connection, resulting in the signal voltage from all remaining channels being significantly skewed. As such, our final sample was made up of 35 participants (19 females, 16 males; age range: 19 – 29, $M = 23.69$, $SD = 2.61$; 33 right-handed). This study was approved by The University of Nottingham's Ethics Committee, with all participants providing informed consent prior to the commencement of the session and receiving monetary compensation for their time, regardless of whether they completed the full experimental task.

3.2.2 Experimental Design

This study was a repeated-measures block design, aimed at investigating whether the phase of low-frequency brain oscillations influence visual detection performance and/or visual ERPs. To achieve this, the

implemented experimental task asked participants to detect a target whilst concurrently undergoing EEG. The staircase and behavioural task for this study were created and presented via custom MATLAB scripts (R2022a, Mathworks, 2022) and Psychtoolbox, formed as a direct replication of Mathewson et al., (2009). These are currently available in our Open Science Framework Repository: https://osf.io/mtv8r.

3.2.3 Procedure and Task

This study comprised of a single session that included practice trials, a staircase procedure and the main task. Participants were first invited to an EEG lab at The University of Nottingham, where they were sat in a Faraday cage, placing their chin on a chinrest to minimise any head movements and ensure that their line of sight was always central to the screen. This chin rest was measured at ~ 57cm from the screen. Central positioning was also aided through the use of a height-adjustable desk which was altered for each participant, achieving an appropriate eye line that was both central and comfortable. The rest of the room was set up with a chair, computer screen and keyboard. It was dimly lit with a lamp positioned in the corner of the room and kept quiet to minimise distractions. The screen that stimuli were presented on was set to a refresh rate of 100 Hz (size: 1226 x 2248 pixels, screen model: Lenovo Legion, computer model: Lenovo ThinkStation P620).

Once participants had the opportunity to read the information sheet, ask any questions and sign their informed consent to be recruited into the study, participants were given instructions on the upcoming task. Each were told that their task was to identify when the solid dot appeared on the screen, pressing ‘b’ on the keyboard to answer yes and ‘n’ for no. To reiterate this further, participants were presented with diagrams of the three trial types that could appear: target only, target and mask, or mask only trials. Correct responses for each of these options were reiterated to ensure that participants understood the task. Importantly, it was emphasised to participants that they must always maintain fixation on the centre of the screen (aided by the presence of the fixation cross). Each part of this session (practice, staircase and main task) followed the same basic design.

Throughout the task, the background of the screen was consistently a light grey colour (RGB: 0.8, 0.8, 0.8). Trials started with a black fixation cross presented centrally on the screen for 250ms, reorienting participants attention at the start of each trial (RGB: 0, 0, 0; size: 0.5 degrees). After its offset, the screen was blank for 400ms, until the target dot appeared for a short 10ms (target size: 1 degrees). In mask only trials (catch trials) the target was replaced by a blank screen of the same duration as the target. Then, after 50ms of

another blank screen (inter-stimulus interval), a mask appeared for 20ms (size: 2 degrees). The aim of this backward mask was to impair the perception of the target so that an accurate measure of target-specific perception could be gained. In target only trials, the mask was replaced by a blank screen for the same duration as the mask. The contrast colour of these two stimuli (target and mask) were titrated to each participants' individual threshold (see below). Participants were instructed to respond to the presence of the target as quickly as they could following its appearance, but were prevented from any responses after 1520ms, as this was considered too late and the trial was moved on (see Figure 3.2). The temporal accuracies of these presentations were evaluated via a photodiode prior to the first participant being recruited.

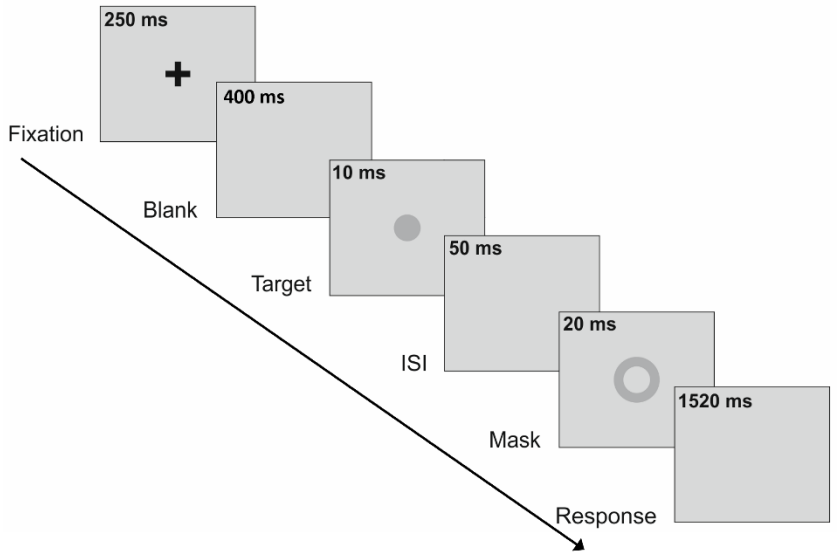


***Figure* 3.2**: Schematic representation of a 'Target plus Mask' trial. Each trial started with a fixation cross presented for 250ms. After a 400ms blank screen, the target appeared at the centre of the screen for one frame (10ms). Following a 50ms delay, a mask was presented for 20ms. Participants were instructed to detect the target and indicate whether they saw the dot or did not see it using two distinct keys on the keyboard. They had 1520ms to respond, after which the next trial began.

After receiving the task instructions, participants were asked to complete a short practice run of the experiment (N = 20 trials) where the presented stimuli had varying levels of contrast. For this, participants were given feedback after each trial response, receiving a red or green fixation for each incorrect or correct response, respectively. If the participant understood the task following this practice, the study then moved onto the staircase procedure.

A staircase was conducted so that the stimuli in the main task (target and mask) could be titrated to each participants' individual threshold. Importantly, this was not something that Mathewson et al., (2009)

conducted in their original study, instead opting to use a pre-set and constant stimuli colour across all subjects. We believe that the addition of titration procedures was a vital modification to the task, as it ensured that results could be accurately collapsed across participants without a confounding effect of task difficulty. Therefore, to implement this, we adopted a 2-up/1-down staircase, meaning that if participants answered correctly twice in a row, stimuli contrast was reduced by four steps, whilst if they got it wrong once, contrast was increased by three steps. After 21 of these reversals, the staircase stopped and a mean contrast threshold was calculated from the final 20 measures (the first response is considered a practice and not included; García-Pérez, 1998). If this number of reversals was not reached, the staircase ceased after 144 trials (split into two blocks of 72 trials) and participants were asked to repeat the procedure up to twice more. If participants successfully completed the staircase, they then moved onto a validation task (N = 72 trials) to check that the contrast value identified by the staircase would yield a performance within the inclusion criteria. The criteria were: A) a $d' > 0$, B) a false-alarm (FA) rate ≤ 25%, and C) a hit-rate (HR) of ≥ 25% and ≤82%. These were chosen for a number of reasons, including the exclusion of data that indicated either below chance performance ($d' < 0$), participants not paying attention (FA ≥ 25% or HR ≤ 25%), or there not being enough 'no' trial answers for subsequent analysis (HR ≥ 82%). If any of these criteria were not met, participants were asked to repeat the staircase. If the participant still did not reach the desired performance threshold after three attempts of the staircase, or staircase and validation, they were thanked for their time and removed from any further testing.

If performance criteria were met within the validation procedure, participants were asked to continue with the study and EEG was set-up for subsequent neural recording.

Following this, the main experiment could commence. This was arranged in a block design, where participants were presented with 72 trials in 16 separate blocks. There was no difference between each of these blocks, with this format chosen only to provide participants with a rest period to avoid fatigue effects confounding results. The timing of these rest periods was controlled by participants themselves, where they were required to press any button on the keyboard to progress onto the next block. Participants were encouraged to use these rest periods and take their time. As previously mentioned, there were three types of trials within this task, with one being the sole presence of the target (25% of trials), another being the sole presence of the mask (25%), or the joint presence of both (50%). These were randomly distributed across and within the blocks.

3.2.4 EEG Acquisition

For EEG acquisition, a Biosemi ActiveTwo system with ActiView software (BioSemi, Amsterdam, Netherlands) was used, with a sampling rate of 1024 Hz. A 64-channel arrangement was also utilised for this study, covering the entire scalp with a 10-20 layout. In the original paper by Mathewson et al., (2009), neural activity was only recorded from 21-channels distributed across the cortex. Whilst we have planned to replicate the analyses conducted within the original investigations and thus do not expect to analyse the activity from our additional channels, recording them provides us with the opportunity of extending into exploratory analysis, should it be needed. Further, in additional contribution to open science, if this data is re-used for related investigations, the increased number of channels will likely mean that appropriate data will be available. Returning to our set-up, six further external electrodes were also used, with two placed on the mastoids (right and left), one placed above the left eye and another below, and the remaining two placed on the outer side of each eye. These were included so that we could re-reference the data offline to the average of the mastoids, and to record horizontal and vertical eye movements (electrooculogram, EOG). The latter of these was especially important as we did not utilise any additional eye tracking techniques, so this provided us with a record of when blinks and saccades occurred, of which could potentially contaminate results. Prior to recording, all electrodes were connected to an amplifier and offsets were checked to ensure an appropriate impedance reading of between 25-50 mV per channel. Set-up was approximated to take around 30 minutes.

3.3 Data Analysis

As with experiment presentation, all analyses were performed in MATLAB (R2022a, MathWorks, 2022) using custom scripts and the FieldTrip toolbox (2021 release, https://www.ru.nl/neuroimaging/fieldtrip; Oostenveld et al., 2011).

3.3.1 Behavioural Data Analysis

As mentioned, participants were excluded from the main analysis if their performance did not reach a certain criteria. This was based on the original paper, where it was argued to ensure that the final dataset was constructed from valid data where participants were performing the task in line with given instructions. To assess this, hit rates (HR), false alarms (FA), perceptual sensitivity (*d'*) and decision criterion (c) were calculated for each participant individually (see specific criteria, above). For the calculation of HR, this was defined as the proportion of correct "yes" (button press 'b') responses for when the target was presented. Similarly, FA was

calculated as the proportion of "yes" (button press 'b') responses for when the target was not present. Both were used in our final calculation of *d'* and *c*, using the following equations:

$$d' = z(HR) - z(FA)$$

$$c = -\frac{1}{2}(z(HR) + z(FA))$$

Here, $z(x)$ is the inverse of the normal cumulative function evaluated at x (Macmillian & Creelman, 1991; Macmillan, 2002). This was calculated within a MATLAB function created by Böckmann-Barthel (2023), implementing a correction for perfect response rates (HR = 1 and/or FA = 0) according to the 1/2N rule (see Stanislaw & Todorov (1999) for justification). This essentially adds 1/(2*N*) to HR or FA measures of 0 and subtracts it from measures of 1, where *N* refers to the number of trials used to calculate HR and FA.

If participants successfully passed our set criteria and their data entered the final analysis, performance was further scrutinised to guarantee the validity of our results. Here, we calculated participants' accuracy first to ensure that they achieved between 20-80% accuracy and less than 25% FA. In an additional step, FA rate was calculated for each task block separately, as it is possible that certain blocks were driving an overall performance that met criteria, whilst others were undesirable for our investigations (Ruzzoli et al., 2019). This extra check was not implemented in the original paper, but here we removed all blocks where FA rate was above 25% (N = 1.3 blocks removed per participant, on average).

Additionally, to assess whether there were any confounding influences of practice or fatigue effects, behaviour measures were calculated at each block individually, with a repeated-measures ANOVA then conducted to assess whether there was a significant effect of block number on performance.

3.3.2 EEG Data Analysis

Pre-processing of EEG data was first conducted to ensure that the data was clean and available in a usable format. Data was primarily band-pass filtered (0.01 – 25 Hz) using a two-pass-reverse filter (Gross, 2014), conducted whilst the data was still continuous. EEG signals were then re-referenced to the average of the two synchronized mastoid signals, creating a cleaner and assumed neural-only signal. Following this, continuous data was then segmented into epochs of -600 to 600ms, where 0ms is defined as the target onset (dot), or absence as the case may be. All epoched data was then resampled to 250 Hz and from this point on,

only two trial conditions were retained for further analysis: target-only and target-masked trials. This choice was based on the experimental aims, where we were only interested in determining whether neural activity could influence perception of the target, and so target-absent trials were not needed.

Next, to continue cleaning the data, ocular artifacts were identified and corrected using a validated method outlined in Gratton et al., (1983). Specifically, this method calculates a 'propagation factor' from EOG and EEG signals at a single-trial level, describing the relationship between the two and correcting for EOG activity in output data, leaving a remaining clean EEG signal. Artifact rejection was then conducted via a semiautomatic process, whereby the signal was demeaned and any signal change that exceeded ± 250 μV was highlighted and removed. Importantly, both of these steps were also adopted within the original Mathewson et al., (2009) paper. In one final pre-processing step, upon visualising the resulting EEG signals, bad channels were manually selected and removed from the datasets (N = 0.97 channels removed per participant, on average). If these removed channels were either Fz and/or Pz, the entire dataset was subsequently removed from the remaining analysis, as these were deemed the two main channels of interest for replication of the original paper (Mathewson et al., 2009). Fortunately, this did not occur within the current dataset.

Alpha Power and Phase

Following the original paper, artifact-free data for trials with target plus mask were used to estimate pre-target alpha power and phase. This analysis was restricted to cover a time window of -200 to 0ms, where 0ms remains the onset of the target. This was based on our aim of uncovering how pre-target power and/or phase can modulate visual perception, alongside analyses by Mathewson et al., (2009) suggesting that fixation offset affected EEG activity for ~ 200ms, and so we eliminated this potential confound by removing such times. Using this newly defined data, a discrete Fourier Transform with no taper was applied to the EEG signal acquired from channel Pz of each participant separately, at a single-trial level. Importantly, this analysis only focused on a single alpha frequency of 10 Hz, in part restricted by analytical limitations meaning that we could only investigate frequencies in multiples of 5, but also based on Mathewson et al., (2009) and previous literature on the influence of alpha oscillations in visual target detection paradigms (e.g., Ergenoglu et al., 2004; Romei, Brodbeck, et al., 2008; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000). By matching our analysis parameters to those chosen by Mathewson et al., (2009), this meant that our results could be directly compared with ease.

For each participant, log-transformed power was used to split trials into those that exhibited high versus low power, based on individual medians. Primary focus for this analysis was on high-powered trials only, as these have previously been assumed to be the only trials with sufficient power for a phase effect to occur (Lindsley, 1952; Mathewson et al., 2009). Thus, high-alpha power trials were divided further into two non-overlapping phase bins, each covering 180 degrees. These bins were calculated based on the mean phase for undetected targets (102.74°). To note, calculated bins in the original paper were determined in the same way, following a phase measure of 134.6° for undetected trials. Based on their relevance to performance, these bins were also termed "hit" and "miss" phases. Once the bins were calculated, trials were assigned to one of the two groups based on their prestimulus alpha phase, with the HR then recalculated for each bin. To examine performance differences between the two bins, a one-tailed paired samples *t*-test ($p < .02$) was conducted to compare HR. It was determined that if the original results held true and visual perception is a cyclic process, then this difference is expected to be significant. This test was additionally repeated on low-powered trials, although this step was not outlined in the registered report.

In a further attempt to replicate the findings from Mathewson et al., (2009) an additional analysis of phase opposition was included to evaluate whether alpha phase is significantly different for hit versus miss trials, at channel Pz. This was conducted with both high and low power trials as this analysis appropriately takes into account the lesser influence of low amplitude trials (Mathewson et al., 2009). For this, methods in the original paper were followed, where the previously calculated phases for each participant and trial (following Fourier transform at 10 Hz) were converted into Cartesian coordinates (i.e., two-dimensional unitarian vectors). This was achieved with the following formula:

$$z = e^{i\emptyset}, |z| = 1$$

Where the calculated z is the phase expressed as a complex number and ϕ is the alpha phase at trial i. To expand, two-dimensional Cartesian coordinates reflect the distance from the origin (or amplitude) and angle (or phase). Mean vectors for both hits (z_{Hit}) and misses (z_{Miss}) were calculated for each participant using this procedure, and then averaged to produce a group mean ($\hat{Z}_{Hit}$ and $\hat{Z}_{Miss}$). Of note, following Mathewson et al.'s (2009) pipeline, the contribution of each participant to the mean was weighted by concentration, such that participants showing a phase distribution concentrated around a preferred value contributed more than to the

grand average than those that did not. The difference between these two means ($\Delta\hat{Z} = \hat{Z}_{Hit} - \hat{Z}_{Miss}$) was then calculated and input into a Hotelling paired bivariate test to determine whether this value significantly differs from zero. To achieve this, a series of equations were followed to reach our final value:

$$(1)\ T^2 = n(\Delta\hat{Z} - \mu_0)^T S^{-1}(\Delta\hat{Z} - \mu_0)$$

where $\mu_0 = [0\ 0]$ is the direction corresponding to the null hypothesis and S^{-1} is the inverse of the sample covariance matrix. This matrix is made up of the differences between the grand average directions for hit and miss trials, per participant. Calculated as follows:

$$(2)\ \Delta\hat{Z} = \frac{z_{Hit}}{|Z_{Hit}|} - \frac{z_{Miss}}{|Z_{Miss}|}$$

In a final step of this calculation, the resulting statistical F value is obtained via a T-squared statistic:

$$(3)\ F_{p,n-p} = \frac{n-p}{(n-1)p} T^2$$

where degrees of freedom can be gained from the number of participants (n) and variables (p), the latter of which is 2 as these are the elements of the vector (amplitude and phase). Resulting statistical *p*-values were acquired from the above *F*-value, with $p < .02$ suggesting that the phase difference between hit and miss trials differs significantly from zero; as expected based on results from the original paper.

Event Related Potentials

Finally, we assessed phase influence on N1 amplitude and latency. Here, latency is defined as the time interval between the presentation of the target and the peak of the related ERP component. Again, this was motivated by the original paper, where Mathewson et al., (2009) used target-only trials to test this aim. Reasoning behind this was centred around that fact that we were interested in response to target only, but we recognised that ERPs would be generated for mask stimuli too, likely disrupting the observed N1 component of interest (i.e., those in response to the target). For this analysis, we sorted trials according to the phase bins calculated in a previous step, at channel Pz (see above). ERPs were then calculated for each bin ("hit" and "miss") and subsequently baseline corrected to 200ms pre-target. It is important to point out that this ERP calculation was solely conducted on channel Fz, as in Mathewson et al., (2009), based on previous research showing that the strongest phase differences are observable at this location (Busch et al., 2009). Using these

ERPs for each participant and each of the phase bins, peak amplitude of component N1 and its latency (between 50-170ms post-target) were determined. In order to assess whether there was a significant difference in either of these N1 features, across the two phase bins, separate one-tailed *t*-tests were conducted for each. If such differences were found to be significant, we could then determine that perceptual processing is indeed characterised by rhythmic behaviours.

3.4 Results

3.4.1 Behavioural Results

In total, after removing blocks that violated our inclusion criteria, the 35 participants had a collective detection rate of 51.54% across all blocks (*SD* = .5; Range = 18.32 – 67.8%). This could be broken down into an accuracy of 84.03% for trials where the target appeared on its own (*SD* = .044; Range = 75.46 – 97.91%), and 54.79% for trials where the target was followed by a mask (*SD* = .034; Range = 47.22 – 67.36%). False alarm rates on the other hand averaged at 9.6% across participants and blocks (*SD* = .011, Range = 5.56 – 12.22%). It is important to note here that participants included within this analysis all passed the initial performance criteria. However, as blocks were then removed if they exceeded 25% FA, this ultimately impacted overall performance measures and accounts for why our final reported accuracy range is as low as 18% in one participant.

Behavioural measures of HR, FA, *d'* and *c* were additionally calculated at each block to determine whether there were any evident practice or fatigue effects appearing within the data (see Figure 3.3, below). Results from an ANOVA revealed that there was a significant effect of block number on HR ($F(6.15, 98.32 = 2.77$, $p < .001$, $\omega = .15$) and *d'* measures ($F(15, 240) = 3.37$, $p < .001$, $\omega = .17$). For both, performance in general became progressively lower as the experimental session continued (block 1: HR = 54.58%, *d'* = 1.65 versus block 16: HR = 47.93%, *d'* = 1.21). In contrast though, FA and criterion rates remained stable across time, with no significant effect of block number ($F(15,240) = 1.54$, $p = .094$, $\omega = .177$ and $F(15, 240) = 1.22$, $p = .26$, $\omega = .071$, respectively).

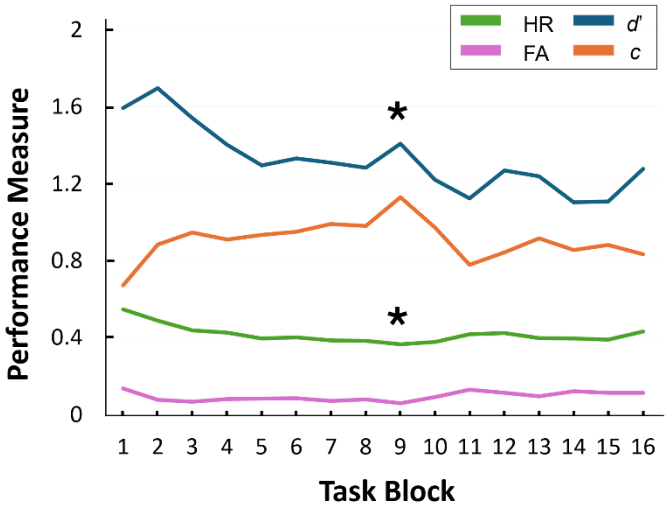


***Figure* 3.3:** Behavioural performance. Average linear trends of task performance measures as a function of the testing block. Perceptual sensitivity (*d'*; blue line), decision criterion (*c*; orange line), hit rates (HR; green) and false alarms (FA; purple). Significant effects of block number on performance are indicated with an asterisk. See Figure 2A in Mathewson et al., (2009) for a comparison.

3.4.2 EEG Results: Phase effects on Performance

After extracting high-power trials and splitting them into our two calculated phase bins ("hit" phases: 193-13° and "miss" phases: 13-193°), a one-tailed paired samples *t*-test on corresponding HR revealed that that there was no significant difference in performance between "hit" phases (M = 59.04%, SD = .18) and "miss" phases (M = 58.83%, SD = .18), $t(34) = .25$, $p = .81$ (difference = .22%, BCa 95% CI [-.016, .02]). Reporting of the BCa 95% method here is a means for calculating a 95% confidence interval using the Bias-Corrected and Accelerated (BCa) bootstrap method (Efron, 1987). Used here as it considered the potential bias and skewness that small sample sizes may introduce within the distribution of bootstrap estimates. When looking at low-powered trials, a *t*-test further revealed no significant difference in performance when alpha oscillations fell within a "hit" phase (M = 61.06%, SD = .18) or "miss" phase (M = 59.38%, SD = .18), $t(34) = 1.61$, $p = .12$ (difference = 1.69%, BCa 95% CI [-.0045, .038]). For an illustration of these measures, see Figure 3.4 (below).

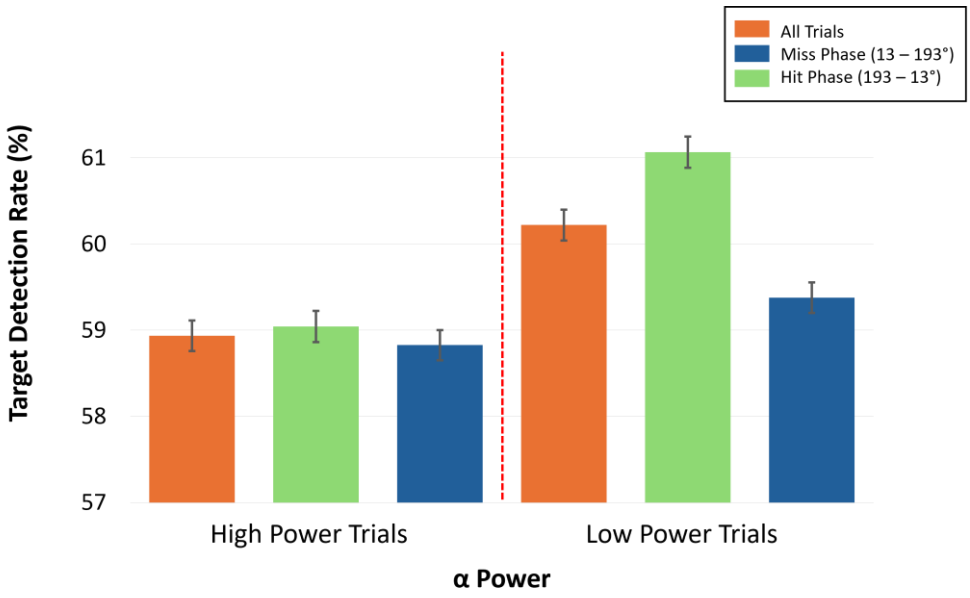


***Figure* 3.4**: Target detection rates at each alpha power as a function of the phase bin. The three bars on the left show the average performance for high-alpha power trials, whilst the three on the right show performance for low-alpha power trials. Green bars illustrate performance when the target appears whilst alpha phase is considered "hit" and between 193-13°, whilst the blue bars represent the performance for "miss" phases of 13-193°. Orange bars show performance averaged across both phase bins. Dispersion measures of *SD* are also plotted. In Mathewson et al., (2009) see Figure 4B as a comparison.

Following this, a Hotelling paired bivariate test was used to assess whether a significant phase opposition was present across all trials (regardless of alpha power). Results revealed that this was indeed the case, with the phase of alpha being significantly different for hit trials (M = 110.93°) than compared to misses (M = 156.65°), $F(2, 33) = 17.3$, $p < .001$ (see Figure 3.5, below).

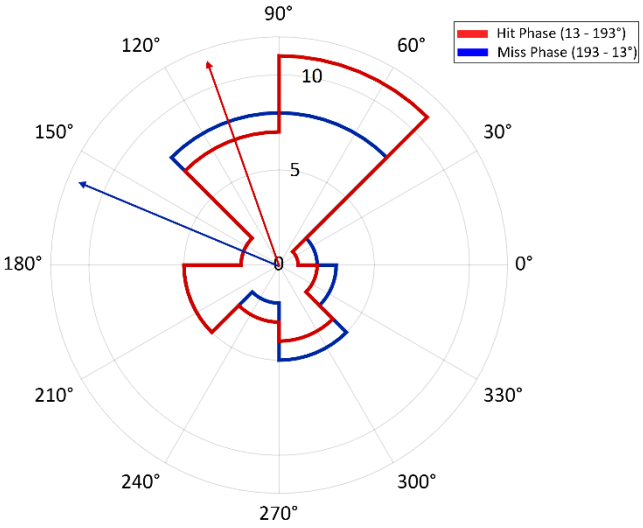


***Figure* 3.5**: Phase-difference between hit and miss trials. Two circular histograms depicting the mean phase of pre-target alpha-band activity for hit (red) versus miss (blue) trials. These phase angles have been obtained from the average of a 10 Hz signal at channel Pz only, for each participant. Matching coloured arrows represent the weighted average phase angle for each condition. See Figure 4D in Mathewson et al., (2009) for a comparison.

3.4.3 EEG Results: Phase effects on N1 Components

Finally, ERPs at channel Fz were calculated for both hit and miss trials (see Figure 3.6, below). These measures were then compared to assess whether there were any additional phase effects on N1 amplitude and/or latency. One-tailed *t*-tests first revealed that there was no significant difference between N1 amplitude when the target onset occurred at the "hit" phase (M = .3 μV, SD = .5), compared to the "miss" phase (M = -.2 μV, SD = 2.3), $t(34) = -1.41$, $p = .084$ (difference = .5, BCa 95% CI [-∞, .099]). In a similar result, there was also no observed significant difference in N1 latency during the "hit" phase (M = 109.14ms, SD = 38.16) compared to the "miss" phase (M = 114.74ms, SD = 36.39), $t(34) = -4.76$, $p = .75$ (difference = -5.6ms, BCa 95% CI [-∞, .02]).

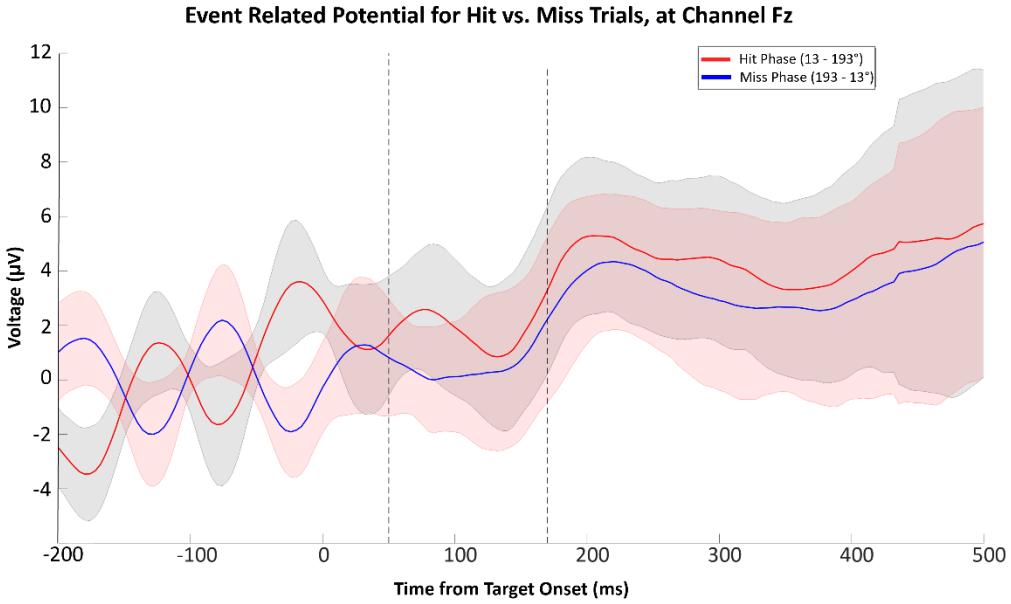


***Figure* 3.6**: Alpha Phase and ERPs. Grand average of the ERP signal for the channel Fz as a function of the pre-target alpha phase for miss (red) vs. hit trials (blue) with standard deviation shading. Averages are time-locked to target onset (time = 0). Two vertical lines (dashed) represent the time window used to detect the N1 amplitude and latency. No significant difference in amplitude or latency of N1 components was found when trials were grouped according to the phase bins. See Figure 3 in Mathewson et al., (2009) for a comparison.

3.5 Discussion

The main aim of this investigation was to replicate a previous study by Mathewson et al., (2009), investigating whether visual perception fluctuates along the phase of pre-target alpha oscillations.

First, we tested the influence of alpha phase when alpha power was high. To this aim we split high-powered alpha trials according to two phase bins (based around the mean phase of undetected trials) and looked at behavioural differences between these “hit” and “miss” phase definitions. We found no indication to suggest that there was indeed a difference in performance across these two bins, rejecting our hypothesis and thus failing to replicate findings from the original study. This is unexpected as the power-phase interaction is at the core of the pulsed inhibition hypothesis suggested by Mathewson at al., (2011), meaning that this study has more generally failed to offer support to such a theory.

Despite our failure to replicate the original results, there may be a number of reasons as to why we have obtained our unanticipated findings, predominantly surrounding the analysis choices that were made in an attempt to reproduce the original study. Firstly, it is important to point out that both power and phase calculations were limited to the signal observed at channel Pz. This choice was made to replicate Mathewson at

al.'s (2009) original analysis, which in turn was based on previous literature suggesting that this channel often exhibits the largest average amplitude of alpha-band activity (Hanslmayr et al., 2005; Ro, 2019; Samaha et al., 2015). However, when looking at the literature that focuses on power effects, many studies include more electrodes in their analyses and are therefore likely to capture a more complete understanding of cortical activity that may modulate visual perception. Additionally, it is true that there are interindividual differences in cortical structures that should be considered (Herwig et al., 2003; Scrivener & Reader, 2022), where the regions underlying our chosen channel may be varied across participants, subsequently meaning that we may be examining the neural signal of different cortical regions across participants. Perhaps this may be one of the reasons as to why we have found inconsistencies when comparing this study to previous literature, but also when considering why Mathewson et al.'s (2009) original findings have not been robustly corroborated since its publication. In addition, our analysis only focused on 10 Hz alpha-band activity, replicating the original method but also potentially missing power effects if they are present at any other frequency of alpha-band oscillation. This also encompasses the lack of consideration for individualised alpha frequencies (IAF), as it is well-known that there will be a disparity across individuals in the alpha frequency that is preferred, with these being evidenced to predict perceptual performance in alternative previous studies (Samaha & Romei, 2024; Tarasi & Romei, 2024). Without accounting for this, this has likely contributed to our resulting non-significant effects of power and phase interactions on visual perception.

Additionally, when delving into the finer details of the current analysis, there is a notable flaw within our approach to investigate phasic behaviours. This encompasses how our phase bins were defined by the average phase of miss trials, with hits being orthogonal to this by default. This could certainly be considered as a limitation within our approach, as it means that hit phases are placed into a bin that perhaps does not appropriately suit them, alongside all participants being forced into the same phase bins even though we know from previous work that there are often individual differences in preferential phase (VanRullen, 2016a; Wolpert & Tallon-Baudry, 2021). With this approach, the effect of oscillatory phase is likely to be reduced, if not eliminated, as our phase bins likely do not contain phases associated with just hits or misses, invalidating our analysis. Further, we should also consider individual differences in the relative orientation of neurons with respect to recording electrodes, conduction delays resulting in shifts of optimal phases and differences in cortical folding resulting in signal polarity reversals (VanRullen, 2016a), each of which stress the limitations of

choosing analyses that adopt phase angle averaging techniques. However, as this approach was utilised in the original paper and pre-registered for the current investigation, we were restricted to its use despite its outlined weaknesses.

Our second hypothesis that hit and miss trials are characterised by a different alpha phase in the interval preceding the stimulus presentation, was confirmed, and we therefore replicated the original findings. The significance testing of the phase differences here was implemented using the Hotelling's paired bivariate test, which importantly did not utilise the previously defined phase-bins and included all trials regardless of power. Information of mean phase vectors for hit versus miss trials from each participant was then combined in a way that weighted individual contributions, creating a more valid reflection of group averages. When directly testing phase opposition with this analysis, we found a significant difference between hit and miss phases, thus replicating the original study and providing evidence that prestimulus alpha phase influences the perception of a subsequent stimulus. Compared to the phase bins method, this test offers a more flexible approach to accounting for individual differences, which may explain why a significant effect was only observed here and not with the previous analysis. We therefore believe that these results should be viewed as robust and convincing evidence in favour of the literature that seeks to demonstrate how visual perception fluctuates along the phase of alpha oscillations (Busch et al., 2009; Mathewson et al., 2009, 2011; Zazio et al., 2022).

However, we should also acknowledge the growing collection of null evidence, finding no indication of alpha phase influences on perceptual outcomes (Benwell et al., 2017, 2022; Michail et al., 2022; Ruzzoli et al., 2019; Van Diepen et al., 2015). One possible explanation for such contradictions may arise from differences in task conditions, where those that have found significant results for phase effects have implemented what could be considered as 'simple' detection designs, i.e., the detection of a small point of light (e.g., Busch et al., 2009) or the detection of a centrally presented dot (e.g., Mathewson et al., 2009; the current experiment also). In comparison, those that have reported no significant effect of phase have often implemented more complex designs, such as through the inclusion of distractors (Van Diepen et al., 2015) or asking participants to discriminate target features rather than just detect their presence (Michail et al., 2022). Additionally, the duration of target presented may likewise impact the role of pre-target phase, where the perception of stimuli on a shorter timescale may rely more heavily on this oscillatory feature (Zazio et al., 2022). These differences

should be considered closely, as each may impact the conclusions that can be drawn from resulting evidence and likely have led to the extensive contradictions within the field.

When going back to our findings, we additionally found no significant difference in N1 amplitude or latency, when comparing hit versus miss trials (as defined by our calculated phase bins). This suggests that occipital alpha phase measures (at channel Pz) observed within this study do not influence cortical excitability levels measured at the frontal cortex (at channel Fz). When linking back with the original study, this again does not match findings from Mathewson et al., (2009) which did indeed find significant differences in both amplitude and latency measures for the N1 component. Whilst these original findings were attributed to reflect changes in brain activation being dependent on pre-target alpha phase, our current results do not support such a theory. However, there is already compelling evidence to suggest that alpha phase does have a modulatory effect on corticospinal excitability, examined through indexes of MEPs and phosphene perception levels (Berger et al., 2014; Bergmann et al., 2019; Dugué et al., 2011; Samaha et al., 2017; Schilberg et al., 2021; Zrenner et al., 2023). Based on the limitations of our analysis choices outlined above (i.e., choice of phase bins) and consideration for previous evidence, it would therefore be premature to view our current findings as robust evidence against the role of alpha phase on cortical excitability. Instead, we have concluded null evidence in support of the pulsed inhibition hypothesis specifically, as outlined above. As Mathewson et al., (2009) utilised the same analytical approach to us, it is possible that they only found significant results due to their investigation being weaker in statistical power than compared to ours (a result of small sample sizes). Whilst low power typically leads to type II errors, i.e., concluding there is no effect when in fact one does actually exist (Button et al., 2013), it may be the case that the original results from Mathewson et al., (2009) are an example of a type I error, i.e., concluding there is an effect when in fact one does not exist. This can occur in low powered investigations when a subset of participants introduce bias to the data and cause the averaged results to become an inaccurate reflection of the true population.

It is also important to acknowledge our behavioural findings, where we found that there was a significant effect of block number on HR and *d'* measures, where both seemed to reduce following performance in the first couple blocks. We can perhaps attribute this to confounding variables of fatigue, aligning with behavioural results obtained by Mathewson et al., (2009) which they extend by correlating with parallel decreases of alpha power across blocks; promoting the additional suggestion that neuronal behaviour

is influential in visual awareness. Curiously, in our study, behavioural measures then increase in the final block, perhaps reflecting participants acquiring a final burst of high concentration as they realised they no longer had to conserve their remaining energy. Further, attention should be drawn to the final performance measures of our participants after we removed trial blocks sitting outside of our desired performance criteria. Whilst the set conditions were implemented to ensure that only valid data was taken forward into our analyses, by excluding these blocks it meant that some participants achieved an adjusted overall accuracy of just above 18%, well below chance level. This likely means that these participants either found the task too challenging, they were not paying attention throughout the study, or perhaps even that they fatigued quickly during the task. As the target contrast was chosen based on staircase performances, it is likely to be one of these latter two suggestions, highlighting how their performance may not be considered reliable enough for inclusion in our analyses. Although arguably still, by ensuring that participants did not have high FA rates, this could be considered enough of a criterion to establish reliability for the purposes of this investigation. It would be interesting if we could exclude and replace these participants in an attempt to determine whether this would differentially impact our resulting statistical conclusions, possibly resulting in a clearer depiction as to the role of alpha on visual perception. Though, this was not something that was registered and therefore was not feasible for the current study.

Finally, it is important to address a single feature of the implemented task which limits our ability to make detailed conclusions surrounding the role of alpha oscillations in perception. This is explicitly the ability of participants to temporally predict the onset of the target during this task (i.e., through no jittered pre-target interval). With this ability, there is a potential confounding influence of target expectations, where the pre-target neural signals may have been biased towards the successful perception of the target (Clementz et al., 2002; Nandi et al., 2023; Samaha et al., 2015). This is something that we aim to address in an additional study as part of the #EEGManyLabs Initiative, where the investigation will be identical to what is currently outlined but with the inclusion of a jittered interval between the fixation and the onset of the target. This will enable us to further determine the validity of the conclusions from Mathewson et al., (2009) and decipher if temporal expectations play a substantial role in the modulatory role of phase in visual perception. Previous attempts to investigate this have offered inconclusive evidence thus far (Ruzzoli et al., 2019), but there is a key acknowledgement of the need for this to be explored in depth, as results may potentially have an impact on

conclusions drawn from a number of studies (e.g. Harris et al., 2018; Myers et al., 2014; Samaha et al., 2015). Both of these points accentuate the need for this additional exploration into the mechanisms that may influence visual perception.

3.6 Conclusion

In conclusion our results partially replicate the original findings observed in the popular study by Mathewson et al., (2009), where we have evidenced a significant pre-target alpha phase difference in detected than compared to undetected trials. Whilst we did not replicate previous results surrounding the effects of alpha power, and phase effects for calculated N1 components, our results still offer similar interpretations, whereby low-frequency oscillations (i.e., alpha) are able to modulate how the brain samples visual stimuli via mechanisms of phase-dependent fluctuations. We believe that we have presented robust evidence of this effect, carried most strongly by our significant Hotelling test result. However, we also acknowledge that our findings here are somewhat inconclusive in establishing a complete understanding of the role of alpha oscillations in visual perception, most notably because our conducted analyses utilising defined phase bins is limiting and unsuitable. This perhaps accounts for why we have not been able to determine the effect of alpha phase on cortical excitability. We hope that with the addition of data from the eight other labs conducting this same experiment, enough evidence will be collected to make the interpretation of our results stronger, establish reliable conclusions and resolve the longstanding debate surrounding alpha oscillations and perception.

Chapter 4: Investigating the Role of Neuronal Oscillations in the Top-Down Control of Visuospatial Attention, an EEG study

4.1 Introduction

With the overwhelming quantity of information in our environment, to achieve any task we need a filtering mechanism so that our limited cognitive resources can be allocated to behaviourally relevant input (Wahn & König, 2017; Veniero et al., 2021). Without such a mechanism, it is conceivable to imagine that attempting to accomplish any ordinary task would become difficult, if not impossible. For example, imagine trying to do a simple food shop if we could not effectively filter out the products that we did not need to buy – it would take forever. Thankfully, attentional processes can be employed to allocate our cognitive resources to specific locations, bringing the objects there into attentional focus, a process that is explicitly known as visuospatial attention (Emrich et al., 2017). By its very definition, this is the selective attention that is allocated to a location in visual space (Kim & Kastner, 2019), allowing the enhanced detectability and discriminability of stimuli at such localities (Antonov et al., 2020; Mathewson et al., 2009; Maunsell & Cook, 2002). To orient this attention, top-down control mechanisms can be employed (or endogenous attention; Richter et al., 2018; Riddle et al., 2019; Spitzer & Haegens, 2017; Veniero et al., 2021), i.e., the attentional deployment to a particular location or stimulus that is modulated by task instructions, goals, and knowledge of the individual (Mozer et al., 2005). This is in contrast to bottom-up mechanisms (or exogenous attention) that reflect involuntary shifts of attention towards salient stimuli (Posner, 1980).

For this chapter, the focus will be on endogenous attention specifically, with such attentional mechanisms being thought to have evolved to not only achieve goal-directed behaviour (Allport, 1987), but also because they offer an evolutionary advantage (Clark et al., 2014). This is based on attention increasing an individual's chances of averting negative stimuli, or decreasing their chances of missing positive ones (Anderson, 2013). Posner was one of the first to empirically verify such advantages, finding that by validly cueing participants with where a target is likely to appear and encouraging shifts of attention, this reliably improved perceptual performance at this location, measured via both accuracy and reaction times (Posner, 1980). Importantly though, endogenous attention is only appropriately engaged if attentional cues are considered predictive, otherwise uninformative cues engage exogenous attention and behavioural performance is instead guided by the perception of salient stimuli (Carrasco, 2011). With this knowledge, we

are becoming more aware of how to validly study attentional mechanisms, with Posner's task design of cueing attention and then presenting targets being regarded as famous in the investigation of visuospatial attention. Thousands of researchers continue to adopt and adapt this cueing paradigm to further our understanding of attentional mechanisms (Hayward & Ristic, 2013; Klein, 2005), including how they may be modulated by both external and internal factors.

When first delving into the topic of visuospatial attention, it is important to understand the two prominent types of attentional orienting: covert and overt. These are two ways in which individuals can shift their attention, with the important distinction being that overt shifts involve saccades that bring a visual location/object into the view of the fovea, whilst covert refers to attentional shifts that are achieved without movement of the eyes. Depending on task instructions, both of these modes can be implemented during the Posner task, and more generally are used daily and across species (Harmening et al., 2011; Nothdurft et al., 2009; Sridharan et al., 2014). When exploring endogenous attention in particular, study designs have been implemented to explore both overt and/or covert shifts of attention, enabling the investigation of how attentional deployment may occur alongside or in the absence of saccades, respectively. Despite our knowledge of how to conduct these studies and decades of research exploring all facets of attention, the study of visuospatial attention has only recently had a resurgence due to experimental techniques now being able to investigate the relationships between neural activity and visual responses (Peylo et al., 2021). This means that our understanding of the neural mechanisms subserving visuospatial attention is continuously evolving, with new theories and empirical evidence often coming to light (Hopfinger et al., 2000; Sherman et al., 2016; Spadone, Betti et al., 2021; Veniero et al., 2021). Specifically, the narrative has shifted from looking at event-related potentials (ERPs) as our main hallmark of cognition, towards the use of neuronal oscillations to illustrate changing dynamics of cognitive processes (Bastiaansen et al., 2011). This is important as ERPs are neural responses to presented stimuli and events (Blackwood & Muir, 1990), meaning that they are time- and phase-locked to the onset of such (Min et al., 2007; Rugg, 2009). These have been especially useful in uncovering the effects of attentional shifts on sensory processing, including how ERPs may correlate with behavioural outcomes. However, by looking towards oscillations instead, this has enabled a better understanding of how neural activity may modulate the attentional shift itself, typically seen by exploring oscillatory signatures as far back as the cue that directed its deployment. As such, this has also meant that we

can explore non-time/phase locked activity that would otherwise have been averaged out in traditional ERP analyses, resulting in the exploration of evolving mechanisms (see Bastiaansen et al., 2011, for a detailed discussion on the topic). Despite these advances though, findings surrounding which oscillatory frequencies are responsible for which (cognitive) behaviours, have often remained contradictory and unclear (Clayton et al., 2015; Thut et al., 2006), with relevant disputes focusing on how they may influence cognition, e.g., the inhibitory or facilitatory nature of alpha oscillations. This is something that will be explored in the continuation of this chapter, as ongoing debates highlight both the challenges associated with understanding the neural mechanisms behind the top-down control of visuospatial attention and the demand for further research within this domain, directing progress towards a field-wide consensus. The overall results and conclusions of this experimental chapter will ultimately look to contribute to this aim.

The present investigation will focus solely on covert shifts of visual attention. We determined that it would be beneficial to avoid the presence of eye movement artifacts, meaning that we could then reliably study attention-related responses without potential ocular confounds, supporting a valid investigation into how attention is modulated by oscillations independently from eye movement processes; a motivation that is shared amongst others in this field (Kulke et al., 2020; Talcott & Gaspelin, 2021). Similarly, the use of a covert paradigm meant that we could reliably investigate shifts of attention on a much shorter temporal scale, as covert attention has been shown to speed up the processing of relevant information (for a review, see Anton-Erxleben & Carrasco, 2013; Carrasco & McElree, 2001). This speed has been attributed at least in part to the absence of saccades, reducing the cost of disengaging attention from a foveated location to reorient it to another (Koevoet et al., 2023). Complementary arguments also state that this lower cost is facilitated by the reduced need for saccadic motor preparation, pre-saccadic attentional shifting and predictive mapping behaviours (Koevoet et al., 2023). It should be emphasised though, that whilst covert attention is thought to be 'cheaper' than overt, some argue that there is still a cost that should be considered. This is underscored by the well-known (but controversial) pre-motor theory of attention, which outlines how covert shifts of attention are accompanied by saccadic motor preparation behaviours, despite no saccades being executed (Rizzolatti et al., 1987). However, newer research is beginning to propose that whilst this may be true for exogenous shifts of covert attention (i.e., triggered by object saliency), it appears that endogenous shifts of covert attention (i.e., cued) can be independent of such oculomotor control (Casteau & Smith, 2020; Liu et al., 2022; Smith & Schenk,

2012). To understand this fully, more research is currently needed to resolve the conflicting research that either continues to offer support to the pre-motor theory (Belopolsky & Theeuwes, 2012; Van Der Stigchel & Theeuwes, 2007) or those that promote its rejection (Smith & Schenk, 2012). For the current investigation though, focus will remain on covert attention for reasons outlined above.

When investigating the neural correlates of visuospatial attention, EEG studies have found evidence to suggest that predominately alpha (8-12 Hz), beta (13-30 Hz), or both of these oscillatory frequency bands may play a key role in the modulation of visuospatial attention (Banerjee et al., 2017; Peylo et al., 2021; Riddle et al., 2019; Sauseng et al., 2005; Spadone, Wyczesany, et al., 2021; Vázquez Marrufo et al., 2001). However, the literature that exists is frequently contradictory and so final conclusions remain out-of-reach. An invaluable review by Carrasco (2011) provides an insight into the extent of this, outlining both robust conclusions surrounding the effects of spatial attention on behavioural outcomes, as well as highlighting debates that exist across electrophysiological and neuroimaging studies, each attempting to offer insights into neuronal mechanisms that may modulate such activities. Considering this, the following sections will seek to further review the associated evidence in relation to visuospatial attention and where relevant, visuospatial perception. Whilst attention and perception are closely related, there is an important distinction between the two: *attention* is the process whereby information from the environment is selected and 'focused' on (Schröger et al., 2015), whilst *perception* is how we become aware of something by means of the senses (e.g., visual and auditory; Wade & Swanston, 2013). Often, these terms are mistakenly used interchangeably, and so this thesis will endeavour to clarify whether important studies focus on either attention, perception, or both, so that a comprehensive understanding of the current literature can be achieved. This chapter will then progress to outline an EEG experimental study that was conducted with the aim of uncovering the precise neural mechanisms involved in the top-down control of visuospatial attention, and how this may modulate the perception of targets, with a conclusion on where our research stands within the current evidence base. To achieve this, we will specifically look to examine the neural signal generated by a covert endogenous attentional shift, helping to bridge the gap in our knowledge of neural mechanisms that modulate shifts of spatial attention, seen specifically in the signal prior to the onset of target stimuli.

4.1.1 The Key Role of Oscillations in Visuospatial Attention

Alpha Oscillations (8-12 Hz)

As mentioned in previous chapters, alpha oscillations are the most prominent features of neural activity in the cortex. Traditionally, these brain waves have been most associated with rest, with alpha oscillations seen as a representation of the brain's 'idle-state' (Ben-Simon et al., 2008). Moving away from this definition, they have now been strongly evidenced to play a key role in attentional processes, amongst other important cognitions, by mediating both the suppression and (or) selection of information during attentional orienting (Foster & Awh, 2019; Foxe & Snyder, 2011; Klimesch, 2012; Schneider et al., 2022). In fact, this research is so compelling that the field no longer considers alpha to reflect idling, instead highlighting it as one of the most important neural signals for healthy cognition (Başar & Güntekin, 2012). When solely focusing on its role within attentional mechanisms, it has been proposed that attentional sampling processes occur at roughly 8 Hz, reflecting the rhythmicity of attention within the alpha band (Landau & Fries, 2012). This effect is found specifically when individuals are sampling a single location though, with such behavioural fluctuations reducing to 4 Hz when two locations are instead present. This 4 Hz rhythm has been attributed to attention essentially shifting concurrently between the two fields, demonstrated further by the antiphase relationship between the spectra of target detection in each of the two locations (Landau & Fries, 2012).

It is well agreed that the typical neural signature of an attentional shift can be seen when an individual shifts their attention to one side of visual space, resulting in a decrease of occipito-parietal alpha power over the hemisphere contralateral to the attended location and an increase over the hemisphere ipsilateral (Kelly et al., 2006; Thut et al., 2006; see Figure 4.1, below). Such findings have been replicated numerous times, particularly in the investigations of top-down attentional control, whereby participants are cued to shift their attention to one side of visual space (Foxe & Snyder, 2011; Limbach & Corballis, 2017; Rihs et al., 2007; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000). Interestingly, when attention is distributed across visual fields equally, with no single hemifield taking primary focus, alpha lateralisation is shown to be replaced by a bilateral decrease in power (Dombrowe & Hilgetag, 2014); in line with the idea that the lateralisation behaviour works to prioritise one visual field over the other. This illuminates towards how alpha power lateralisation within the visual cortex is able to modulate performance, with improved performance being observed at regions where (a majority of) attention has been shifted, i.e., during lateralisation occurrence (Anton-Erxleben

& Carrasco, 2013; Carrasco, 2011). Thut et al., (2006) demonstrated this effect by presenting empirical findings of a significant relationship between alpha lateralisation and detection speed in a visual attention task, where detection was faster when there was larger lateralisation. Importantly though, this same effect was not seen when considering detection rates as a performance measure within Thut et al.'s study. It could therefore be argued that alpha lateralisation here may reflect response preparation rather than attentional deployment, although the authors of this study have argued that this is unlikely. If this were true, then significant results should only be observed in the left hemisphere of the brain as participants responded with their right hands, meaning response preparation processes should be restricted to the corresponding left cortex. Instead, this effect was observed across both hemispheres, therefore suggesting that the lack of lateralisation effects on detection rates likely reflect the impact of attentional reorienting. If a target is presented at an uncued location, participants can simply reorient their attention to this location if the stimulus is presented for long enough, thus still perceiving the target and successfully responding in the trial. This reorientation of attention would only occur after the 'invalid' presentation of the target and so it would not be appropriate to correlate target detection in these cases with pre-target alpha power measures, perhaps accounting for why a non-significant relationship has been observed within this study. Reaction times on the other hand would be affected by the reorienting process as it is shown to be time costly, and so the correlative relationship between lateralisation and reaction times would persist, as seen. To account for this, the chosen analysis should have instead focused only on valid trials where the target was presented in the cued position, allowing for a more accurate evaluation on the impact of alpha power lateralisation on behavioural performance as indexed by accuracy. This valid-only selection of trials is something that has been carried forward, where appropriate, for use in the current investigation. We have also chosen to present our targets on a short time scale, partially in an attempt to prevent such reorientation behaviours from impacting our results.

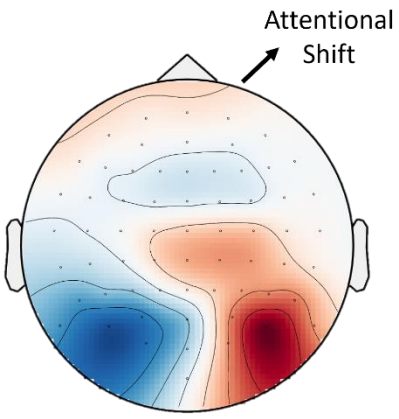


***Figure* 4.1**: Illustration of hemisphere specific alpha power changes that result from shifts of visual attention. The typical signature follows a pattern of decreased alpha power (blue shading) at the occipital hemisphere contralateral to where attention has been shifted, with increased alpha power (red shading) at the ipsilateral hemisphere.

Observed alpha lateralisation behaviours make up the foundations of the well-known inhibition theory, proposing that increases in alpha power can suppress irrelevant/distractor input (Jensen & Mazaheri, 2010; Klimesch, 2012). In the investigation of this, many studies have presented clear evidence of this effect (Gould et al., 2011; Kelly et al., 2006; Rihs et al., 2009; Rihs et al., 2007; Sauseng et al., 2005; Thut et al., 2006). For example, Kelly et al., (2006), found that there was a significant pre-target increase of alpha power in the hemisphere contralateral to where distractors were presented, with this effect being significantly higher when the task was more difficult. This demonstrates how changes in alpha power could be considered a mechanism of active attentional suppression, adapting to task demands and working to aid our visual performance abilities by minimising interference. In more recent studies, this finding was replicated, with empirical evidence showing that when the perceptual load of the target increases, i.e., when identifying the target requires more cognitive resources, alpha power also increases within the visual cortex contralateral to distractors (e.g., Gutteling et al., 2022; Jokisch & Jensen, 2007). These results were found in parallel to behavioural evidence showing how such increases in alpha power were predictive of smaller distractor interference effects on performance reaction times (Gutteling et al., 2022). Beyond this, manipulations of stimuli within this same study by Gutteling et al., (2022) showed that by making the distractors more prominent and therefore increasing their interference abilities, it appeared that pre-target alpha oscillations responded by increasing in power, likely accentuating their suppression abilities. Together, these results work to advocate for the theory

that alpha power is inhibitory, operating via mechanisms that allocate our perceptual resources to the target by reducing resources to distractors.

When linking alpha power lateralisation to the topic of visuospatial attention specifically, a blocked design study was conducted by Rihs et al., (2009), exploring posterior alpha power during a spatial attention paradigm, where participants were cued at the start of a block with where to shift their attention for an upcoming target at each trial. As is standard, this target would then either appear at the cued or uncued position and participants would have to respond with where it was presented. When reviewing the resulting neural recordings from EEG, there was a clear reduction in alpha power during pre-target time windows, which was maximal in the hemisphere contralateral to the attended visual field. This was then followed by an increase of alpha power in the hemisphere ipsilateral to the attended side, which was an effect argued to be seen only when attention needed to be sustained over longer intervals, i.e., during the period between cue to target in a blocked design. These results maintain the idea that alpha power works via inhibitory mechanisms, but it also extends knowledge to include the temporal interpretation of a delayed increase in alpha power reflecting the later suppression of input from uncued locations. Although, despite its popularity, the design of this experiment is arguably limiting as there are no distractors present throughout the task, meaning we cannot assume a role of alpha power in their suppression. It should therefore be stressed that the inhibitory role of alpha has not validly been tested here, with interpretations surrounding this theory potentially being unsubstantiated when considering that the findings of this popular study have often been viewed as foundational evidence for such (Foxe & Snyder, 2011; Mathewson et al., 2011; Peylo et al., 2021). This is not an uncommon weakness in the investigations of visuospatial attention though, meaning that across the field there is subsequently a lack of empirical evidence for the role of alpha in the suppression of to-be-ignored distractors (Foster & Awh, 2019; Wöstmann et al., 2019). Without distractors being included in task designs, there is a chance that success on Posner-like tasks could be attributed to exogenous attention instead, rather than the assumed endogenous attention. To explain, when participants are responding with where they believe the target to be, they may have become aware of this by means of target saliency rather than cognitive resources being allocated to the location they believe the target will appear at (Macaluso & Doricchi, 2013), reflecting the invalid investigation of endogenous attention.

Poor task designs have become a common limiting factor within the literature investigating visuospatial attention and the role that oscillations play in such, with some of these likely contributing to the

contrasting or null results that are often seen, complicating any emerging patterns within the literature. One of the most recent reviews in the field outlines this clearly, with Bonnefond and Jensen (2024) proposing that perhaps the literature is so muddied when attempting to understanding the inhibitory role of alpha, mainly because of the choice of task distractor. Beyond what has been previously mentioned on advocating for the presence of distractors, this review highlights how distractors may differentially influence alpha oscillations, possibly accounting for why some studies may have found null results. It is possible that if targets and distractors within a task are too dissimilar, this will result in the reduced need for alpha oscillations to suppress any interfering stimuli, as the target can easily be identified without this resource. Arguably, this is what occurred in a study by Noonan et al., (2016), investigating the preparatory attentional mechanisms for inhibiting distractors. From their study, it was concluded that there was null evidence for the modulatory role of alpha oscillations during the top-down control of visuospatial attention; going against all previous knowledge of alpha inhibition. However, when delving into their task design, it appears that their distractors were easily recognisable from targets, with the former created by superimposing two Gabor patch targets on top of one another to create a distinguishably different checkboard pattern. With this contrast in stimuli, it is possible that the low interference from distractors has meant that alpha power did not need to significantly increase to prevent distractor interference. Further, this study includes an additional limitation of sometimes presenting both the distractor and target in the same visual hemifield concurrently, making it difficult to determine whether any lateralised alpha effects exist within the cortex. Such design flaws, along with others, prompt the need for new and carefully designed studies to be conducted within this field, with the addition of theoretically sound analysis choices, highlighting how there needs to be a shift in the way that this topic is studied. To guide this, Wöstmann et al., (2019) published ten simple rules, including outlining how task distractors should be potent enough to interfere with the target, as outlined previously. With this in mind, despite the current assessment of the literature revealing failings and inadequacies based on inappropriate designs, there are inklings that the tide is slowly changing. Acknowledgment of paradigm weaknesses has meant that some newer studies are emerging with adoption of more suitable designs (see Zhao et al., 2023, for a good example of this), likely resulting in more valid investigations of the top-down control of attention via neuronal mechanisms; something that this thesis investigation similarly aims to achieve.

When taking a step back, despite contradictions within the field meaning that there is yet no clear understanding surrounding the exact role of alpha oscillations in visual attention processes, one thing we do

know is that alpha oscillations undoubtedly play an essential role in the top-down control of attention, regardless of whether this is faciliatory, inhibitory, or both (see Foster & Awh, 2019; Schneider et al., 2022). In an attempt to decipher methods of 'how', Bonneford and Jensen (2024) hint at how to conclude the true nature of this effect, suggesting that more research should be conducted in a way that enables the behavioural observation of sustained distractor suppression, i.e., through the implementation of blocked designs. It has been suggested that only with this design type can true inhibition behaviours become observable, as attention is sustained for periods of time long enough to reveal reliable neural mechanisms of attentional allocation (Couperus & Mangun, 2010; Noonan et al., 2016; Zhao et al., 2023). Further, Bonneford and Jensen (2024) advise the field to begin exploring the mechanistic role that alpha oscillations play in attentional processes as a whole. Specifically, they argue that new avenues of research should be opened to investigate alternative but vital roles of alpha, such as whether these signals are able to control the flow of information within the cortex, thus influencing our visual processing capabilities and subsequently target detection performance. There is promising research to suggest that this may indeed be the case, with reduced occipital alpha power being responsible for increased excitability that often then leads to improved visual processing (Iemi et al., 2017; Lange et al., 2013; Romei, Brodbeck, et al., 2008; Romei, Rihs, et al., 2008). On a neurophysiological basis, we know that alpha power is a signature of neural excitability and can thus characterise cortical states, with low alpha power reflecting active/enhanced neuronal processing and high-power reflecting its suppression (Pfurtscheller, 2001; Pfurtscheller & Lopes Da Silva, 1999).

Moving on from alpha power, we must also reflect on how alpha phase measures can have an influence over performance in visuospatial attention tasks (Busch et al., 2009; Mathewson et al., 2009, 2011; Sherman et al., 2016). Current theories have been presented to suggest that the role of alpha phase takes on an extension to the alpha inhibition theory, renamed as the 'pulsed inhibition theory' (Mathewson et al., 2011; Mazaheri, 2010). Here, the emphasis is on how alpha cycles reflect periodic fluctuations of inhibition, whereby suppression behaviours are increased at certain alpha phases as well as stronger amplitudes (Jensen & Mazaheri, 2010; Klimesch, 2012). This same relationship has also been seen in neurophysiology, with neuronal firing rates becoming inhibited with stronger magnitudes of alpha power and also rhythmically within the oscillatory cycle, dependant on phase (Haegens et al., 2011). Simply put, this means that neuronal firing rates will fluctuate along the phase of alpha, resulting in the similar cyclic modulation of performance on a behavioural task. As an example of this, Haegens et al., (2011) trained a single monkey to perform a

somatosensory discrimination task whilst their neuronal activity was recorded using intracranial techniques at five locations in the somatosensory, premotor and motor cortices. Resulting data first found that alpha power decreases were associated with better task performance and increased neuronal spiking activity in the primary somatosensory cortex (S1), secondary somatosensory cortex (S2), dorsal premotor cortex (DPC), left medial premotor cortex (MPC-left; lateralised to the left because stimuli was delivered to the right hand) and the primary motor cortex (M1). In extension, they also found that alpha phase predicted the observed neuronal spiking activity, revealing that firing rates were significantly higher during falling phases and troughs, than compared to alpha peaks. Such findings are in line with the pulsed-inhibition hypothesis, showing that alpha oscillations create periods of inhibited neuronal firing and therefore reduce our processing abilities during such times. This therefore promotes the idea that alpha oscillations are not only able to influence cortical regions, but also set the state of cortical networks (i.e., the sensorimotor network; Palva & Palva, 2011; Sadaghiani & Kleinschmidt, 2016). However, as important as this study is for expanding our knowledge on the topic, this was conducted with a single monkey and so it is difficult to determine whether such results can be extrapolated and generalised across to humans. When reviewing the literature, it appears that a lot of the cortical state evidence here is conducted in non-human primates, justified by the ease of utilising higher resolution but invasive neuronal recording methods here, e.g., single cell recordings (Combrisson et al., 2017; Jensen et al., 2014; Montemurro et al., 2008; Ng et al., 2013). It would also be fair to conclude that the outlined study by Haegens et al., (2011), is not an exploration of attentional mechanisms, leaving us with a remaining question of how attentional cues may modulate oscillatory behaviours in cueing paradigms, and how this would impact perceptual behavioural performance (i.e., by encouraging fluctuations).

In response to this, there has been relatively little in the way of attentional investigations that explore the pulsed-inhibition hypothesis and thus the impact of alpha phase. Instead, there has been a focus on perception, with human studies suggesting that when individuals are presented with close-to-threshold visual targets, the phase of neuronal oscillations between the frequencies of 7-10 Hz (i.e., alpha) are related to the likelihood of perceiving them (Busch & VanRullen, 2010; Mathewson et al., 2009). A popular example of this was conducted by Mathewson et al., (2009), who highlighted that alpha phase significantly influences visual awareness in a detection task, but that this effect was only reliable when alpha power was increased (see Chapter 3). This is further supported by Busch and VanRullen (2010), who concluded from their EEG study that the phase of ongoing alpha oscillations in the occipital cortex, when the stimulus is presented centrally, can

influence the strength of neuronal responses (indexed via ERPs) and modulate reaction times that have often been used as a measure of perceptual performance. However, whilst these are useful studies to enhance our understanding of the roles that oscillations play in visual perception, without a cueing element we cannot gain a deeper understanding of how oscillations modulate visual *attention*.

Samaha et al., (2015) conducted one of the first investigations to explicitly explore the effect of top-down attention on the phase of oscillatory activity, hypothesising that shifting temporal attention would bias the phase of alpha oscillations towards optimal angles for successful performance. To study this, participants were cued with the time at which a visual target would likely appear on the screen, with these cues being labelled as either predictive or unpredictive and participants being informed of this. After the appearance of the target in each trial, these were masked with noise and participants were tasked with discriminating the target orientation (left or right). As expected in all attentional studies, top-down (temporal) predictions improved visual discrimination performance in the task. In keeping with the predicted hypothesis, it was also found that task success could be attributed to the modulation of alpha phase prior to target onset, and interestingly this finding was independent from any alpha power differences that were observed in the data. However, it should be highlighted that the analysis for this study was only conducted on EEG electrode Pz, as this was the electrode that showed maximal pre-target alpha power. Whilst this is a common approach to optimise analyses and resources, it means that resulting conclusions cannot provide a holistic view of cortical activity. Despite this, it is a useful example for emphasising the interplay that oscillations have with attentional mechanisms, albeit temporal and not spatial, unlike the focus of this chapter (see Chapter 3 for further corroborating evidence).

As noted in the introductory chapter, it is also important to address the existing neuromodulation evidence within this topic to determine whether alpha oscillations can causally modulate how we shift our visuospatial attention. One of the earliest examples of this was a study conducted by Romei et al., (2010) who investigated the role of prestimulus alpha rhythms in the occipital cortex during visual perception. Whilst this study did not utilise a cue to engage attention, the authors aimed at imitating the neural signals of attentional deployment by using rhythmic TMS at alpha (10Hz) and then also two control frequencies (5 and 20Hz), delivered to the occipito-parietal regions of the hemisphere contra- or ipsilateral to the visual field where the stimulus would appear. This was conducted under the assumption that by doing so the neural activity at the stimulation site would be entrained to match the delivered frequency and reflect what should occur following

attentional shifts (Thut, Schyns, et al., 2011). To achieve this, a series of 5 TMS pulses were delivered prior to the onset of a thresholded target stimulus (a black dot) that appeared in either the right or left hemifield for a short amount of time. Participants were then tasked with simply identifying where this target appeared. Upon analysing behavioural outputs of hit rates and false alarms, it was found that when stimulation was delivered at 10 Hz and on the hemisphere ipsilateral to the visual stimulus presentation, this resulted in a significantly higher hit rate than compared to when it was delivered contralaterally or at either 5 or 20 Hz stimulation frequencies. Interestingly, no difference was found in false alarms across conditions though, suggesting that alpha oscillations may causally bias the perception of stimuli by impairing contralateral target detection and enhancing ipsilateral targets. Whilst this seems like a clear-cut depiction into the causal role of alpha, there are limitations within this study that should be expanded on. These include the lack of distractors, as mentioned before, alongside the lack of an attentional cueing component, both of which would enable a better application of these findings towards understandings of visuospatial attention specifically. Further, this study only looked at the behavioural outcomes of hit rates and false alarms, which whilst able to provide a general overview of performance, are also limited in their ability to reveal extensive evidence into the causal effects of alpha and the consequences of this neural activity (for more information, see Chapter 4.1.2 Signal Detection Theory).

It should also be noted that some attempts to reinforce alpha-related results with causal evidence, have also fallen short. One such study that lands within this category used transcranial alternating current stimulation (tACS) techniques at individualised alpha frequencies, modulating alpha oscillations during a visual perception task (no cueing). This was conducted whilst sinusoidal gratings appeared in either the left or right visual hemifield of a screen and participants had to respond with its perceived location (Graaf et al., 2020). Importantly, the presentation of this visual stimuli was timed to the onset of predefined phases of the entraining tACS signal, meaning that subsequent behavioural results would be able to determine whether perception was preferentially improved during certain alpha phases. This was not the case though, with performance hit rates not being modulated by alpha phase. Yet, despite this, during post-hoc analyses it was found that there was some evidence of alpha phase effects on reaction times, suggesting that perhaps alpha phase does modulate performance after all, but just by improving speed rather than accuracy. Such effects on reaction times have been further reinforced in an attentional rTMS study by Sauseng et al., (2011), who used an rTMS protocol to exert an inhibitory effect on neural activity by applying a low stimulation of 1 Hz

frequency. This stimulation was delivered to both the vertex (as a control site) and the right frontal eye field (rFEF), an area that is widely reported to control the allocation of spatial attention through goal-directed mechanisms (i.e., endogenous attention; Gregoriou et al., 2014; Martinez-Trujillo, 2022; Wardak et al., 2006, 2011); explored more in subsequent sections of this chapter. This protocol was utilised with the aim of suppressing the excitability of the rFEF whilst participants performed a covert visuospatial attention task and simultaneously undertook EEG recordings. Behavioural results determined that response times were significantly delayed after the inhibition of the rFEF compared to the vertex, but only during valid cueing trials, reflecting an impairment of attentional control towards the cued location. Beyond this, EEG analysis showed that 1Hz rTMS over the rFEF, caused a significant change in alpha power at the occipital electrodes, finding that the typically observed lateralisation was virtually absent, only present in control trials. With this, the accumulation of results converge towards the suggestion that alpha oscillations play a causal role in the top-down control of visuospatial attention, via signals generated from FEF regions that then propagated towards the occipital cortex.

However, these results should be interpreted carefully, as despite these being seemingly convincing pieces of research, the evidence is muddied with the appearance of additional contradictory evidence that has attempted and failed to establish causality (e.g., Kasten et al., 2020; Schuhmann et al., 2019). Of this, more recent literature has begun to explore the possibility that modulations of alpha oscillations are not a causal mechanism but instead a consequence of visuospatial attention (for a critical discussion, see Peylo et al., 2021). Specifically, Antonov et al., (2020) identified a potential flaw within the literature, where previous studies have not determined whether increases in alpha power reflect an active mechanism of distractor suppression, logically supposing that if this were true then increasing power should be seen prior to the onset of contralateral distractors – something that studies often do not evaluate as focus is predominately on neural activity following target presentations. Some even go so far as to argue that there is no (convincing) evidence for the modulation of alpha-band oscillations as a mechanism for controlling neuronal responses to stimuli (Gundlach et al., 2020; Zhigalov & Jensen, 2020). For additional reviews and descriptions of these, refer to Chapter 5. Our research will seek to make this trial period separation by looking only at pre-target time windows, resulting in a clearer investigation of how our oscillatory activity may modulate visual processing following shifts of attention.

In summary of the research surrounding the role of alpha oscillations, despite all the contradictions, it is crucial to reiterate that based on the extensive observation of alpha power lateralisation, we can confidently consider this to be a key signature of shifting visuospatial attention. We therefore expect it to appear as a result of our implemented paradigm, with participants instructed to engage top-down control mechanisms of attention and thus demonstrating a modulation of alpha power. Without this pattern of results, it could be argued that our participants did not appropriately engage with the task, resulting in the invalid investigation of visuospatial attention as a whole. The role of alpha phase on the other hand is less clear and not yet well established within the literature. Subsequently, this has meant that it is difficult to decipher whether our study will determine any significant modulations of this specific measures in how we shift our attention, with much of the research only acknowledging its importance for visual perception.

Beta Oscillations (8-12 Hz)

Alongside the arguments for the importance of alpha in visuospatial attention, there is also emerging literature that acknowledges the contribution of beta oscillations (Gola et al., 2013; Richter et al., 2018; Spitzer & Haegens, 2017; Van Ede et al., 2011; Wróbel, 2000). This is made particularly apparent within a review by Di Dona and Ronconi (2023), who recently published an exploration of beta oscillations in vision, particularly focusing on perception. Here, it was outlined that whilst alpha has traditionally been the focus of this topic, there is compelling evidence to suggest that beta activity modulates several important processes too. For the purpose of this thesis, the most important one to acknowledge here is the evidence they put forward for the role of beta power modulations in FEF regions, leading to the suppression of saccades during covert attentional shifting, the top down modulation of these and thus the control of visuospatial attention as a whole (Fiebelkorn et al., 2018). They expand this perspective by highlighting the role of beta oscillations in the magnocellular-dorsal (M-D) visual pathway, which is commonly known as the ‘where’ pathway and is key in motion processing (Chapman et al., 2004; Fortes & Merchant, 2006; Livingstone & Hubel, 1987). Within their review, Di Dona and Ronconi (2023) refer to a number of important studies that have all evidenced beta contributions in visual processes, for example through the functional connectivity of spatiotopically organised regions within the M-D pathway (Rogala et al., 2020; Yordanova et al., 2017) and maintaining cognitive states required for the maintenance of representations in space (Engel & Fries, 2010). Through the acknowledgment of these, they conclude that beta oscillations appear to be the core neuronal rhythm within the M-D pathway, acting as a vital modulator in the orientation of spatial attention. Despite these admissions though, they

acknowledge that the evidence contributing to such conclusions is still in its infancy, but there is the start of what they term to be a coherent picture of the role that beta band rhythms play in visual perception.

When reviewing this evidence base ourselves, beta oscillations clearly demonstrate value and possess the ability to modulate our attention and perception of upcoming stimuli (Di Dona & Ronconi, 2023). This has been seen in a breadth of studies, including those of visual attention (Riddle et al., 2019), perception (Piantoni et al., 2010), but most prominently in those that investigate motor and somatosensory functions (Lundqvist et al., 2024). This is because beta oscillations are most generally associated with the sensorimotor system, often reflecting motor preparation and execution behaviours (Barone & Rossiter, 2021; Pavlidou et al., 2014; Zhang et al., 2008). Whilst we will be focusing on their role within visual and attentional systems, it is important to acknowledge this historical link as most tasks that are used to investigate such topics require participants to make task-related responses on a keyboard or mouse. This of course means that participants will be both planning and carrying out motor behaviours, resulting in neuronal beta activity that could be misinterpreted as relevant for the investigated cognition. With this in mind, when studying the role of beta oscillations in visuospatial attention, it is vital to convincingly dissociate neuronal mechanisms that support motor response behaviours from those that reflect the cognitive signal of attention. This can be achieved by implementing certain analytical steps (see Lundqvist et al., 2018), or even through careful task designs that consider how the two can be separated (Zagha et al., 2022). For example, some studies have achieved this by only revealing response keys after the window of interest, preventing participants from preparing their response (e.g., Rahnev et al., 2011). In review of appropriate task designs, Zagha et al., (2022) introduces suggestions on how to isolate sensory and cognitive from movement-related neuronal activity, outlining how studies should consider implementing 2-alternative forced choice (2AFC) designs with a delayed response time window. This enables researchers to disentangle choice responses from other sources of modulation, ensuring that signals of interest are not contaminated by motor responses. With this in mind, our conducted study addressing the aims of this chapter utilises both a 2AFC model and has a 300ms delay between the target offset and response window. Additionally, as we are only exploring pre-target time windows, we expect the impact of motor behaviours to be minimal. For extra reassurance, studies that are outlined in the following sections, and our own, have all explored beta oscillations in regions of the cortex located beyond the motor region, emphasising a reduced

likelihood that the evidenced signals reflect motor responses, strengthening our ability to make interpretations of the modulatory role of beta in visuospatial attention.

When focusing on the field of visual processes exclusively, research has demonstrated that beta exhibits differential behaviours than compared to alpha, where increases in beta power are shown to support target processing (Gola et al., 2013; Vázquez Marrufo et al., 2001). Much like alpha though, this effect of beta is also suggested to be under the influence of attentional shifts (Thorpe et al., 2012). This is supported by Gola et al., (2013), who asked participants to locate a specified target in a matrix, amongst a group of distractors. The orientation of this target was varied during each trial and participants were cued on a trial-by-trial basis with which orientation they needed to subsequently search for. Through EEG recordings, it was determined that correct responses were preceded by an increase in beta power within the occipital cortex, something that was not seen with incorrect trials. Interestingly also, this study included two groups of participants, younger versus older adults. When comparing these two, it was found that if older adults had similar beta activity to those who were younger, performance did not differ between the two groups. However, when older adults had differential activity, represented by decreases of beta power during difficult task conditions (i.e., when there was a shorter presentation of the target), these individuals had a higher number of incorrect responses. As such, it was interpreted that 'healthy' beta increases may indicate sufficient activation of attentional processes and the ability to sustain this throughout the period of an attentional task. Whilst this is a good insight into the way in which beta oscillations may help to modulate visual attention, it could be argued that this study is not a perfect illustration of visuo-*spatial* attention. Here, participants were not cued with where to shift their attention but instead asked to explore a visual area; the lack of attentional shifts being emphasised by the lack of lateralisation effects seen within their EEG signals. It would be interesting therefore to continue investigating the role of beta in tasks involving more explicit shifts of spatial attention, allowing us to gain insight into how such neural activity can help to orient attention towards targeted regions. With this knowledge we would be able to better assess how to guide our cognitive resources to a chosen location in anticipation of upcoming visual processing.

One of the early and few studies that have examined the role of beta specifically using spatially cueing task designs, are those conducted by Wróbel and his team of researchers (Bekisz & Wróbel, 1993, 1999, 2003; Wróbel et al., 1994, 2007). During these studies, electrodes were implanted into the visual cortex of cats and

their neural signals were recorded whilst they performed a visuo-spatial attention task, whereby a light would indicate which of two doors should be opened for a food reward. By examining their neural recordings, in the event of a successful trial (i.e., correct selection of the door) an enhancement of beta burst activity was seen in the anticipatory period between cue onset and the opening of the door, something that was not apparent during unsuccessful trials. Importantly, this was seen in the occipital cortex, so the neural behaviour could be separated from movement preparation accounts. In a review of these studies together, they proposed that this increase in beta activity could be interpreted as a marker of enhanced attention (Wróbel, 2000). Though, whilst such conclusions have been strengthened by replications within this research group, increasing its reliability, it should be stressed that it is difficult to extrapolate these findings onto the human cortex, as Wróbel's studies only recruited cats as their subjects. When it comes to examining the role of beta in visuospatial attention in humans, the literature is sparse and there is a definite need for further investigations to be conducted in this area. Only lately have Wróbel's findings been replicated in human subjects, by a unique study that explored sustained visual attention in a classroom setting (Ko et al., 2017). By asking students to identify visual targets during lectures and recording neural activity via EEG methods, Wróbel's findings were indeed imitated in the human cortex, with students exhibiting increases of beta power in temporal and occipital lobes during periods of increased attention (Ko et al., 2017).

Of the minimal research that does exist, there are additional studies that extend our beta knowledge, implementing task designs whereby participants are cued to covertly shift their attention to either the left or right visual hemifield, each containing a drifting Gabor patch (Spadone, Betti, et al., 2021; Spadone, Wyczesany, et al., 2021). For each trial, the given cue would either stay the same as the previous trial or change to direct attention towards the alternate hemifield, encouraging participants to either sustain or shift their attention, respectively. After the onset of this cue, participants were tasked with identifying a brief orientation change in the target Gabor, which was 80% likely to be in the cued hemifield. Upon analysing concurrent MEG results, Spadone's research found that beta band oscillations were responsible for aiding the communication between the prefrontal dorsal attention network (DAN) and parietal regions that are required for visual processing. Specifically, this communication started at the frontal eye fields (FEFs) and propagated downstream. Importantly for our interpretations of this, such an effect was only evidenced during trials where participants were required to reorient their attention, suggesting that beta oscillations play a role in the top-down control

of orienting attention between spatial regions. Similarly, prior research corroborates this, with proposals of increased beta power reflecting the reorienting of attention by updating goal-driven schemas, ensuring that participants are focused on attending to the targets spatial position and preventing automatic (pre-potent) responses caused by perception (Hampshire et al., 2010; Wiesman et al., 2017). This is imperative empirical evidence of the correlational relationship between beta oscillations and reorienting top-down attention (see also Gross et al., 2004).

Frontal Eye Fields and Beta Oscillations

Before continuing to explore the existing and relevant beta literature in more depth, it is fundamental to address the briefly mentioned FEFs and their involvement in endogenous attention. The FEFs are an area of the frontal cortex (one located on each hemisphere of the brain), that have been evidenced to contain visual, motor and visuo-motor neurons (Bruce et al., 1985). This has meant that the FEFs have been associated with a range of functions, most notably of which include the preparation/planning of saccades (Herbet, 2021), visual scene analysis (Muggleton et al., 2003) and the creation of attention-related signals (Herbet, 2021; Martinez-Trujillo, 2022; Veniero et al., 2021). The data that has been collected to support such suggestions has come from an assortment of studies, including lesion investigations (e.g., Schiller & Chou, 1998; Van Der Stigchel et al., 2012), stimulation protocols (e.g., Blanke et al., 2000; Grosbras & Paus, 2002) and direct (and indirect) neural recordings (Meehan et al., 2017; Popov et al., 2017; Wang et al., 2016); the latter two of which can explore the propagation of task-relevant signals across the cortex, particularly when combined. This has created an extensive collection of evidence to conclude the importance of the FEFs in successful visual functioning, particularly in the realm of visual attention. For the purpose of this chapter, the most important function of the FEFs that should be acknowledged is their proven ability to generate attention-related signals, which can then influence subsequent activity in visual areas that are located downstream (Herbet, 2021; Martinez-Trujillo, 2022; Veniero et al., 2021). Whilst the literature for this is relatively established, and previously explored within this chapter, what is less apparent is the neuronal mechanisms that may enable the FEFs to achieve their proposed role in visual functioning.

New research is beginning to come to light though, with one recent study by Veniero et al., (2021) investigating the modulatory effects of oscillations in the FEFs. In this study, single-pulse TMS methods were applied to the rFEF, resulting in its activation and thus the generation of an attentional signal. To note, the term

'attentional signal' here is used on the assumption that rFEF activation by TMS generates a signal that is comparable to one that is generated during voluntary shifts of attention, in analogy with animal studies that have demonstrated this to be the case when using invasive electrical stimulation (Moore & Fallah, 2004). This signal was then tracked with EEG as it propagated across the cortex towards occipital regions. Interestingly, it was found that when the rFEF was activated, this caused a phase reset of beta activity at occipital sites, reinforcing the notion that FEFs have top-down influence but more specifically via the phasic feature of oscillations. To emphasise this top-down effect further, this same protocol was repeated whilst participants performed a visual motion discrimination task, finding that the onset of the TMS pulse caused changes in visual perception abilities (i.e., hit rates) that fluctuated along the phase of beta oscillations too. When determining how the FEFs achieve this, this study implemented a dual site TMS procedure by delivering single pulses to the rFEF and then the right V5/MT region, an area known for processing moving stimuli (Chawla et al., 1998), like those used in the outlined paradigm. This protocol was chosen as it was hypothesised that the FEFs can modulate visual perception via their ability to cause fluctuations in excitability at recruited visual areas. So, whilst the first pulse at the rFEF was applied to cause an activation and trigger the propagation of an attentional signal towards the visual cortex, the second pulse at region V5 was used to evoke moving phosphenes so that participant reports of these could be used to assess the excitability of this region (i.e., stronger phosphene perception = higher regional excitability). Through the successful completion of this, it was found that pulses over the rFEF caused moving phosphene perception rate to fluctuate over time, again along the phase of beta frequencies (17 Hz; see Figure 4.2, below). Thus, in summary, it can be determined that top-down control of visual perception is instructed by the FEFs and can causally shape perception (as measured with hit rates and phosphene perception) through the modulation of beta oscillations.

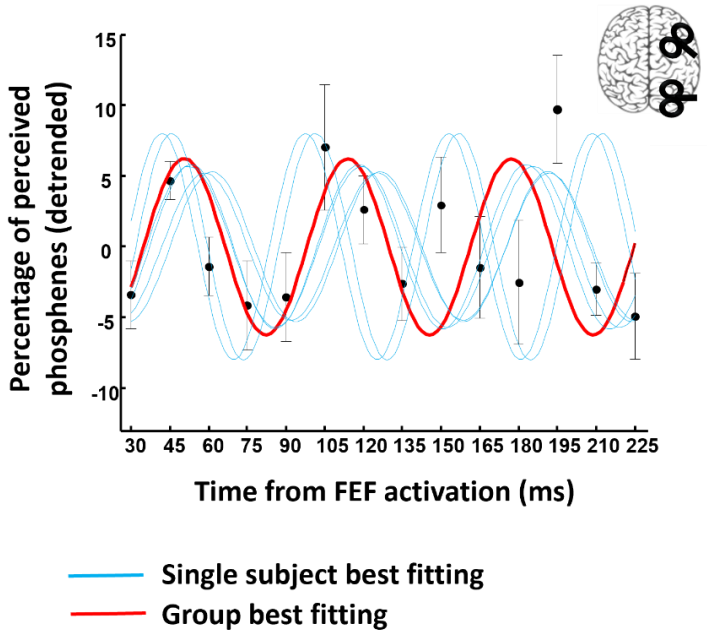


***Figure* 4.2**: Results from Veniero et al., (2021) following dual pulse TMS of the rFEF and rV5. Here, phosphene perception is used as a measure of V5 excitability. The average percentage of phosphenes perceived (black dots) is plotted for each time point from rFEF activation (30 – 225ms). The bold red signal shows a superimposed best-fitting cosine model for the group on average, calculated at 17 Hz. Single subject best-fitting cosine models are similarly plotted in blue. Adapted figure provided by D Veniero.

Considering this, whilst the paper by Veniero et al., (2021), and its conclusions significantly contribute to our understanding of endogenous control over visual perception, there are still open questions surrounding whether there is any causal evidence to support the role of beta phase in visuospatial attention. To our knowledge, this literature is very limited, with very few papers exploring this potentially causal beta-attention relationship. Of those that are currently available, there is one study to look towards by Romei et al., (2011), who used frequency-specific TMS to induce oscillations of 20 Hz (beta) and 5 Hz (theta) in the right intraparietal sulcus (rIPS), just before participants were required to perform a visual attention task. This region of the brain was chosen as previous work has demonstrated its activation during attention-requiring tasks, including shifts of attention and orienting spatial attention (Coull & Frith, 1998; Wojciulik & Kanwisher, 1999; Gillebert et al., 2011; Lückmann et al., 2014). At the same time as the last pulse in the delivered TMS train (5 out of 5 pulses), a stimulus would appear on the screen comprising of a modified version of Navon hierarchical letters (Navon, 1977; influenced by Mevorach et al., 2006), where, for example, combinations of either small ‘H’, ‘S’ or ‘D’ letters would be grouped in a larger letter shape, e.g., ‘H’. These stimuli would either be clear for the participant to see or blurred, reflecting a task of either local or global visual perception where participants

had to identify the presence or absence of the large *global* letter 'H' or the small *local* 'H' (see Romei et al., 2011 for further clarification). Results determined that during right parietal TMS at the induced 20 Hz beta frequency, this selectively enhanced visual processing of local stimuli. Such findings suggest that increased beta at this region of the brain can reduce the interference of distractors appearing from concurrent global stimuli, with this study providing causal evidence of such an effect. Though, perhaps from this we can instead conclude that beta oscillations in this region are able to bias visual processing towards local properties of stimuli, whereas theta stimulation was found to have the opposite effect and bias the visual processing of global properties. Regardless, these results suggests that beta oscillations are causally involved in visual processing during visual attention tasks, particularly in top-down attention, as participants were asked to pay attention to either global or local features of stimuli. Whilst the findings of this study reflect the causal role of beta oscillations in endogenous visual attention, there is still a question surrounding whether these findings would carry over to studies of visuo-*spatial* attention, a question that often reappears and is something that currently lacks transparent answers from within the present literature. It is this specific gap in our knowledge that this our implemented study will aim to bridge, explicitly examining the role of oscillations during visuospatial attention paradigms.

In summary of the evidence presented for beta oscillations thus far, one of the key take home messages here is that beta appears to be the frequency of choice for FEFs to exert their top-down influence on visual regions of the brain. This subsequently leads us to believe that during visuospatial attention tasks, it is likely that both behavioural performance (i.e., hit rates) and occipital neural recordings will exhibit beta fluctuations, based on the assumptions that each is under the control of the FEFs directing attentional resources. It remains to be seen however whether this effect is observable only when participants reorient their attention, as previously suggested. To determine the reliability of this suggestion, we have implemented a block design, where participants are assumed to sustain their attention at an increased likelihood than compared to shifts.

4.1.2 Signal Detection Theory, Attention and Brain Oscillations

Prior to commencing our own investigations though, we must first consider the best methods for achieving this. In the past, to resolve the scientific debate surrounding the role of oscillations in visuospatial attention, researchers both previously and continuously have sought to relate neuronal oscillations to

measures of performance, i.e., accuracy and reaction times. However, we are now striving beyond this and moving to investigate a more comprehensive measure of performance, which can be achieved through the utilisation of theoretical frameworks such as signal detection theory (SDT; Macmillian & Creelman, 1991). When making decisions, individuals are often in a situation of uncertainty, forced to make choices based on detecting a signal against background noise (Anderson, 2015). SDT offers a reliable method of empirically measuring this decision-making process in performance tasks, offering us a unique insight into our sensitivity and bias to certain targets; adding a level of complexity to our acquired knowledge. Accordingly, this model has been applied within research in an attempt to uncover the precise mechanisms of attention (MacMillan, 2002; Zhou et al., 2021) and explore how internal neural excitability changes can influence behavioural outcomes.

By adopting this framework, as mentioned, researchers have endeavoured to quantify perceptual performance achieved by visuospatial attention processes, based on a combination of both perceptual sensitivity (*d'*) and decision criterion (*c*; Zhang et al., 2019). By definition, *d'* is a measure of an individual's ability to discriminate signals of interest from noise, whilst *c* is a measure of an individual's willingness to select one perceptual decision over another (Bohil et al., 2015; Zhou et al., 2021). An improvement in performance can be achieved by a decrease in *c* and/or an increase in *d'* (Luo & Maunsell, 2018).

When looking towards the available literature, there are several studies that have endeavoured to reveal the impact of spatial cues on SDT measures, the majority here being behavioural. The first study to introduce this focus, provides a good foundation of knowledge towards the changes in both *d'* and *c* that are influenced by shifting attention. Here, Vernet et al., (2019), conducted a behavioural study implementing a visuospatial attention task, where participants were cued with which direction to shift their attention for an upcoming target that would be masked after brief presentation. Upon applying SDT analyses to their results, they found that shifting attention reliably increased perceptual sensitivity measures across participants and resulted in the adoption of a more liberal decision criterion. When reflecting on the former effect in particular, increased sensitivity has been described most often as caused by signal noise being reduced by means of attentional focus, enabling targets to become more distinct from potential distractors (Dosher & Lu, 2000a, 2000b; Lu et al., 2002). This contrasts with a smaller number of studies who theorise that attentional mechanisms increase sensitivity through means of target enhancement, leading to its increased perception (Carrasco et al., 2002; Ling & Carrasco, 2006).

Less studied is the influence that spatial attention has on decision criterion, also known as decision *bias*. With this measure, it is theorised that when an individual is cued to shift their attention to a spatial location, if they consider this cue to be valid they will set a lower decision criterion for stimuli appearing in this newly attended location (Smith & Ratcliff, 2009), resulting in perceptual decisions made with less evidence (Vernet et al., 2019). In a similar outlay of results, an investigation of visuospatial attention in mice found that by utilising a Posner-type paradigm, both valid and invalid spatial cueing resulted in *d'* and *c* changes, aiding perceptual performance in the task (Wang & Krauzlis, 2018). Specifically, it was found that decision criterion for valid trials was significantly lower than invalid trials, resulting in much shorter reaction times. This has been replicated in human subjects, finding that the predictive cues significantly lowered *c* measures from baseline, however when the cues were considered neutral, this did not result in a baseline change (Rahnev et al., 2011). This suggests that criterion setting is a dynamic process that can be modulated by the presence and reliability of task-related cues. Though, whilst these behavioural studies can improve our understanding of how shifting attention can impact our decision-making processes, we are limited in our ability to decipher how these changes occur from within the cortex, i.e., via neuronal mechanisms.

Moving forward to review evidence that extends beyond behavioural, it is essential to outline some key investigations that have led to the consideration that both *c* and *d'* are modulated by brain oscillations, setting the internal state of the brain (Zhou et al., 2021). Despite the history of this topic extending back decades (Carrasco, 2011), there is surprisingly little research that investigates oscillations and SDT alongside attentional components (Luo & Maunsell, 2018). Instead, studies have mostly explored perception, examining the influence of pre-target alpha phase and power on *c* and *d'* measures in perceptual tasks without attentional components. Here it has been demonstrated that ongoing pre-target alpha phase predicts *c* but not *d'* (Sherman et al., 2016), whilst others find that ongoing trial-by-trial alpha power fluctuations predict changes in *d'* (Zhou et al., 2021). Explicitly, Zhou et al., (2021) found that lower pre-target alpha power in occipital regions amplified neural responses so that the signal of interest was more distinct from noise, improving perceptual sensitivity (*d'*). However, this study found no evidence of a modulation of pre-target alpha activity in criterion changes, contradicting previous research that often presents such findings (Iemi et al., 2017; Limbach & Corballis, 2016; Samaha et al., 2020). In yet more contrast, alternative research states that reduced pre-target alpha power can bias an individual to report the presence of stimuli more often than their actual occurrence, reflecting a decrease in *c* measures (Iemi et al., 2017; Samaha et al., 2017, 2020).

Importantly, these latter studies clearly state that there is no effect of alpha oscillations on *d'* measures, and thus alpha rhythms arguably modulate baseline neural excitability rather than the precision of sensory processing (Iemi et al., 2017). But it is critical to point out that these findings have no explicit link to visuospatial attention and instead focus simply on how ongoing neuronal activity can influence perception. The tasks that were implemented asked participants to identify whether a target was either present or absent, not requiring any shifts of visuospatial attention based on the presence of a cue. This again leaves the open question surrounding whether endogenous shifts of attention would modulate perception via neuronal mechanisms in the same way, or perhaps differentially.

In another study of visual perception, there is evidence to suggest that high-beta oscillations (30 Hz) can enhance perceptual sensitivity to near-threshold targets, whilst oscillations as high as 50 Hz are responsible for changes in criterion (Chanes et al., 2013). This was put forward in a study by Chanes et al., (2013), who utilised frequency-specific TMS protocols during pre-target time windows to entrain frequencies of both 30 and 50 Hz in the rFEF. During trials with 30 Hz entrainment and when targets were displayed in the right visual field, this resulted in a significantly higher *d'* than compared to when they were presented in the left visual field. Alike, during the 50 Hz stimulation condition and when targets were displayed in the left visual field, this resulted in a significantly reduced *c* than compared to when they were presented in the right visual field. This is interesting as it suggests that not only are these two SDT measures modulated by different neural mechanisms, shown additionally in studies of auditory perception (Ho et al., 2017), but it also reinforces the importance of the FEFs in causally modulating visual processes. Even though the implemented task did not require participants to shift their attention based on a cue, there is cause for generalisation of these results towards visuospatial attention, as the rFEF was chosen as the site of stimulation; an area that is previously evidenced in visuospatial attentional orienting (Corbetta & Shulman, 2002). Thus, by stimulating this area the researchers are able to make inferences about the role of neuronal oscillations in attentional orienting processes, despite their task not directly testing attention. To reinforce this, refer back to the study by Veniero et al., (2021), where the FEFs were stimulated to create a neuronal signal which we can assume, based on previous literature, mimics attentional processes.

Through collating and reviewing the outlined research surrounding the role of neuronal oscillations in the top-down control of visuospatial attention, it is clear that there is currently not enough evidence to reveal

a clear and detailed picture of neural influences in this domain. In light of this, the following study has been conducted with the aim of gaining an in depth understanding of how shifting visuospatial attention can be modulated by neuronal oscillations, in the occipital cortex predominately. By adopting a 2AFC attentional paradigm with cueing elements, we sought to explore this empirically through both behavioural measures and complimentary EEG neuronal recordings. Both types of data were collected so that we could examine the full time window between a trigger event that signified the beginning of the task and the onset of the target (i.e., pre-target epoch). To note, this trigger event was included as a salient non-informative cue, resetting the phase of ongoing oscillations so that we could accurately examine the rhythmicity of attentional sampling between the two cued hemifields (Fries, 2023), i.e., the sequential selection of discrete locations. Further, our dual approach to data acquisition was required due to event related potentials resulting from the implemented trigger onset, meaning that we could not reliably look at EEG signal recordings immediately after this event. Importantly also, this unique study has been designed with the previous literature in mind, taking into account previous limitations of task designs and analytical approaches that have contributed to inconsistent findings amongst the field. For example, we have chosen to include potent distractors within our task, where they appear alongside targets to enable the valid assessment of endogenous attentional mechanisms, critically without confounding influences of exogenous processes. We additionally designed both our task and analysis pipeline to provide an equal chance to uncovering the effects of both alpha- and beta-band frequencies, where previous literature may have masked or enhanced either of these by utilising a trial-by-trial design and presenting a cue at the start of each, causing strong alpha-band activity that often results from shift cues (Spadone, Betti, et al., 2021), or simply by restricting their analytical frequencies. By conducting this, we expect to determine whether alpha or beta-band oscillations (focusing on phase) can predict *d'* and/or *c* measures when individuals engage in the top-down control of visuospatial attention. By including measures of SDT within our investigations, we are able contribute to the growing number of studies that are forming a deeper understanding of how visual perception may be achieved. When linking our behavioural and EEG results, we expect to find rhythmicity in the behaviour of *d'* and (separately) *c*. Based on previous literature, we also hypothesise that the neuronal mechanisms and topographies of these measures will be distinct from one another (e.g., Zhou et al., 2021), although based on the literature being so limited, we cannot predict for sure what these specific results will be.

4.2 Materials and Methods

4.2.1 Subjects

Forty healthy volunteers were recruited for the current study (32 female, 8 male), all of whom had normal-to-corrected vision. All participants completed an initial behavioural session and from this, thirty-one participants were invited back to complete a following EEG session (25 female, 6 male). The other participants were removed due to insufficient performance on the behavioural task (for criteria, see 'Session One: Behavioural', below). Five participants (3 female, 2 male) were further excluded from analysis due to insufficient performance on the EEG session (same criteria). The resulting sample size for subsequent analysis was thus 26 participants (M = 22.23 years, SD = 3; 22 females), which is in line with (or close to) a number of related previous investigations (e.g., Ho et al., 2017; Zhou et al., 2021). The study was approved by The University of Nottingham Ethics Committee, with all participants providing informed consent prior to the study and receiving monetary compensation for their time.

4.2.2 Experimental Design

This study was a repeated-measures design aimed at investigating if and how brain oscillations can be associated with changes in perceptual sensitivity (d') and/or criterion (c). To achieve this, the experimental task explored both participants' behavioural performance and neural signals when they covertly shifted their spatial attention based on a cue. This design mimicked a Posner cueing paradigm, but unlike classic studies, participants here were informed of which visual side to attend to in a block design, rather than being presented with a symbolic cue at the beginning of each trial (e.g., as in Thut et al., 2006). This choice had two aims, firstly reducing the evoked potentials resulting from the presentation of a cue, and minimising the strong alpha-band activity that often results from cues containing spatial information, as demonstrated by Spadone et al., (2021). Further, we wanted to ensure that participants sustained their attention for an adequate amount of time across the task, so that an accurate measure of attentional mechanisms could be obtained without reorienting behaviours potentially confounding results. The implemented task was created and presented via PsychoPy (version 2021.2.3; Peirce et al., 2019), using a QUEST staircase to titrate the stimuli so that participants achieved approximately 75% performance accuracy, ensuring that all participants were performing at the same baseline and to be able to confirm any advantage of valid cues.

4.2.3 Main Task

The main task was a motion discrimination task, where participants were instructed to always maintain fixation on a constant black fixation bullseye (RGB: -1, -1, -1; font: Arial; letter height: 1 degree) and make a response based on their perception of target motion. A schematic representation of this task is shown in Figure 4.3 (below).

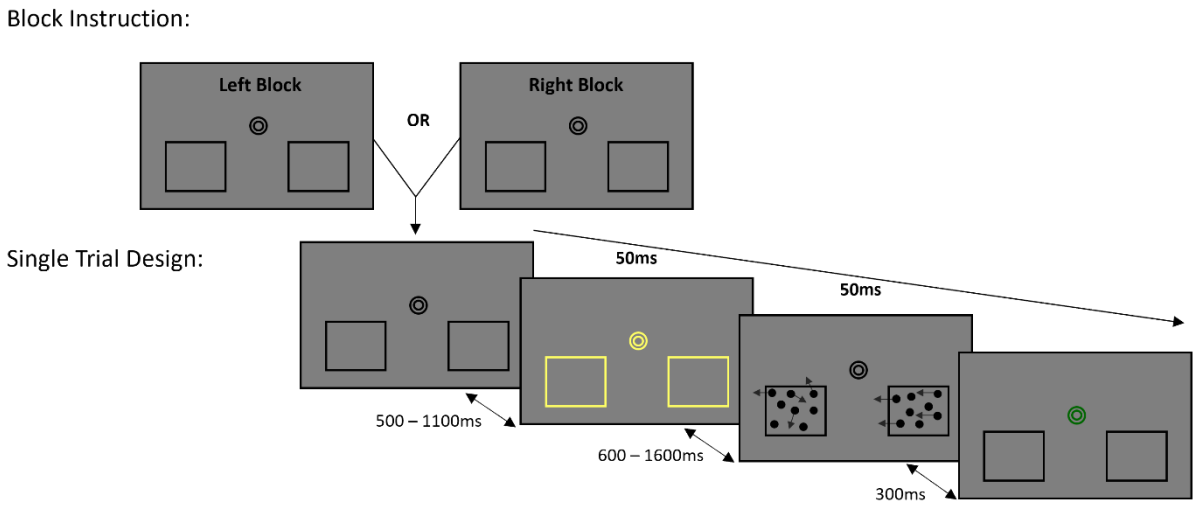


***Figure* 4.3**: Schematic representation of the experimental task. On the first screen of each block, participants were cued to covertly shift their attention to either the left or right placeholder. After a jittered interval between 500-1100ms, the fixation and placeholders briefly flashed for 50ms to notify the participant that the trial was starting. Moving dots then appeared after a variable interval (600-1600ms) in both placeholders for 50ms, however, only the dots in one placeholder moved coherently. Arrows are included for illustrative purposes only to indicate the direction of dot movement. In the example, the dots on the right moved coherently, the left randomly. 300ms after the offset of these dots, the fixation turned green prompting participants to respond with the direction of the coherent motion.

Stimuli were presented on a mid-grey luminance (RGB: 0.6549, 0.6549, 0.6549) screen that stayed consistent throughout. At the beginning of each testing block, participants were instructed on which side the target was more likely to appear via a simple instruction screen, i.e., 'Left Block' or 'Right Block'. This task was made up of eight blocks overall which were counterbalanced (4 Right, 4 Left) so that participants alternated their shift at each succeeding block (e.g., Right then Left), minimising fatigue effects. The start of the block was self-initiated by participants pressing any button on the keyboard. After the button press and throughout the block, a central bullseye and the two placeholders were displayed on the screen consistently. After a jittered interstimulus interval (ISI) of between 500-1100ms, the fixation and the placeholders flashed for 50ms, indicating that the trial was starting. This flash occurred as a colour change of yellow (RGB: 1, 0.5529, -0.2),

which was chosen and adjusted to be isoluminant alongside the background, minimising evoked potentials and afterimages that could confound both neuronal data and performance. This flash was included as a salient non-informative cue to reset attentional sampling (Fiebelkorn et al., 2013, 2018; Fries, 2023; Lakatos et al., 2008). Importantly, when participants received instructions for the task, they were made aware of the flash being indicative of the trial starting. Following this, after a jittered interval that varied depending on session number (see sections on each session below, for further details), moving dots appeared for 50ms in both placeholders. The stimuli consisted of two sets of 180 moving black dots (size: 5 degrees; field space: 5.8, speed: 0.04; lifetime: -1), each located in a square placeholder either side of the fixation (right position: (7, -7) degrees; left position: (-7, -7) degrees, size = 6 x 6 degrees, with a black outline width of 2.5). One set of these dots moved coherently (set to the participants' individual threshold) and was, therefore, the target. The other set moved randomly and acted as a distractor. Importantly, the side at which the coherent dots were presented was dependent on the block type, where 80% of the time, the coherent dots appeared in the cued position (e.g., Right Block = right placeholder dots move coherently 80% of the time); this is termed the valid/congruent condition. The other 20% of the time, coherent dots appeared at the uncued location (e.g., left placeholder dots move coherently 20% of the time during a 'Right Block'), this is termed the invalid/incongruent condition. We presented both the target and distractor at the same time for each trial so that we could validly test endogenous attention without the risk of target saliency engaging mechanisms of exogenous attention (i.e., attentional grabbing effects). The order of valid and invalid trials was randomised within blocks, and target movement direction was equally likely to be either right or left for each trial.

Then, after 300ms from the dot's disappearance, the fixation turned green (RGB: -1, 0.0040, -0.4980) to indicate that participants could respond. This delay was implemented to reduce motor preparation behaviours during pre-target time points. Participants were asked to respond with which direction they thought the coherent dots were moving. During the valid trials, coherence of these was set to match the threshold result of the staircase (see 'Session One: Behavioural', below), however during the invalid trials, titrated coherence was increased by 10% to ensure that participants were given a reasonable opportunity to decipher movement direction, as the target did not appear where we assume their attention was oriented. We also reasoned that being able to discriminate dot movement in invalid trials would further encourage attentional sampling. Conversely, if the invalid trials were too difficult—leading to chance-level performance—

participants might disengage from the unattended location and focus solely on the cued position. Using the keyboard, participants had to press ‘m’ if they thought the dots were moving right, or ‘z’ if they thought they were moving left, with no time limit for response.

After the completion of each block, participants were visually presented with their accuracy scores (%) for both valid and invalid conditions. This was to encourage them to continue performing to the best of their ability and perhaps even increase their attentiveness if they were underperforming. They were then given a rest period to reduce fatigue. Participants started the next block when they were ready by pressing any button to continue with the task.

Importantly, after each block, the dot coherence was adjusted if participants were under or over performing. If participants scored below 70% performance accuracy, then coherence was increased by 5%, and if it dropped below 60% performance accuracy, then coherence was increased by 10%. On the other hand, if participants scored above 80% performance accuracy, then coherence was decreased by 5%, and if it reached 90%, then coherence was decreased by 10%. This was included within the task design as it meant that both practice and fatigue effects could be accounted for if participants started exhibiting either improved or impaired performance, respectively.

Overall, this study comprised of two sessions, a behavioural and an EEG session (see corresponding sections below). During both sessions, participants were invited to the lab where they were seated in a Faraday cage, placing their chin on a chinrest to minimise head movements and position their line of sight central to the screen. This chinrest was measured at ~57cm from the screen. The room was set up with a desk, chair, computer screen and keyboard. The room was dimly lit and quiet to minimise distractions. The screen that stimuli were presented on was set to a refresh rate of 100 Hz (size: 1226 x 2248 pixels, screen model: Lenovo Legion, computer model: Lenovo ThinkStation P620).

An EyeLink 1000 system (version 1.0.18; SR Research, Mississauga, Ontario, Canada) was used throughout both sessions to carry out video-based monocular eye tracking at 1000 Hz. This ensured participants were fixated on the central bullseye throughout the experiment. Trials that showed deviation from this were excluded as they did not reflect covert attention. A standard 5-point calibration and validation

procedure was used to calibrate the eye tracker, conducted at the start of the experiment and then every block following (N = 4 calibrations per session, N = 8 in total).

4.2.4 Session One: Behavioural

This first behavioural session was comprised of three parts: practice task, staircase task and the main behavioural task. In total, session one lasted approximately one hour.

During the practice, participants were given a chance to familiarise themselves with the task outlined above by completing 20 practice trials (N = 17 valid, N = 3 invalid) whilst covertly shifting their attention to the right. This lasted approximately 1 minute in total. Coherence of the practice stimuli was set to 99% during this stage to allow for participants to clearly understand the task. If, after this practice, it became apparent that participants did not understand the task design, this practice was repeated to ensure that the main task would be completed properly.

The next section was the staircase titration, designed to adjust the coherence of the stimuli to match each participants' perceptual threshold; defined as the dot coherence value needed to achieve 75% accuracy in the motion discrimination task. The coherence of the stimuli started at 99% and reduced with correct responses at a standard deviation of 2. In the event of incorrect responses, coherence similarly increased. The titration automatically stopped when participants' threshold reached a 95% confidence interval, or they have reached 200 trials. Two staircases were performed prior to the main tasks of both sessions, one for the stimuli appearing in the right and another for stimuli appearing in the left placeholder. Importantly, the cue for these staircases were 100% valid to ensure accurate calculation of thresholds.

Following this, the main task began. Details for this are all outlined above in 'Main Task'. During this session, the intervals between the flash onset and the target ranged from between 600-920ms (in steps of 20ms, 24 trials per interval, per block). In total, there were 102 trials in each block of this session, meaning that across the eight blocks Session One included 816 trials (N = 680 valid, 136 invalid).

Following the completion of this session, if participants achieved an overall performance accuracy of >70% on valid trials and >50% on invalid trials, they were invited back to participate in the EEG session. Our justification behind this invalid threshold is embedded in the task aims, where we wanted to ensure that participants were sampling from both placeholders as they were told that there was a chance that the target

stimulus could appear in either. Thus, we needed to ensure that invalid performance was above chance (50%). In addition, performance had to be better for valid than invalid trials, ensuring that the participants were covertly shifting their attention accurately based on the cue.

4.2.5 Session Two: EEG

Session two was a replication of the previous session, but with the addition of EEG protocols and some modified parameters. In total, session two lasted approximately 2 hours including EEG setup.

The staircase titration was repeated for this session, to account for any practice effects that may have occurred during the previous session. Following the completion of this, the main task was repeated but with the addition of extra intervals of 1000-1160ms (steps of 40ms), between the flash and the onset of the target. This meant that Session Two included a total of 162 trials per block, with 24 trials per interval. These extra times were included to provide trials with a flash to target interval long enough to investigate oscillatory dynamics with EEG, avoiding ERP contamination of oscillatory activity in the window of primary interest (pre-target) due to the flash. In total, there were 1296 trials (N = 1080 valid, 216 invalid) across the whole of this experiment, meaning that across the two sessions there were 2112 trials collected for each participant (N = 1760 valid, N = 352 invalid).

For EEG acquisition, a Biosemi ActiveTwo system and ActiView software (BioSemi, Amsterdam, Netherlands) was used, with a sampling rate of 1024 Hz. A 64-channel arrangement was chosen for this study, covering the whole head with a 10-20 international system. Three additional electrodes were also used, one placed on each mastoid (right and left) to use as an off-line reference and another on the right cheek to measure eye movements (electrooculogram; EOG). Prior to recording, electrodes were connected to an amplifier and offsets were checked, ensuring a level between 25-50 mV at each channel. Set up was approximated to take 30 minutes.

4.3 Data Analysis

All analyses were performed in MATLAB (R2022a, MathWorks, 2022) using custom scripts and the FieldTrip Toolbox (2021 release, https://www.ru.nl/neuroimaging/fieldtrip; Oostenveld et al., 2011).

4.3.1 EEG Data Analysis

Although EEG data was collected throughout the whole of session two, only trials where the target was presented ≥1000ms after the flash onset (phase-resetting event) were included in this section of analysis. This later EEG interval time was chosen to reduce the risk of evoked potentials contaminating pre-target activity. The EEG signal was initially epoched (N = 480 epochs per participant), beginning 1 second before the flash onset (flash = time 0) to 2.26 seconds after (total epoch time = 3.26 seconds). This signal was then referenced to the mastoids, zero-padded to 5 seconds (to avoid filter artifacts), band-pass filtered (1-48 Hz), two-pass reverse filtered (Gross, 2014) and demeaned to achieve baseline correction. Next, vertical EOG (VEOG) was calculated to detect blinks and saccades, using the external cheek electrode and Fp2 channel. VEOG was then subjected to the same pre-processing steps as the EEG signal, where both were combined and resampled to 256 Hz.

Eye-tracking (ET) data from each participant was also imported and concatenated with EEG signals, so that the timeline of the ET matched that of EEG. This ET signal was similarly resampled to 256 Hz. This combination enabled an easier illustration of when ET artifacts (e.g., blinks and saccades) occurred so that appropriate decisions on trial exclusions could be made (see below).

Artifact rejection was carried out on all EEG trials, with MATLAB automatically highlighting artifacts at a cut-off at 6 SDs from the mean. Each trial was then visually inspected for artifacts, resulting in the manual removal of whole trials with saccades, movement artifacts, and blinks around the flash or target presentation. On average, 14% of trials were removed from each participants EEG dataset (N = 405 trials remaining, on average for each participant). Bad channels were also interpolated during this step (N = 0.5 channels, on average from each participant), and the resulting signal was re-referenced to the average of all channels. Independent component analysis (ICA) was then conducted to identify and separate 20 independent sources of signal present within the EEG (via PCA reduction), i.e., eye movement sources. The produced components topographies, time courses and average activities were then plotted and visually inspected to assess whether they were in fact an artifact and needed to be removed from the signal. An example of removed components included cardiac artifacts and head movement/muscle noise. On average, 5 of these ICA identified sources were removed from each participants EEG signal. Following this, a further final post-processing step was taken

to ensure that the data was thoroughly clean. This included plotting the variance and standard deviation of each trial and channel, where those that presented as extreme outliers were removed.

Preparatory Data Steps

To prepare the data for subsequent analysis, the same initial preliminary steps were followed throughout. Since we were particularly interested in the activity immediately preceding the event of interest, i.e., the flash or the target, to avoid any leakage of post-event activity in these periods and remove the evoked response, we created a 1000ms long epoch for each of these events. This consisted of the original EEG signal between -500 to -10ms with respect to the flash or target, and a copy of this epoch then flipped along the time axes. Real and mirror epochs were then concatenated so that any post-event/stimulus-evoked activity was removed from the data. Note that by analysing both the pre-flash and pre-target periods, we aimed to ensure that the resetting event functioned as a salient stimulus and that participants were following instructions.

A spectral estimation of the data was then computed for a range of frequencies, the choice of which was dependent on each analysis (see each section below). This was achieved by first bandpass filtering the raw EEG signals (two-pass reverse) between a range of [*fc – hw, fc + hw*], where *fc* is the centre frequency and *hw* is frequency width, which determined the spectral smoothing. We set *hw* to be 0.3 times the centre frequency.

Data was then passed through a Hilbert Transform to obtain the analytic signal, from which amplitude (1) and/or phase angle (2) were extracted for each frequency and time point according to the following formulas:

$$(1)\ pow(n,f,t) = \left|\left(\frac{\mathrm{Im}(n,f,t)}{\mathrm{Re}(n,f,t)}\right)\right|^2$$

$$(2)\ \theta(n,f,t) = tan^{-1}\left(\frac{\mathrm{Im}(n,f,t)}{\mathrm{Re}(n,f,t)}\right)$$

where *n* is the trial number, *f* is the centre frequency and *t* is the time point. *Im* is then the imaginary part of the complex value from Hilbert transformation, whilst *Re* is the real value. Remaining flipped data was then discarded from further analysis.

Depending on the analysis being conducted, either the calculated phase or power signals were taken forward to investigate each oscillatory feature in detail. The specifics of these are reported in detail below.

Sanity Checks

Following the outlined preparatory steps, analysis started by calculating time-frequency representations (TFR) of power for both pre-flash and pre-target time points. This first analysis was conducted to ensure that individuals were shifting their attention in line with the given cues. Whilst behavioural measures are considered to be a good indication of this, we wanted to ensure that this was further confirmed by the well-known alpha power lateralisation effect presented extensively in previous literature (Peylo et al., 2021).

When implementing the Hilbert Transform for this analysis, we chose a wide range of frequencies from 5-25 Hz to prevent the exclusion of any important findings within the current study, stopping at 25 Hz as we were predominately interested in the alpha range. The impact of shifting attention on oscillatory power was then assessed by comparing the two conditions (leftward versus rightward covert attention) and testing for the presence of significance differences with a *t*-test analysis, correcting for multiple comparisons with Bonferroni correction (2500 permutations). As we were interested in the classic alpha-signature of attentional orienting at the occipital cortex, whilst power measures were calculated for each channel separately, the comparison analysis focused on just occipital channels (O1, O2, PO3, PO4, PO7 and PO8). To note, central electrodes were removed from this step as we were only interested in determining alpha lateralisation behaviours.

Event Related Potentials

Before moving to the main analysis, event related potentials (ERPs) elicited by the flash and by the target were examined at both the individual and group level. Besides offering a useful visualisation of how the two cued signals behaved, we deemed it necessary to assess whether the results from the upcoming phase analyses were truly testing the effects of phase and not resulting from stimulus-evoked activity (Brüers & VanRullen, 2017). By accounting for this, we can make assured interpretations of our data, assessing how shifts of visuospatial attention may be able to modulate neural oscillations via phasic mechanisms (Vinao-Carl et al., 2024). For this control analysis, artifact-free epochs were used to assess any difference in the pre-flash or pre-target windows of ERPs between leftward and rightward attentional shift conditions. We reasoned that if any phase differences between attentional shifts were observed in upcoming analyses (POS and MVPA, see below), we needed to rule out the possibility that they were driven by stimulus onsets rather than true phase effects. Therefore, it was essential to confirm that no significant ERP differences existed between signals following leftward versus rightward attentional shifts. To this aim, EEG data for each participant was used to compute the

time-locked average ERP for each window (pre-flash and pre-target). In both cases, we used a baseline correction of -500 to 0ms and ERPs for the two cueing conditions were averaged across trials for each participant individually and then as a group (grand average). The impact of shifting attention on resulting ERPs was then assessed via a cluster analysis with 2500 permutations and a *maxsum* cluster statistic, where we specifically examined intervals of 0 to 400ms post-flash and target.

Phase Opposition Sum

To investigate whether the direction of the attentional orienting was accompanied by a phase difference, we used the Phase Opposition Sum (POS) calculation to achieve this aim (VanRullen, 2016). This is a non-parametric method to assess phase differences between two conditions, i.e., shift left versus right. We assumed that if participants were sampling between the visual hemifields, then at any given point the attentional signals relating to shift left and right should be in phase opposition. Thus, we calculated POS for both pre-flash and pre-target epochs, following the preparatory steps outlined above. It was determined that this analysis would be desirable over alternative phasic measures of Phase Opposition Product (POP) or Phase Bifurcation Index (PBI), as sum is considered a more stable analytical technique (VanRullen, 2016a). To achieve this, phase angles were calculated for both shift conditions following VanRullen's (2016) method of evaluating phase differences with the following equation:

$$POS = ITPC_A + ITPC_B - 2ITPC_{All}$$

Where ITPC is the inter-trial phase coherence of A, 'Shift Right' and B, 'Shift Left', with the two conditions together being represented as All. This analysis therefore involves a comparison of ITPC measured over all trials and separately calculated for each condition. Following traditional calculations, each ITPC is calculated via the following equations:

$$\boldsymbol{ITPC_{All}} = \left| \sum_{[\boldsymbol{i}=\boldsymbol{1}:\boldsymbol{n}]} \boldsymbol{\omega_i}/|\boldsymbol{\omega_i}| \right| / \boldsymbol{n_{All}}$$

$$\boldsymbol{ITPC_A} = \left| \sum_{[\boldsymbol{i} \in \boldsymbol{group_A}]} \boldsymbol{\omega_i}/|\boldsymbol{\omega_i}| \right| / \boldsymbol{n_A}$$

$$\boldsymbol{ITPC_B} = \left| \sum_{[\boldsymbol{i} \in \boldsymbol{group_B}]} \boldsymbol{\omega_i}/|\boldsymbol{\omega_i}| \right| / \boldsymbol{n_B}$$

Here, the use of these assumes that $\boldsymbol{\omega_i}$ is a complex number representing the analytic signal for trial i. Oscillatory amplitude and phase are then represented by $|\boldsymbol{\omega_i}|$ and $\boldsymbol{angle}(\boldsymbol{\omega_i})$, respectively (Lachaux et al., 1999; Tallon-Baudry et al., 1996). As before, A and B subscripts represent the two cueing conditions, with their combination being All. As we were most interested in how phasic behaviours at the occipital region were modulated by attentional shifts, POS analysis was conducted separately for channels O1, Oz, O2, PO3, POz, PO4, PO7 and PO8 only. Resulting POS values will be positive if the ITPC of each condition exceeds the overall ITPC. Statistical significance was then calculated for each participant, channel and frequency of interest following a permutation whereby trial assignment to condition A ('Shift Right) and B ('Shift Left') was randomly shuffled 1000 times (VanRullen, 2016a). For each of these, the final calculated *p*-value was the proportion of permutations that yielded a higher measure than in the original dataset. In the first instance we determined that it was especially important to review POS at the individual participant-level, as it has been well established that there are often neural differences across participants meaning that averaged analyses may mask variation in oscillatory behaviours (Donoghue et al., 2022). To achieve this, for each individual the calculated POS *p*-values were combined across channels, correcting for multiple comparisons by combining dependent *p*-values using a method first outlined by Fisher, (1932). Here, *p*-values were combined in the log domain using the following equation:

$$P_{Combined} = -2 \sum_{n=1}^{N} \log (p_n)$$

where p_n represents the *p*-value of channel n, with the final combination of *p*-values calculated under the null hypothesis and a Chi-squared distribution with $2N$ degrees of freedom. Importantly, POS analysis already corrects for time and frequency multiple comparisons, so this did not need to be considered within our analysis steps.

Following this, POS analysis was extended to gain an overview of averaged phase behaviour across participants (and channels). To do this we took the combined channel *p*-values (see above) and combined them across participants using a method developed by Stouffer et al., (1949) as implemented by VanRullen (2016), taking the inverse normal cumulative distribution function of each individual participants' independent *p*-values and transforming them into equivalent z-scores. These z-scores could then be combined as they are evaluated in standard deviation terms, meaning that individual variability is accounted for. These were then

converted back into probability *p*-values using the normal cumulative function. The following equation details this procedure:

$$P_{Combined} = 1 - \Phi(\frac{\sum_{[i=1:N]}\Phi^{-1}(1-p_i)}{\sqrt{N}})$$

Here, both normal and inverse normal cumulative function are represented by Φ and Φ^{-1}, respectively. N, P and i are then the number of participants, the *p*-value and trial number, correspondingly.

For both the single-participant and group level analyses here, we reasoned that we would not need to consider the impact of lateralisation effects across the two hemispheres, as this analysis only considers the difference between phase angles. However, to further validate this assumption, group-level POS was additionally calculated at the midline (Oz and POz), the right (PO8, PO4 and O2) and left (PO7, PO3 and O1) occipital hemisphere separately.

Multivariate Pattern Analysis

Based on results from POS analysis, modulatory effects of phase were explored further using a multivariate pattern analysis (MVPA). This was first carried out at a single participant level and only during pre-target time points, looking solely at trials where participants responded to the target correctly and thus suggesting that attention was shifted appropriately, regardless of whether this was during a valid or invalid trial. Further, we looked at classifier performance across all EEG channels to gain a holistic understanding of oscillatory behaviour across the scalp. However, this analysis was also replicated with just occipital channels (matching POS analysis), as this was our primary region of interest.

Artifact-free trials were first filtered between 14-30 Hz (beta), chosen based on POS findings. MVPA analysis was then conducted using a time-by-time generalisation procedure which trained and tested a linear discriminant analysis (LDA) classifier on each time point of the calculated phase data. LDA is believed to be the optimal classifier for data that follows a normal distribution, minimising the risk of misclassification for new samples of the same distribution (Blankertz et al., 2011). This created a 2D matrix of classification performance, calculated at each combination of training and test time (Treder, 2020). Implementing this in MATLAB involved using Treder's (2020) MVPA-Light toolbox (available at https://github.com/treder/MVPA-Light.git), with selected cross-validation parameters of 'kfold' type, repeated 15 times with a default number of five folds.

Cross validation is an important step in classification as it ensures that the model is tested on an independent dataset outside of the training sets, preventing overfitting and resulting in a realistic estimate of model performance (Treder, 2020). To outline this process further, drawing on our chosen parameters, we have implemented a model that splits the data into five different sets (folds) and with only one of these folds being used as the test dataset at any one time and the remaining four being reserved for classifier training. This cross-validation check is then repeated 15 times, with a new test fold at each reiteration. Finally, a performance output metric of area under the curve (AUC) was selected over accuracy, as AUC is considered to be more robust against class imbalances (i.e., Right vs. Left cueing trials).

Upon successful completion of this MVPA process, significance of classifier performance was then tested using a threshold-free cluster enhancement (TFCE) method, avoiding the risk of choosing a cluster threshold that impacts the sensitivity of the statistics (Smith & Nichols, 2009) whilst still accounting for multiple comparison corrections. This was repeated for 1000 permutations using the collapsed data across all participants. Ultimately, this assessed whether there was a significant difference between 'real' AUC measures calculated from the previous MVPA and permuted values of this metric. If our observed phase opposition in the beta frequency held true and the two cueing conditions could be predicted by different phases at any one time, we expect that resulting performance of the classifier will appear as a 2D matrix that takes on the appearance of a checkerboard pattern (King & Dehaene, 2014; see Figure 4.4, below). In other words, if there is a phase opposition in beta, the classification performance at a given training time will be above chance when the two conditions are at their maximal phase distance, moving to below chance when the phase difference approaches zero (crossing points).

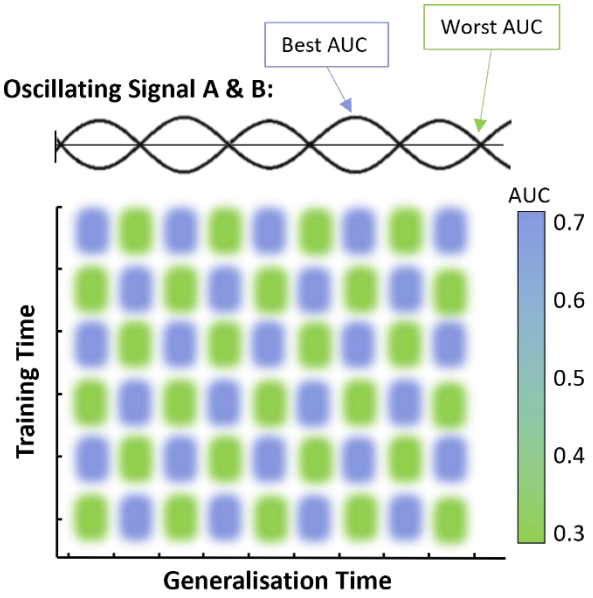


***Figure* 4.4**: Example of our predicted temporal generalisation matrix following MVPA analysis of an oscillating signal (pictured at the top). Here, we expect classifier performance (AUC) to fluctuate rhythmically along the phase of the oscillation to form a checkerboard pattern. Specifically, when the phase of two signals are maximally opposite, we expect the classifier to exhibit improved performance (increased AUC) than compared to when phases are similar (decreased AUC).

4.3.2 Behavioural Data Analysis

Behavioural data obtained from both sessions were combined and analysed together. First, the eye-tracking data was reviewed and trials where saccades or blinks occurred anywhere between 100ms pre- to 60ms post-target onset, were removed from the final dataset. This ensured that the participant did not miss the target due to blinks or gain an advantage by making a saccade toward its location. Following these exclusions, an average of 1505 behavioural trials remained for each participant.

Sanity checks: Behavioural

An overview of task performance (accuracy) was then calculated for both valid and invalid task conditions across session one and two, individually and in combination. Accuracy data was then input into a two-way ANOVA to determine whether there was a significant effect of cue reliability (valid vs. invalid cues) and cue direction ('Shift Right' vs. 'Left') on performance accuracy.

Signal Detection Theory

Signal detection theory methods were then used to calculate perceptual sensitivity (*d'*) and decision criterion (*c*) at each of the flash-to-target intervals (time between flash to dot onset), temporally reconstructing the data. This was conducted just for valid trials, using the following equations:

$$d' = z(HR) - z(FA)$$

$$c = -\frac{1}{2}\big(z(HR) + z(FA)\big)$$

Where HR and FA are the hit rate and false alarm rate, respectively, and $z(x)$ is the inverse of the normal cumulative function evaluated at x (Macmillian & Creelman, 1991; Macmillan, 2002; Zhou et al., 2021). For this study, dots moving to the right were defined as signal, whereas dots moving to the left were considered noise. Therefore, if participants correctly identified that the dots were moving to the right and pressed the 'm' key in response, the trial was recorded as a Hit. In turn, FA was reported when participants incorrectly indicated that the dots were moving right. This choice was arbitrary and could feasibly be the reverse.

The *d'* and *c* were calculated for each participant and interval, using data from session one and two, but only looking at behavioural trials where the target was presented <1000ms after the phase-resetting event (flash). This yielded a time course of visual performance (*d'* and *c*) covering a flash-to-target interval from 600 to 920ms (steps of 20ms) post flash, which was then subsequently analysed for the presence of cyclic patterns.

Additionally, whilst we only looked at trials where the flash-to-target interval was <1000ms, to ensure that there were no differences between the two flash-to-target interval windows (<1000ms and 1000 to 1160ms), *d'* and *c* measures were calculated for these collapsed time bins and a paired samples *t*-test was used to statistically verify the assumption that behaviour did not differ across windows.

Irregular Resampling Auto-spectral Analysis

Resulting *d'* and *c* temporal data was linearly detrended to remove the linear effects across inter-stimulus intervals and retain any cyclic patterns around the mean. This behavioural data was then upsampled to 100 Hz for further analysis, facilitating a comparison with EEG signals and enabling a better estimation of effects at higher frequencies (note the original sampling frequency was 50 Hz, thus allowing us to investigate up to 25 Hz at its Nyquist frequency). To ensure that our subsequent analyses only looked at oscillatory activity, irregular resampling auto-spectral analysis (IRASA; Wen & Liu, 2016) was applied to *d'* and *c* time-courses. This enabled us to distinguish rhythmic activity from concurrent power-spectral 1/*f* modulations. Only frequencies

where the oscillatory signals were evidenced as a higher power than aperiodic (1/*f*) fractal signals were then kept for further interpretations (as in Helfrich et al, 2018).

Curve Fitting Procedure

To test whether *d'* and *c* measures showed significant fluctuations over time, a curve-fitting procedure was applied to each participants' data separately, employing robust nonlinear least-squares fitting procedures. For each measure and participant, cosine models $C(t)$ between 15 and 40 Hz (steps of 1 Hz) were fit to the data according to the following formula:

$$C(t) = A\cos(2\pi f t + \theta)$$

Where A, f and θ are the amplitude, frequency, and phase of the cosine, respectively. To note, the lower limit of the frequency range chosen here was motivated by prior IRASA results indicating only oscillatory activity within the beta frequency band. Resulting R-squared values for each frequency model were then extracted and tested for significance using a bootstrap procedure. Here, R-squared is a measure of how well the model fits the data, with higher values reflecting a better fit. As our null hypothesis was the absence of a temporal structure in *d'* and *c* time courses, interval labels were randomly permuted over 500 iterations, with cosine models fitted to the resulting behavioural pattern of each participant, generating a null distribution of 500 R-squared values. R-squared values for the real and null distribution were then averaged across participants. The R-squared values obtained from the actual data were compared to the null distribution and considered to be significant if they fell in the top 97.5th percentile.

4.3.3 Main Analysis: Regression

For our main and concluding analysis, we aimed to bring together our behavioural and EEG findings, applying a regression model to the data to determine whether oscillatory phase in the pre-target window can reliably predict *d'* and/or *c* at the single-trial level. Due to the time-consuming nature of this analysis, we selected 54 channels and pre-target timepoints between -250 to -10ms, only looking at alpha and beta frequencies between 7 and 35 Hz, as these were of most interest following the results from our prior analyses and research cited within the introduction. This resulted in 1 hour computation time per channel, justifying why we removed channels that are known to contribute noise to the analysis and were also not considered to be essential to our investigations (i.e., Fp1, Fp2, AF8, Fpz, FT8, AF7, AF3, AF4, T7 and T8). When conducting this

analysis, signals from the two cueing conditions were looked at separately to prevent the potential opposite phase measures from cancelling each other out. We then only selected valid trials to ensure that we were accurately examining the impact of attentional shifts without confounding effects of reorienting behaviours, including trials that resulted in both correct and incorrect responses, as these were needed for the calculation of *d'* and *c* measures. As with the previous analyses, preparatory data steps were taken at the start, with phase angle calculations taken forward.

Following this, regression models were applied to each participants' data individually, designed as a modified version of a procedure outlined by Zoefel et al., (2019), implemented here to examine whether oscillatory phase can predict *d'* and *c* measures during the conducted visuospatial attention task. It was determined that the optimal method for achieving this would be by conducting an ordinal, probit link regression with circular predictors (sine and cosine). These circular predictors were included in our model alongside the predictors of target movement direction and their combined predictive value (phase angle*movement). For each participant, we modelled the response (target presence/absence) at each trial as the results of these factors according to the following formula:

$$p(Y = 1) = \beta_0 + \beta_1 M + \beta_2 \theta + \beta_3 \theta * M$$

For this, $p(Y = 1)$ is the probability of answering 'dots are moving right' (our signal), M is the direction the target movement during each trial and θ is the phase angle. Within this, $\beta_2\theta$ and $\beta_3\theta * M$ are the root-mean squares of the two regression coefficients, scripted as $\sqrt{(\beta_{2.1} cos\theta)^2 + (\beta_{2.2} sin\theta)^2}$ and $\sqrt{(\beta_{3.1} cos\theta * M)^2 + (\beta_{3.2} sin\theta * M)^2}$, respectively. To note, the choice of our probabilities focusing only on when participants answer that dots are moving right, is arbitrary and could feasible be the opposite. This choice does however follow our behavioural calculations of *d'* and *c*, and so we have opted to remain consistent in our signal versus noise approach. The output of this model provided beta coefficient values for each of our predictors and their interactions. In analogy to a model used by Zhou et al., (2021) to investigate the effect of alpha we then utilised the coefficient outputs from the regression analysis to calculate corresponding beta values for *d'* as follows:

$$d' = \beta_1 + \beta_3 M,$$

$$\beta_{d'} = \beta_3.$$

Alongside a similar procedure for *c* values, as follows:

$$c = -\beta_0 - \frac{1}{2}\beta_1 + \left(-\beta_2 - \frac{1}{2}\beta_3\right)M,$$

$$\beta_c = \left(-\beta_2 - \frac{1}{2}\beta_3\right).$$

These equations mirror traditional calculations of behavioural *d'* and *c*. Besides repeating this analysis for each participant, the regression was also repeated 100 times for each channel, frequency and timepoint, where each of these iterations differed by utilising randomly shuffled participant response data, across trials (permutation number reduced due to this being a resource and time intensive analysis). Both real and permuted distribution of $\beta_{d'}$ and β_c were hence obtained for each participant. Group level significance was then assessed via a cluster analysis, correcting for multiple comparisons. This was used to determine whether there was a significant difference between the real and permuted distribution of beta values, both generated from the previous regression step. For this, a dependent samples *t*-test was conducted, which generated random samples of both datasets 2500 times and compared them to calculate a test statistic for each permutation (cluster statistic = *maxsum*). A final *p*-value was subsequently calculated as the proportion of these random samples that resulted in larger *t*-statistics than the real distribution. As this was a two-tailed test, the critical alpha-level used for this permutation analysis was $p = .025$.

4.4 Results

4.4.1 EEG Results

Sanity Checks: EEG

First, we wanted to verify that the performance in the behavioural (latency: 600 – 920ms from flash) and EEG window (latency: 1000 – 1160ms from the flash) was comparable. On average, performance was near identical for both *d'* (behavioural window 1: $M = 1.37$, $SD = .40$, window 2: $M = 1.35$, $SD = .38$) and *c* (EEG window 1: $M = -.075$, $SD = .21$, window 2: $M = -.08$, $SD = .24$), with a *t*-test confirming that there was no statistically significant difference across the two time windows for *d'* ($t(25) = .38$, $p = .71$, $d = .074$) and *c* ($t(25) = .21$, $p = .84$, $d = .04$) measures. This therefore suggested that the two windows contained the same signals and so we can extrapolate findings from one window into the other.

To confirm that the behavioural manipulation then caused our participants to orient their attention according to the block instruction, we compared the two conditions (leftward versus rightward attentional shifts) to verify the presence of the known alpha-signature of attentional orienting. To this aim, time-frequency representations (TFRs) of power over occipital electrodes were calculated for both pre-flash and pre-target timepoints, during both cueing conditions separately, and compared. When first examining time points around the flash (time zero = flash onset; Figure 4.5A, below), there appeared to a bilateral decrease of alpha power across the occipital cortex (channels PO7, PO3 and O1). When matching this with the evidence from our cluster analysis, there was no significant difference in power measures between left versus right shifts of attention (1 negative cluster, t = -4.21, p = .22). Our results also suggested that participants validly used the cue to shift their attention for upcoming target onset, but only after the onset of the flash. This is seen when looking towards the latter epoch of pre-target times (time zero = target onset; see Figure 4.5B, below). When comparing the signal from both shift conditions, there is a clear lateralisation of alpha-band activity, demonstrated by a significant decrease of alpha power in the left occipital cortex (1 negative cluster, t = -58.14, p = .018) and an increase in the right (1 positive cluster, t = 35.59, p = .036). When drawing on previous literature, this matches what we already know about alpha power behaviours during shifts of attention, where decreases and increases of alpha are thought to facilitate and inhibit visual processing in their contralateral hemifields, respectively (Thut et al., 2006).

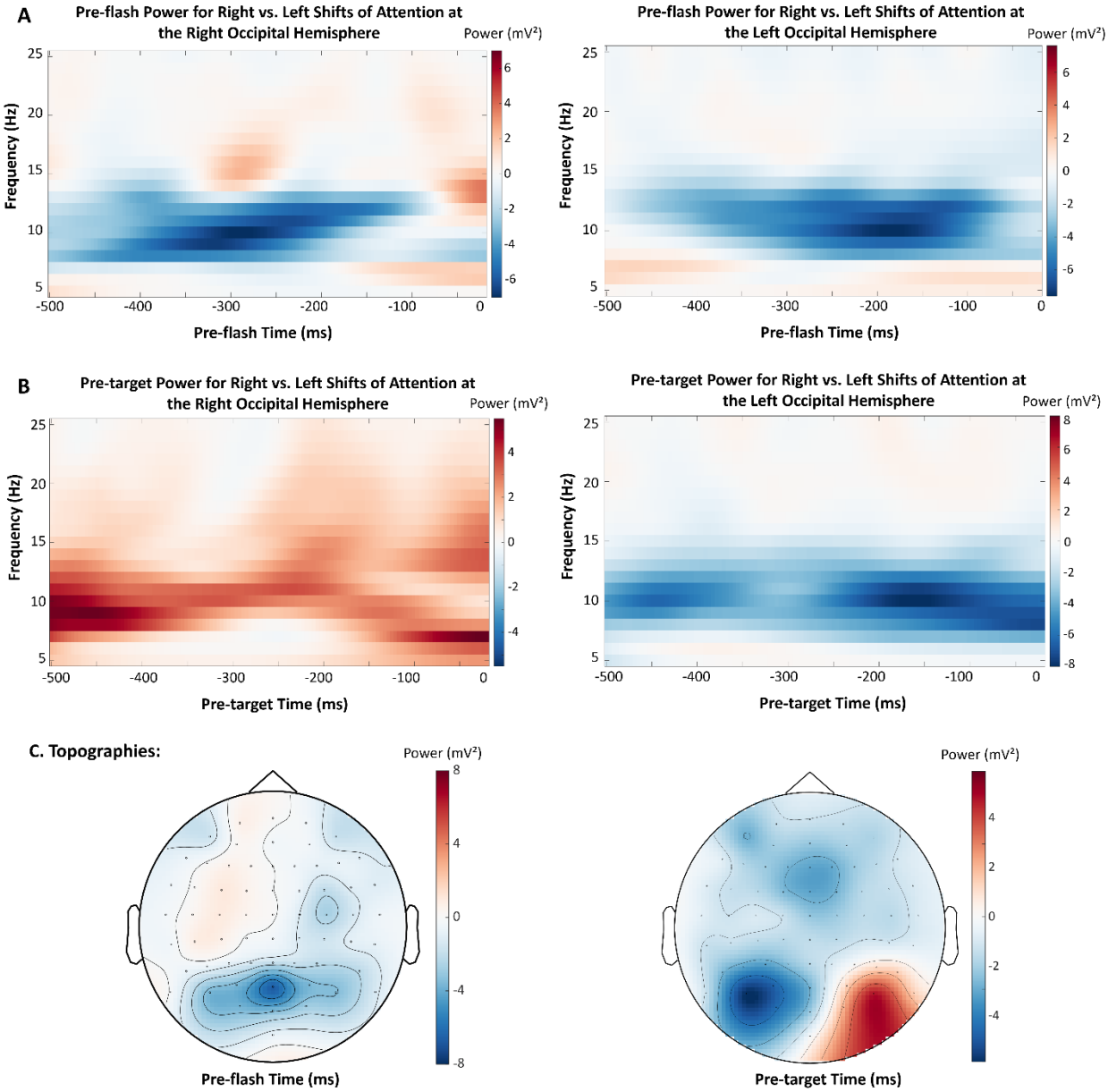


***Figure* 4.5**: Observed EEG power when the neural signal is time locked to the onset of the flash (A) and the target (B). All figures here represent the calculated power difference between shift right vs. left attentional signals, when averaged across participants and trials. The two right TFRs depict power differences observed in the left occipital cortex (PO3, PO1 and PO7), whilst the left two show differences in the right (PO4, PO2 and PO8). The topographies plotted here (C) also illustrate corresponding alpha power behaviours between the frequencies of 8-12 Hz and across all occipital channels (POz, Oz, PO8, PO7, PO4, PO3, O1 and O2). Again, this is presented for both pre-flash (left) and pre-target (right) time points. Blue colours on all figures are indicative of decreases in power measures, whereas red represents increases.

Event Related Potentials

Next, we wanted to test whether leftward and rightward attentional shifts evoked ERPs of different amplitudes following both the flash (see Figure 4.6, below) and target (see Figure 4.7, below). Both windows were split by cueing conditions and assessed alongside one another at individual channels separately. When looking at individual averages, we noticed that the averaged signals of the two cueing conditions were seemingly in phase opposition. This was specifically noticeable during the pre-target window between -600ms and up to -50ms, as well as somewhat post-stimulus. In fact, it is perhaps more precise to state that these opposition behaviours were only absent at times surrounding the stimulus onset (i.e., time 0 – 300ms). This procedure was conducted at both the single participant level and also averaged across the group, but focus should be centred at the single level due to phase angles likely being inconsistent across participants and thus cancelling each other out during averaging (see Figure 4.6 & 4.7A, below for a single participant example; see Figure 4.6 & 4.7B, below for the group average).

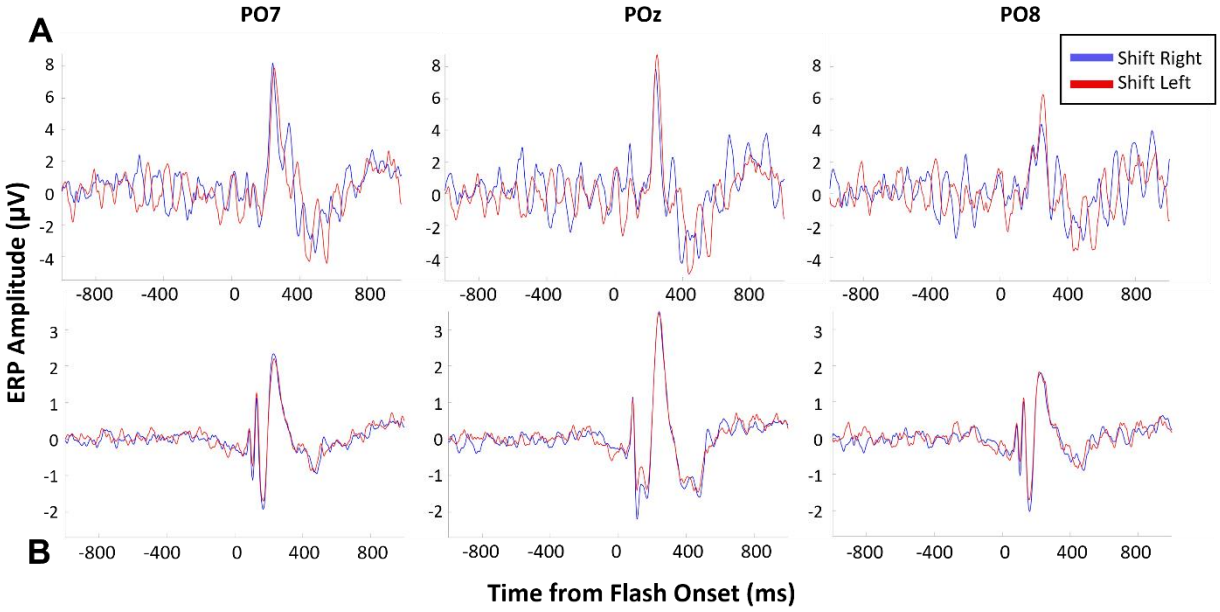


***Figure* 4.6**: ERPs for shift right (blue trace) and shift left (red trace) conditions, where time zero is the onset of the flash. This is plotted for three occipital channels (left: PO7, middle: POz, right: PO8) to provide an overview of activity across the visual cortex, as we expect that behaviour may differ based on lateralisation effects. The top row depicts a representative participant (A), whereas the bottom shows the group average (B).

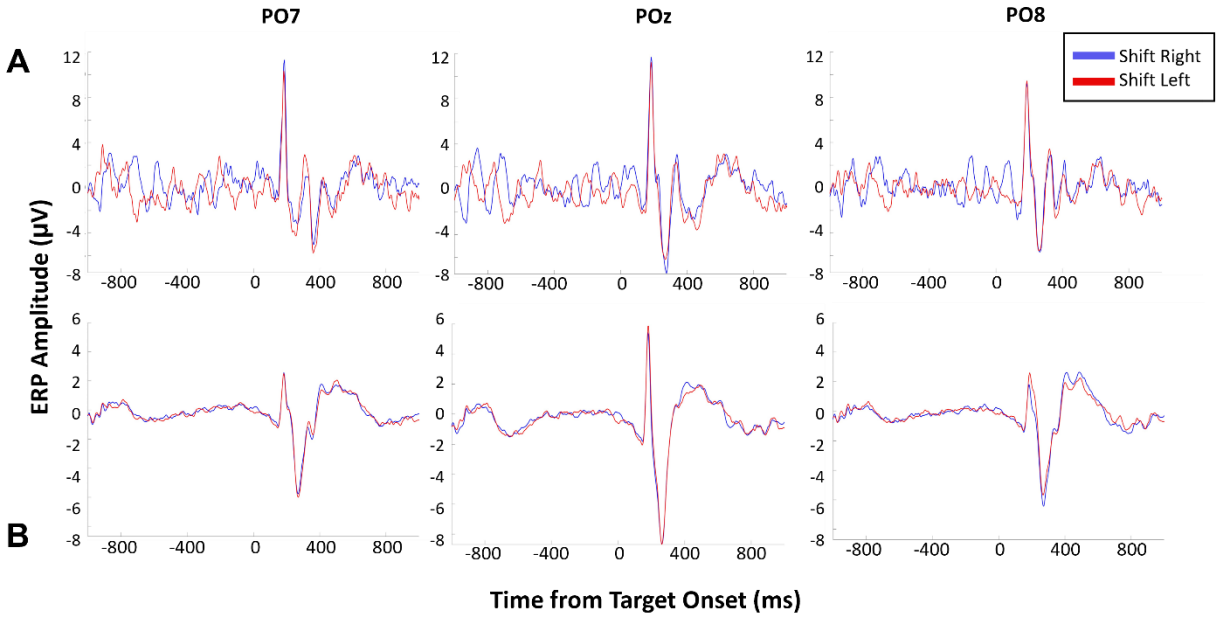


***Figure* 4.7**: ERPs for both shift right (blue trace) and shift left (red trace) conditions, where time zero is the onset of the target. This is plotted for three occipital channels (left: PO7, middle: POz, right: PO8) to provide an overview of activity across the visual cortex, as we expect that behaviour may differ based on lateralisation effects. The top row depicts a representative participant (A), whereas the bottom shows the group average (B).

Cluster analysis revealed that there was no significant difference between ERPs recorded during right versus left shifts of attention, for both post-flash (14 positive clusters, lowest p = .24; 9 negative clusters, lowest p = .09) and post-target windows (14 positive clusters, lowest p = .88; 10 negative clusters, lowest p = .9). This suggests that we can rule out the risk of any phase effects observed in the upcoming analyses (POS and MVPA) being driven by stimulus onset rather than representing true phase effects.

Phase Opposition Sum

Following the incidental finding that the pre-flash and pre-target activity seemed to be in phase opposition, we formally assessed these differences using the POS calculation (VanRullen, 2016a). This was conducted for both pre-flash and pre-target time windows, at the single participant (see Figure 4.8 and 4.9, below) and group-level (see Figure 4.10, below). When first looking at the single participant data, the plotted pre-flash results reveal that there were a number of significant phase opposition points, varying in time and frequency, but importantly exhibiting huge variation across participants. From examining the visualisations, it is difficult to decipher any prominent patterns across participants, with some exhibiting temporally sustained alpha phase oppositions, and others exhibiting temporally intermittent phase oppositions in the beta-band.

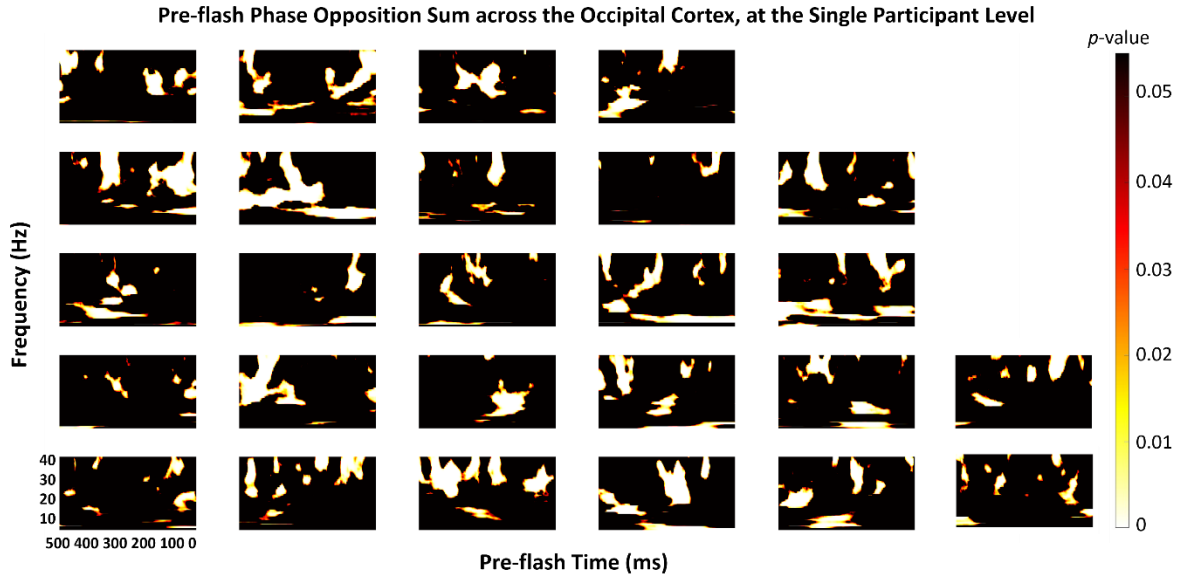


***Figure* 4.8**: Phase opposition sum between leftward and rightward attentional shift conditions at pre-flash time windows. This is calculated at the single-participant level, where each panel represents an individual participant. All significant *p*-values are highlighted in non-black colours ($p < .001$ = white). *P*-values are plotted as an average of across the occipital cortex (POz, Oz, PO8, PO7, PO4, PO3, O2, O1).

Similarly, when examining pre-target signals (see Figure 4.9, below), there was again notable variety in POS across participants, making it difficult to uncover patterns of significance. Arguably, it could be suggested that during this time there was a shift in significant POS findings moving closer to the onset of the target, as well as more activity within the higher ranges of beta-band activity. It should be stressed though, without considering group averages it is difficult to extrapolate descriptions of these results.

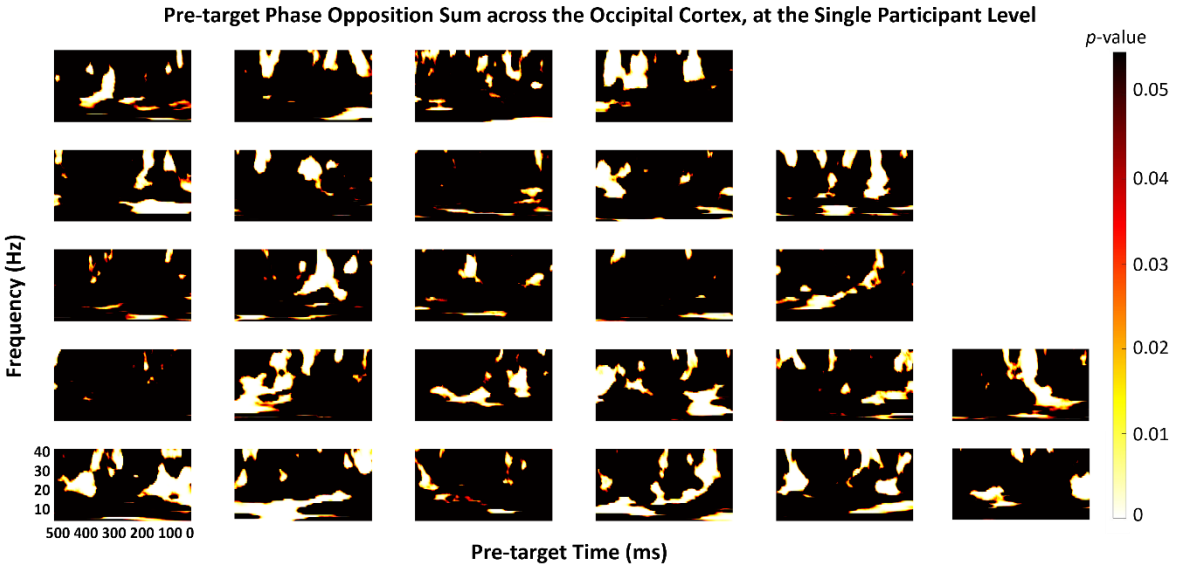


***Figure* 4.9**: Phase opposition sum between leftward and rightward attentional shift conditions at pre-target time windows. This is calculated at the single-participant level, where each panel represents an individual participant. All significant *p*-values are highlighted in non-black colours ($p < .001$ = white). *P*-values are plotted as an average of across the occipital cortex (POz, Oz, PO8, PO7, PO4, PO3, O2, O1).

When looking at the group-level data to provide an overview of phasic behaviours, the averaged figure (4.10, below) depicts how there was a broad range of frequencies exhibiting opposition behaviours across both pre-flash and pre-target time points. The pre-flash calculations illustrate phase opposition behaviours that suggest participants were utilising the information of the cue prior to the trial even commencing (represented by flash onset). Such behaviours are mainly localised in beta-band frequencies, which is a pattern that carries across to pre-target time points also. With this latter stage, phase opposition behaviours are more constrained towards a time closer to the onset of the target (~ -100 to 0ms). Interestingly also, phase opposition appears in the alpha-band frequencies too, but this is predominately seen immediately before the cue.

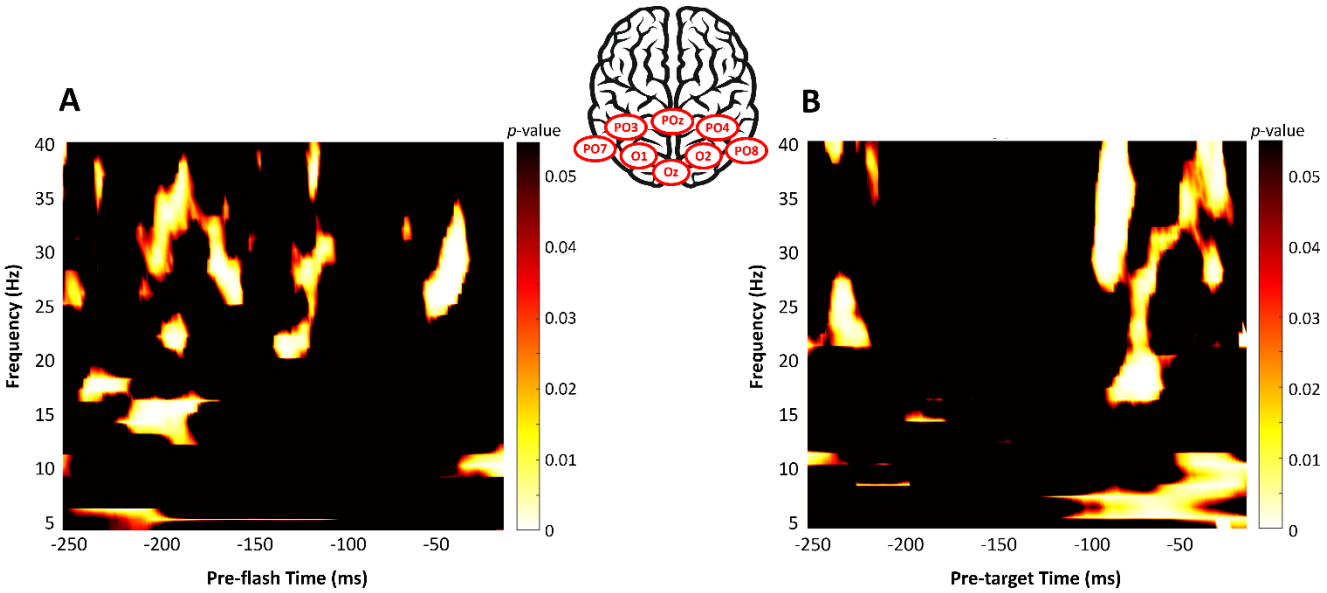


***Figure* 4.10**: Significant phase opposition effects observed when comparing the two attentional signals, shift right versus left. Plotted here are heat maps of *p*-values, for pre-flash (A) and pre-target (B) signals, where significant *p*-values are shown in non-black colours ($p < .001$ = white). This is calculated at the group-level, averaging across both participants and occipital channels highlighted in the middle figure (POz, Oz, PO8, PO7, PO4, PO3, O2, O1).

To ensure that we were not mistakenly removing any lateralised effects by averaging over the occipital cortex, POS was additionally calculated for neural signals over the left, right and central occipital channels separately (see Figure 4.11, below). From this we can see that patterns of POS did not differ considerably between the three locations, especially in the beta-band, meaning that interpretations surrounding attentional phase differences can validly be drawn from whole occipital averages (see above).

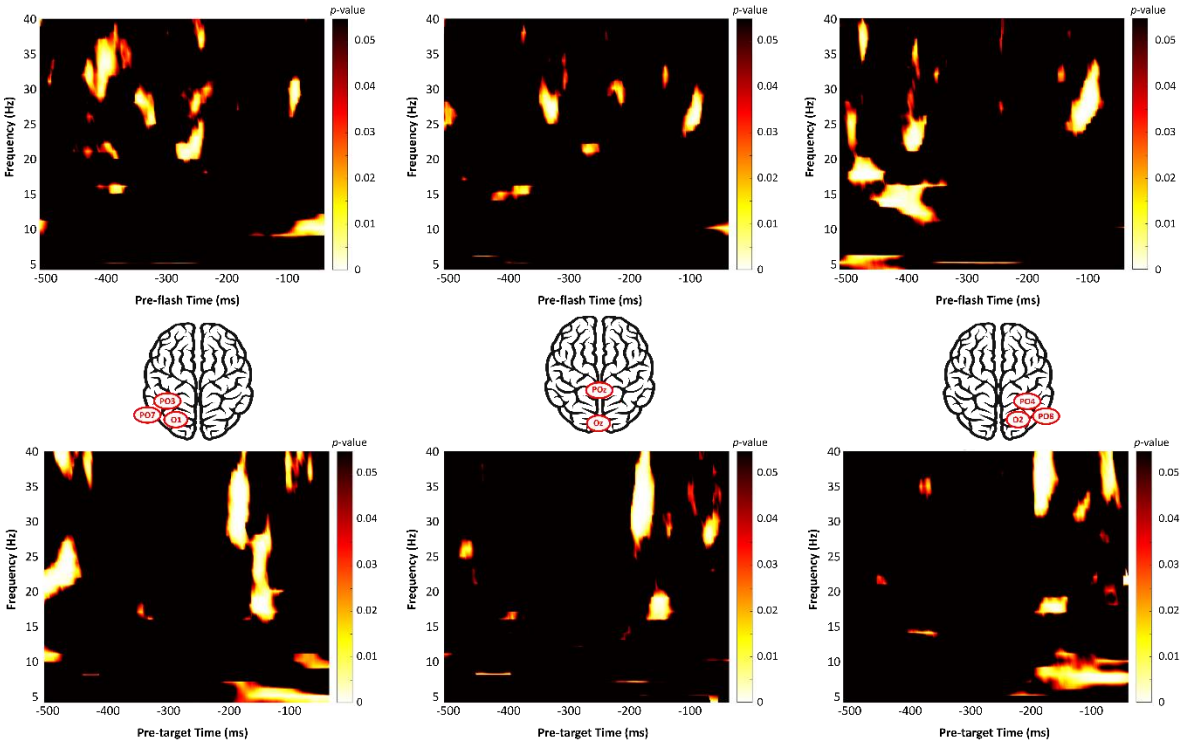


***Figure* 4.11**: POS effects observed when comparing the two attentional conditions, shift right versus left. Here, we calculated these at the left (O1, PO3 & PO7; left column), central (Oz & POz; middle column) and right occipital hemisphere (O2, PO4 & PO8; right column). Plotted are heat maps of *p*-values, for pre-flash (top row) and pre-target signals (bottom row), where significant *p*-values are shown in non-black colours ($p < .001$ = white). This is calculated at the group-level, averaging across participants.

Multivariate Pattern Analysis

From our previous POS results, we determined that there were some similarities across participants, but we also acknowledge that there was a lot of variation too. Thus, we resolved that to potentially capture more subtle changes in phase behaviours, a MVPA should additionally be conducted.

Thus, MVPA analysis was first conducted across all available channels of the cortex after filtering the signal in the beta frequency. As hypothesised, the LDA classifier exhibited fluctuating performance accuracy (indexed by area under the curve measures) in its ability to predict cue instructions (i.e., Shift Right) based on neural phase during pre-target time windows. Following a TFCE cluster analysis, this was found to be significant during select times of the matrix ($p < .001$; see Figure 4.12A, below). Specially, there was a clear 'checkboard' pattern visually apparent within the observed matrix, aligning with our initial predictions. When repeating this procedure across occipital channels alone, similar results were observed ($p < .001$; see Figure 4.12B, below).

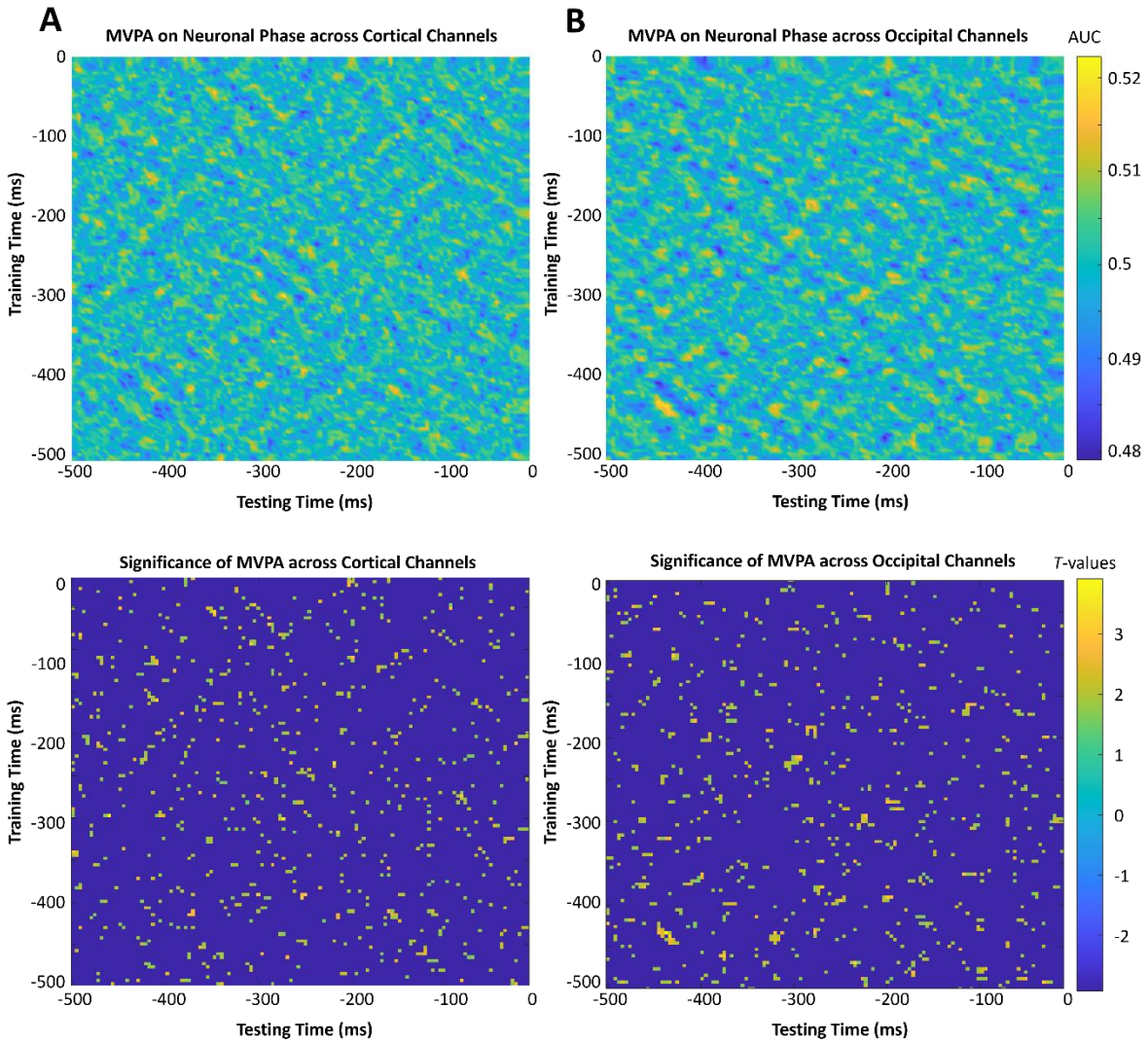


Figure 4.12: MVPA results when calculated across participants at either all channels (A; left column) or just occipital channels (B; right column). Top row figures show classifier performance (AUC) across pre-target epochs. The bottom row of figures presents corresponding *t*-values from a cluster analysis, masking non-significant classifier performance in dark blue. In line with our predicted matrix, fluctuating AUC performance of the classifier can be seen with the presence of a visually observable checkboard (top row), with statistical masking supporting the significance of this effect (bottom row).

4.4.2 Behavioural Results

Sanity checks: Behavioural

To confirm that our behavioural manipulation was successful, behavioural data across the two sessions, were submitted to a two-way ANOVA. As expected, we found a significant effect of task validity on performance accuracy. Specifically, it was shown that valid trials resulted in a significantly higher accuracy (M = 75%, SD = 1.2%) than compared to invalid trials (M = 61%, SD = 1%), $F(1, 25) = 83.57$, $p < .001$, $\eta_p^2 = .77$. In contrast, the choice of cueing instructions (shift right vs. left) and the interaction between cueing and validity,

had no significant effect on performance accuracy ($F(1, 25) = .005$, $p = .94$ and $F(1, 25) = 3.67$, $p = .067$, respectively).

Signal Detection Theory: Rhythmicity in Behaviour

To assess whether measures of *d'* and/or *c* demonstrated rhythmic behaviours, signal detection theory methods were applied to the valid trials from this dataset, with the original and upsampled data plotted alongside one another for visual inspection (see Figure 4.13A and B, below). From the figures it can be concluded that the pattern of behaviour did not differ when comparing detrended with upsampled data, meaning that we could reliably take forward upsampled data for the following analyses without being concerned about whether it reflects the true signal.

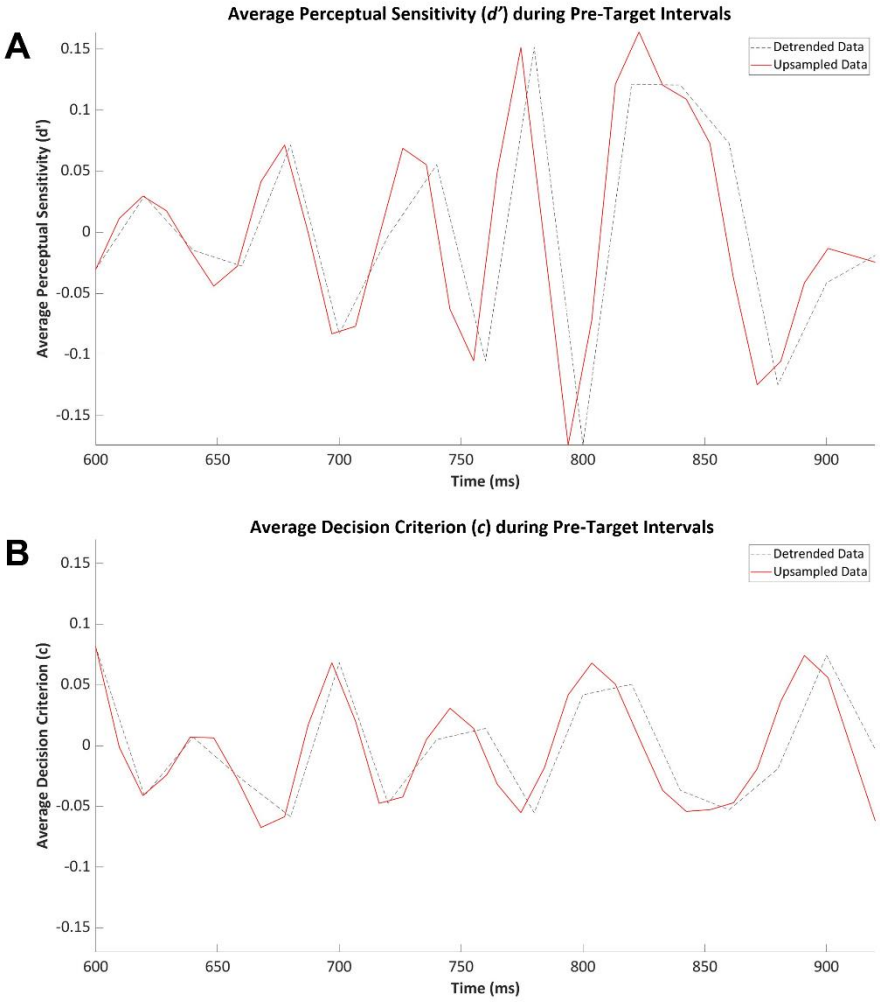


***Figure* 4.13**: Average time course of *d'* (A) and *c* (B). Each panel shows the original (black dashed line) and upsampled (red line) detrended data, calculated as an average across participants. The x-axis represents the time of target presentation from the flash (behavioural trials: 600 – 920ms from flash).

Using this data, Figure 4.14 (below) shows the new interpolated data for both *d'* and *c*, with the addition of measures of variability. Here, time courses were plotted at both the single-participant and group-average level, illustrating the average fluctuation behaviours of these measures but also highlighting the extensive differences that were observed between our participants.

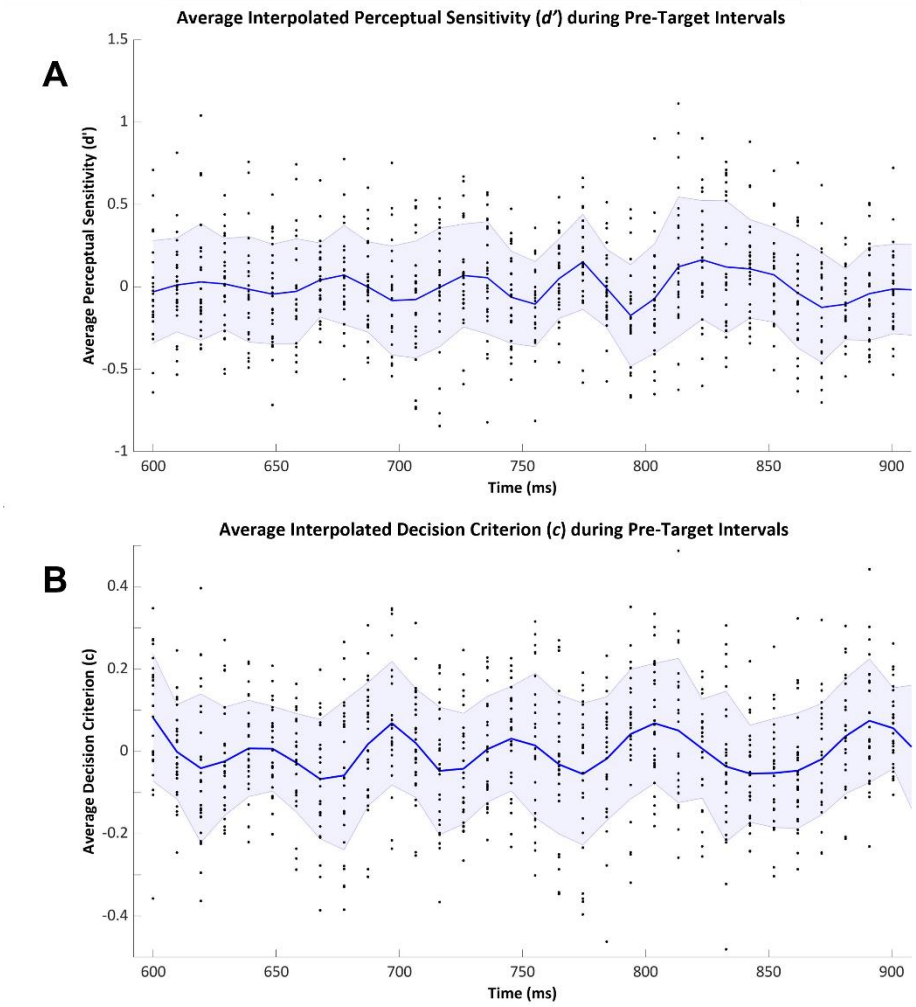


***Figure* 4.14**: Average time course of *d'* (A) and *c* (B) at the single-participant (single dots) and the group-average level (bold blue line). The shaded area represents the standard deviation around the mean. The x-axis denotes the time of target presentation from the flash (behavioural trials: 600 – 920ms from flash).

Irregular Resampling Auto-spectral Analysis

IRASA was then applied to these reconstructed *d'* and *c* measures, separating the oscillatory spectra from aperiodic signals at both the single-participant and group-average level (see Figure 4.15, below). When examining the average, oscillatory peaks exhibiting larger power than fractal components appear to be present solely in the beta-band frequency range for both *d'* and *c* measures. At the individual level, whilst there is some

variability there is nothing to suggest that this finding is being driven by any one or few participants, suggesting that our calculated average is a reliable representation of IRASA results for both *d'* and *c* measures. With this data, all subsequent analyses that investigate beta-band oscillations can thus make valid interpretations surrounding the contribution of this oscillatory component in the top-down control of visuospatial attention, as we now know that this rhythmic activity holds more power than aperiodic components for both *d'* and *c*.

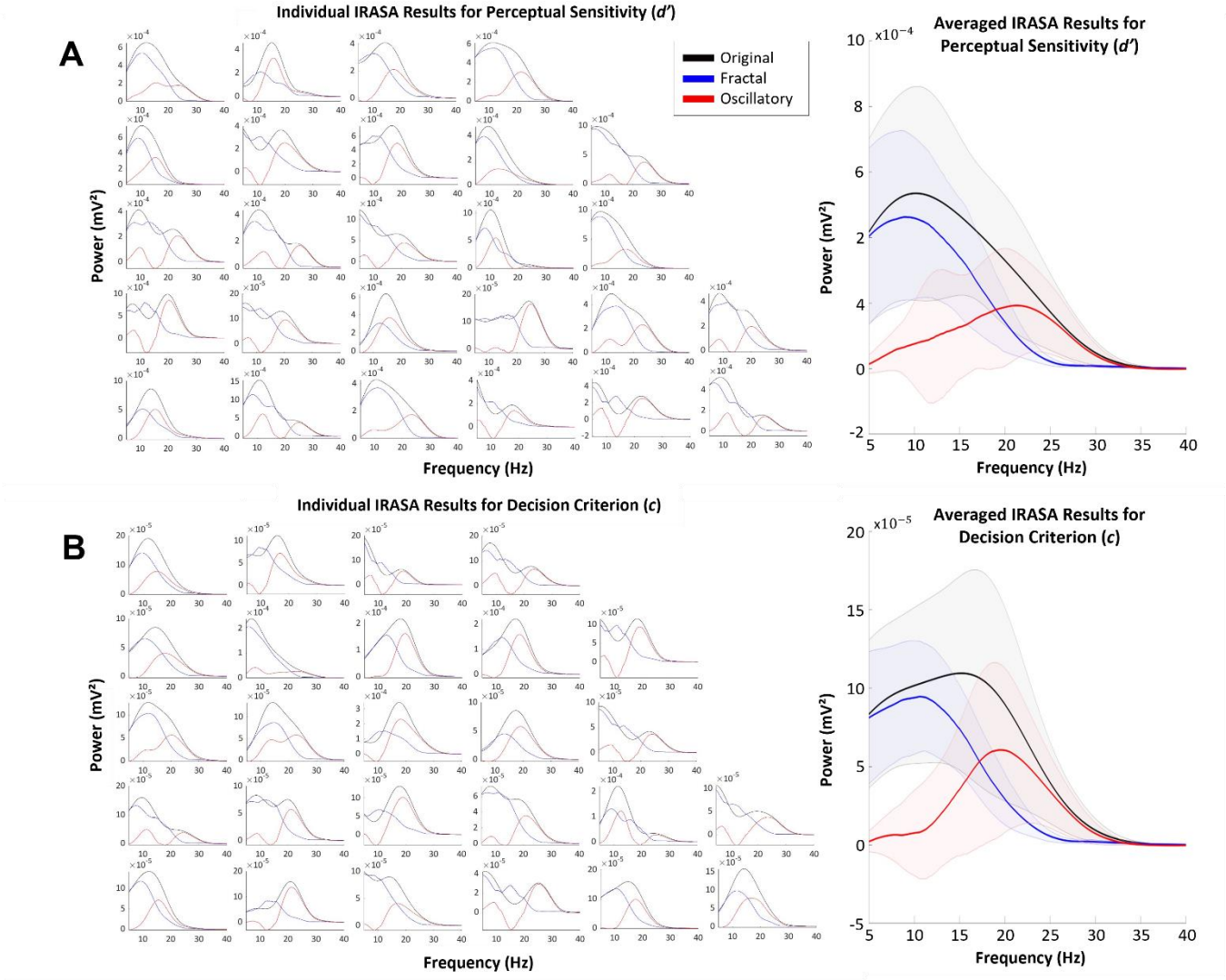


***Figure* 4.15**: IRASA results for *d'* (A) and *c* (B) measures calculated at the single-participant level (left figures) and the group average (right figures). IRASA was conducted to separate oscillatory (red) and fractal signals (blue) from the original (black) EEG signal

Curve Fitting Procedure

Finally, to test statistical significance of the oscillatory frequencies that exhibited a higher power than alternative spectra, we adopted a procedure that compared R-squared values obtained from the actual data with those from a null distribution. Resulting evidence determined that for measures of *d'*, models of between 15 – 25 Hz had a significantly improved fit with the real data that compared to null distributions. This frequency band was marginally reduced for measures of *c*, with significance stretching from 15 to just below 24 Hz (see Figure 4.16, below). Interestingly to note also, when plotting the calculated R-squared values for these measures, there is a reduction of individual variance at higher frequencies. Additionally, when looking at *d'*, measures the highest R-squared value sit at 16 Hz, whilst for *c* it is equal at both 15 and 20 Hz; both exhibiting significant best fitting models within the beta-band.

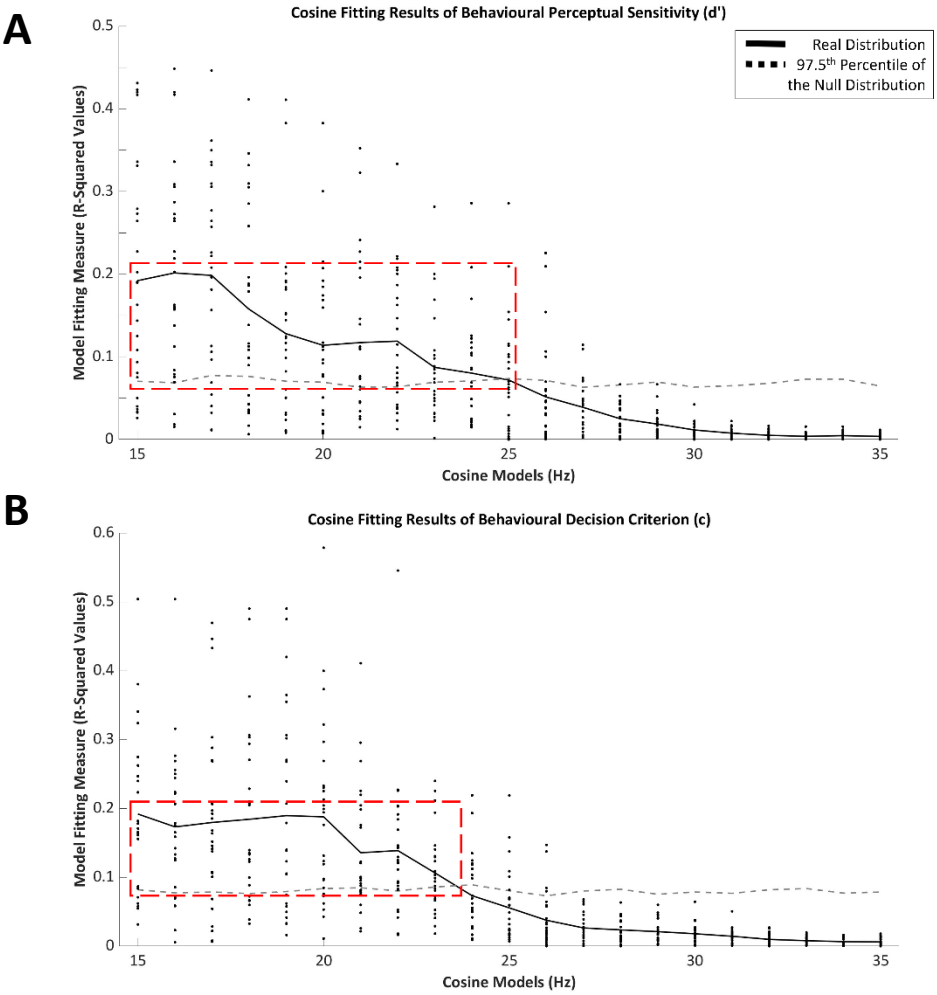


***Figure* 4.16**: R-squared values for the real distribution of oscillatory spectra from *d'* (A) and *c* (B) behavioural measures. The dashed black line is illustrative of the 97.5th percentile of the null distribution. Cosine models are considered to be significant fits of the data when R-squared values for the real distribution are above this 97.5th threshold. For ease for visualisation, significant models have been outlined with a red dashed box.

4.4.3 Bringing all together: Phase effects on behaviour

The main aim of the study was to test whether phase could predict *d'* and *c* measures, at single trial level. To this aim, we tested a model defining *d'* and *c* as a function of pre-target phase and presence of the signal. To establish significance, we ran a cluster-based permutation test comparing real and permuted β_d, and β_c. Our results showed that oscillatory phase significantly predicted both *d'* and *c*, at the occipital channels (see Figure 4.17, below). When looking at perceptual sensitivity first, we found a significant positive cluster (t = $1.09e^6$, p = .002) centred around 25 Hz (22-27 Hz), emerging 150ms before the target appearance and persisting until its onset. This cluster also included a significant alpha effect within the same time window, though over a more limited frequency range. These effects were significant over the occipital channels bilaterally. For the decision criterion, we found a similar pattern, with a significant negative cluster (t = $-1.28e^6$, p = .002) at a matching frequency and centred around 25 Hz, again extending from around 140ms (pre-target) to target onset. Significant effects within the alpha band were also present with this measure, although slightly reduced in frequency width than compared to *d'*.

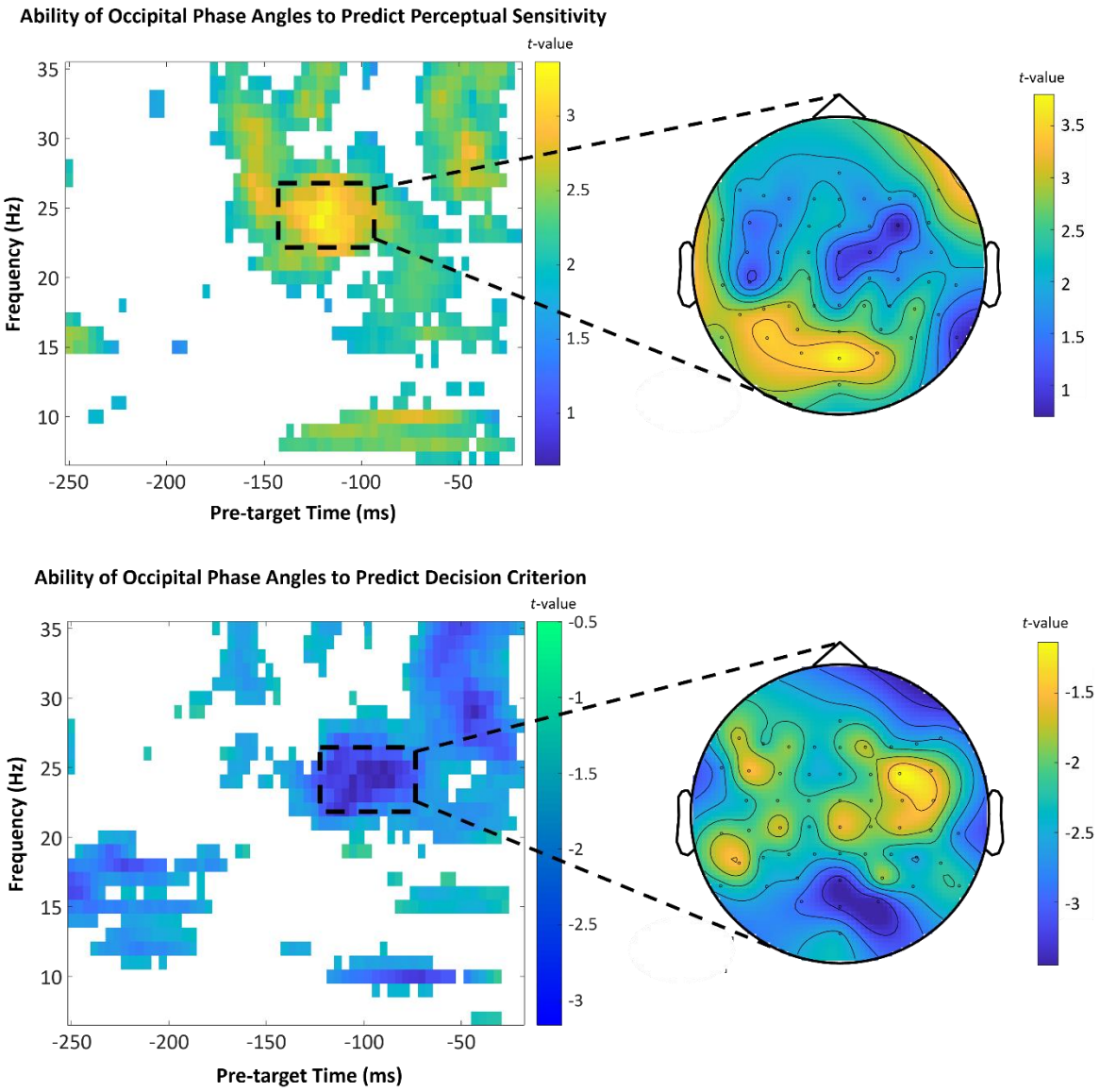


***Figure* 4.17:** Results of the cluster analysis for A) perceptual sensitivity (*d'*) and B) decision criterion (*c*) during pre-target windows. The implemented cluster analysis compares the real and permuted distribution of regression calculated beta values for *d'* and *c*. Plotted here are resulting statistical *t*-values obtained from the cluster, where orange colours in figures A are indicative of large positive t-values, whereas orange in figures B are indicative of large negative *t*-values. All results here are masked by significance, so only significant values are plotted

4.5 Discussion

The main aim of this investigation was to explore how visual attention modulates perception via neural oscillations. To do so, we chose to investigate performance through signal detection theory (SDT) indexes of perceptual sensitivity (*d'*) and decision criterion (*c*), enabling a deeper exploration of how oscillations may uniquely influence our ability to perform a visual detection task that requires shifts of attention.

Importantly, before diving into our results, it is essential to highlight how participants within this study appropriately engaged with the task and shifted their attention based on the provided cues. This can be seen in both EEG and behavioural results, where we have observed a significant alpha-signature of attentional orienting (i.e., alpha power lateralisation), alongside congruent trials resulting in a significantly higher performance accuracy than incongruent trials. Both findings here work together to suggest that participants accurately shifted their attention based on the cue, therefore making this study a valid investigation of visuospatial attention.

Next, we investigated any effects of attentional shift direction on ERPs as a reassurance that any pre-target phase effect was not due to difference in ERP size between the two conditions. To this aim we split data into rightward and leftward shifts of attention and found no significant difference between the two, thus excluding post-stimulus activity changes as a confounding factor in our phase analysis. However, when plotting ERPs at the individual level, we incidentally found that the attentional signals preceding the ERPs were in relative anti-phase with one another. This was true for both pre-flash and pre-target time points, suggesting that there was an effect of the attentional cue even prior to participants being given the signal for the trial commencing (i.e., flash onset). Interestingly also, when looking at individual ERPs, it appears that whilst the phase of the attentional signals align (i.e., no phase opposition) after the onset of the flash and target (time = zero), as time progresses the original antiphase relationship only resumes after the flash and not after the target onset. This is likely indicative of participants no longer sampling either side of visual space during post-target windows, as the relevant visual stimulus had passed and there was no longer a need to do so. Crucially though, these patterns were observed when looking at ERPs at the single-participant level only. When extending our investigation into group-level plots, this resulted in the differences between signals being reduced to such an extent that it became no longer discernible. This is important to acknowledge as it highlights the necessity of considering individual differences when exploring neural data, without doing so there is a risk of noteworthy findings being overlooked through the implementation of averaged analyses.

To reinforce these interpretations and examine whether the direction of attentional orienting is accompanied by a phase difference in oscillatory activity, we utilised POS calculations. Results here found that there were significant phase differences present most notably within the beta-band (~16 - 30 Hz), highlighting phase dependence on which direction participants shifted their attention (right vs. left). It can therefore be

interpreted that the phase of beta oscillations is implicated in attentional sampling behaviours, reinforced by the effect appearing strongest at time points closest to the target onset (pre-target epochs); when we would expect participants to engage endogenous attention the most. When looking only at pre-target epochs, analyses at the occipital cortex show significant phase oppositions predominately between 100 - 10ms pre-target. However, it should also be noted that there is an additional significant phase opposition appearing within the low-alpha/theta band, which appears to be sustained for 100ms approaching the target onset also. These findings could reflect the periodic inhibition of each hemifield sequentially, with both alpha and beta phase working to aid the allocation of resources to one side of visual space at a time. This is a conclusion that previous studies have similarly reached, with findings restricted to frequencies of 4 Hz (Landau & Fries, 2012) and interpreting this as evidence of how attentional sampling behaviours fluctuate at 8 Hz when there is a single location, with this then being divided by the number of additional locations that demand resources (VanRullen et al., 2007). Whilst this is interesting to consider, it does not account for our phase effect findings in the beta band though, despite the fact that this previous study was also an investigation of visuospatial attention.

It becomes important to then consider whether these differences may be a result of task designs variations, where it is possible that our choice of moving stimuli may have biased our results towards beta frequencies. This suggestion is based on presented evidence from a number of studies, suggesting that beta-band frequencies are modulated during visual movement perception tasks (for a review, see Pavlidou et al., 2014); although they note that this is primarily observed within sensorimotor cortices. Further, the use of a block design in this study has likely contributed to a different observation of results, where an attentional cue was only given once at the start of a block, meaning that individuals were tasked with sustaining attention for around five minutes (approximate time to complete a block). The impact of this choice is crucial to consider as beta oscillations have previously been correlated with sustaining attention across a prolonged period of time (Gola et al., 2013; Ko et al., 2017), potentially accounting for why our results may contrast prior knowledge. However, in our view, we argue that whilst both of these design choices may carry some limitations, they have likely contributed to creating a more accurate exploration of visuospatial attention, as sustaining attention and perceiving moving stimuli is a reflection of real-world behaviours and thus offers enhanced external validity.

Additionally, it is important to acknowledge that the phase effects outlined here (and across previous studies) are gained from examining averaged neural phase behaviours, across individuals. Whilst this is an essential part of determining general neural behaviours across a sample, aiding investigational interpretations, it is also important not to overlook individual differences when exploring such features, especially phase (Donoghue et al., 2022). The presence of these differences is abundantly evident within our findings, as it is clear to see that there is a huge variation in phase opposition measures (at both pre-flash and -target time points) when comparing participants. This is not entirely an unexpected finding, as it is well known across the field that individuals have different preferential phases (VanRullen, 2016a; Wolpert & Tallon-Baudry, 2021). Although, despite this acknowledgment, the degree of differences observed within our phase opposition calculations are somewhat larger than expected, with some individuals exhibiting many clusters of significant phase oppositions and others exhibiting none. Similarly, there is a broad range of frequencies that these significant clusters appear at, bringing into question the generalisability of our interpretations. Fortunately, this is not a new discovery within the field of attentional investigations, with a previous study also finding that there is a wide stretching range of individual differences in selective attention and the attentional modulation of neural phase angles that result from this (Laffere et al., 2020), albeit in a study of auditory attention. With this in mind, we stress that the use of POS measures to obtain these results offers a reliable method of accounting for such individual differences. This is important as phase angles can be influenced by a number of aspects, such as differential conduction delays between cortical regions, variations in cortical folding, as well as the orientation of neurons underlying the recording electrode (VanRullen, 2016a). Thus, by looking at the opposition of phases rather that absolute angles, this offers a more optimal approach to assessing such neural features and gaging how they are modulated or their role in modulating.

The role of beta oscillations in shifts of visuospatial attention was further extended through our MVPA classifier results, where we found that beta phase (14-30 Hz) could be used to significantly determine whether a single trial was assigned to the shift right or left cueing condition. Essential to our interpretation of this, classifier performance fluctuated across time, exhibiting a checkboard pattern of performance that has previously been identified as illustrative of an oscillatory component in the classifier input (King & Dehaene, 2014). In other terms, this suggests that whilst there were certain phases that the classifier was repeatedly

able to use to differentiate between the two shifting conditions, there were equally times when this ability was reduced, emphasising the role of attention in modulating the phasic behaviours of beta-band oscillations.

Each of these outlined analyses have explored how visual attention modulates perception most notably via fluctuating beta-band phases. However, we are still yet to explore how these oscillations may uniquely influence SDT measures of *d'* and *c,* where we hypothesized that if oscillatory activity is perceptually relevant, its induced periodicity should also manifest in behaviour. To test this, we sampled *d'* and *c* at various time points across trials (without EEG). We also used IRASA to identify the activity that exhibited higher power compared to 1/*f* components. Specifically, this was the case for frequencies of ~19-25 Hz for *d'* and ~17-23.5 Hz for *c* measures, suggesting that it is at these beta rhythms that the two measures fluctuate. This contrasts the majority of the (limited) literature that is available, as most often there is evidence to support these measures fluctuating at alpha frequencies instead (Benwell et al., 2017; Sherman et al., 2016; Zhang et al., 2019; Zhou et al., 2021); although importantly these are not in studies of attention. Although, with these previous studies and those that generally explore rhythmic signals, results should always be viewed with some caution, as it is often unclear whether they separate oscillatory components from aperiodic/fractal. This oversight may lead to invalid conclusions, as fractal components can introduce peaks in the neural signal which can then be misinterpreted as oscillatory activity (Donoghue et al., 2022). From our searches, there is only one piece of evidence to corroborate our findings surrounding the beta fluctuations of *d'* measures, where Chanes et al., (2013) found that when stimulating the right FEF at 30 Hz, to mimic an attentional orienting behaviour (visuospatial), *d'* also fluctuated at beta frequencies. By comparing this to studies of visual perception, it could be that attention gives rise to beta frequencies that then modulate behavioural measures, causing them to fluctuate within the same frequency band. This is in line with studies on the role of the FEFs, demonstrating top-down attentional signals from this area propagating downstream towards regions such as the occipital site, resulting in beta activity modulation (Martinez-Trujillo, 2022; Sauseng et al., 2011; Veniero et al., 2021).

Our finding that *d'* fluctuates at beta frequencies can be interpreted further, where the previous literature has suggested that fluctuations in *d'* create periodic windows that facilitate the occurrence of attentional shifts (Fiebelkorn & Kastner, 2019). Although, it should be noted that the research suggesting this, by Fiebelkorn and Kastner (2019), looks at the theta-rhythmic behaviours of *d'* specifically, and so this interpretation is potentially limited in its relation to the beta results from our study. Still, it is possible that as

our task presented target stimuli on such a short time scale, perhaps *d'* fluctuated at a faster rate in anticipation of the potential need to reorient attention within a brief period, increasing the chances of performance success during invalid trials (Spadone, Betti, et al., 2021; Spadone, Wyczesany, et al., 2021). In comparison, less literature exists for *c* measures, meaning that it becomes challenging to determine why our results may contrast those that have previously emphasised the role of alpha (Benwell et al., 2017; Limbach & Corballis, 2016; Samaha et al., 2017), or even gamma (Chanes et al., 2013; Wyart & Tallon-Baudry, 2009). It could be that the beta-band fluctuations for *c* reflect how participants are using cue directed top-down expectations to adjust their decision criterion throughout the task. This is something that has been suggested previously, although often without the use of an attentional paradigm, possibly accounting for why there is a lack of prior evidence for the role of beta frequencies (Lange et al., 2013; Sherman et al., 2016). Despite this, to reiterate, the existing literature is currently sparse and mostly focuses on perceptual studies without an attentional element. We therefore believe that even our behavioural findings can offer a new insight into the role of beta oscillations in modulating measures of signal detection, including highlighting the similarity between *d'* and *c* in attention-related processes.

To bring our behavioural and EEG findings together, in our final analysis we utilised a regression approach to determine if *d'* and/or *c* could be predicted by phase angles in the occipital cortex. Interestingly, we indeed found that the phase of beta-band activity could influence response criterion measures during a visual detection task, which has been corroborated only in an unpublished thesis by Chanes, (2014). Here, Chanes (2014) found that the phase of beta oscillations indirectly modulated response criterion by changing gamma band oscillations. Our results cannot attest to this gamma-band effect, however it does highlight the interesting relationship that signal detection measures have with neural oscillations. Additionally, this study by Chanes (2014) found evidence to suggest that *d'* measures were independent of beta phase behaviours, contrasting our current results. Although, it is important to point out that this study found such an effect when investigating frontal regions of the cortex, whilst our focus remained on occipital regions. Additionally, these results were found during implemented tasks of conscious visual detection, unlike our current investigation of perceptual discrimination, with both points likely contributing to our observed differences in results.

Within our regression analysis also, we found similar effects between the two measures of *d'* and *c*. This is somewhat unexpected as previous literature has frequently noted that such measures differ in both

frequency and topography (e.g., Ho et al., 2017). Thus, our findings of similarity may simply be due to our post-regression calculations of *d'* and *c* only differing in the 'smaller' coefficient, meaning that there is numerically only a small difference in their distributions. However, when looking at our results as a whole, it seems that attentional shifts involve beta activity, regardless of the used metric (i.e., POS, MVPA), in line with the idea that beta is a top-down rhythm (Michalareas et al., 2016). Within this interpretation, distinct beta phase could facilitate stimulus processing (Veniero et al., 2021) and lead to a better sensitivity (*d'*) and consequently to a more conservative criterion (*c*). In this scenario, the two measures would be highly correlated and possibly driven by the phase of beta oscillations. However, based on the number of studies exploring this topic being far and few between, it is difficult to judge whether this is indeed the case.

As a whole, this experiment successfully determined that neural oscillations in the beta-band were most influenced by shifts of attention, where the behaviours of oscillatory power and phase were defined by whether participants shifted their attention to the left or right visual hemifield. This beta-band relationship similarly extended into SDT measures of *d'* and *c*, where we found that beta phase can be used to predict both measures. Thus, through the application of several analytical techniques, this study has evidenced that shifting visuospatial attention is able to modulate perceptual performance via mechanisms of occipital beta-band oscillations.

Throughout the discussion of these findings, it is clear that the narrative is continuing to emphasise the importance of beta. Despite these seemingly clear findings though, it is important to continue to question why these may differ from previous literature, which frequently correlates visual task performance with alpha-band oscillations instead. One reason for this contrast may simple be due to the employed task within this study, where we uniquely designed the current paradigm to take into account potential flaws observed in previous studies; addressed in the introduction, e.g., inadequate distractor stimuli. As such, one could argue that the findings here offer a more accurate reflection of the role that oscillations play in visuospatial attention. Task differences are something that have been considered previously too, with a number of reviews on the topic of visuospatial attention/perception highlighting this same line of thought (Bonnefond & Jensen, 2024; Wöstmann et al., 2022). It is increasingly likely that task differences are a contributing factor towards why there is a contrast between the current findings and previous literature. This could extend as far as previous findings failing to observe effects of beta oscillations, simply because their implemented tasks were too easy.

Whilst alpha power lateralisation has been consistently reported in previous studies of attention, arguably offering support to the well-known theory of alpha inhibition, the task designs that have previously been adopted to reach this conclusion are often not challenging enough, presenting targets or distractors in one visual hemifield at any single time (for an example of this, see Rihs et al., 2009). This means that whilst participants may indeed shift their attention to a cued location (i.e., endogenous attention), if a stimulus is only presented in one hemifield, it is likely they will become aware of this by means of exogenous attention instead (i.e., salient stimuli drawing attention). By increasing the difficulty of our task and presenting near-identical targets and distractors in both hemifields at the same time (i.e., target in the right hemifield, distractor in left), only differing in their movement coherence, we believe that our investigation into how visuospatial attention modulates perception via neural oscillations, offers an exciting and fresh perspective to the literature.

4.6 Conclusion

In summary of our findings, this study has successfully evidenced the significant role of beta-band oscillations in visuospatial attention. Specially, we have found that shifting endogenous attention results in the top-down control of beta-band oscillations within the occipital cortex, subsequently resulting in the modulation of perceptual performance abilities in a visual discrimination task. To our knowledge, this is one of the first investigations that has implemented a valid visuospatial attention task to assess the rhythmic behaviours of *d'* and *c* measures, importantly in both behavioural and neuronal recordings. By designing our task to address potential limitations within previous studies, we are confident in the approach we have taken to explore this topic, offering new insights and contributing to the progression of knowledge in this topic.

Chapter 5: Probing the causal role of brain oscillations in visuospatial attention, a TMS study

5.1 Introduction

Of the studies that have guided our understanding of neuronal mechanisms in cognitive neuroscience, including that from the previous chapter, these have been dominated by neural recordings that provide correlational evidence over causal. Whilst these are essential for the continual growth of our knowledge, they only go so far as to explain the modulatory effects of oscillations on cognitive behaviours, such as shifting attention across a visual field. Studies must also seek to validate EEG (and MEG) findings to strengthen interpretations through the implementation of neuromodulation protocols and in this case, manipulating oscillations to causally establish their role in cognition. The current experimental chapter will endeavour to address this need, building on the evidence from the EEG study outlined in Chapter 4 and using its results to guide a TMS study to assess causal relationships between oscillations and visuospatial attention, specifically focusing on SDT measures. The beginning of this chapter will re-introduce some of the important correlational evidence outlined previously, aiming to provide an overview of the topic and helping to justify the need for our subsequent investigation. Whilst some of this information will be repeated across the two chapters, it is important to additionally address the previous evidence here so that this chapter can be presented as a standalone investigation. Related causal evidence will be introduced where possible, however the focus of these largely remains on visual perception rather than attention, and so often only general assumptions can be made with this literature.

As the previous chapter's evidence dictates, there appears to be a correlation between measures of perceptual sensitivity (*d'*) and decision criterion (*c*) with pre-target occipital beta-band oscillations, in a visuospatial attention task. As of current, there is no published neuromodulation evidence to corroborate this finding, which is unsurprising considering the lack of research on this specific area of focus. There have instead been a number of attempts to use stimulation techniques to determine the causal role of oscillations in visual attention, but without looking at the SDT measures that we remain interested in (e.g., Capotosto et al., 2009; Peylo et al., 2021; Romei et al., 2010; Sauseng et al., 2011; Taylor & Thut, 2012; Thut et al., 2006). These have obtained relatively robust findings, supporting what we know from correlational EEG studies and determining that alpha power is under top-down attentional control by the prefrontal cortex (i.e., FEFs), where shifting

visuospatial attention reliably results in decreases of alpha power in the occipital hemisphere contralateral to the shift (e.g., Capotosto et al., 2009; Marshall et al., 2015; Romei et al., 2010; Sauseng et al., 2011; Taylor & Thut, 2012; Thut et al., 2006). Of these, Marshall et al., (2015) determined that when performing a visuospatial attention task and concurrently inhibiting the right or left FEF with theta burst stimulation, this resulted in the absence of an alpha power modulation in the occipitoparietal cortex. When repeating this task with theta stimulation at the vertex instead (control), the typical alpha power signature of attention was reintroduced, i.e., alpha power reduction in the hemisphere contralateral to stimulation. Interestingly also, they additionally found that FEF inhibition resulted in slower reaction times on trials that required shifts of covert attention. Whilst they did not explicitly examine SDT measures, they attribute this change to FEF inhibition influencing attentional bias, perhaps due to the modulation of alpha oscillations meaning that participants were unable to inhibit distractors within the task. Again, this seeks to reinforce the top-down control of oscillations in the visual system, but it also begins to suggest that these oscillations may uniquely influence performance in such tasks.

Whilst these studies offer a good foundation of knowledge surrounding the neuronal mechanisms of visuospatial attention, they still lack any robust and valuable information as to how oscillations may impact measures of SDT that are now considered critical to our decisions during such tasks. To explore this, we must instead look towards studies of visual perception, rather than attention, as the neuromodulation literature is currently unable to illuminate towards an answer for our open question. However, it is important to note that often these studies choose to stimulation the FEFs, a region of the cortex which is most associated with controlling the allocation of visuo-spatial attention through goal-directed mechanisms (Gregoriou et al., 2014; Martinez-Trujillo, 2022; Veniero et al., 2021; Wardak et al., 2006, 2011). Therefore, whilst the implemented behavioural tasks may be related to visual perception investigations, by stimulating the FEFs we can assume that this evokes a neuronal signal that mimics attentional orienting, meaning that we can make generalisations of resulting evidence towards visuospatial attention instead.

Thus, the most relevant study to first draw upon is one by Chanes et al., (2013) who used TMS to entrain oscillations of both 30 and 50 Hz at the right FEF, during pre-target time windows, whilst participants performed a visual perception task of detecting near-threshold stimuli. As a control, they also included a matched stimulation condition that was non-frequency specific (i.e., arrhythmic), as well as a sham TMS

protocol. The task asked participants to either discriminate the orientation of a Gabor target presented in the right or left hemifield of the screen (discrimination task), or simply to report whether it was present (conscious detection task) and on which side it appeared. When calculating performance measures for each stimulation condition, results suggested that during the first discrimination task there was no significant modulation of either accuracy, *d'* or *c* measures based on stimulation. Conversely, there were significant results from the conscious detection task, where pre-target TMS bursts of 30 Hz increased *d'*. This effect was not seen in the non-frequency specific control, sham condition or during the 50 Hz stimulation, proposing that high beta oscillations pre-target may causally enhance perceptual sensitivity during visual perception. Interestingly, this finding was reversed when looking towards *c* measures, with TMS bursts of 50 Hz significantly reducing *c*. This means that after a 50 Hz (gamma) stimulation at the rFEF,, participants were more liberal with their responses, an effect that again was not seen during sham or non-frequency specific control conditions. Considering these findings, it can be concluded that different oscillation frequencies have distinct causal effects on visual perception. Specifically, the results here suggest that the rFEF, may behave as a higher-order cortical region that can causally impact lower-order areas of the visual cortex through the modulation of neural oscillations. This is based on our understanding of the visual system operating in a hierarchical manner, where the FEFs are evidenced to provide 'feedback' to lower visual areas such as V1, or V5 if dealing with moving stimuli (for more information on visual pathways, see Gilbert & Li, 2013).

More support for the role of beta-band oscillations in visual processes comes from another aforementioned study by Veniero et al., (2021). To briefly reiterate this study, single-pulse TMS was applied to the rFEF whilst EEG recordings tracked the propagation of the resulting signal across the cortex. It was found that this single pulse would cause a phase reset of beta-band oscillations in the lower-level occipital regions, in the absence of a visual task. When repeating this procedure whilst participants performed a visual motion discrimination task, performance appeared to fluctuate along the phase of beta frequencies too, suggesting that the FEFs have top-down influence over occipital regions by causally influencing beta oscillations. To test whether this interpretation was true, in an extension of their investigation this procedure was repeated but with the additional dual-stimulation site of region V5. This was implemented to determine whether activating the FEFs could then causally influence the excitability of V5, as indexed by a change in moving phosphene rate. This was indeed the case, where the moving phosphene perception rate did fluctuate over time in a regular

beta frequency; a behaviour which was not replicated with a control dual stimulation over the vertex and then region V5. This works to emphasise the top-down control of higher-order visual areas via the modulation of beta oscillations. However, despite being an elegant investigation into how oscillations may influence perceptual performance, contributing essential knowledge to aid our understanding of neuronal mechanisms, the analysis of this study did not include any SDT measures. This makes it difficult to assess whether *d'* and *c* measures would show a similar (beta) fluctuation to the hit rates observed in Veniero et al.'s first study, which is important to determine as both contribute to performance (for more details, see Hawkins et al., 1990; Luo & Maunsell, 2018). It is also important to note that this study similarly adopted an investigation of perception, with very minimal studies to our knowledge seeking to discover whether the causal effects that are seen here would hold true in studies of visuospatial attention (i.e., Marshall et al., 2015), particularly in the top-down control of this. Although again, as this protocol did stimulate the FEF region and thus reproduce an attentional signal, we can once more use this study to guide our understanding of the neuronal mechanisms associated with attention.

Amongst our literature searches, there appears to be only a couple of neuromodulation studies that do causally investigate the role of beta-band oscillations in the top-down control of visual *attention* directly, but again lack the inclusion of SDT measures. The first of these was an investigation by Riddle et al., (2019) who asked participants to perform a visual search task and identify the presence of a target (defined by colour and orientation) amongst three distractors. Each distractor was unique but shared one common feature with the target (i.e., colour or orientation), making the target hard to identify by saliency alone and thus restricting the role of bottom-up attentional mechanisms (Macaluso & Doricchi, 2013). Prior to the onset of this search array, a cue was used to probe participants with the target features to search for in the upcoming task. Crucially, a 4-pulse TMS train of either 20 Hz (beta) or 50 Hz (gamma) at either high (110% MT) or low (50% MT) intensities, were delivered to the superior precentral sulcus (sPCS) or the intraparietal sulcus (IPS) during this task; two areas that have previously been implicated in visual attention (Corbetta & Shulman, 2002). TMS was also delivered to the primary sensory cortex (S1), chosen as a control stimulation site. Importantly to highlight though, these pulses started and ended after the onset of the probe, leaving a period of 320ms before the commencement of the search array. Without the inclusion of EEG, it is difficult to determine whether the effects of their stimulations were lasting enough to influence activity at the time of the task – perhaps a flaw

within their design. Additionally, this study only collected an average number of 34.5 trials per experimental condition (i.e., beta TMS at 110% MT intensity) in a total of 16 usable participants. This is a very low number even when considering safety restrictions on TMS protocols meaning that there is a limit on the amount of TMS pulses that can be delivered to a single participant per day (Rossi et al., 2009). Whilst it is common for TMS studies to have relatively smaller sample sizes and trial numbers than compared to behavioural or electrophysiological studies (Chipchase et al., 2012), it emphasises how caution should be applied when inferring potential conclusions from these results in particular. It may be the case that this study is underpowered and perhaps not able to contribute robust conclusions towards the neuronal mechanisms of top-down visual attention. With this in mind, when looking towards their results, it was revealed that beta-band TMS disrupted search accuracy when it was applied to both the sPCS and IPS, with an increased number of errors being made when the target was presented in the hemifield ipsilateral to the stimulation site. On one hand, this suggests that the entrainment of beta frequencies can causally disrupt top-down attentional processes and impair behavioural performance. Although, on the other hand, it could also suggest that an increase of beta could increase top-down attentional signals to the contralateral hemifield alone, meaning that participants' focus is biasedly shifted here during visual attention tasks. This would account for the reduction in task performance, of which could be driven by contralateral increases in *d'* measures, as previously outlined by Chanes et al., (2013).

For those who are familiar with the literature surrounding this topic, it is perhaps identifiable that the task used by Riddle et al., (2019) has previously been validated most famously by Buschman and Miller, (2007, 2009), who first investigated shifts of attention amongst two monkeys. In a similar depiction of results, they too found that top-down shifts of visual attention are preceded by spiking activity of local field potentials between the frequencies of 18-35 Hz, of which was located in the frontal regions of the cortex (i.e., FEF). Before moving beyond these studies, it is worth highlighting that there are some limitations for the adoption of this task design that should be addressed, including how during the visual search task the location of the target is unpredictable, with no spatial cue being offered to guide this. The impact of this is twofold, where first it is difficult to link this with our investigation of the top-down control of visuospatial attention, as participants here have no task information to guide endogenous shifts of focus. Secondly, without such a cue, prestimulus visual attention is arguably not engaged, and so this may fundamentally account for why no modulation of alpha-

band oscillations can be seen within this investigation (Peylo et al., 2021). This is important to consider when evaluating the literature, as it highlights that there is a clear lack of investigations that validly explore the causal role of neural oscillations in the top-down control of visuospatial attention, utilising important behavioural indexes of *d'* and *c*. Whilst similar themes have been addressed within the previous chapter, here we seek to emphasise how sparse the causal evidence is than compared to the already limited correlational.

In light of this, when looking at neuromodulation studies, this is as much as the current literature can offer. Accordingly, prior to commencing our own investigations into the topic, we must again seek to explore the correlational evidence to help us build our understanding further. This includes our previous investigation outlined in Chapter 4, suggesting that shifting attention results in the top-down control of beta-band oscillations, which subsequently play a key role in the perception of moving stimuli within a visuospatial attention paradigm. One of the only other studies to our knowledge that has also investigated signal detection theory (SDT) measures utilising a visuospatial attention paradigm, was an MEG investigation conducted by Wyart and Tallon-Baudry (2009), where participants were cued to covertly shift their attention to either the left or right lower visual field of a screen. A titrated contrast grating with a random orientation then appeared at either the cued or uncued of these locations, or sometimes not at all. Following its offset, participants were asked to choose which of two orientations matched the previously presented target and whether a grating was even presented. This study was one of the first to explore perceptual sensitivity (*d'*) and decision bias (*c*) and reported that gamma band activity could explain fluctuations in observed criterion measures, whilst alpha-band frequencies could be responsible for sensory baseline shifts (i.e., *d'*), affecting the strength of perceptual response to stimuli. These results work to suggest that performance in a visuospatial attention task relies on separate mechanisms of modulating neuronal activity – alpha and gamma-band frequencies. Despite this important conclusion, whilst these results are unique in highlighting potential neuronal mechanisms associated with SDT measures, there is one vital limitation that should be addressed, of which may account for the contrast in findings between their study and those from Chapter 4. As already discussed, despite the inclusion of a cueing paradigm suggesting that this is a valid approach to investigate attention, without the addition of distractors it makes it tricky to discriminate whether the detection of the target was validly achieved by endogenous attention alone (based on the cue), and not exogenous attention (based on the saliency of a single target appearing on the screen). The likelihood of this confound is accentuated by literature that has evidenced

how gamma oscillations are considered to most associated with bottom-up processes (Michalareas et al., 2016) and so the validity of this study should be carefully considered.

In one final attempt to explore related literature, we can move again to studies of visual perception, which regrettably also offer contradictory results to our own correlational findings. Evidence here can be drawn from two studies by Zhang et al., (2019) and Zhou et al., (2021) where both implemented different visual perception tasks to determine the role of alpha oscillations in SDT measures. The first of these studies was a behavioural investigation only, where participants were tasked with discriminating the orientation of stimulus gratings at a titrated contrast threshold. When calculating *d'* and *c* measures, it was clear that these fluctuated at ~8 Hz and ~10 Hz, respectively. However, a permutation test revealed that only *d'* fluctuations were significant. The fact that they only found significant results for one measure of SDT further offers support to criterion and sensitivity oscillating at separate frequencies (Wyart & Tallon-Baudry, 2009), as their analysis only explored a range of between 3-13 Hz, so perhaps *c* measures oscillate significantly outside of this. Further, the difference between the two measures are extended by suggestions of separate brain structures for each (Luo & Maunsell, 2015, 2018), but as Wyart and Tallon-Baudry (2009) did not increase their analysed frequency range or record neural signals from the cortex, it is difficult to confirm for certain whether this holds true. Next, Zhou et al., (2021) conducted an EEG study with a visual detection task to show that pre-target alpha oscillations in the occipital-parietal areas may shape *d'* measures, with lower alpha power improving *d'*. In this study, they asked participants to respond to each trial with whether they saw a target appear, or not. Interestingly also, prior to this they manipulated participants' decision criterion (*c*) throughout the task, by instructing participants that during the upcoming block the target would appear either 20% or 80% of the time, resulting in participants being either less or more biased to report the presence of the target, respectively. In reality, besides a priming block at the start of the experiment where these percentages held true, during the main task the targets were instead presented at a constant rate of 50%. This subsequently means that we can use these results to investigate top-down effects to some extent, as it can be supposed that manipulating criterion prior to the blocks means that participants will use this knowledge to endogenously influence their performance. Whilst the aim of this study differs from ours (perception vs. attention), their criterion results arguably did not contradict our findings, with both showing no evidence of a significant alpha-band modulatory effect in top-down criterion changes. By extending their frequency range beyond alpha (7-14 Hz), perhaps they would have

reached equal conclusions to ours in establishing the role of beta oscillations in criterion. These two studies are useful in guiding our understanding of how neural oscillations are modulatory in visual processes. However, to reiterate a former narrative, these are investigations of *perception* and so links to our attentional investigations remain tenuous. Additionally, it is possible that as we asked participants to covertly shift their attention and included near identical-to-target distractors, our task could be considered more difficult. This may be important to consider as previous research has determined that certain neural oscillations can be differentially modulated by task difficulty, as seen in investigations of visual attention (e.g., Chen et al., 2017; Roijendijk et al., 2013), perception (e.g., Li et al., 2013; Senkowski & Herrmann, 2002) and other cognitive processes (e.g., Dugue & VanRullen, 2014). Specifically, some studies have suggested that harder tasks lead to a reduction in alpha power, with this possibly resulting in a reduced variability of alpha and consequently masking any modulating effects that would otherwise be present (for more detail, see Limbach & Corballis, 2016).

In reflection of this literature, it is clear that more research is needed to determine the causal relationship between neural oscillations and the top-down control of visuospatial attention, including how this impacts measures of perceptual sensitivity (*d'*) and decision criterion (*c*). The following neuromodulation study has been conducted with this aim, but also in the hope of extending our previous EEG research to corroborate the importance of beta oscillations in visuospatial attention. By implementing a modified version of the task outlined in Chapter 4, we have sought to obtain causal evidence that can be easily related to our EEG findings. We have modified our cueing task to include a neutral shift condition for this purpose, as we were interested in determining whether any potential behavioural effects were due to shifts of attention or simply the perception of stimuli. Additionally, whilst previous studies within this field chose to stimulate the FEFs for reasons previously noted (i.e., the generation of attentional signals), we have instead chosen to stimulate region V5. We reasoned that performing a visuospatial attention task would activate the FEFs and, in turn, induce changes in V5 oscillatory activity. Therefore, by stimulating V5, we aimed to enhance the effects of attentional orienting on the visual cortex—the region ultimately responsible for stimulus processing. Based on our previous conclusions, we expect to find that stimulating region V5 at beta frequencies will result in improved perceptual performance, as defined by indexes of *d'* and *c*. We are also interested to see whether stimulation of the right V5 will causally impact the allocation of attention, where we hypothesise that the entrainment of alpha oscillations may inhibit performance of congruent trials in the left visual field (as only the rV5 is stimulated).

5.2 Materials and Methods

5.2.1 Subjects

A total of 24 healthy (no neurological, psychiatric or another medical condition that could alter brain functioning) participants were recruited for the current study (19 females, 5 males), all of whom had normal-to-corrected vision. Ages ranged from 18 – 42 years (*M* = 22, *SD* = 6.3) and all besides two participants reported being right-handed. Due to the nature of this study, participants were not recruited if they did not meet the safety criteria for TMS and MRI protocols (Rossi et al., 2009). This study was approved by The University of Nottingham's Ethics Committee, with all participants providing informed consent prior to the two experimental sessions and receiving monetary compensation for their time. Due to one participant's disengagement in the task, this dataset was excluded from any analysis.

After reviewing each participants performance to ensure that they were engaging with the task accurately and using the information of the cue, four further participants needed to be removed from analysis due to their invalid trial accuracy being above their valid trial accuracy. This suggests that they did not shift their attention based on the cue and so their data was removed to preserve the validity of any subsequent results. Thus, data from 19 participants (14 females; *M* = 21 years old, *SD* = 1.9) was used to create the final dataset of this study.

5.2.2 Experimental Design

This study is a repeated measures design aimed at investigating if and how neural oscillations can modulate motion discrimination performance in a visuospatial attention task, including the exploration of how changes could be related to perceptual sensitivity and/or criterion measures. The behavioural task here is a variation of that presented within Chapter 4 and was similarly created and presented via PsychoPy (version 2023.1.3, Peirce et al., 2019). Again, the task used a QUEST staircase to titrate the stimuli so that participants achieved approximately 75% performance accuracy. Throughout, participants were instructed to maintain fixation on a central bullseye and make a response using a keyboard. Unlike the previous experiment, here we used non-invasive brain stimulation methods (i.e., rTMS) to manipulate neural activity prior to the onset of stimuli, at frequencies of alpha (10 Hz), beta (20 Hz) and a control condition named arrhythmic (AR, see below). We chose these first two active frequency bands (alpha and beta) based on contradictions within the previous literature meaning that it is currently unclear which oscillatory frequency is able to modulate measures of *d'*

and/or *c*. Thus, we determined that it would be in our best interest to include both so that we could explore either possible effect. Further, we chose to include arrhythmic stimulation as a control condition, to determine whether the delivery of TMS itself resulted in any observed effects, rather than the rhythmicity of our stimulations (as in Thut et al., 2011), i.e., via phase resetting mechanisms. Stimulation was delivered to the right V5/MT, chosen based on our moving stimuli task design, with this region being specialised for the processing of such (Zeki, 2015). Additionally, we reasoned that as our stimuli were fast in motion (see below), these would arrive at region V5 via a fast input pathway which by-passes region V1 (Ffytche et al., 1995; Grasso et al., 2018); a parallel pathway phenomenon originally named dynamic parallelism.

5.2.3 Main Task

The main task was a motion discrimination task, where participants were instructed to maintain fixation on a constant black fixation bullseye (RGB: -1, -1, -1; font: Arial; letter height: 1) and make a response based on their perception of target motion. A schematic representation of this task is shown in Figure 5.1 (below).

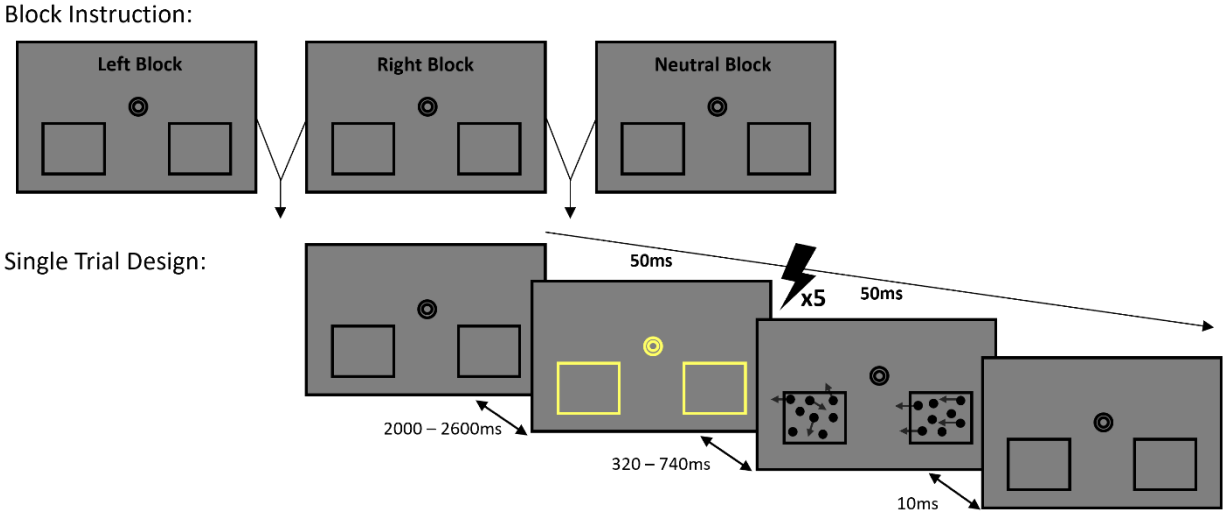


***Figure* 5.1**: Visual representation of the trial structure. Participants are first cued with which direction to shift their attention to (e.g., 'Right Block' means shift attention to the right placeholder). After a jittered ISI between 2-2.6s, the stimuli on the screen flashes to notify the participants that the trial is starting. Then, after another jittered ISI of between 300-700ms, the first TMS pulse is delivered in a train of 5, the duration of which dependant on pulse condition (alpha = 40ms duration, beta = 20ms, AR = 30ms). During the final fifth pulse, moving dots will appear for 50ms in the placeholders, this can occur any time between 320-740ms after the flash. When the dots disappear, participants respond with which direction the dots are coherently moving.

Stimuli were presented on a mid-grey luminance (RGB: 0.6549, 0.6549, 0.6549) screen that stayed consistent throughout. At the beginning of each testing block, participants were instructed on which side the target was most likely to appear via a simple instruction screen, i.e., 'Left Block', 'Right Block' or 'Neutral Block'. Essentially, this Neutral Block represented a condition where participants were not cued with which side of the visual field to shift their attention. The resulting task was made up of nine blocks which were counterbalanced by cue (3 Right, 3 Left, 3 Neutral) so that participants alternated their shift at each succeeding block (e.g., Right then Left then Neutral), minimising fatigue effects. There was a total of 20 trials in each block (N = 180 total trials).

The start of the block was self-initiated by participants via a press of any button on the keyboard. After the button press and throughout the block, a central bullseye and two placeholders were displayed on the screen consistently. After a jittered interstimulus interval (ISI) of between 2000-2600ms, the fixation and the placeholders flashed for 50ms, indicating that the trial was starting. This flash occurred as a colour change of yellow (RGB: 1, 0.5529, -0.2), which was chosen and adjusted to be isoluminant alongside the background, minimising afterimages that could confound performance. This flash was included as a salient non-informative cue to reset attentional sampling (Fiebelkorn et al., 2013, 2018; Fries, 2023; Lakatos et al., 2008). Importantly, when participants received instructions for the task, they were made aware of the flash being indicative of the trial starting. Following this, after a sampling interval of between 300-700ms, a train of 5 TMS pulses (5 pulses x 180 trials = 900 total pulses) were delivered to V5 at varying frequencies (alpha: 10 Hz, beta: 20 Hz and AR). For alpha frequency (10 Hz), the train lasted for 40ms with a 10ms gap between each pulse. For beta (20 Hz), the train lasted for 20ms with a 5ms gap between each pulse. Finally for arrhythmic, the train lasted for 30ms with varying gaps of 50, 60, 80 and 110ms, the order of which was randomised across trials. Importantly, each of these stimulation conditions included the same number of stimuli over the same overall duration, meaning that each should be comparable without confounding influences. Upon the final pulse, moving dots appeared for 50ms in both placeholders. These stimuli consisted of two sets of 180 moving black dots (size: 5 degrees; field space: 5.8, speed: 0.04; lifetime: -1), each located in a square placeholder either side of the fixation (right position: (7, -7) degrees; left position: (-7, -7) degrees, size = 6 x 6 degrees, with a black outline width of 2.5). One set of these dots moved coherently (set to the participants' individual threshold) and was, therefore, the target, whilst the other set moved randomly and acted as a distractor. The side at which the coherent dots

were presented was dependent on the block type, where during attention blocks (i.e., shift right or left) the coherent dots appeared in the cued position 80% of the time (e.g., Right Block = right placeholder dots move coherently 80% of the time); this was termed the valid/congruent condition. The other 20% of the time, coherent dots appeared at the uncued location (e.g., left placeholder dots move coherently 20% of the time during a 'Right Block'), this was termed the invalid/incongruent condition. In these cases, titrated coherence of 'invalid' targets was increased by 10% to ensure that participants were given a reasonable opportunity to decipher movement direction based on salient perception of the target. We also reasoned that being able to discriminate dot movement in invalid trials would further encourage attentional sampling. Conversely, if the invalid trials were too difficult—leading to chance-level performance—participants might disengage from the unattended location and focus solely on the cued position. Finally, during neutral cues, the target could appear at either the left or right placeholder with an equal likelihood (50%). We presented both the target and distractor at the same time for each trial so that we could validly test endogenous attention without the risk of target saliency engaging mechanisms of exogenous attention (i.e., attentional grabbing effects). The order of valid and invalid trials was randomised within blocks, and target movement direction was equally likely to be either right or left for each trial. Following the disappearance of these dots, participants could then respond 10ms later with which direction they thought the coherent dots were moving. Using the keyboard, participants pressed 'm' if they thought the dots were moving right, or 'z' if they thought left, there was no time limit for response.

After the completion of each block (~ 5 minutes), participants were visually presented with their accuracy scores (%) for both sides of the visual field. This was to encourage them to continue performing to the best of their ability and perhaps even increase their attentiveness if they were underperforming. Additionally, after each third block (neutral block) the dot coherence could be adjusted if participants were under or over performing due to either fatigue or practice effects, respectively. If participants scored below 70% performance accuracy, then coherence was increased by 5%. If it dropped below 60% accuracy, then coherence was increased by 10%. On the other hand, if participants scored above 80% accuracy, then coherence was decreased by 5%. Similarly, if it reached above 90% accuracy, then coherence was decreased by 10%. Between each block participants were given the opportunity to take a break and resume the task whenever they were ready. Importantly, trial numbers varied across task conditions, where in total, there were 30 congruent trials

per stimulation frequency (3 stimulation frequencies x 30 trials = 90 congruent trials) but only 10 incongruent trials per stimulation (3 stimulation frequencies x 10 trials = 30 incongruent trials). For the neutral shift condition separately, there were 10 trials per stimulation and location of target presentation (3 stimulation frequencies x 2 VFs x 10 trials = 60 total 'neutral' trials).

This study comprised of two sessions, an initial MRI acquisition and a behavioural/TMS session (see their corresponding sections below). On average, there was roughly one week in between these sessions to ensure that there was enough time to process the obtained MRI's and locate region V5 coordinates required for TMS delivery.

4.2.4 Session One: MRI

Participants were first invited to an MRI session to acquire an anatomical T1-weighted image of their brain. This was conducted on a 3.0 Tesla Phillips Ingenia MR system, at The Sir Peter Mansfield Imaging Centre in Nottingham. The duration of this was approximately 15 minutes and participants were simply asked to lie still in the scanner during the session.

Resulting DICOM images were then imported into BrainVoyager QX 2.8 (Brain Innovation, Maastricht, The Netherlands; www.brainvoyager.com) where they were corrected, transformed into Talairach space and segmented based on the position of the mid-sagittal plane (MSP), anterior commissure (AP), posterior commissure (PC) and the superior-/interior- cortical points (SP and IP). To ensure that the region of interest (ROI: right V5/MT) was accurately located, we used the Cortex-based Alignment (CBA) algorithm (Duecker et al., 2014). Briefly, the cortical surface was reconstructed for each participant using anatomical data acquired from the initial MRI session. This was then aligned to a cortical atlas that included the probabilistic Talairach group maps of region V5, as described in Frost and Goebel (2012). Group maps were back transformed to individual cortical anatomy and the TMS target was subsequently defined as the centre of gravity for the area with the highest probability of reflecting this area. Talairach coordinates were obtained from this location and subsequently used for the positioning of the TMS coil during the session (see *Figure* 5.2, below, for a single participant example).

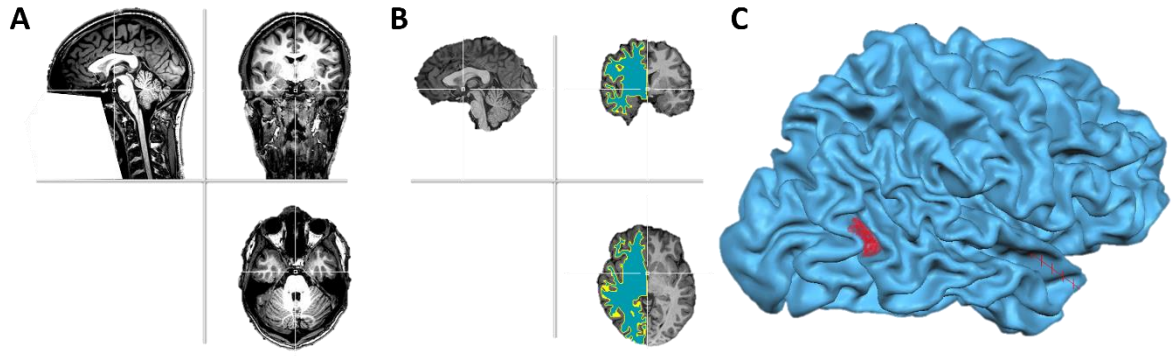


***Figure* 5.2**: A simplified example of anatomical MRI processing steps, conducted in BrainVoyager. A T1-weighted image is first imported into the software (A), which then undergoes an inhomogeneity correction where the brain is extracted from the skull (B). Hemispheres are segmented from one another and expressed in Talaraich space. Focus is on the right hemisphere only, where a functional atlas is overlayed onto the inflated hemisphere, highlighting the location of rV5/MT (shown in red shading; C).

5.2.5 Session Two: Behavioural and TMS

This session was comprised of four sections: set-up and calibration, practice task, staircase task and the main behavioural task (outlined above). In total, session two lasted approximately one hour.

During the set-up, participant's MRI files were imported into the neuronavigational system Brainsight ® (version 2.5.1; Rogue Research, Canada, http://www.rogue-research.com), where a skin model was reconstructed from individual MRI files, allowing setting of anatomical landmarks (i.e., nasion, tip of nose, right and left preauricular points). The obtained Talairach coordinates were then input as a target, stored in Brainsight and used to monitor the coil position throughout the session, ensuring the location of the TMS coil was consistently correct.

During the task, participants were seated in a comfortable armchair with their chin on a chinrest to minimise head movements. This chin rest was positioned central to the monitor at approximately 57cm from the screen. The room was dimly lit and quiet to minimise distractions. The screen that stimuli were presented on had a refresh rate of 100 Hz (size 1134 x 2003 pixels, screen model: BenQ LCD Monitor, computer model: Lenovo ThinkStation P620).

Participants were invited to complete the practice task first, where they were given a chance to familiarise themselves with the task outlined above (see 'Main Task') by completing 20 practice trials (N = 17 valid, N = 3 invalid) whilst covertly shifting their attention to the right. This lasted approximately 1 minute.

Coherence of the practice stimuli was set to 99% during this stage to allow for participants to clearly understand the task. If after this practice it became apparent that participants did not understand the task design, this practice was repeated to ensure that the main task would be completed accurately. Crucially, whilst both the practice and upcoming staircase were versions of the main task, they did not include any stimulation protocols.

The next section was the staircase titration, designed to adjust the coherence of the stimuli to match each participants' perceptual threshold; defined as the dot coherence value needed to achieve 75% accuracy in the motion discrimination task. The coherence of the stimuli started at 99% and reduced with correct responses at a standard deviation of 2. In the event of incorrect responses, coherence similarly increased. The titration automatically stopped when participants' threshold reached a 95% confidence interval, or they reached 200 trials. Two staircases were performed prior to the main tasks of both sessions (one for the stimuli appearing in the right and another for stimuli appearing in the left placeholder). Importantly, the cue for these staircases were 100% valid to ensure accurate calculation of thresholds.

Following this, a cap with a Brainsight tracking sensor was then placed onto the participants head, allowing the co-registration of pre-set anatomical landmarks using a digitiser stylus. Once completed, this co-registration was validated at different points across the scalp (most importantly the posterior of the head), ensuring a co-registration error of below 3mm. The target was then located using the stylus and marked on the cap to allow for ease of coil placement. Once the TMS coil was then placed over the target/V5, it was held at 90 degrees orientation during the entirety of the task, perpendicular to the scalp midline (see *Figure* 5.3, below). The main task then began.

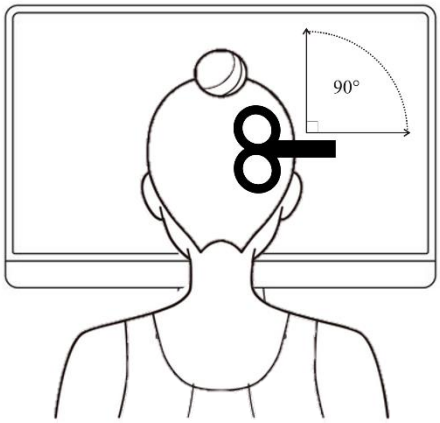


***Figure* 5.3**: Example of TMS setup. Whilst participants are sat in front of the computer screen, the TMS coil is placed over participant specific MT/V5 co-ordinates and held at a constant 90-degree angle whilst delivering pulses

TMS intensity was initially set at 60% machine stimulator output (MSO) for all participants. However, if participants complained about the stimulation being uncomfortable, intensity was lowered in 2% increments until reached a comfortable level (50% being the lowest admissible). On average, intensity was at 57.79% across all participants (*SD* = 3.26).

Once the task finished, participants were given a post-experiment questionnaire to determine whether their perception/vision during the task was affected by the TMS protocol (i.e., via phosphene induction). They were asked whether they saw something unusual when TMS was applied, where it was, how often it appeared, and were then encouraged to draw it. All participants answered no to the former question.

5.3 Data Analysis

Signal Detection Theory

Once the behavioural data was collated for each participant, the data was cleaned by removing all trials where reaction time was +/- 3 standard deviations away from the mean. The resulting data was then split into the separate conditions (3 stimulation types x 3 cues x 2 visual fields = 18 conditions total), ready for statistical analysis.

During the experiment, both reaction times (RTs) and accuracy measures were collected for each trial. Signal detection theory measures of perceptual sensitivity (*d'*) and decision criterion (*c*) were also calculated for each participant and condition, using the following equations:

$$d' = z(HR) - z(FA)$$

$$c = -\frac{1}{2}\big(z(HR) + z(FA)\big)$$

From the equation, HR and FA are hit rate and false alarm rate, respectively, and $z(x)$ is the inverse of the normal cumulative function evaluated at x (DeCarlo, 1998; Macmillan, 2002; Macmillian & Creelman, 1991). For this study, identical to that of the previous EEG investigation (see Chapter 4), we have chosen to calculate HR based on participants correctly answering that the dots were moving right, by pressing the 'm' response key. In turn, FA is calculated based on participants incorrectly answering that the dots were moving right.

When calculating these, a correction was also applied to account for cases where HR or FA rates equated to 0 or 1. This is essential as without this correction the corresponding z-score value would reach a value of +/- ∞ (Stanislaw & Todorov, 1999). For our chosen correction, the 1/(2*N*) rule was applied, adding 1/(2*N*) to either HR or FA measures of 0 and subtracting from measures of 1, where *N* refers to the number of trials used to calculate HR and FA (see Macmillan & Kaplan, 1985). To implement this, a MATLAB function created by Böckmann-Barthel (2023) was used.

Analysis of Variance

Resulting data meant there were four final performance measures collected for each participant and task condition, including accuracy, RTs, *d'* and *c*. Following this, a 3x3x2 repeated-measures analysis of variance (ANOVA) was conducted on each performance measure separately to determine whether these were uniquely influenced by the given attentional cues (3 levels: Shift Right, Left or Neutral), stimulation type (3 levels: Alpha, Beta or AR) and/or where the targets were presented on the screen (2 levels: Right or Left VF). This analysis was conducted in (*IBM SPSS Statistics*, Version 28) and all reported post-hoc tests were Bonferroni corrected.

General Linear Mixed Effect Models

After obtaining our ANOVA results, we deemed it necessary to implement a second analysis, examining instead the predictive abilities of our three variables (cue, target location (VF) and stimulation) on performance measures. This was in part motivated by the need to consider individual differences, a step that became apparent when examining our previous ANOVA results. Alongside this, we also determined that it would be valuable to compare the fitting ability of each model and thus decipher which variable could be

considered a 'best' predictor. Thus, for each of the performance measures separately, three general linear mixed-effects models (GLME) were fitted to the data using the *fitglme* function in MATLAB. By using this additional approach, we could control for the confounding influence of individual variability by introducing a random effects input in each of our models, something that may be advantageous when examining the large error bars resulting from our ANOVA output. To note also, whilst accuracy and RT values were input into the model at the single-trial level, both *d'* and *c* were instead calculated per condition. Such models were written as follows:

$$Model\ One\text{:}\ \ y \sim 1 + cue * VF + (1|participants)$$

$$Model\ Two\text{:}\ \ y \sim 1 + stim + (1|participants)$$

$$Model\ Three\text{:}\ \ y \sim 1 + stim * cue * VF + (1|participants)$$

where y is the outcome measure (i.e., accuracy, RT, *d'* or *c*), with $stim, cue, and\ VF$ input as the fixed predictor variables. To account for the individual differences that may be present within our results, $participants$ are chosen as a random effects variable within the model. Importantly, model parameters differed depending on the outcome measure being modelled. Specifically, when modelling accuracy, we utilised a binomial distribution and logit link function, with the Approximate Laplace fitting method to estimate coefficients. Both *d'* and *c* are similarly modelled but with a normal distribution and Identity link function instead. Finally, when looking at RTs, we used an Inverse Gaussian distribution and Identity link function (based on the review by Lo & Andrews, 2015). Dummy variables for each of these models were created with a reference group for each factor, which we chose to be AR stimulation, neutral shifts of attention and when the target was presented in the right visual field.

Model One was chosen based on the hypothesis that there will be a congruency effect present in the data, showing that participants perform significantly better when they were cued to shift their attention to a valid location (where the coherent dots would appear). This is tested by examining whether there is an interaction between cue and the visual field that the target is presented in. If congruency effects are present, this would be reflected by improved performance during valid (i.e., shift right and targets presented in the right visual field) compared to invalid conditions (i.e., shift right and targets presented in the left visual field). This is in line with previous literature which has replicated this effect consistently, including our own data in the

previous chapter. The results from this model are arguably more of a sanity check to confirm that participants were effectively using the cue to shift their attention. Following this, *Model Two* was conducted to explore the singular impact of stimulation type on performance measures, aimed specifically to determine whether our hypothesis held true and beta stimulation influences performance measures, particularly those of *d'* and *c*. Finally, *Model Three* was applied to assess whether the inclusion of the stimulation condition influenced the congruency effect that we expected to see from *Model One*. If the output of either of these models showed any significant main or interaction effects, fixed effects coefficients were explored to determine where such effects were presented (i.e., post-hoc acquired from the original *fitglme* function). All model *p*-values were corrected for multiple comparisons using Bonferroni correction (adjusted *p*-value = .017).

To assess which model best fit the data, Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) values were calculated for each GLME model using the formula:

$$AIC = -2logL_M + 2K$$

$$BIC = -2logL_M + \log(n)\,K$$

Where $logL_M$ is the maximum log likelihood determined by the Approximate Laplace fitting, K is the total number of parameters estimated in the model and n is the number of observations. For binomial distributions, this parameter is equal to the number of fixed and random effects, plus one $(nc + p + 1)$. For alternate distributions, this is just the number of fixed plus random effects $(nc + p)$.

Whilst this analysis provided a comprehensive understanding of how the predictors contributed to the four different performance measures, we chose to extend our approach further and replicate an analysis that was conducted in the previous chapter. This analysis looked to determine *d'* and *c* measures at a single trial level by fitting a multinomial regression model, using the *fitmnr* function in MATLAB. Prior this this, we removed trials associated with neutral shifts of attention, as we were exploring the congruency effect that is established by valid and invalid cues only. As we were primarily interested in stimulation effects, to implement this we first split the data by stimulation type and separately tested whether the congruency effect predicted responses at the single-trial level for each participant, with the following formula:

$$p(Y = 1) = \beta_0 + \beta_1 M + \beta_2 C + \beta_3 M * C$$

where $p(Y = 1)$ is the probability of answering 'dots are moving to the right', M is the direction that the dots are moving and C is whether a trial is congruent, defined by $cue * VF$ (modification of analysis utilised by Zhou et al., 2021). Resulting coefficient values (β) were then used to calculate coefficients for the SDT measures of *d'* as follows:

$$d' = \beta_1 + \beta_3 C,$$

$$\beta_{d'} = \beta_3.$$

Alongside a similar procedure for *c* values, as follows:

$$c = -\beta_0 - \frac{1}{2}\beta_1 + \left(-\beta_2 - \frac{1}{2}\beta_3\right) C,$$

$$\beta_c = \left(-\beta_2 - \frac{1}{2}\beta_3\right).$$

As a result, for each participant there were three coefficient values for both *d'* and *c* measures, one for each stimulation type. These were input into another general linear mixed effects model to determine whether the addition of stimulation type (alpha, beta or AR) changed the influence of the previous congruency effect on measures of *d'* and/or *c*. Again, this was fit to a normal distribution, an Identity link function and an Approximate Laplace fit method.

5.4 Results

Overall, this analysis aimed to explore whether performance on a visuospatial attention task could be casually modulated by the entrainment of distinct neural oscillations (i.e., alpha and/or beta) at region rV5/MT. To achieve this, performance was assessed via measures of accuracy, reaction time (RT), perceptual sensitivity (*d'*) and criterion (*c*).

The data was primarily checked for any outliers, based on the criteria that reaction time was +/- 3 standard deviations away from the mean (calculated for each participant separately). This resulted in an average of 3.1 trials being removed from each participants dataset.

5.3.1 MRI

To ensure that we were stimulating the chosen region of interest, we used BrainVoyager software to localise region rV5/MT on individual T1-weighted MRI anatomical scans. Resulting average (±SD) Talairach coordinates were calculated at: $x = 35.29\ (\pm 7.5),\ y = -59.09\ (\pm 9.9),\ z = 3.96\ (\pm 7.1)$.

5.3.2 Behavioural Results

Upon completing the task detailed above (see, Session Two: TMS), performance scores of accuracy, RT, *d'* and *c* were collated across participants and conditions. Figure 5.4 (below) depicts the descriptive statistics for each of these.

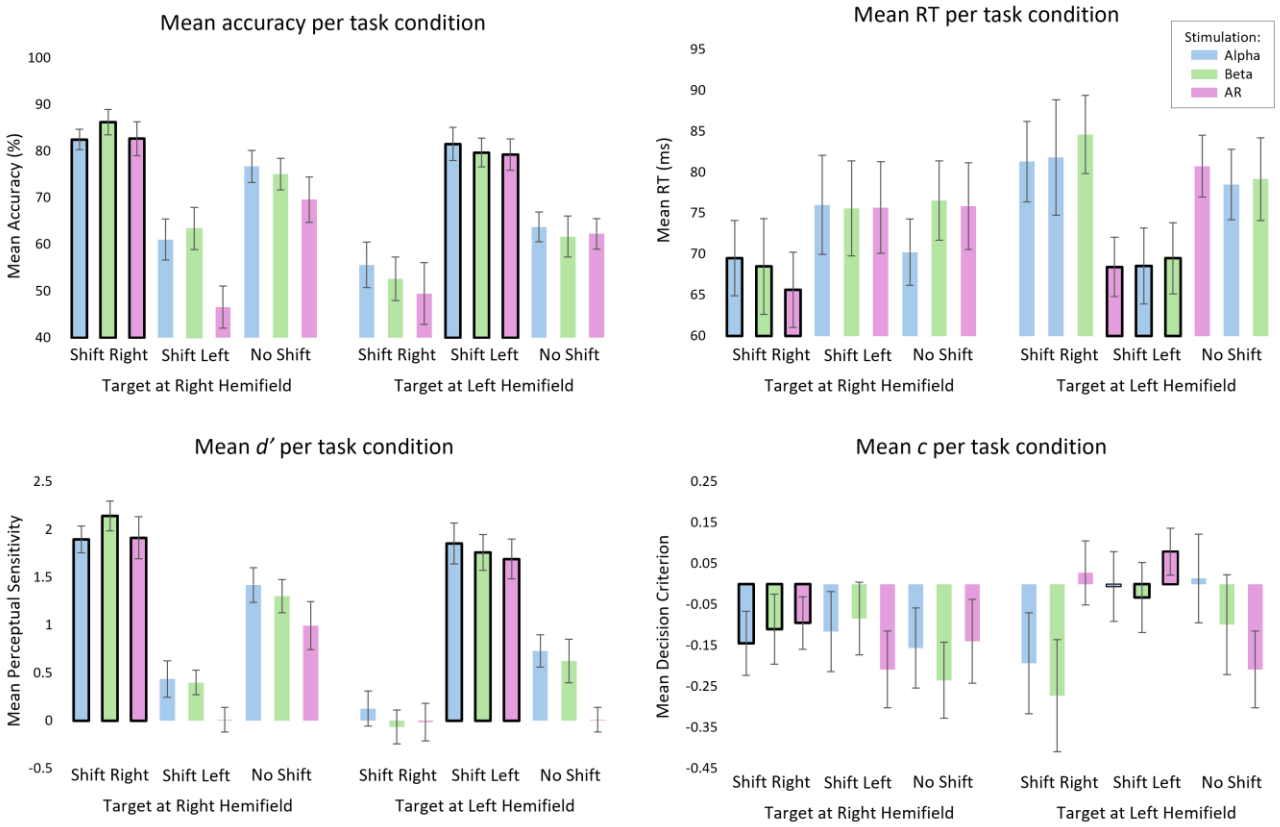


***Figure* 5.4**: Average and standard error bars for each performance measure — accuracy (top left), RT (top right), *d'* (bottom left) and *c* (bottom right). In each panel, the measure of interest is plotted according to the visual field where the target was presented (i.e., Right Hemifield and Left hemifield) and then for the cue instruction (Shift Right, Left, No Shift). Blue bars represent alpha stimulation conditions, green represent beta and pink AR. When the conditions are congruent (e.g., shift attention right and coherent dots presented in the right VF), bars are outlined in black.

Analysis of Variance (ANOVA)

To start our analysis, ANOVA was conducted for each of our performance measures separately, exploring whether our independent variables of cue (3 levels: shift right, left or no shift), target location (2 levels: coherent dots presented in the right or left visual field) and/or stimulation frequency (3 levels: alpha, beta or AR) had any significant main and/or interaction effects on resulting task performance.

Performance Accuracy:

When investigating measures of performance accuracy, there was a significant main effect of both VF ($F(1, 18) = 5.02$, $p = .038$, $\eta_P^2 = .22$) and stimulation type ($F(2, 36) = 5.39$, $p = .009$, $\eta_P^2 = .23$). As expected, we also found a significant interaction effect of cue*VF ($F(2, 36) = 49.85$, $p < .001$, $\eta_P^2 = .74$). In contrast, there was no significant main effect of cue on its own ($F(2,36) = .023$, $p = .98$), nor any interactions that included stimulation: cue*stim ($F(4, 72) = .71$, $p = .59$), VF*stim ($F(2, 36) = 2.07$, $p = .14$) and cue*VF*stim ($F(4, 72) = 1.02$, $p = .4$). For a depiction of these results, see Figure 5.5 (below).

When exploring the significant effects further, it appeared that performance was significantly better when the target was presented in the right hemifield ($M = 71.5\%$, $SE = 2.2$) than compared to the left ($M = 65.1\%$, $SE = .022$), $p = .038$, 95% CI [.004 .13]. Additionally, when looking at the main effect of stimulation, post-hoc tests showed that performance was significantly improved following alpha ($M = 70.2\%$, $SE = .017$) than compared to arrhythmic stimulation ($M = 65\%$, $SE = .023$), $p = .017$, 95% CI [.008 .096]. No difference was found between alpha and beta stimulation ($p = 1$), nor between beta and AR ($p = .08$).

Finally, when investigating the congruency interaction effect (cue*VF), we confirmed the attentional advantage leading to a better performance when the target appeared in the attended VF. Performance was significantly improved for trials where participants shifted their attention to the right and the target was presented in the right (Congruent trials: $M = 83.8\%$, $SE = .023$) versus left (Incongruent trials: $M = 52.6\%$, $SE = .037$) visual field, $p < .001$, 95% CI [.22 .41]. Similarly, when participants shifted their attention to the left, performance was significantly improved when the target was presented on the left (Congruent trials: $M = 80.2\%$, $SE = .027$) than compared to the right (Incongruent trials: $M = 57\%$, $SE = .033$), $p < .001$, 95% CI [.14 .32]. Interestingly, for the uncued condition, there was still a significant difference in performance, where right target presentations ($M = 73.8\%$, $SE = .032$) resulted in a significantly improved performance accuracy than compared to left ($M = 62.6\%$, $SE = .028$), $p = .01$, 95% CI [.03 .2], indicating a rightward attentional bias.

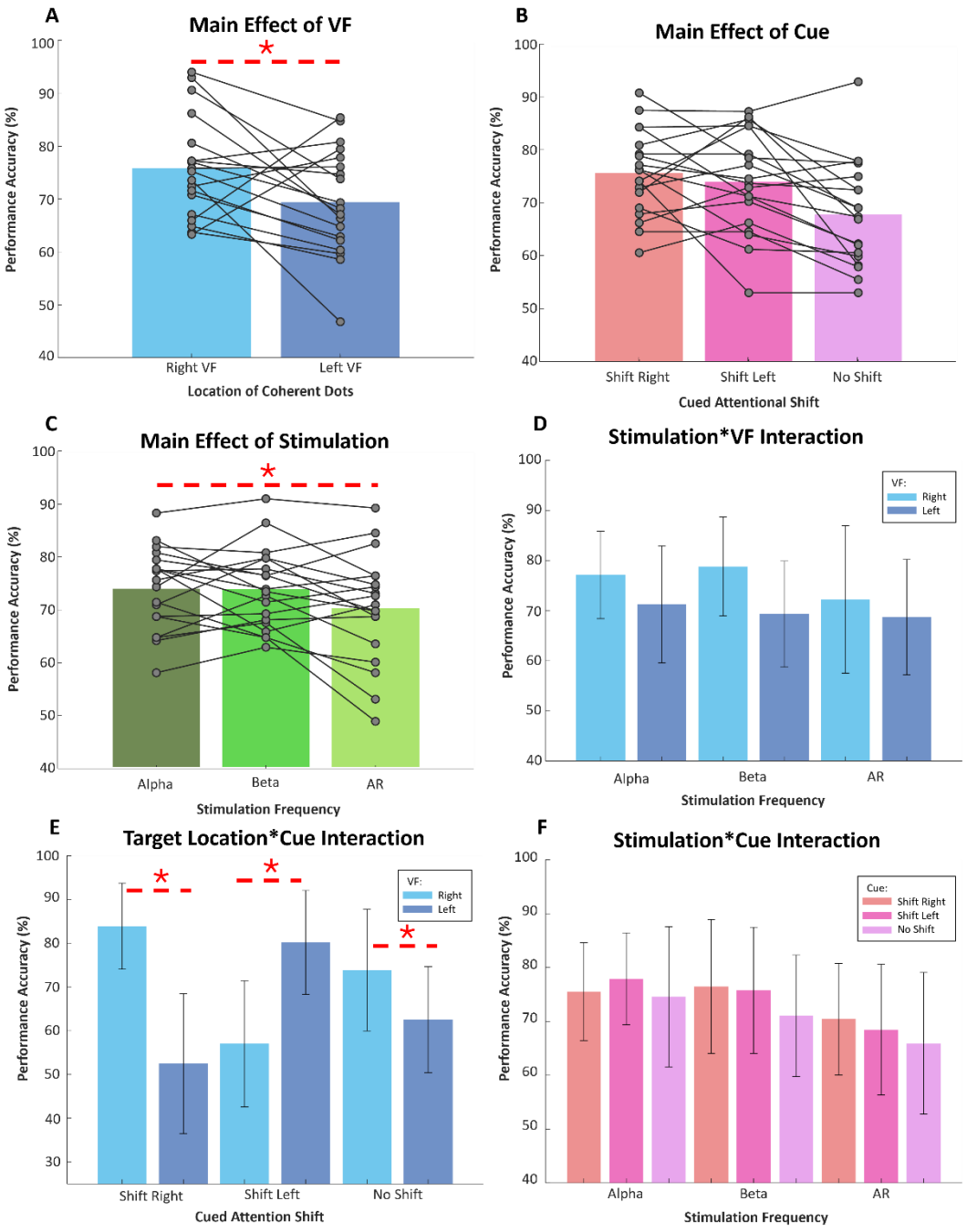


***Figure* 5.5**: Performance accuracy for each independent variable (VF = panel A; cue = B; stimulation = C), alongisde their interaction (stimulation*VF = panel D; VF*cue = E; stimulation*cue = F). Bars are coloured for additional guidance, where blues represent the two visual fields (light blue = right VF, dark blue = left), pinks represent the cueing condition (pink-orange = shift right, bright pink = left and purple = no shift) and greens represents the different stimulation conditions (dark green = alpha stimulation, bright green = beta, light green = AR). Where there is a significance difference between conditions, this is illustrated with a red dashed line and red asterisk.

Reaction Time:

When looking at measures of RT, there was a significant main effect of VF again (F(1, 18) = 5.68, p = .028, η_P^2 = .24), but no main effect of either cue (F(2, 36) = 1.2, p = .31) or stimulation (F(2, 36) = .13, p = .88). There was again a significant interaction effect of cue*VF (F(2, 36) = 10.53, p < .001, η_P^2 = .37), but no interaction effect of cue*stimulation (F(4,72) = .16, p = .96) or VF*stimulation (F(2,36) = .41, p = .67). The final three way interaction was also non-significant, cue*VF*stim (F(4,72) = 1.35, p = .26). For a depiction of these results, see Figure 5.6 (below).

When exploring these significant effects, RTs were significantly faster when the target was presented in the right VF (M = 726ms, SE = .042) compared to the left (M = 770ms, SE = .038), p = .028, 95% CI [-.082 -.005]. When looking at the cue*VF interaction, RTs were also significantly faster for congruent trials but only following rightward cues (Congruent trials: M = 679ms, SE = .049 vs Incongruent trials: M = 826ms, SE = .047), demonstrating a congruency effect, p < .001, 95% CI [-.2 -.091]. In contrast, when participants shifted their attention to the left or were presented with neutral cues, there was no significant difference between RTs when targets were then presented in the former (Congruent trials: M = 688ms, SE = 40; M = 795ms, SE = .039) or latter visual field (Incongruent trials: M = 758ms, SE = .055; M = 742ms, SE = .044), p = .093, 95% CI [-.15 .013] and p = .11, 95% CI [-.014 .12].

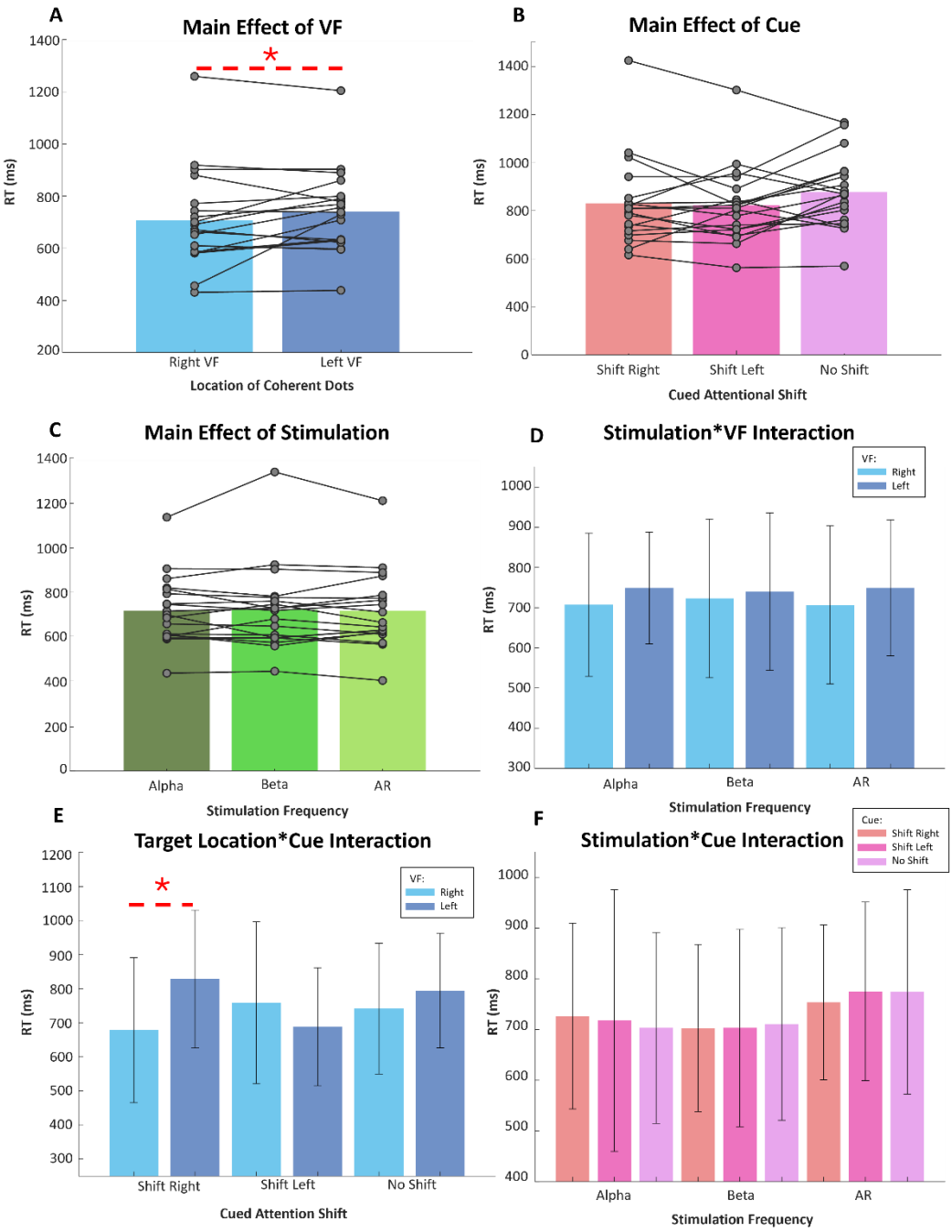


***Figure* 5.6**: Reaction times for each independent variable (VF = panel A; cue = B; stimulation = C), alongisde their interaction (stimulation*VF = panel D; VF*cue = E; stimulation*cue = F). Bars are coloured for additional guidance, where blues represent the two visual fields (light blue = right VF, dark blue = left), pinks represent the task cueing type (pink-orange = shift right, bright pink = left and purple = no shift) and greens represents the different stimulation conditions (dark green = alpha stimulation, bright green = beta, light green = AR). Where there is a significance difference between conditions, this is illustrated with a red dashed line and red asterisk.

Perceptual Sensitivity:

Next, when looking at measures of *d'*, there was a significant main effect of VF ($F(1,18) = 11.4$, $p = .003$, $\eta_P^2 = .39$) and stimulation ($F(2,36) = 7.12$, $p = .002$, $\eta_P^2 = .28$), but no significant effect of cue here ($F(2,36) = 2.28$, $p = .12$). When looking at interaction effects, there was only one significant interaction between cue*VF ($F(2,36) = 94.48$, $p < .001$, $\eta_P^2 = .84$). Both cue*stimulation ($F(4,72) = 1.73$, $p = .15$) and VF*stimulation ($F(2,36) = .19$, $p = 54$) effects were non-significant. The final three-way interaction was also non-significant, cue*VF*stim ($F(4,72) = .76$, $p = .55$). For a depiction of these results, see Figure 5.7 (below).

When examining just the significant effects further, it was revealed that *d'* was higher when the targets were presented in the right visual field (*M* = 1.17, *SE* = .1) compared to the left (*M* = .74, *SE* = .1), *p* = .003, 95% CI [.16 .69]. When looking at the effect of stimulation type, *d'* significantly increased following alpha (*M* = 1.08, *SE* = .087) and beta stimulation (*M* = 1.03, *SE* = .079) compared to AR (*M* = 77, *SE* = .12), *p* = .014, 95% CI [.056 .56] and *p* = .031, 95% CI [.02 .5], respectively. Interestingly though, there was no significant difference in *d'* measures when comparing alpha and beta stimulations, *p* = 1.

Finally, the interaction between cue and VF revealed a clear congruency effect. When participants shifted their attention to the right, there was a significant increase in *d'* measures when targets were presented in the right VF (*M* = 1.99, *SE* = .14) compared to those presented in the left (*M* = .015, *SE* = .12), *p* <.001, 95% CI [1.56 2.39]. Similarly, when participants shifted their attention to the left, there was a significant increase in *d'* measures in trials where the target was presented in the left VF (*M* = 1.77, *SE* = .17) compared to right (*M* = .28, *SE* = .11), *p* <.001, 95% CI [1.05 1.93]. Interestingly also, these significant differences extended into the uncued shift condition, where *d'* was significantly increased for trials where the target was presented in the right visual field (*M* = 1.24, *SE* = .17) compared to the left (*M* = .45, *SE* = .11), *p* <.001, 95% CI [.43 1.16].

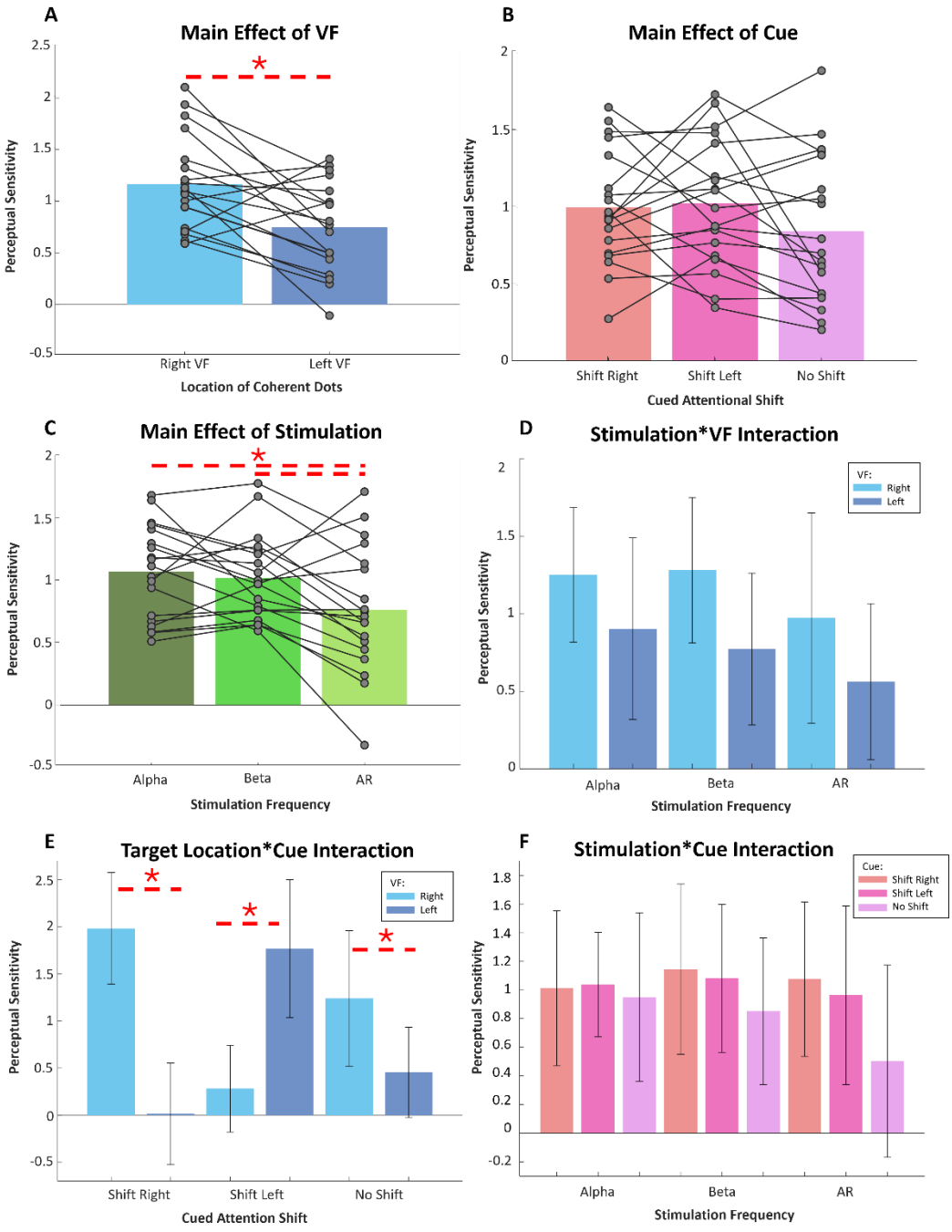


***Figure* 5.7**: Perceptual sensitivity (*d'*) for each independent variable (VF = panel A; cue = B; stimulation = C), alongisde their interactions (stimulation*VF = panel D; VF*cue = E; stimulation*cue = F). Bars are coloured for additional guidance, where blues represent the two visual fields (light blue = right VF, dark blue = left), pinks represent the cueing condition (pink-orange = shift right, bright pink = left and purple = no shift) and greens represents the different stimulation conditions (dark green = alpha stimulation, bright green = beta, light green = AR). Where there is a significance difference between conditions, this is illustrated with a red dashed line and red asterisk.

Decision Criterion:

Finally, when looking at the last performance measure of decision criterion, there was no significant effect of either cue ($F(2,36) = .63$, $p = .54$), VF ($F(1,18) = 1.41$, $p = .25$) or stimulation ($F(2,36) = .64$, $p = .53$), including their interactions of cue*VF ($F(2,36) = 1.7$, $p = .2$), cue*stimulation ($F(4,72) = 1.45$, $p = .23$) and VF*stimulation ($F(2,36) = .74$, $p = .49$). The final three-way interaction was also non-significant, cue*VF*stim ($F(2.65,47.61) = .1.54$, $p = .22$, with Greenhouse-Geisser correction due to sphericity violations). For a depiction of these results, see Figure 5.8 (below).

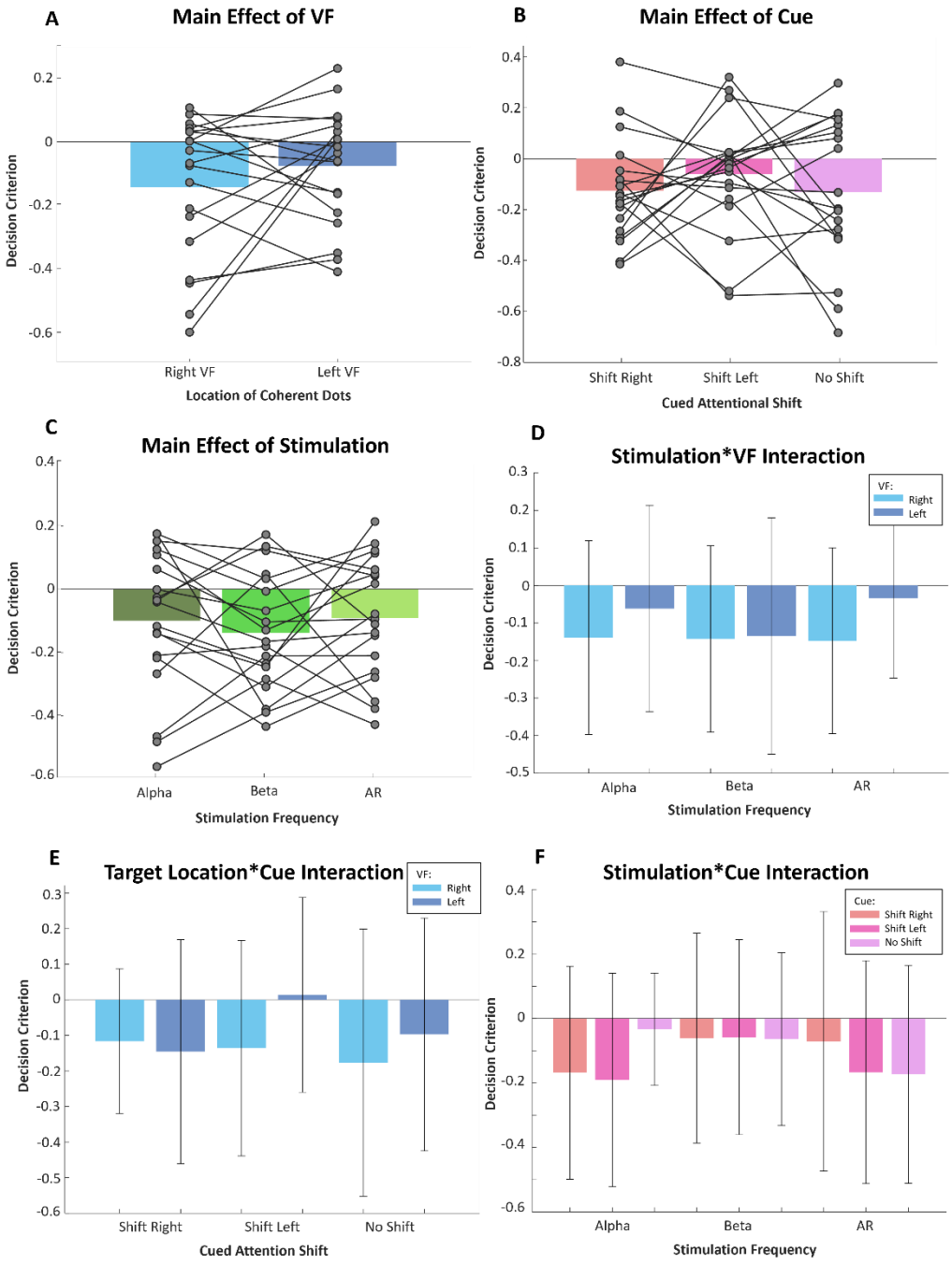


***Figure* 5.8**: Decision criterion (*c*) for each independent variable (VF = panel A; cue = B; stimulation = C), alongisde their interaction (stimulation*VF = panel D; VF*cue = E; stimulation*cue = F). Bars are coloured for additional guidance, where blues represent the two visual fields (light blue = right VF, dark blue = left), pinks represent the task cueing type (pink-orange = shift right, bright pink = left and purple = no shift) and greens represents the different stimulation conditions (dark green = alpha stimulation, bright green = beta, light green = AR). Here there are no significant main or interaction effects of task conditions on criterion measures.

General Linear Mixed Effect Models

Each of our four calculated performance measures were then input into separate GLME analyses to assess whether they could be predicted by our independent variables of cue (3 levels: shift right, left or neutral shift), target location (2 levels: coherent dots presented in the right or left visual field) and/or stimulation frequency (3 levels: alpha, beta or AR). When exploring these results, the following sections will be split by model, with each exploring all four of the calculated task performance measures.

Model One: The Congruency Effect (Cue*VF)

To first explore whether task congruency could predict performance, a GLME model was created for each of the four performance measures of accuracy (AIC = 3677.76; BIC = 3720.58), reaction time (AIC = -9.77; BIC = 39.16), *d'* (AIC = 813.01; BIC = 843.69) and *c* (AIC = 366.79; BIC = 397.47). From these, it was determined that both the cue and the visual field in which the coherent dots appeared ($p < .001$), could predict three out of the four performance measure (not criterion). This was followed by a significant interaction between these two predictors ($p < .001$), but again only for the same three measures (see Table 1 for full output, below).

Table 1

Results obtained from a GLME determining the predictive relationship between task congruency and performance measures of accuracy, RT, perceptual sensitivity (*d'*) and decision criterion (*c*). GLME output provided statistical indications for whether the given attentional cue and/or the visual field that the target was presented in had individual effects on performances, alongside assessing their combined interaction effect (i.e., congruency effect). Significant results are highlighted in bold ($p < .017$).

		***F*-stat**	**DF1, DF2**	***p*-value**
Accuracy	Cue	41.03	2, 3344	**< .001**
	VF	17.64	1, 3344	**< .001**
	Cue*VF	82.64	2, 3344	**< .001**
RT	Cue	20.52	2, 3344	**< .001**
	VF	9.88	1, 3344	**.0017**
	Cue*VF	34.72	2, 3344	**< .001**
Perceptual Sensitivity	Cue	74.28	2, 336	**< .001**
	VF	31.93	1, 336	**< .001**
	Cue*VF	157.48	2, 336	**< .001**
Decision Criterion	Cue	.35	2, 336	.7
	VF	1.18	1, 336	.28
	Cue*VF	1.52	2, 336	.22

Post Hoc Analysis for Model One

Performance Accuracy:

When investigating performance accuracy for each attentional cue, this was significantly higher for rightward attention shifts (*M* = 76.07%, *SD* = 7.96) compared to the neutral shifts (*M* = 68.22%, *SD* = 9.91; difference = 7.85%, BCa 95% CI [.35 .88], *t*(3344) = 4.51, *p* < .001). Similarly, leftward shifts (*M* = 74.45%, *SD* = 9.52) outperformed the neutral condition also (difference = 6.22%, BCa 95% CI [-1.09 -.48], *t*(3344) = -5.02, *p* < .001). Both of which are in line with what we would expect when investigating the effects of cues on task performance. Additionally, accuracy was significantly improved when targets were presented in the right (*M* = 76.11%, *SD* = 9.53) versus left (*M* = 69.75%, *SD* = 10.06) visual field (difference = 6.36%, BCa 95% CI [-.82 -.3], *t*(3344) = -4.2, *p* < .001), which was unexpected considering there was no task advantage to stimuli presented in the right visual field.

For interaction effects, an expected congruency effect was observed, where accuracy was significantly reduced in the right cue condition for trials where the target was presented in the left VF (*M* = 52.48%, *SD* = 16) compared to the right (*M* = 83.87%, *SD* = 9.83; difference = 31.39%, BCa 95% CI [-1.43 -.63], *t*(3344) = -5.08, *p* < .001). In an identical pattern, for the left cue condition, accuracy was again significantly reduced for trials where the target was presented in the right VF (*M* = 57.02%, *SD* = 14.41) compared to the left (*M* = 80.19%, *SD* = 11.86; difference = 23.17%, BCa 95% CI [1.31 2.1], *t*(3344) = 8.48, *p* < .001). When considering the neutral cue, there was again a significant difference in performance accuracy, where participants were better at discriminating targets in the right visual field (*M* = 74.06%, *SD* = 13.88) than compared to the left (*M* = 62.41%, *SD* = 12.12; difference = 11.65%, BCa 95% CI [.63 1.43], *t*(3344) = 5.08, *p* < .001).

Reaction Times:

For measures of RTs, these were significantly increased for neutral trials (*M* = 767.7ms, *SD* = 166.6) compared to right cue (*M* = 715.6ms, *SD* = 204.3; difference = 52.1ms, BCa 95% CI [-.095 -.044], *t*(3344) = -5.4, *p* < .001). However, there was no significant difference when comparing shift left versus neutral cues (*p* = .58), suggesting that participants did not find the left cue to be advantageous. Additionally, RT was significantly faster when targets were presented in the right (*M* = 712.1ms, *SD* = 187.7) versus left (*M* = 746.2, *SD* = 161.6) visual field (difference = 34.1ms, BCa 95% CI [.019 .082], *t*(3344) = 3.14, *p* = .0017), following the same pattern

observed for accuracy, but again this was unexpected considering that there was no difference between the visual hemifields.

For interaction effects, the standard congruency effect was similarly present within this measure, where during right shifts of attention RTs were significantly slower when the target was presented in the left (*M* = 828.15ms, *SD* = 202.42) visual field than compared to the right (*M* = 678.47ms, *SD* = 212.78; difference = 149.68ms, BCa 95% CI [.063 .16], *t*(3344) = 4.44, *p* < .001). In parallel, during left shifts of attention, RTs were significantly slower when the target was presented in the right (*M* = 758.98ms, *SD* = 237.3) visual field than compared to the left (*M* = 688.3ms, *SD* = 173.26; difference = 70.68ms, BCa 95% CI [-.15 -.059], *t*(3344) = -4.46, *p* < .001). Lastly, for the neutral cue condition, there was a significant difference in RTs, where participants were quicker at responding to targets in the right visual field (*M* = 741.44, *SD* = 191.73ms) than compared to the left (*M* = 794.38, *SD* = 168.13ms; difference = 52.94ms, BCa 95% CI [-.16 -.063], *t*(3344) = -4.44, *p* < .001).

Perceptual Sensitivity:

Finally, *d'* was significantly increased when comparing right (*M* = .99, *SD* = .37) versus neutral (*M* = .85, *SD* = .48) cues (difference = .14, BCa 95% CI [.47 1.02], *t*(336) = 5.33, *p* < .001), as well as left (*M* = 1.03, *SD* = .41) versus neutral cues (difference = .18, BCa 95% CI [-1.23 -.68], *t*(336) = -6.83, *p* < .001). Both highlighting a clear effect of a given cue in promoting perceptual sensitivity measures. Again though, *d'* was significantly increased when targets were presented in the right (*M* = 1.17, *SD* = .45) versus left (*M* = .75, *SD* = .44) visual field (difference = .42, BCa 95% CI [-1.07 -.52], *t*(336) = -5.65, *p* < .001), continuing our unexpected findings that suggest perceptual preference for one hemifield over the other.

For interaction effects, there was a significant interaction between cue and VF (i.e., congruency effects) for *d'* measures. In the right cue condition, *d'* was significantly reduced for trials where the target was presented in the left VF (*M* = .015, *SD* = .54) compared to the right (*M* = 1.99, *SD* = .59; difference = 1.98, BCa 95% CI [-1.57 -.79], *t*(336) = -5.95, *p* < .001). The same was true for left cue conditions, where *d'* was significantly reduced for trials where the target was presented in the right (*M* = .28, *SD* = .46) compared to the left VF (*M* = 1.77, *SD* = .73; difference = 1.49, BCa 95% CI [1.89 2.67], *t*(336) = 11.51, *p* < .001). Similarly, during neutral cues, *d'* was significantly reduced when the target was presented in the left (*M* = .45, *SD* = .48) than compared to the right visual hemifield (*M* = 1.24, *SD* = .72; difference = .79, BCa 95% CI [.79 1.57], *t*(336) = 5.96, *p* < .001).

Model Two: The Stimulation Effect

Next, with similar models for accuracy (AIC = 3868.21; BIC = 3892.67), RT (AIC = 128.36; BIC = 158.94), *d'* (AIC = 1037.04; BIC = 1056.21) and *c* (AIC = 367.83; BIC = 387), we looked to determine whether stimulation frequency could significantly predict performance outcomes, finding that this was not the case (see Table 2 for full output, below).

Table 2

Results obtained from a GLME determining the statistical relationship between the stimulation frequency of region V5/MT and performance measures of accuracy, RT, perceptual sensitivity (*d'*) and decision criterion (*c*). Significant results are highlighted in bold ($p < .017$).

	***F*-stat**	**DF1, DF2**	***p*-value**
Accuracy	2.51	2, 3347	.081
RT	.43	2, 3347	.65
Perceptual Sensitivity	2.73	2, 339	.066
Decision Criterion	.49	2, 339	.61

Post Hoc Analysis for Model Two

Results of this model suggested that there were no significant main effects of stimulation type on any of the performance measures.

Model Three: The 'Full' Effect

For the final model, we wanted to determine how our three predictors might interact with one another to predict participant performance. Thus, models were again created for accuracy (AIC = 3688.9; BIC = 3805.12), RT (AIC = 3.27; BIC = 125.6), *d'* (AIC = 816.99; BIC = 893.69) and *c* (AIC = 378.68; BIC = 455.38). Here, the previously determined significant interaction effect between cue and VF were again observed for three out of four performance measures (not criterion), exhibiting a congruency effect. See Table 3 for full output (below).

Table 3

Results obtained from a GLME determining the statistical relationship between each of our three task conditions (cue, VF and stimulation frequency) and performance measures of accuracy, RT, perceptual sensitivity (*d'*) and decision criterion (*c*). This was assessed for each variable independently, as well as also examining all combinations of these variables to provide a full overview of how performance measures were manipulated in this experiment. Significant results are highlighted in bold ($p < .017$).

		F-stat	DF1, DF2	*p*-value
Accuracy	Cue	22.68	2, 3332	**< .001**
	VF	2.72	1, 3332	.1
	Stimulation	1.35	2, 3332	.26
	Cue*VF	37.64	2, 3332	**< .001**
	Cue*Stim	1.07	4, 3332	.37
	VF*Stim	.53	2, 3332	.59
	Cue*VF*Stim	.68	4, 3332	.61
RT	Cue	11.36	2, 3332	**< .001**
	VF	1.06	1, 3332	.3
	Stimulation	2.06	2, 3332	.13
	Cue*VF	15.01	2, 3332	**< .001**
	Cue*Stim	1.67	4, 3332	.15
	VF*Stim	2.44	2, 3332	.087
	Cue*VF*Stim	.88	4, 3332	.48
Perceptual Sensitivity	Cue	32.8	2, 324	**< .001**
	VF	17.53	1, 324	**< .001**
	Stimulation	1.75	2, 324	.18
	Cue*VF	63.42	2, 324	**< .001**
	Cue*Stim	.65	4, 324	.63
	VF*Stim	.51	2, 324	.6
	Cue*VF*Stim	.78	4, 324	.54
Decision Criterion	Cue	.42	2, 324	.66
	VF	.3	1, 324	.58
	Stimulation	.33	2, 324	.72
	Cue*VF	2.04	2, 324	.13
	Cue*Stim	.47	4, 324	.76
	VF*Stim	1.09	2, 324	.34
	Cue*VF*Stim	1.4	4, 324	.23

Post Hoc Analysis for Model Three

Accuracy:

Similar to *Model One*, the significant predictive value of cue was observed for accuracy measures, where accuracy was significantly higher following shift right cues ($M = 76.07\%$, $SD = 7.96$) than compared to neutral ($M = 68.22\%$, $SD = 9.91$; difference = 7.85%, BCa 95% CI [.31 1.2], $t(3332) = 3.31$, $p < .001$). Following

this, significance again extended to accuracy being significantly higher for left cues (M = 74.45%, SD = 9.52) than compared to neutral (difference = 6.22%, BCa 95% CI [-1.55 -.5], t(3332) = -3.85, p < .001).

For interaction effects, accuracy was significantly reduced following right shifts of attention and when the target was presented in the left (M = 52.48%, SD = 16) visual field than compared to the right (M = 83.87%, SD = 9.83; difference = 31.39%, BCa 95% CI [-1.95 -.59], t(3332) = -3.65, p < .001). During left shifts of attention, accuracy was instead significantly reduced when the target was presented in the right (M = 57.02%, SD = 14.41) visual field than compared to the left (M = 80.19%, SD = 11.86; difference = 23.17%, BCa 95% CI [1.24 2.58], t(3332) = 5.58, p < .001). Finally, when the cue was neutral, there was a similar pattern of observation seen whereby participants demonstrated a rightward bias and performed significant better during right target presentations (M = 73.85%, SD = 13.88) than compared to left (M = 62.49%, SD = 12.12; difference = 11.36%, BCa 95% CI [.034 1.42], t(3332) = 2.06, p = .04).

Reaction Time:

Following, RTs were significantly increased for uncued shifts of attention (M = 76.77ms, SD = 16.66) than compared to right (M = 71.56ms, SD = 20.43; difference = 5.21ms, BCa 95% CI [-.14 -.049], t(3332) = -4.18, p < .001), but there was no significant difference between shift left versus neutral (p = .97). Again, this works to reinforce the suggestion that participants did not view left cues as informative enough.

For interaction effects between cue and VF conditions, congruency effects were again observed, where during right shifts of attention RT was significantly slower when the target was presented on the left (M = 82.82ms, SD = 20.24) visual field than compared to the right (M = 67.85ms, SD = 21.28; difference = 14.97ms, BCa 95% CI [.081 .26], t(3332) = 3.78, p < .001). Similarly, during left shifts of attention, RT was significantly slower when the target was presented in the right (M = 75.9ms, SD = 23.73) visual field than compared to the left (M = 68.83ms, SD = 17.33; difference = 7.07ms, BCa 95% CI [-.16 -.00089], t(3332) = -1.98, p = .048). In comparison, there was no difference in RT during neutral shifts of attention when targets were presented in the right (M = 741.22ms, SD = 191.73) compared to the left visual field (M = 794.39ms, SD = 168.13; p = .21)

Perceptual Sensitivity:

Finally, when investigating whether *d'* measures could be significantly predicted by any of our task conditions, this model revealed that *d'* was significantly increased when comparing right (M = .99, SD = .37)

versus neutral (*M* = .85, *SD* = .48) attentional shifts (difference = .14, BCa 95% CI [.46 1.38], *t*(324) = 3.91, *p* < .001). This pattern repeated and *d'* significantly increased for shift left (*M* = 1.03, *SD* = .41) versus neutral conditions (difference = .18, BCa 95% CI [-1.45 -.52], *t*(324) = -4.19, *p* < .001). Similarly, *d'* was significantly increased when targets were presented in the right (*M* = 1.17, *SD* = .45) versus left (*M* = .75, *SD* = .44) visual field (difference = .42, BCa 95% CI [-1.45 -.52], *t*(324) = -4.19, *p* < .001).

For interaction effects, one final example of a congruency effect was observed, where during right shifts of attention *d'* was significantly reduced when the target was presented in the left (*M* = .015, *SD* = .54) visual field than compared to the right (*M* = 1.99, *SD* = .59; difference = 1.98, BCa 95% CI [-1.6 -.29], *t*(324) = -2.84, *p* = .0048). During left shifts of attention, *d'* was instead significantly reduced when the target was presented in the right (*M* = .28, *SD* = .46) visual field than compared to the left (*M* = 1.77, *SD* = .73; difference = 1.49, BCa 95% CI [2.01 3.32], *t*(324) = 8.02, *p* < .001). Here, a rightward bias was demonstrated further within the neutral shift condition, where *d'* was significantly reduced when targets were presented in the right visual field (*M* = 1.24, *SD* = .72) than compared to the left (*M* = .45, *SD* = .48; difference = .76, BCa 95% CI [.41 1.72], *t*(324) = 3.21, *p* = .0014).

Model Comparisons

When looking at the observed AIC and BIC values for each model, it appears that the congruency effect (cue*VF) demonstrated the best model for all performance measures. See Table 4 (below) for an overview.

Table 4

AIC and BIC values for each model (cue*VF, stimulation and cue*VF*stimulation), assessing their ability to fit each of the performance measures (accuracy, RT, *d'* and *c*). The lowest values of AIC and BIC for each measure are highlighted in bold font, illustrating the overall best fitting model for the data.

	Model One **Cue*VF**		***Model Two*** **Stimulation Type**		***Model Three*** **Cue*VF*Stimulation**	
	AIC	BIC	AIC	BIC	AIC	BIC
Accuracy	**3677.76**	**3720.58**	3868.21	3892.67	3688.9	3805.12
Reaction Time (RT)	**-9.77**	**39.16**	128.36	158.94	3.27	125.6
Perceptual Sensitivity (d')	**813.01**	**843.69**	1037.04	1056.21	816.99	893.69
Decision Criterion (c)	**366.79**	**397.47**	367.83	387	378.68	455.38

Regression Analysis and Additional GLME Models

From our results we can clearly see evidence of a congruency effect (interaction between cue and VF), but nothing to suggest that our implemented stimulations have had any effect on behavioural measures. Thus, to ensure that we have explored this fully, we conducted a regression analysis to first obtain beta values for *d'* and *c* measures on a single-trial level, corresponding to the predictive value of the congruency effect. Using a GLME model to then examine whether stimulation type influenced these, we determined that beyond the congruency effect, there was no significant main effect of stimulation for either *d'* ($F(2, 54) = .4$, $p = .67$) or *c* ($F(2, 54) = .81$, $p = .45$).

Summary of ANOVA and GLME Similarities and Differences

In the completion of this results section, it is important to end by highlighting the single main similarity and difference seen across the results of our ANOVA and GLME analysis approaches.

Firstly, our main similarity to acknowledge is that both approaches evidenced a significant effect of trial congruency for three out of four of our chosen performance measures ($p < .001$); all besides decision criterion. When referring to trial congruency here, we are specifically describing the interaction effect observed between the trial cue and the visual field in which the target was presented. Secondly, when considering differences, the main one to note is that of the stimulation effect. Whilst the ANOVA analyses showed

significant effects of stimulation conditions on measures of *d'* and performance accuracy, these did not replicate across to our GLME analyses, suggesting that individual differences contributed largely to our initial determination of significance.

5.5 Discussion

The main aim of this investigation was to corroborate our EEG results from the previous chapter and determine whether beta-band oscillations causally influenced measures of perceptual sensitivity (*d'*) and decision criterion (*c*), in a visuospatial attention paradigm.

Our primary findings suggested that participants accurately engaged in the given task, utilising the cues appropriately to shift their visual attention for discrimination of the upcoming target. This can clearly be seen through the presence of a significant congruency effect within the data for measures of performance accuracy, reaction times and perceptual sensitivity (*d'*). In contrast, this effect was not seen in measures of decision criterion, suggesting that participants did not adjust their decision-making criteria based on knowledge from the cue. This is interesting as it suggests that participants were not flexible in how they made their decisions during this task, but instead exhibited constant measures of *c* regardless of all conditions.

Following on from this, it is important to note that when exploring the interaction between neutral shifts of attention and where the target was presented, as well as when looking at the main effect of target location alone (VF) it appears that participants may have had a bias to allocate more attentional resources to the right visual field than compared to the left, illustrated in measures of performance accuracy, *d'* and RT. Perhaps it is the case that participants appeared to be more accurate here, simply because they had a more successful guess rate for the right visual field than compared to the left. With the task design being a two alternative forced choice (2AFC) paradigm and the fact that there is a small number of trials, there is a notable likelihood that this could indeed be the case. However, as performance is above chance, the risk of this is relatively reduced, as well as this suggestion arguably not suiting the observed measures of RT. It is also interesting to note that it contradicts previous literature proposing a general left visual field bias for perceptual judgments, response speed and discrimination accuracy (Meyyappan et al., 2023). This relates to similar literature that has previously illustrated right hemispheric dominance in visuospatial attention, suggesting that performance in the left hemifield should naturally exhibit improved performance (Shulman et al., 2010; Wang et al., 2024), unlike our observed right visual field advantages. This relates to pseudoneglect behaviours, which

is a phenomenon exhibited in healthy individuals whereby there is a natural tendency to favour the left visual hemifield (Bowers & Heilman, 1980; Jewell & McCourt, 2000). It becomes interesting therefore to determine why our healthy participants have not demonstrated this pseudoneglect behaviour and instead present evidence of the reverse (i.e., rightward bias). Perhaps this could be attributed to our largely female sample, where one previous study found evidence to suggest that visual processing within the female brain is selectively lateralised to the left hemisphere in response to local targets (Roalf et al., 2006). Though we believe this to be unlikely as previous studies have found evidence of rightward biases even when studies have included subjects with matched sex distributions (see Szczepanski & Kastner, 2013). Thus, we propose that this is perhaps more dependent on the implemented task features than it is our selection of participants. Within our study we have asked participants to discriminate the motion direction of fast moving and briefly presented targets, of which the left hemisphere may be more attuned to the requirements of high temporal resolution (Brown & Nicholls, 1997; Laycock et al., 2007; Nicholls, 1996), resulting in the enhanced perception of such stimuli in the right visual field. For example, Brown and Nicholls, (1997) tested this theory with auditory stimuli, finding that when brief (in time) auditory events were presented to participants, performance was significantly better for those presented within the right field than left, demonstrating left hemisphere advantages that can be used to account for our similar findings within the visual domain.

Additionally, perhaps we could attribute this bias to TMS only being delivered to the right cortical hemisphere within our current study. There is a chance that the somatosensory activation caused by the TMS served as an additional attentional grabber, working beyond the given task cues of shift left, right and neutral. This could feasibly have drawn participants to focus on the right visual field and thus resulted in improved behavioural measures at this location, a suggestion which is especially feasible when considering that the target onset was timed to match the final TMS pulse. However, without having a 'no TMS' condition, it is difficult to determine the accuracy of this suggestion. There is also the possibility that this preference in visual field may be due to our stimulation protocols resulting in a relative inhibition of the left visual space. This would be a convincing argument if looking solely at the impact of alpha-band oscillations, as increases in alpha have been frequently shown to inhibit stimuli that appear in the contralateral hemifield (e.g., Jensen & Mazaheri, 2010; Kelly et al., 2006; Klimesch, 2012; Rihs et al., 2009; Rihs et al., 2007; Sauseng et al., 2005; Thut et al., 2006). However, this pattern of behaviour is seen across all stimulation conditions, meaning that we

cannot, therefore, address these unexpected findings as a result of rTMS disrupting the normal functioning of the brain, or entraining oscillations to causally modulate behaviour. Therefore, we believe that the most convincing explanation would be surrounding the TMS pulses capturing participants' attention, or perhaps even the brief presentation of targets. Regardless of the reasoning though, based on the significant congruency effects observed with right and left shifts of attention, we can be assured that the task was carried out appropriately and thus reflects an accurate test of visuospatial attention.

This leads us to then investigate whether our hypothesised effect held true, where ANOVA results revealed that there was a significant main effect of stimulation type on measures of both performance accuracy and perceptual sensitivity (*d'*). Specifically, task accuracy significantly increased following alpha band stimulation than compared to AR, but interestingly there was no significant difference when comparing alpha band stimulation with beta. From our results, we can see that the mean difference between these frequency stimulations was relatively small, suggesting that perhaps the effects of stimulation here were not frequency specific. When looking next at *d'*, both alpha and beta rTMS resulted in a significantly increased *d'* measure than compared to AR stimulation, suggesting that stimulation of the rV5/MT resulted in improved performance by significantly separating the target signal from noise. Again, there was no observable difference between these two active stimulation conditions (alpha and beta), reinforcing suggestions that our observed results are not frequency specific. These results go to both support and contrast our predictions, where we hypothesised that there would be a significant improvement of perceptual performance following beta-band stimulation, specifically reflected in indexes of *d'* and *c* measures. Whilst we did indeed find that beta-band stimulation resulted in increases of *d'*, it is also true that alpha-band stimulation matched this effect. This could possibly highlight that *d'* can be causally influenced by a broad range of frequencies, the extent of which cannot be revealed by this study alone as we only attempted to entrain 10 and 20 Hz oscillations. Crucially, this does not in fact contrast our previous EEG results, as our main regression analysis found that the phase of beta-band oscillations could predominately predict *d'* measures, but also that this predictive ability did extend into alpha frequencies, just less so.

We should also highlight here that the similar results for both 10 Hz and 20 Hz stimulation frequencies could result from the fact that they are considered harmonics of one another. Previous studies have suggested that when stimulating the cortex to entrain oscillations at alpha frequencies, similar effects can be seen at the

next harmonic frequency (Lin et al., 2021; Zmeykina et al., 2020). This is seen most notably in a study by Lin et al., (2021), where stimulating the occipital cortex (around channel Oz, O2 and PO4) at a frequency of 10 Hz (alpha) resulted in the induction of both 10 Hz and 20 Hz oscillations, i.e., alpha and it's beta harmonic. Importantly, the entrainment of the harmonic within their study only lasted one cycle beyond the last TMS pulse. However, as our investigation delivered the last pulse at the time of target onset, it is feasible that our 10 Hz stimulation procedure resulted in the entrainment of both alpha and beta oscillations, accounting for why we have not observed any notable differences in performance between the two.

Whilst this is an interesting result showing alpha and beta effects for *d'*, we did not find any causal influence of stimulation type on *c* measures, suggesting that perhaps decision criterion is not causally modulated by alpha or beta oscillations, pointing towards possible alternative mechanisms that may be responsible for influencing this measure. Based on previous literature, this could feasibly be gamma-band oscillations instead, where stimulation of the rFEF at 50 Hz has found that this caused participants to be more liberal in their response criterion (i.e., reducing measures of *c*; Chanes et al., 2013), although it is important to remember that this particular study by Chanes et al., (2013) uses a conscious detection task and is arguably more reflective of bottom-up mechanisms.

Alternatively, it could be that the stimulation frequencies we chose for our rTMS protocols during this experiment were not optimal to achieve our desired effect, particularly when investigating the causal influence of beta oscillations. Here we chose to entrain oscillations at 20 Hz, which was a choice driven by an underlying aim of being able to compare our results with previous literature that has typically utilised this same definition of beta-band activity (e.g., Corbetta & Shulman, 2002; Riddle et al., 2019). However, it is also true that the beta-band stretches up to frequencies of 30 Hz and so in hindsight, it would have been equally justified to utilise a higher frequency within this study, based specifically on the results from our previous EEG investigation. It was here that we found phase effects were present predominantly in frequency ranges around 25 Hz. Whilst the difference between 20 and 25 Hz may seem non-substantial, it could feasibly account for why we did not see the hypothesised effects and so it would be interesting to repeat this experiment with different definitions of both alpha- and beta-band frequencies. With more time available to us, perhaps this experiment could have also been extended into two sessions, so that the effects of gamma-band stimulation could be additionally explored. Whilst not embedded within the aims of this investigation, by including gamma-band

frequencies we would have been able to comment on the reliability of previous studies that have evidenced a role of these oscillations in determining decision criterion measures (Chanes et al., 2013). Since we did not find such effects with either alpha or beta oscillations in our current investigation, it brings into question whether we have overlooked the role of gamma oscillations here. This is something that should be taken into consideration for future investigations.

Moreover, perhaps the most valid method to adopt when choosing stimulation parameters for this investigation would be through utilising individualised frequencies or even through matching the 'natural' frequency of the biological oscillator (i.e., region V5); which can vary across individuals. This is proposed on the basis that delivering rhythmic TMS does not create new, artificial oscillations but instead interacts with and entrains a naturally occurring oscillation (Coldea et al., 2022). By implementing TMS protocols that match these rhythms, studies have shown that this may increase the efficacy of TMS by facilitating entrainment processes (Pikovskij et al., 2003). On the other hand, without this, it is feasible that our delivered TMS has impaired the 'natural' frequency of V5, resulting in the varied modulation of performance across participants, ultimately causing problems when averaging across our performance measures (Coldea et al., 2022).

When exploring our results further, it is also interesting to note that there is no interaction effect between stimulation type and the visual field that the target was presented in. When drawing on knowledge from previous literature, this is an effect that we would expect to see based on our understanding of the lateralised behaviours for both alpha and beta band oscillations. To expand, prior evidence has clearly outlined that by increasing alpha or beta oscillatory activity in one hemisphere of the brain, we can typically expect to see an effect that presents itself in the contralateral hemifield (Brewer & Barton, 2012; Marshall et al., 2015). Beyond just the effects of neural activity, this reflects how the visual system is mapped out (i.e., right occipital hemisphere controls left visual inputs), shown for example when previous studies have stimulated the right V5/MT (identical to our region of interest) to induce moving phosphenes in the left visual field (Veniero et al., 2021). It is challenging to determine why we have not replicated this within our results, where we would expect participants' performance in the left hemisphere to be causally influenced by our implemented active TMS protocols (alpha and beta). Crucially though, this lack of significance may be due to our reliance on assumptions of oscillatory entrainment being achieved through our stimulation protocols. Here we refer to the delivery of rhythmic TMS causing neural activity at region V5 to synchronise with our stimulation frequencies

(Thut, Veniero, et al., 2011), i.e., at alpha or beta frequencies. In reality, without concurrent EEG we are unable to assess whether this was truly achieved. Additionally, we are further limited by our choice of stimulation intensity, where all participants began the experiment with stimulation delivered at 60% MSO, with this only reduced incrementally if participants were feeling uncomfortable or muscular twitches were evoked. Whilst this is a legitimate approach that has been successfully utilised in previous investigations (Garcia-Sanz et al., 2022; Turi et al., 2021), we acknowledge that it is suboptimal for stimulation protocols due to individual differences such as skull thickness (Stokes et al., 2007), grey matter volume, and other anatomical and/or functional individual differences (Rosso et al., 2017). Without controlling for this the 'dosage' of TMS will likely differ across participants (Herbsman et al., 2009). Instead of using MSO to define our stimulation intensities, arguably we could have utilised phosphene thresholds, however this would have likely resulted in a high number of participant exclusions based on the likely induction of phosphenes interfering with participant's vision during the visual task.

Despite these interesting displays of results, what we can also see from our findings is that there are individual differences present throughout all the performance measures, specifically when looking at stimulation effects; illustrated by large confidence interval ranges and when plotting participant data. Whilst this is not unexpected as previous literature has revealed that there is often high inter-subject variability when entraining oscillations via TMS (Gießing et al., 2020; Trajkovic et al., 2024; Wasserman et al., 2008), it has ultimately resulted in our GLME analyses offering only non-significant findings for the effect of stimulation on all performance measures (accuracy, RT, *d'* and *c*). Here, we chose to implement these models so that we could account for the random effects observed across individuals and thus evaluate the confounding influence of individual differences. In a broad overview of such results, they first offer contradictions to our previous ANOVA results by no longer offering support to our hypothesis of beta oscillations casually modulating *d'*. In detail, when examining whether stimulation type could predict both *d'* and *c* measures either in a model on its own or in combination with our other predictors (cue and VF), all stimulation conditions had non-significant effects. This suggests that neither alpha nor beta stimulation had any causal influence on perceptual performance in a visuospatial task when accounting for individual differences, contradicting our previous EEG findings. This is further emphasised with the non-significant results from our final regression analysis corroborating no effect of stimulation on predicting SDT measures of *d'* and *c*. Reasons surrounding why this may be have been previously

outlined already within this discussion, where it would be interesting to repeat this experiment with stimulation intensities set to consider individual thresholds (i.e., phosphene thresholds), 'natural' frequencies of region V5, and perhaps even to utilise functional MRI techniques as a localisation tool for region V5, arguably leading to more accurate coordinates than compared to relying on atlases. By adopting these approaches, it is likely that our observed individual differences would be reduced and offer a more robust reflection of our stimulation effects, which would perhaps be larger than we are currently seeing (Trajkovic et al., 2024). These approaches were not adopted within the current study due to a lack of resources.

Caution in the interpretation of these results is stressed though as it is likely that our investigation is not sufficiently powered. Whilst we did aim for a sample size of around 25 participants, due to poor performances and the exclusion of some datasets, we ended our recruitment period with a total collection of 19 evaluable participants. Due to MRI-related funding being restricted and not covering any additional image acquisition needed for rV5/MT localisation, we could not replace the five excluded participants within our overall sample. With this in mind, we think it would be most appropriate to label these results as somewhat inconclusive. Though they embody trends that suggest there is some modulatory effect of alpha and beta oscillations on measures of *d'*, much like our hypothesis, there is not yet enough evidence to suggest that this is a robust finding.

5.6 Conclusion

In summary of our findings, this study has determined inconclusive results as to the role of beta-band oscillations in causally modulating the top-down control of visuospatial attention, as indexed by measures of perceptual sensitivity (*d'*). Whilst we found evidence that pointed towards this effect, individual differences and a potential lack of statistical power have resulted in these GLME effects remining non-significant. Despite this, this study, alongside our EEG experiment, has prompted a review of the current literature suggesting that we arguably have not been investigating visuospatial attention in an optimal way. We hope that these two studies will be used as a reference for future investigations examining whether neural oscillations may modulate how we shift our attention in visual space, and how perception is subsequently influenced by this.

Chapter 6: General Discussion

As a whole, this thesis explored the role of neuronal oscillations in modulating the top-down control of visuospatial attention, perception and more generally, cortical excitability. Specifically, we focused on oscillations within the occipital cortex, identifying the influence of oscillatory rhythms that were either under the control of higher-order areas, i.e., beta oscillations controlled by FEF regions, or categorised as ongoing, i.e., alpha oscillations present at rest.

To achieve such investigations, we adopted several methods ranging from different neuroimaging techniques to improved design paradigms, to explorative analysis methods and the use of open-science procedures. Each of these approaches were applied throughout this thesis to deepen of understanding of how our brain waves cause our cortical processes to fluctuate rhythmically, often resulting in the waxing and waning of cognitive performance and behaviour.

6.1 Summary of Findings

To briefly summarise our findings, in our initial investigation we first explored the role of oscillations in establishing cortical excitability levels, finding that the amplitude and phase of occipital alpha-band frequencies could influence motor cortex excitability at rest. These findings work to underscore the importance of global modulatory mechanisms in shaping network interactions, as we were able to reveal how ongoing oscillations influence visuo-motor connections within the cortex, perhaps demonstrating their underlying cognitive function in these integration pathways.

Next, we looked towards the role of occipital alpha-band oscillations in modulating visual perception, attempting to replicate the findings of a popular study by Mathewson et al., (2009). By repeating their previous design, we found evidence in partial support of their original results, evidencing a significant alpha phase effect on visual perception, but independently of power.

By extending such investigations, we then explored related mechanisms to determine that when oscillations were under the influence of higher-order areas, i.e., the FEFs during shifts of attention, this attentional orienting was accompanied by a modulation in the phase of occipital beta, consistent with alternating sampling of both visual fields. Such results were matched with fluctuations of perceptual sensitivity

and decision criterion which could be further predicted by the beta phase, suggesting that this oscillatory mechanism extended into the behavioural domain.

Though, when attempting to add a level of causality to our findings, we did not find robust evidence to support our proposed role of beta oscillations in shifts of visual attention. This was the outcome of our subsequent TMS investigation, where we attempted to entrain alpha, beta and arrhythmic frequencies at region V5/MT whilst participants performed a modified version of our original visuospatial attention task. Resulting performance revealed that whilst there was some suggestion of an effect of stimulation type on performance, this did not appear to be frequency specific and was diminished when accounting for individual differences. However, it is important to note that there are clear limitations to our investigation here, making interpretations of our results relatively constrained.

6.2 Contribution to Knowledge

From this accumulation of research evidence, we have been able to clearly establish the importance of neuronal oscillations, predominantly those within alpha and beta frequencies, in modulating our cognitive processes and causing them to fluctuate rhythmically over time. Of course, this is not new knowledge, a reality that we hope has been reiterated through the extensive literature that has been referenced throughout this thesis. However, we have been able to offer contributions to this field which should be accentuated clearly. Firstly, we believe that our results show evidence of an occipital preference for which oscillatory mechanisms are engaged at any one time. To detail this, our results are perhaps reflective of how when individuals are at rest, cortical modulations are led by ongoing alpha oscillations, whilst 'controlled' beta oscillations seem to exert their effects most often when individuals are engaged in a task, i.e., shifting attention.

Following this, it is important to acknowledge that our findings build upon previous research to account for potential pitfalls in earlier study designs, creating what we consider to be increasingly valid methods of investigation. This is particularly true for our EEG study (Chapter 4) where we studied endogenous visuospatial attention, whilst controlling for the impact of salient stimuli and ensuring the presence of prominent distractors. We have also explored measures of signal detection theory to continue to advance knowledge within the field, where few studies to date have looked to explore the neuronal mechanisms of perceptual sensitivity and decision criterion within a visuospatial task. By doing so, we have been able to gain a deeper understanding of how our perceptual decisions are guided by oscillatory behaviours. When exploring

the literature also, a surprising number of studies have restricted their analyses to only explore alpha-band frequencies, as these have traditionally been most popular. Whilst this is considered to be a valid method to implement when conducting investigations, it runs the risk of missing important findings and means that the literature often overlooks the importance of beta-band oscillations in modulating cognitive processes. Our results have thus promoted its inclusion in future research, as we have clearly presented evidence of its significance.

Additionally, two of our experimental chapters (Chapter 2 & 3) have been written in part to promote the adoption of open-science techniques to continue examinations into the mechanisms of oscillatory influence. By embracing these collaborative techniques, as a field we can establish both valid paradigms and eventually a robust, shared dataset that we can draw more reliable conclusions from. This is something that is growing within the field of neuroscience specifically, and we are excited to be a part of its development.

In terms of how this research fits into the broader understanding of vision, we provide clear evidence that neural oscillations in the occipital cortex play a significant role in modulating cognitive processes related to visual perception, including when this is preceded by goal-directed shifts of attention. Specifically, our findings highlight the importance of ongoing alpha-band oscillations in facilitating communication between occipital and parietal brain regions—an interaction that underpins our ability to perceive and respond to visual stimuli within our environment. Our studies also demonstrates that our visual processes fluctuate with the phase of both alpha- and beta-band oscillations, suggesting that the brain samples visual input in a phase-dependent manner. While alpha oscillations appear to be more influential during ongoing, spontaneous activity, beta-band oscillations seem more closely tied to goal-directed behaviour. Reflecting on our earlier analogy of why we sometimes notice a distant flash of lightning and other times do not. These natural fluctuations in visual processing offer a compelling explanation for such variability in perception.

6.3 Applications

Beyond the theoretical contributions of this thesis, it is also important to consider how these findings may inform real-world applications, particularly within the field of clinical neuroscience. By providing insight into what may constitute ‘normal’ neural activity for the processes of visual cognition, our research lays the groundwork for developing interventions that could enhance visual perception, attention, and related cognitive behaviours. For instance, neurostimulation techniques such as transcranial alternating current stimulation

(tACS) or repetitive transcranial magnetic stimulation (rTMS), could be designed to selectively enhance beta-band oscillations within the visual cortex, potentially improving goal-directed visual attention and increasing perceptual sensitivity at task-relevant spatial locations. Furthermore, understanding what 'typical' oscillatory patterns look like puts us in a position to better identify deviations from this norm, offering potential biomarkers for visual/attentional disorders such as visual neglect (i.e., hemispatial neglect) or attention deficit disorder (ADD). However, it is essential to note that whilst this may present exciting opportunities, we are still a long way off this achievement. As our findings here are arguably still preliminary, a substantial amount more research is required to establish reliable distinctions between 'normal' and 'non-normal' oscillatory activity, with our study representing just one step towards that larger goal.

6.4 Limitations

We should also make it clear that there are some limitations to our investigations which potentially restrict the evaluations that can be drawn. These are addressed within the chapters themselves but for the purpose of this discussion, some points will be condensed and broadly reviewed here also.

The first of these is our smaller-than-optimal sample sizes of 10 and 19 participants during our two TMS experiments. These were mainly due to limited resources, consequently meaning that our studies may be underpowered. This is not unusual for TMS studies though, as participants often remain apprehensive about participating in neuromodulation experiments due to the strict inclusion criteria and the acknowledgement that it can sometimes be uncomfortable, as well as the fact that conducting these studies is quite resource intensive – particularly with concurrent EEG. However, when looking at some of the literature that we are comparing against, the majority of these sit within our sample window, where Sauseng et al., (2011) recruited only 12 participants, Riddle et al., (2019) recruited 17, and Mäki and Ilmoniemi, (2010) recruited a similar 16 – to name a few. This is important to recognise as it suggests that perhaps our results are not so removed from previous evidence within the field, alongside reinforcing the notion that small sample sizes remain an issue that should be tackled in future research. To account for this, we can again look to open-science methods, where we have presented an example of a multi-lab experiment (see Chapter 3) aimed at recruiting large participant numbers that would not be feasible within a single lab. By adopting these methods, findings across the domain of neuroscience would hugely benefit and become notably more reliable.

Next, our second limitation to address is our reliance on assumptions within our TMS experiment, exploring the causal relationship between oscillations and visuospatial attention. As we were not able to collect EEG data in parallel to implementing TMS, we can only assume that we achieved neuronal entrainment of the desired frequencies (10 and 20 Hz). In reality, this may not be the case and underlying brain rhythms may not have synchronised with our delivered pulses. We have instead based our assumptions of entrainment on a wealth of previous literature, where findings have predominately revealed evidence for the successful entrainment of oscillations via rTMS methods (Thut, Veniero, et al., 2011; Wang et al., 2024). This has included a previous investigation by Ruzzoli and Soto-Faraco (2014) who were able to successfully induce 10 and 20 Hz oscillations by using rTMS techniques, with pulse timings matched to our chosen protocol (i.e., last pulse synchronised with onset of stimuli). In the future, it would be interesting to repeat this experiment with EEG recordings acquired in parallel, alongside a larger sample size to achieve greater statistical power.

Lastly, whilst not necessarily a limitation within the studies that make up this thesis, it is important to acknowledge the common pattern of results arising from our investigations, where high levels of individual differences have been observed across each of our studies. Whilst we believe that we have appropriately accounted for these differences by implementing analyses such as those that weight individual contributions to the data, it is important to discuss this variation for the purpose of future investigations. As with all explorations in neuroscience, we expect there to be some level of noise within the data, based predominately on individual variances in neural signals, cognitive patterns and even biological structures across subjects. This is centred on the unavoidable fact that as humans we are all slightly different. However, the level of variation that we have observed here is arguably somewhat greater than we would expect, with some individuals demonstrating opposite neuronal activity to one another. As individual data is often not presented within the literature, it is difficult to tell where our experience of this lies within the field, where the large majority of studies simply choose to report averaged results; perhaps considered more robust. We wish to argue that regardless of the ‘main’ result (i.e., the final averaged EEG signal), future research should endeavour to be transparent with single-level analyses, so that readers are able to gain an insight into individual contributions and how they may vary across the sample. Further, it should also be stressed that where possible, researchers should seek to implement analyses that do indeed consider individual differences, much like our own investigations, so that any averaged data is not misleading based on skewness and bias, dominated by a few

'leading' participants. Without embracing methodological frameworks to account for variability, such as increasing sample sizes, employing individualised neuroimaging techniques and applying advanced statistical methods such as mixed-effects modelling, it is difficult to determine whether averaged results are generalisable or even reliable. To accentuate the importance of this, consider our previous results from Chapter 5, whereby our significant effect of neural stimulation was eliminated when employing a more appropriate analysis that accounted for individual differences. With this knowledge, it is feasible to imagine that there are previous investigations whose significant results would also be subject to this same fate if their analyses were modified in similar ways.

6.5 Conclusion

In short, we hope that each of these experimental investigations can be viewed as a direct contribution to the growing attempts to resolve uncertainties when investigating rhythms in cognition. The need for this research is a direct result of contradictory and unclear evidence currently dominating the field, even despite investigations into this topic having been ongoing for decades. Whilst it has been well evidenced that characteristics of oscillations (i.e., their periodicity) are able to orchestrate cognition (e.g., Fries, 2015; Thut et al., 2012; Thut & Miniussi, 2009; VanRullen, 2016), recent reviews have revealed just how extensively varied the evidence base currently is, with some revealing that the literature currently stands 50/50 in support of rhythmic sampling theories (Keitel et al., 2022; Kienitz et al., 2022). Alongside this, new evidence is still coming to light that challenges findings we have previously considered to be robust, i.e., the inhibitory nature of alpha oscillations. We have argued throughout this thesis that it is likely such debates and differences in findings are a result of poor study designs and inconsistencies in the approaches used by researchers. Subsequently, we have used this piece of work to illustrate more valid methods of investigating some of these topics, alongside promoting the use of open-science methods to increase our sample sizes, data and collaborative efforts. We hope that this thesis has demonstrated the exciting potential that can arise from implementing these changes, moving one step closer to uncovering the true role of occipital oscillations.

References

Adrian, E. D., & Matthews, B. H. C. (1934). The Berger rhythm: Potential changes from the occipital lobes in man. *Brain*, *57*(4), 355–385. https://doi.org/10.1093/brain/57.4.355

Ah Sen, C. B., Fassett, H. J., El-Sayes, J., Turco, C. V., Hameer, M. M., & Nelson, A. J. (2017). Active and resting motor threshold are efficiently obtained with adaptive threshold hunting. *PLOS ONE*, *12*(10), e0186007. https://doi.org/10.1371/journal.pone.0186007

Albouy, P., Weiss, A., Baillet, S., & Zatorre, R. J. (2017). Selective Entrainment of Theta Oscillations in the Dorsal Stream Causally Enhances Auditory Working Memory Performance. *Neuron*, *94*(1), 193-206.e5. https://doi.org/10.1016/j.neuron.2017.03.015

Albuquerque, R. M., Antonino, G. B., Do Nascimento, A. C. R., De Lima, B. S. N., Lima, F. A., De Melo, D. G., Araújo, C. S., Guerra, S. V. C., Brito, R. D. M., & Machado, K. K. D. M. S. (2023). A practical guide to the evaluation of the functional integrity of the corticospinal tract by transcranial magnetic stimulation in post-stroke patients. *Brain Imaging and Stimulation*, *2*, e5097. https://doi.org/10.17267/2965-3738bis.2023.e5097

Allport, A. (1987). Selection for action: Some behavioural and neurophysiological considerations of attention and action. In *Perspectives on Perception and Action* (H. Heuer&Sanders (Eds), pp. 395–419). L. Erlbaum Associates.

Anand, S., & Hotson, J. (2002). Transcranial magnetic stimulation: Neurophysiological applications and safety. *Brain and Cognition*, *50*(3), 366–386. https://doi.org/10.1016/S0278-2626(02)00512-2

Anderson, B. A. (2013). A value-driven mechanism of attentional selection. *Journal of Vision*, *13*(3), 7–7. https://doi.org/10.1167/13.3.7

Anderson, N. D. (2015). Teaching signal detection theory with pseudoscience. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.00762

Anton-Erxleben, K., & Carrasco, M. (2013). Attentional enhancement of spatial resolution: Linking behavioural and neurophysiological evidence. *Nature Reviews Neuroscience*, *14*(3), 188–200. https://doi.org/10.1038/nrn3443

Antonov, P. A., Chakravarthi, R., & Andersen, S. K. (2020). Too little, too late, and in the wrong place: Alpha band activity does not reflect an active mechanism of selective attention. *NeuroImage*, *219*, 117006. https://doi.org/10.1016/j.neuroimage.2020.117006

Babiloni, C., Del Percio, C., Arendt-Nielsen, L., Soricelli, A., Romani, G. L., Rossini, P. M., & Capotosto, P. (2014). Cortical EEG alpha rhythms reflect task-specific somatosensory and motor interactions in humans. *Clinical Neurophysiology*, *125*(10), 1936–1945. https://doi.org/10.1016/j.clinph.2014.04.021

Babiloni, C., Pizzella, V., Gratta, C. D., Ferretti, A., & Romani, G. L. (2009). Chapter 5 Fundamentals of Electroencefalography, Magnetoencefalography, and Functional Magnetic Resonance Imaging. In *International Review of Neurobiology* (Vol. 86, pp. 67–80). Elsevier. https://doi.org/10.1016/S0074-7742(09)86005-4

Badawy, R. A. B., Loetscher, T., Macdonell, R. A. L., & Brodtmann, A. (2012). Cortical excitability and neurology: Insights into the pathophysiology. *Functional Neurology*, *27*(3), 131–145.

Banerjee, S., Grover, S., & Sridharan, D. (2017). Unraveling Causal Mechanisms of Top-Down and Bottom-Up Visuospatial Attention with Non-invasive Brain Stimulation. *Journal of the Indian Institute of Science*, *97*(4), 451–475. https://doi.org/10.1007/s41745-017-0046-0

Banich, M. T. (with Compton, R. J.). (2018). *Cognitive Neuroscience* (4th ed). Cambridge University Press.

Bánki, A., Brzozowska, A., Hoehl, S., & Köster, M. (2022). Neural Entrainment vs. Stimulus-Tracking: A Conceptual Challenge for Rhythmic Perceptual Stimulation in Developmental Neuroscience. *Frontiers in Psychology*, *13*, 878984. https://doi.org/10.3389/fpsyg.2022.878984

Barker, A. T. (1991). An Introduction to the Basic Principles of Magnetic Nerve Stimulation: *Journal of Clinical Neurophysiology*, *8*(1), 26–37. https://doi.org/10.1097/00004691-199101000-00005

Barker, A. T., Jalinous, R., & Freeston, I. L. (1985). Non-invasive magnetic stimulation of human motor cortex. *The Lancet*, *325*(8437), 1106–1107. https://doi.org/10.1016/S0140-6736(85)92413-4

Barnett, M. W., & Larkman, P. M. (2007). How to understand it: The action potential. *Practical Neurology*, *7*(3), 192–197.

Barone, J., & Rossiter, H. E. (2021). Understanding the Role of Sensorimotor Beta Oscillations. *Frontiers in Systems Neuroscience*, *15*, 655886. https://doi.org/10.3389/fnsys.2021.655886

Başar, E., & Güntekin, B. (2012). A short review of alpha activity in cognitive processes and in cognitive impairment. *International Journal of Psychophysiology*, *86*(1), 25–38. https://doi.org/10.1016/j.ijpsycho.2012.07.001

Bastiaansen, M., Mazaheri, A., & Jensen, O. (2011). Beyond ERPs: Oscillatory neuronal dynamics. In *Oxford handbook of event-related potential components* (ES. Kappenman, SJ. Luck (Eds.), pp. 31–49). Oxford University Press. https://doi.org/10.1093/oxfordhb/9780195374148.013.0024

Bastos, A. M., Vezoli, J., Bosman, C. A., Schoffelen, J.-M., Oostenveld, R., Dowdall, J. R., De Weerd, P., Kennedy, H., & Fries, P. (2015). Visual Areas Exert Feedforward and Feedback Influences through Distinct Frequency Channels. *Neuron*, *85*(2), 390–401. https://doi.org/10.1016/j.neuron.2014.12.018

Bates, J. a. V. (1951). Electrical activity of the cortex accompanying movement. *The Journal of Physiology*, *113*(2–3), 240–257. https://doi.org/10.1113/jphysiol.1951.sp004569

Baumgarten, T. J., Schnitzler, A., & Lange, J. (2016). Prestimulus Alpha Power Influences Tactile Temporal Perceptual Discrimination and Confidence in Decisions. *Cerebral Cortex*, *26*(3), 891–903. https://doi.org/10.1093/cercor/bhu247

Bekisz, M., & Wróbel, A. (1993). 20 Hz rhythm of activity in visual system of perceiving cat. *Acta Neurobiologiae Experimentalis*, *53*(1), 175–182.

Bekisz, M., & Wróbel, A. (1999). Coupling of beta and gamma activity in corticothalamic system of cats attending to visual stimuli: *NeuroReport*, *10*(17), 3589–3594. https://doi.org/10.1097/00001756-199911260-00023

Bekisz, M., & Wróbel, A. (2003). Attention-dependent coupling between beta activities recorded in the cat's thalamic and cortical representations of the central visual field. *European Journal of Neuroscience*, *17*(2), 421–426. https://doi.org/10.1046/j.1460-9568.2003.02454.x

Belopolsky, A. V., & Theeuwes, J. (2012). Updating the premotor theory: The allocation of attention is not always accompanied by saccade preparation. *Journal of Experimental Psychology: Human Perception and Performance*, *38*(4), 902–914. https://doi.org/10.1037/a0028662

Ben-Simon, E., Podlipsky, I., Arieli, A., Zhdanov, A., & Hendler, T. (2008). Never Resting Brain: Simultaneous Representation of Two Alpha Related Processes in Humans. *PLoS ONE*, *3*(12), e3984. https://doi.org/10.1371/journal.pone.0003984

Benwell, C. S. Y., Coldea, A., Harvey, M., & Thut, G. (2022). Low pre-stimulus EEG alpha power amplifies visual awareness but not visual sensitivity. *European Journal of Neuroscience*, *55*(11–12), 3125–3140. https://doi.org/10.1111/ejn.15166

Benwell, C. S. Y., Tagliabue, C. F., Veniero, D., Cecere, R., Savazzi, S., & Thut, G. (2017). Prestimulus EEG Power Predicts Conscious Awareness But Not Objective Visual Performance. *Eneuro*, *4*(6), ENEURO.0182-17.2017. https://doi.org/10.1523/ENEURO.0182-17.2017

Berger, B., Minarik, T., Liuzzi, G., Hummel, F. C., & Sauseng, P. (2014). EEG Oscillatory Phase-Dependent Markers of Corticospinal Excitability in the Resting Brain. *BioMed Research International*, *2014*, 1–8. https://doi.org/10.1155/2014/936096

Berger, H. (1929). Über das Elektrenkephalogramm des Menschen. *Archiv für Psychiatrie und Nervenkrankheiten*, *87*(1), 527–570. https://doi.org/10.1007/BF01797193

Bergmann, T. O. (2018). Brain State-Dependent Brain Stimulation. *Frontiers in Psychology*, *9*, 2108. https://doi.org/10.3389/fpsyg.2018.02108

Bergmann, T. O., & Hartwigsen, G. (2021). Inferring Causality from Noninvasive Brain Stimulation in Cognitive Neuroscience. *Journal of Cognitive Neuroscience*, *33*(2), 195–225. https://doi.org/10.1162/jocn_a_01591

Bergmann, T. O., Lieb, A., Zrenner, C., & Ziemann, U. (2019). Pulsed Facilitation of Corticospinal Excitability by the Sensorimotor μ-Alpha Rhythm. *The Journal of Neuroscience*, *39*(50), 10034–10043. https://doi.org/10.1523/JNEUROSCI.1730-19.2019

Bergmann, T. O., Mölle, M., Schmidt, M. A., Lindner, C., Marshall, L., Born, J., & Siebner, H. R. (2012). EEG-Guided Transcranial Magnetic Stimulation Reveals Rapid Shifts in Motor Cortical Excitability during the Human Sleep Slow Oscillation. *The Journal of Neuroscience*, *32*(1), 243–253. https://doi.org/10.1523/JNEUROSCI.4792-11.2012

Bestmann, S., & Krakauer, J. W. (2015). The uses and interpretations of the motor-evoked potential for understanding behaviour. *Experimental Brain Research*, *233*(3), 679–689. https://doi.org/10.1007/s00221-014-4183-7

Bishop, Geo. H. (1933). Cyclic changes in excitability of the optic pathway of the rabbit. *American Journal of Physiology*, *103*, 213–224.

Blackwood, D. H. R., & Muir, W. J. (1990). Cognitive Brain Potentials and their Application. *British Journal of Psychiatry*, *157*(S9), 96–101. https://doi.org/10.1192/S0007125000291897

Blanke, O., Spinelli, L., Thut, G., Michel, C. M., Perrig, S., Landis, T., & Seeck, M. (2000). Location of the human frontal eye field as defined by electrical cortical stimulation: Anatomical, functional and

electrophysiological characteristics. *NeuroReport*, *11*(9), 1907–1913. https://doi.org/10.1097/00001756-200006260-00021

Blankertz, B., Lemm, S., Treder, M., Haufe, S., & Müller, K.-R. (2011). Single-trial analysis and classification of ERP components—A tutorial. *NeuroImage*, *56*(2), 814–825. https://doi.org/10.1016/j.neuroimage.2010.06.048

Bloomfield, P. (2000). *Fourier Analysis of Time Series: An Introduction* (1st ed.). Wiley. https://doi.org/10.1002/0471722235

Böckmann-Barthel, M. (2023). *Sensitivity index d'* (Version 3.1.1.0) [MATLAB Central File Exchange]. https://www.mathworks.com/matlabcentral/fileexchange/65377-sensitivity-index-d

Bohil, C. J., Szalma, J. L., & Hancock, P. A. (2015). Psychophysical Methods and Signal Detection: Recent Advances in Theory. In R. R. Hoffman, P. A. Hancock, M. W. Scerbo, R. Parasuraman, & J. L. Szalma (Eds.), *The Cambridge Handbook of Applied Perception Research* (1st ed., pp. 22–38). Cambridge University Press. https://doi.org/10.1017/CBO9780511973017.007

Bolognini, N., & Ro, T. (2010). Transcranial Magnetic Stimulation: Disrupting Neural Activity to Alter and Assess Brain Function. *Journal of Neuroscience*, *30*(29), 9647–9650. https://doi.org/10.1523/JNEUROSCI.1990-10.2010

Bonnefond, M., & Jensen, O. (2024). The role of alpha oscillations in resisting distraction. *Trends in Cognitive Sciences*, S136466132400295X. https://doi.org/10.1016/j.tics.2024.11.004

Boon, L. I., Geraedts, V. J., Hillebrand, A., Tannemaat, M. R., Contarino, M. F., Stam, C. J., & Berendse, H. W. (2019). A systematic review of MEG-based studies in Parkinson's disease: The motor system and beyond. *Human Brain Mapping*, *40*(9), 2827–2848. https://doi.org/10.1002/hbm.24562

Borroto-Escuela, D. O., Gonzalez-Cristo, E., Ochoa-Torres, V., Serra-Rojas, E. M., Ambrogini, P., Arroyo-García, L. E., & Fuxe, K. (2024). Understanding electrical and chemical transmission in the brain. *Frontiers in Cellular Neuroscience*, *18*, 1398862. https://doi.org/10.3389/fncel.2024.1398862

Bowers, D., & Heilman, K. M. (1980). Pseudoneglect: Effects of hemispace on a tactile line bisection task. *Neuropsychologia*, *18*(4–5), 491–498. https://doi.org/10.1016/0028-3932(80)90151-7

Bowyer, S. M. (2016). Coherence a measure of the brain networks: Past and present. *Neuropsychiatric Electrophysiology*, *2*(1), 1. https://doi.org/10.1186/s40810-015-0015-7

Brascamp, J., Sterzer, P., Blake, R., & Knapen, T. (2018). Multistable Perception and the Role of the Frontoparietal Cortex in Perceptual Inference. *Annual Review of Psychology*, *69*(1), 77–103. https://doi.org/10.1146/annurev-psych-010417-085944

Brewer, A., & Barton, B. (2012). Visual Field Map Organization in Human Visual Cortex. In S. Molotchnikoff (Ed.), *Visual Cortex—Current Status and Perspectives*. InTech. https://doi.org/10.5772/51914

Brown, S., & Nicholls, M. E. R. (1997). Hemispheric asymmetries for the temporal resolution of brief auditory stimuli. *Perception & Psychophysics*, *59*(3), 442–447. https://doi.org/10.3758/BF03211910

Bruce, C. J., Goldberg, M. E., Bushnell, M. C., & Stanton, G. B. (1985). Primate frontal eye fields. II. Physiological and anatomical correlates of electrically evoked eye movements. *Journal of Neurophysiology*, *54*(3), 714–734. https://doi.org/10.1152/jn.1985.54.3.714

Brüers, S., & VanRullen, R. (2017). At What Latency Does the Phase of Brain Oscillations Influence Perception? *Eneuro*, *4*(3), ENEURO.0078-17.2017. https://doi.org/10.1523/ENEURO.0078-17.2017

Brüers, S., & VanRullen, R. (2018). Alpha Power Modulates Perception Independently of Endogenous Factors. *Frontiers in Neuroscience*, *12*, 279. https://doi.org/10.3389/fnins.2018.00279

Busch, N. A., Dubois, J., & VanRullen, R. (2009). The Phase of Ongoing EEG Oscillations Predicts Visual Perception. *Journal of Neuroscience*, *29*(24), 7869–7876. https://doi.org/10.1523/JNEUROSCI.0113-09.2009

Busch, N. A., & VanRullen, R. (2010). Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proceedings of the National Academy of Sciences*, *107*(37), 16048–16053. https://doi.org/10.1073/pnas.1004801107

Buschman, T. J., & Miller, E. K. (2007). Top-Down Versus Bottom-Up Control of Attention in the Prefrontal and Posterior Parietal Cortices. *Science*, *315*(5820), 1860–1862. https://doi.org/10.1126/science.1138071

Buschman, T. J., & Miller, E. K. (2009). Serial, Covert Shifts of Attention during Visual Search Are Reflected by the Frontal Eye Fields and Correlated with Population Oscillations. *Neuron*, *63*(3), 386–396. https://doi.org/10.1016/j.neuron.2009.06.020

Button, K. S., Ioannidis, J. P. A., Mokrysz, C., Nosek, B. A., Flint, J., Robinson, E. S. J., & Munafò, M. R. (2013). Power failure: Why small sample size undermines the reliability of neuroscience. *Nature Reviews Neuroscience*, *14*(5), 365–376. https://doi.org/10.1038/nrn3475

Buzsáki, G., & Draguhn, A. (2004). Neuronal Oscillations in Cortical Networks. *Science*, *304*(5679), 1926–1929. https://doi.org/10.1126/science.1099745

Capilla, A., Pazo-Alvarez, P., Darriba, A., Campo, P., & Gross, J. (2011). Steady-State Visual Evoked Potentials Can Be Explained by Temporal Superposition of Transient Event-Related Responses. *PLoS ONE*, *6*(1), e14543. https://doi.org/10.1371/journal.pone.0014543

Capotosto, P., Babiloni, C., Romani, G. L., & Corbetta, M. (2009). Frontoparietal Cortex Controls Spatial Attention through Modulation of Anticipatory Alpha Rhythms. *The Journal of Neuroscience*, *29*(18), 5863–5872. https://doi.org/10.1523/JNEUROSCI.0539-09.2009

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*(13), 1484–1525. https://doi.org/10.1016/j.visres.2011.04.012

Carrasco, M., & McElree, B. (2001). Covert attention accelerates the rate of visual information processing. *Proceedings of the National Academy of Sciences*, *98*(9), 5363–5367. https://doi.org/10.1073/pnas.081074098

Carrasco, M., Williams, P. E., & Yeshurun, Y. (2002). Covert attention increases spatial resolution with or without masks: Support for signal enhancement. *Journal of Vision*, *2*(6), 4. https://doi.org/10.1167/2.6.4

Casteau, S., & Smith, D. T. (2020). Covert attention beyond the range of eye-movements: Evidence for a dissociation between exogenous and endogenous orienting. *Cortex*, *122*, 170–186. https://doi.org/10.1016/j.cortex.2018.11.007

Caton, R. M. D. (1875). Electrical Currents of the Brain. *British Medical Journal*, *2*, 278.

Caton, R. M. D. (1877). Interim Report on Investigation of the Electrical Currents of the Brain. *British Medical Journal*, *Suppl 1*, 62–65.

Chanes, L. (2014). *Frontal and parietal contributions to visual perception in humans* [Université Pierre et Marie Curie]. https://theses.hal.science/tel-00989767v1

Chanes, L., Quentin, R., Tallon-Baudry, C., & Valero-Cabré, A. (2013). Causal Frequency-Specific Contributions of Frontal Spatiotemporal Patterns Induced by Non-Invasive Neurostimulation to Human Visual Performance. *The Journal of Neuroscience*, *33*(11), 5000–5005. https://doi.org/10.1523/JNEUROSCI.4401-12.2013

Chapman, C., Hoag, R., & Giaschi, D. (2004). The effect of disrupting the human magnocellular pathway on global motion perception. *Vision Research*, *44*(22), 2551–2557. https://doi.org/10.1016/j.visres.2004.06.003

Chawla, D., Phillips, J., Buechel, C., Edwards, R., & Friston, K. J. (1998). Speed-Dependent Motion-Sensitive Responses in V5: An fMRI Study. *NeuroImage*, *7*(2), 86–96. https://doi.org/10.1006/nimg.1997.0319

Chen, A., Wang, A., Wang, T., Tang, X., & Zhang, M. (2017). Behavioral Oscillations in Visual Attention Modulated by Task Difficulty. *Frontiers in Psychology*, *8*, 1630. https://doi.org/10.3389/fpsyg.2017.01630

Chen, K.-H., & Huang, Y.-Z. (2018). The change of motor cortical excitability between eyes open and closed conditions. *NeuroReport*, *29*(3), 214–218. https://doi.org/10.1097/WNR.0000000000000955

Chen, R., & Seitz, R. J. (2001). Changing cortical excitability with low-frequency magnetic stimulation. *Neurology*, *57*(3), 379–380. https://doi.org/10.1212/WNL.57.3.379

Cheyne, D. O. (2013). MEG studies of sensorimotor rhythms: A review. *Experimental Neurology*, *245*, 27–39. https://doi.org/10.1016/j.expneurol.2012.08.030

Chipchase, L., Schabrun, S., Cohen, L., Hodges, P., Ridding, M., Rothwell, J., Taylor, J., & Ziemann, U. (2012). A checklist for assessing the methodological quality of studies using transcranial magnetic stimulation to study the motor system: An international consensus study. *Clinical Neurophysiology*, *123*(9), 1698–1704. https://doi.org/10.1016/j.clinph.2012.05.003

Chrobak, J. J., & Buzsáki, G. (1998). Gamma Oscillations in the Entorhinal Cortex of the Freely Behaving Rat. *The Journal of Neuroscience*, *18*(1), 388–398. https://doi.org/10.1523/JNEUROSCI.18-01-00388.1998

Clark, V. P., Coffman, B. A., Trumbo, M. C. S., & Wegele, A. R. (2014). An Evolutionary Perspective on Attentional Processes. In *Cognitive Electrophysiology of Attention* (pp. 207–215). Elsevier. https://doi.org/10.1016/B978-0-12-398451-7.00016-6

Clayton, M. S., Yeung, N., & Cohen Kadosh, R. (2015). The roles of cortical oscillations in sustained attention. *Trends in Cognitive Sciences*, *19*(4), 188–195. https://doi.org/10.1016/j.tics.2015.02.004

Clayton, M. S., Yeung, N., & Cohen Kadosh, R. (2018). The many characters of visual alpha oscillations. *European Journal of Neuroscience*, *48*(7), 2498–2508. https://doi.org/10.1111/ejn.13747

Clementz, B. A., Barber, S. K., & Dzau, J. R. (2002). Knowledge of Stimulus Repetition Affects the Magnitude and Spatial Distribution of Low-Frequency Event-Related Brain Potentials. *Audiology and Neurotology*, *7*(5), 303–314. https://doi.org/10.1159/000064444

Coffin, S., & Ganz, L. (1977). Perceptual correlates of variability in the duration of the cortical excitability cycle. *Neuropsychologia*, *15*(2), 231–241. https://doi.org/10.1016/0028-3932(77)90031-8

Cohen, L. G., Roth, B. J., Nilsson, J., Dang, N., Panizza, M., Bandinelli, S., Friauf, W., & Hallett, M. (1990). Effects of coil design on delivery of focal magnetic stimulation. Technical considerations. *Electroencephalography and Clinical Neurophysiology*, *75*(4), 350–357. https://doi.org/10.1016/0013-4694(90)90113-X

Cohen, M. X., Elger, C. E., & Fell, J. (2008). Oscillatory Activity and Phase–Amplitude Coupling in the Human Medial Frontal Cortex during Decision Making. *Journal of Cognitive Neuroscience*, *21*(2), 390–402. https://doi.org/10.1162/jocn.2008.21020

Coldea, A., Veniero, D., Morand, S., Trajkovic, J., Romei, V., Harvey, M., & Thut, G. (2022). Effects of Rhythmic Transcranial Magnetic Stimulation in the Alpha-Band on Visual Perception Depend on Deviation From Alpha-Peak Frequency: Faster Relative Transcranial Magnetic Stimulation Alpha-Pace Improves Performance. *Frontiers in Neuroscience*, *16*, 886342. https://doi.org/10.3389/fnins.2022.886342

Cole, S. R., & Voytek, B. (2017). Brain Oscillations and the Importance of Waveform Shape. *Trends in Cognitive Sciences*, *21*(2), 137–149. https://doi.org/10.1016/j.tics.2016.12.008

Colgin, L. L., Denninger, T., Fyhn, M., Hafting, T., Bonnevie, T., Jensen, O., Moser, M.-B., & Moser, E. I. (2009). Frequency of gamma oscillations routes flow of information in the hippocampus. *Nature*, *462*(7271), 353–357. https://doi.org/10.1038/nature08573

Columbus, A. (2008). *Advances in psychology research. Volume 53*. Nova Science Publishers.

Combrisson, E., Perrone-Bertolotti, M., Soto, J. L., Alamian, G., Kahane, P., Lachaux, J.-P., Guillot, A., & Jerbi, K. (2017). From intentions to actions: Neural oscillations encode motor processes through phase, amplitude and phase-amplitude coupling. *NeuroImage*, *147*, 473–487. https://doi.org/10.1016/j.neuroimage.2016.11.042

Conway, B. A., Halliday, D. M., Farmer, S. F., Shahani, U., Maas, P., Weir, A. I., & Rosenberg, J. R. (1995). Synchronization between motor cortex and spinal motoneuronal pool during the performance of a

maintained motor task in man. *The Journal of Physiology*, *489*(3), 917–924. https://doi.org/10.1113/jphysiol.1995.sp021104

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201–215. https://doi.org/10.1038/nrn755

Cortese, F., Coppola, G., Di Lenola, D., Serrao, M., Di Lorenzo, C., Parisi, V., & Pierelli, F. (2017). Excitability of the motor cortex in patients with migraine changes with the time elapsed from the last attack. *The Journal of Headache and Pain*, *18*(1), 2. https://doi.org/10.1186/s10194-016-0712-z

Coull, J. T., & Frith, C. D. (1998). Differential Activation of Right Superior Parietal Cortex and Intraparietal Sulcus by Spatial and Nonspatial Attention. *NeuroImage*, *8*(2), 176–187. https://doi.org/10.1006/nimg.1998.0354

Couperus, J. W., & Mangun, G. R. (2010). Signal enhancement and suppression during visual–spatial selective attention. *Brain Research*, *1359*, 155–177. https://doi.org/10.1016/j.brainres.2010.08.076

Creel, D. (1995). Visually Evoked Potentials. In H. Kolb, E. Fernandez, B. Jones, & R. Nelson (Eds.), *Webvision: The Organization of the Retina and Visual System*. University of Utah Health Sciences Center. http://www.ncbi.nlm.nih.gov/books/NBK107218/

DeCarlo, L. T. (1998). Signal detection theory and generalized linear models. *Psychological Methods*, *3*(2), 186–205. https://doi.org/10.1037/1082-989X.3.2.186

Di Dona, G., & Ronconi, L. (2023). Beta oscillations in vision: A (preconscious) neural mechanism for the dorsal visual stream? *Frontiers in Psychology*, *14*, 1296483. https://doi.org/10.3389/fpsyg.2023.1296483

Ding, N., & Simon, J. Z. (2013). Power and phase properties of oscillatory neural responses in the presence of background activity. *Journal of Computational Neuroscience*, *34*(2), 337–343. https://doi.org/10.1007/s10827-012-0424-6

Ding, Z., Guan, L., He, W., Gu, H., Wang, Y., & Li, X. (2023). Spatial characteristics of closed-loop TMS-EEG with occipital alpha-phase synchronized. *Biomedical Signal Processing and Control*, *83*, 104650. https://doi.org/10.1016/j.bspc.2023.104650

Doelling, K. B., Assaneo, M. F., Bevilacqua, D., Pesaran, B., & Poeppel, D. (2019). An oscillator model better predicts cortical entrainment to music. *Proceedings of the National Academy of Sciences*, *116*(20), 10113–10121. https://doi.org/10.1073/pnas.1816414116

Dombrowe, I., & Hilgetag, C. C. (2014). Occipitoparietal alpha-band responses to the graded allocation of top-down spatial attention. *Journal of Neurophysiology*, *112*(6), 1307–1316. https://doi.org/10.1152/jn.00654.2013

Donoghue, T., Haller, M., Peterson, E. J., Varma, P., Sebastian, P., Gao, R., Noto, T., Lara, A. H., Wallis, J. D., Knight, R. T., Shestyuk, A., & Voytek, B. (2020). Parameterizing neural power spectra into periodic and aperiodic components. *Nature Neuroscience*, *23*(12), 1655–1665. https://doi.org/10.1038/s41593-020-00744-x

Donoghue, T., Schaworonkow, N., & Voytek, B. (2022). Methodological considerations for studying neural oscillations. *European Journal of Neuroscience*, *55*(11–12), 3502–3527. https://doi.org/10.1111/ejn.15361

Dosher, B. A., & Lu, Z.-L. (2000a). Mechanisms of perceptual attention in precuing of location. *Vision Research*, *40*(10–12), 1269–1292. https://doi.org/10.1016/S0042-6989(00)00019-5

Dosher, B. A., & Lu, Z.-L. (2000b). Noise Exclusion in Spatial Attention. *Psychological Science*, *11*(2), 139–146. https://doi.org/10.1111/1467-9280.00229

Duecker, F., Frost, M. A., De Graaf, T. A., Graewe, B., Jacobs, C., Goebel, R., & Sack, A. T. (2014). The Cortex-based Alignment Approach to TMS Coil Positioning. *Journal of Cognitive Neuroscience*, *26*(10), 2321–2329. https://doi.org/10.1162/jocn_a_00635

Duecker, K., Doelling, K. B., Breska, A., Coffey, E. B. J., Sivarao, D. V., & Zoefel, B. (2024). Challenges and Approaches in the Study of Neural Entrainment. *The Journal of Neuroscience*, *44*(40), e1234242024. https://doi.org/10.1523/JNEUROSCI.1234-24.2024

Dugué, L., Marque, P., & VanRullen, R. (2011). The Phase of Ongoing Oscillations Mediates the Causal Relation between Brain Excitation and Visual Perception. *The Journal of Neuroscience*, *31*(33), 11889–11893. https://doi.org/10.1523/JNEUROSCI.1161-11.2011

Dugue, L., & VanRullen, R. (2014). The dynamics of attentional sampling during visual search revealed by Fourier analysis of periodic noise interference. *Journal of Vision*, *14*(2), 11–11. https://doi.org/10.1167/14.2.11

Efron, B. (1987). Better Bootstrap Confidence Intervals. *Journal of the American Statistical Association*, *82*(397), 171–185. https://doi.org/10.1080/01621459.1987.10478410

Emrich, S. M., Lockhart, H. A., & Al-Aidroos, N. (2017). Attention mediates the flexible allocation of visual working memory resources. *Journal of Experimental Psychology: Human Perception and Performance*, *43*(7), 1454–1465. https://doi.org/10.1037/xhp0000398

Engel, A. K., & Fries, P. (2010). Beta-band oscillations—Signalling the status quo? *Current Opinion in Neurobiology*, *20*(2), 156–165. https://doi.org/10.1016/j.conb.2010.02.015

Epstein, C. M., Meador, K. J., Loring, D. W., Wright, R. J., Weissman, J. D., Sheppard, S., Lah, J. J., Puhalovich, F., Gaitan, L., & Davey, K. R. (1999). Localization and characterization of speech arrest during transcranial magnetic stimulation. *Clinical Neurophysiology*, *110*(6), 1073–1079. https://doi.org/10.1016/S1388-2457(99)00047-4

Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., & Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Cognitive Brain Research*, *20*(3), 376–383. https://doi.org/10.1016/j.cogbrainres.2004.03.009

Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, *41*(4), 1149–1160. https://doi.org/10.3758/BRM.41.4.1149

Ferree, T. C. (2006). Spherical Splines and Average Referencing in Scalp Electroencephalography. *Brain Topography*, *19*(1–2), 43–52. https://doi.org/10.1007/s10548-006-0011-0

Ffytche, D. H., Guy, C. N., & Zeki, S. (1995). The parallel visual motion inputs into areas V1 and V5 of human cerebral cortex. *Brain*, *118*(6), 1375–1394. https://doi.org/10.1093/brain/118.6.1375

Fiebelkorn, I. C., & Kastner, S. (2019). A Rhythmic Theory of Attention. *Trends in Cognitive Sciences*, *23*(2), 87–101. https://doi.org/10.1016/j.tics.2018.11.009

Fiebelkorn, I. C., Pinsk, M. A., & Kastner, S. (2018). A Dynamic Interplay within the Frontoparietal Network Underlies Rhythmic Spatial Attention. *Neuron*, *99*(4), 842-853.e8. https://doi.org/10.1016/j.neuron.2018.07.038

Fiebelkorn, I. C., Saalmann, Y. B., & Kastner, S. (2013). Rhythmic Sampling within and between Objects despite Sustained Attention at a Cued Location. *Current Biology*, *23*(24), 2553–2558. https://doi.org/10.1016/j.cub.2013.10.063

Fisher, R. A. (1932). *Statistical methods for research workers* (4th Ed.). Oliver & Boyd.

Fitzgerald, P., Fountain, S., & Daskalakis, Z. (2006). A comprehensive review of the effects of rTMS on motor cortical excitability and inhibition. *Clinical Neurophysiology*, *117*(12), 2584–2596. https://doi.org/10.1016/j.clinph.2006.06.712

Fletcher, A. (2011). Action potential: Generation and propagation. *Anaesthesia & Intensive Care Medicine*, *12*(6), 258–262. https://doi.org/10.1016/j.mpaic.2011.03.010

Fortes, A. F., & Merchant, H. (2006). Investigating Higher Order Cognitive Functions in the Dorsal (magnocellular) Stream of Visual Processing. In R. Pinaud, L. A. Tremere, & P. De Weerd (Eds.), *Plasticity in the Visual System* (pp. 285–306). Springer US. https://doi.org/10.1007/0-387-28190-8_13

Foster, J. J., & Awh, E. (2019). The role of alpha oscillations in spatial attention: Limited evidence for a suppression account. *Current Opinion in Psychology*, *29*, 34–40. https://doi.org/10.1016/j.copsyc.2018.11.001

Foxe, J. J., & Snyder, A. C. (2011). The Role of Alpha-Band Brain Oscillations as a Sensory Suppression Mechanism during Selective Attention. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00154

Fries, P. (2005). A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, *9*(10), 474–480. https://doi.org/10.1016/j.tics.2005.08.011

Fries, P. (2015). Rhythms for Cognition: Communication through Coherence. *Neuron*, *88*(1), 220–235. https://doi.org/10.1016/j.neuron.2015.09.034

Fries, P. (2023). Rhythmic attentional scanning. *Neuron*, *111*(7), 954–970. https://doi.org/10.1016/j.neuron.2023.02.015

Frost, M. A., & Goebel, R. (2012). Measuring structural–functional correspondence: Spatial variability of specialised brain regions after macro-anatomical alignment. *NeuroImage*, *59*(2), 1369–1381. https://doi.org/10.1016/j.neuroimage.2011.08.035

Garcia-Sanz, S., Ghotme, K. A., Hedmont, D., Arévalo-Jaimes, M. Y., Cohen Kadosh, R., Serra-Grabulosa, J. M., & Redolar-Ripoll, D. (2022). Use of transcranial magnetic stimulation for studying the neural basis of numerical cognition: A systematic review. *Journal of Neuroscience Methods*, *369*, 109485. https://doi.org/10.1016/j.jneumeth.2022.109485

García-Pérez, M. A. (1998). Forced-choice staircases with fixed step sizes: Asymptotic and small-sample properties. *Vision Research*, *38*(12), 1861–1881. https://doi.org/10.1016/S0042-6989(97)00340-4

Gießing, C., Alavash, M., Herrmann, C. S., Hilgetag, C. C., & Thiel, C. M. (2020). Individual differences in local functional brain connectivity affect TMS effects on behavior. *Scientific Reports*, *10*(1), 10422. https://doi.org/10.1038/s41598-020-67162-8

Gilbert, C. D., & Li, W. (2013). Top-down influences on visual processing. *Nature Reviews Neuroscience*, *14*(5), 350–363. https://doi.org/10.1038/nrn3476

Gillebert, C. R., Mantini, D., Thijs, V., Sunaert, S., Dupont, P., & Vandenberghe, R. (2011). Lesion evidence for the critical role of the intraparietal sulcus in spatial attention. *Brain*, *134*(6), 1694–1709. https://doi.org/10.1093/brain/awr085

Gola, M., Magnuski, M., Szumska, I., & Wróbel, A. (2013). EEG beta band activity is related to attention and attentional deficits in the visual performance of elderly subjects. *International Journal of Psychophysiology*, *89*(3), 334–341. https://doi.org/10.1016/j.ijpsycho.2013.05.007

Gould, I. C., Rushworth, M. F., & Nobre, A. C. (2011). Indexing the graded allocation of visuospatial attention using anticipatory alpha oscillations. *Journal of Neurophysiology*, *105*(3), 1318–1326. https://doi.org/10.1152/jn.00653.2010

Graaf, T. A., Thomson, A., Janssens, S. E. W., Bree, S., Oever, S., & Sack, A. T. (2020). Does alpha phase modulate visual target detection? Three experiments with tACS-phase-based stimulus presentation. *European Journal of Neuroscience*, *51*(11), 2299–2313. https://doi.org/10.1111/ejn.14677

Grasso, P. A., Làdavas, E., Bertini, C., Caltabiano, S., Thut, G., & Morand, S. (2018). Decoupling of Early V5 Motion Processing from Visual Awareness: A Matter of Velocity as Revealed by Transcranial Magnetic Stimulation. *Journal of Cognitive Neuroscience*, *30*(10), 1517–1531. https://doi.org/10.1162/jocn_a_01298

Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, *55*(4), 468–484. https://doi.org/10.1016/0013-4694(83)90135-9

Gregoriou, G. G., Rossi, A. F., Ungerleider, L. G., & Desimone, R. (2014). Lesions of prefrontal cortex reduce attentional modulation of neuronal responses and synchrony in V4. *Nature Neuroscience*, *17*(7), 1003–1011. https://doi.org/10.1038/nn.3742

Groppa, S., Oliviero, A., Eisen, A., Quartarone, A., Cohen, L. G., Mall, V., Kaelin-Lang, A., Mima, T., Rossi, S., Thickbroom, G. W., Rossini, P. M., Ziemann, U., Valls-Solé, J., & Siebner, H. R. (2012). A practical guide

to diagnostic transcranial magnetic stimulation: Report of an IFCN committee. *Clinical Neurophysiology*, *123*(5), 858–882. https://doi.org/10.1016/j.clinph.2012.01.010

Grosbras, M.-H., & Paus, T. (2002). Transcranial Magnetic Stimulation of the Human Frontal Eye Field: Effects on Visual Perception and Attention. *Journal of Cognitive Neuroscience*, *14*(7), 1109–1120. https://doi.org/10.1162/089892902320474553

Gross, J. (2014). Analytical methods and experimental approaches for electrophysiological studies of brain oscillations. *Journal of Neuroscience Methods*, *228*, 57–66. https://doi.org/10.1016/j.jneumeth.2014.03.007

Gross, J., Schmitz, F., Schnitzler, I., Kessler, K., Shapiro, K., Hommel, B., & Schnitzler, A. (2004). Modulation of long-range neural synchrony reflects temporal limitations of visual attention in humans. *Proceedings of the National Academy of Sciences*, *101*(35), 13050–13055. https://doi.org/10.1073/pnas.0404944101

Gundlach, C., Moratti, S., Forschack, N., & Müller, M. M. (2020). Spatial Attentional Selection Modulates Early Visual Stimulus Processing Independently of Visual Alpha Modulations. *Cerebral Cortex*, *30*(6), 3686–3703. https://doi.org/10.1093/cercor/bhz335

Gutteling, T. P., Sillekens, L., Lavie, N., & Jensen, O. (2022). Alpha oscillations reflect suppression of distractors with increased perceptual load. *Progress in Neurobiology*, *214*, 102285. https://doi.org/10.1016/j.pneurobio.2022.102285

Haegens, S., Nácher, V., Luna, R., Romo, R., & Jensen, O. (2011). α-Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proceedings of the National Academy of Sciences*, *108*(48), 19377–19382. https://doi.org/10.1073/pnas.1117190108

Haegens, S., Vergara, J., Rossi-Pool, R., Lemus, L., & Romo, R. (2017). Beta oscillations reflect supramodal information during perceptual judgment. *Proceedings of the National Academy of Sciences*, *114*(52), 13810–13815. https://doi.org/10.1073/pnas.1714633115

Hallett, M., Di Iorio, R., Rossini, P. M., Park, J. E., Chen, R., Celnik, P., Strafella, A. P., Matsumoto, H., & Ugawa, Y. (2017). Contribution of transcranial magnetic stimulation to assessment of brain connectivity and networks. *Clinical Neurophysiology*, *128*(11), 2125–2139. https://doi.org/10.1016/j.clinph.2017.08.007

Hallez, H., Vanrumste, B., Grech, R., Muscat, J., De Clercq, W., Vergult, A., D'Asseler, Y., Camilleri, K. P., Fabri, S. G., Van Huffel, S., & Lemahieu, I. (2007). Review on solving the forward problem in EEG source analysis. *Journal of NeuroEngineering and Rehabilitation*, *4*(1), 46. https://doi.org/10.1186/1743-0003-4-46

Hampshire, A., Chamberlain, S. R., Monti, M. M., Duncan, J., & Owen, A. M. (2010). The role of the right inferior frontal gyrus: Inhibition and attentional control. *NeuroImage*, *50*(3), 1313–1319. https://doi.org/10.1016/j.neuroimage.2009.12.109

Händel, B., & Haarmeier, T. (2009). Cross-frequency coupling of brain oscillations indicates the success in visual motion discrimination. *NeuroImage*, *45*(3), 1040–1046. https://doi.org/10.1016/j.neuroimage.2008.12.013

Handy, T. C. (Ed.). (2005). *Event-related potentials: A methods handbook*. MIT Press.

Hannah, R., Muralidharan, V., & Aron, A. R. (2022). Motor cortex oscillates at its intrinsic post-movement beta rhythm following real (but not sham) single pulse, rhythmic and arrhythmic transcranial magnetic stimulation. *NeuroImage*, *251*, 118975. https://doi.org/10.1016/j.neuroimage.2022.118975

Hanslmayr, S., Klimesch, W., Sauseng, P., Gruber, W., Doppelmayr, M., Freunberger, R., & Pecherstorfer, T. (2005). Visual discrimination performance is related to decreased alpha amplitude but increased phase locking. *Neuroscience Letters*, *375*(1), 64–68. https://doi.org/10.1016/j.neulet.2004.10.092

Hanslmayr, S., Volberg, G., Wimber, M., Dalal, S. S., & Greenlee, M. W. (2013). Prestimulus Oscillatory Phase at 7 Hz Gates Cortical Information Flow and Visual Perception. *Current Biology*, *23*(22), 2273–2278. https://doi.org/10.1016/j.cub.2013.09.020

Harmening, W. M., Orlowski, J., Ben-Shahar, O., & Wagner, H. (2011). Overt attention toward oriented objects in free-viewing barn owls. *Proceedings of the National Academy of Sciences*, *108*(20), 8461–8466. https://doi.org/10.1073/pnas.1101582108

Harris, A. M., Dux, P. E., & Mattingley, J. B. (2018). Detecting Unattended Stimuli Depends on the Phase of Prestimulus Neural Oscillations. *The Journal of Neuroscience*, *38*(12), 3092–3101. https://doi.org/10.1523/JNEUROSCI.3006-17.2018

Harvey, B. M., Vansteensel, M. J., Ferrier, C. H., Petridou, N., Zuiderbaan, W., Aarnoutse, E. J., Bleichner, M. G., Dijkerman, H. C., Van Zandvoort, M. J. E., Leijten, F. S. S., Ramsey, N. F., & Dumoulin, S. O. (2013).

Frequency specific spatial interactions in human electrocorticography: V1 alpha oscillations reflect surround suppression. *NeuroImage*, *65*, 424–432. https://doi.org/10.1016/j.neuroimage.2012.10.020

Hawkins, H. L., Hillyard, S. A., Luck, S. J., Mouloua, M., Downing, C. J., & Woodward, D. P. (1990). Visual attention modulates signal detectability. *Journal of Experimental Psychology: Human Perception and Performance*, *16*(4), 802–811. https://doi.org/10.1037/0096-1523.16.4.802

Hayward, D. A., & Ristic, J. (2013). Measuring attention using the Posner cuing paradigm: The role of across and within trial target probabilities. *Frontiers in Human Neuroscience*, *7*. https://doi.org/10.3389/fnhum.2013.00205

Herbet, G. (2021). Frontal Eye Fields. In E. Mandonnet & G. Herbet (Eds.), *Intraoperative Mapping of Cognitive Networks* (pp. 41–57). Springer International Publishing. https://doi.org/10.1007/978-3-030-75071-8_3

Herbsman, T., Forster, L., Molnar, C., Dougherty, R., Christie, D., Koola, J., Ramsey, D., Morgan, P. S., Bohning, D. E., George, M. S., & Nahas, Z. (2009). Motor threshold in transcranial magnetic stimulation: The impact of white matter fiber orientation and skull-to-cortex distance. *Human Brain Mapping*, *30*(7), 2044–2055. https://doi.org/10.1002/hbm.20649

Hernandez Pavon, J. C., Garces, N. S., Begnoche, J. P., Miller, L., & Raij, T. (2022). *TMS-EEG-MRI-fMRI-DWI data on paired associative stimulation and connectivity (Shirley Ryan AbilityLab, Chicago, IL)* [Dataset]. Openneuro. https://doi.org/10.18112/OPENNEURO.DS004024.V1.0.1

Hernandez-Pavon, J. C., Schneider-Garces, N., Begnoche, J. P., Miller, L. E., & Raij, T. (2022). Targeted Modulation of Human Brain Interregional Effective Connectivity With Spike-timing Dependent Plasticity. *Neuromodulation: Technology at the Neural Interface*, S1094715922013332. https://doi.org/10.1016/j.neurom.2022.10.045

Herrmann, C. S. (2001). Human EEG responses to 1-100 Hz flicker: Resonance phenomena in visual cortex and their potential correlation to cognitive phenomena. *Experimental Brain Research*, *137*(3–4), 346–353. https://doi.org/10.1007/s002210100682

Herwig, U., Satrapi, P., & Schönfeldt-Lecuona, C. (2003). Using the International 10-20 EEG System for Positioning of Transcranial Magnetic Stimulation. *Brain Topography*, *16*(2), 95–99. https://doi.org/10.1023/B:BRAT.0000006333.93597.9d

Ho, H. T., Leung, J., Burr, D. C., Alais, D., & Morrone, M. C. (2017). Auditory Sensitivity and Decision Criteria Oscillate at Different Frequencies Separately for the Two Ears. *Current Biology*, *27*(23), 3643-3649.e3. https://doi.org/10.1016/j.cub.2017.10.017

Hochstein, S., & Ahissar, M. (2002). View from the Top. *Neuron*, *36*(5), 791–804. https://doi.org/10.1016/S0896-6273(02)01091-7

Hodgkin, A. L., & Huxley, A. F. (1939). Action Potentials Recorded from Inside a Nerve Fibre. *Nature*, *144*(3651), 710–711. https://doi.org/10.1038/144710a0

Hohaia, W., Saurels, B. W., Johnston, A., Yarrow, K., & Arnold, D. H. (2022). Occipital alpha-band brain waves when the eyes are closed are shaped by ongoing visual processes. *Scientific Reports*, *12*(1), 1194. https://doi.org/10.1038/s41598-022-05289-6

Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, *3*(3), 284–291. https://doi.org/10.1038/72999

Hordacre, B., Lotze, M., Jenkinson, M., Lazari, A., Barras, C. D., Boyd, L., & Hillier, S. (2021). Fronto-parietal involvement in chronic stroke motor performance when corticospinal tract integrity is compromised. *NeuroImage: Clinical*, *29*, 102558. https://doi.org/10.1016/j.nicl.2021.102558

Huber, D. E., Potter, K. W., & Huszar, L. D. (2019). Less 'story' and more 'reliability' in cognitive neuroscience. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *113*, 347–349. https://doi.org/10.1016/j.cortex.2018.10.030

Hummel, F., & Gerloff, C. (2005). Larger Interregional Synchrony is Associated with Greater Behavioral Success in a Complex Sensory Integration Task in Humans. *Cerebral Cortex*, *15*(5), 670–678. https://doi.org/10.1093/cercor/bhh170

Hurtado, J. M., Rubchinsky, L. L., & Sigvardt, K. A. (2004). Statistical Method for Detection of Phase-Locking Episodes in Neural Oscillations. *Journal of Neurophysiology*, *91*(4), 1883–1898. https://doi.org/10.1152/jn.00853.2003

Hussain, S. J., Claudino, L., Bönstrup, M., Norato, G., Cruciani, G., Thompson, R., Zrenner, C., Ziemann, U., Buch, E., & Cohen, L. G. (2019). Sensorimotor Oscillatory Phase–Power Interaction Gates Resting Human Corticospinal Output. *Cerebral Cortex*, *29*(9), 3766–3777. https://doi.org/10.1093/cercor/bhy255

IBM SPSS Statistics (Version 28.0.0.0). (2021). [Computer software]. IBM Corp.

Iemi, L., & Busch, N. A. (2018). Moment-to-Moment Fluctuations in Neuronal Excitability Bias Subjective Perception Rather than Strategic Decision-Making. *Eneuro*, *5*(3), ENEURO.0430-17.2018. https://doi.org/10.1523/ENEURO.0430-17.2018

Iemi, L., Chaumon, M., Crouzet, S. M., & Busch, N. A. (2017). Spontaneous Neural Oscillations Bias Perception by Modulating Baseline Excitability. *The Journal of Neuroscience*, *37*(4), 807–819. https://doi.org/10.1523/JNEUROSCI.1432-16.2016

Ilmoniemi, R. J., & Kičić, D. (2010). Methodology for Combined TMS and EEG. *Brain Topography*, *22*(4), 233–248. https://doi.org/10.1007/s10548-009-0123-4

İnce, R., Adanır, S. S., & Sevmez, F. (2021). The inventor of electroencephalography (EEG): Hans Berger (1873–1941). *Child's Nervous System*, *37*(9), 2723–2724. https://doi.org/10.1007/s00381-020-04564-z

Jasper, H., & Penfield, W. (1949). Electrocorticograms in man: Effect of voluntary movement upon the electrical activity of the precentral gyrus. *Archiv Fur Psychiatrie Und Nervenkrankheiten*, *183*(1–2), 163–174. https://doi.org/10.1007/BF01062488

Jensen, O., Gips, B., Bergmann, T. O., & Bonnefond, M. (2014). Temporal coding organized by coupled alpha and gamma oscillations prioritize visual processing. *Trends in Neurosciences*, *37*(7), 357–369. https://doi.org/10.1016/j.tins.2014.04.001

Jensen, O., & Mazaheri, A. (2010). Shaping Functional Architecture by Oscillatory Alpha Activity: Gating by Inhibition. *Frontiers in Human Neuroscience*, *4*. https://doi.org/10.3389/fnhum.2010.00186

Jensen, O., Spaak, E., & Zumer, J. M. (2019). Human Brain Oscillations: From Physiological Mechanisms to Analysis and Cognition. In S. Supek & C. J. Aine (Eds.), *Magnetoencephalography* (pp. 1–46). Springer International Publishing. https://doi.org/10.1007/978-3-319-62657-4_17-1

Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia*, *38*(1), 93–110. https://doi.org/10.1016/S0028-3932(99)00045-7

Jia, X., & Kohn, A. (2011). Gamma Rhythms in the Brain. *PLoS Biology*, *9*(4), e1001045. https://doi.org/10.1371/journal.pbio.1001045

Jokisch, D., & Jensen, O. (2007). Modulation of Gamma and Alpha Activity during a Working Memory Task Engaging the Dorsal or Ventral Stream. *The Journal of Neuroscience*, *27*(12), 3244–3251. https://doi.org/10.1523/JNEUROSCI.5399-06.2007

Jones, M. W., & Wilson, M. A. (2005). Phase precession of medial prefrontal cortical activity relative to the hippocampal theta rhythm. *Hippocampus*, *15*(7), 867–873. https://doi.org/10.1002/hipo.20119

Jones, S. R. (2016). When brain rhythms aren't 'rhythmic': Implication for their mechanisms and meaning. *Current Opinion in Neurobiology*, *40*, 72–80. https://doi.org/10.1016/j.conb.2016.06.010

Karekal, A., Miocinovic, S., & Swann, N. C. (2022). Novel approaches for quantifying beta synchrony in Parkinson's disease. *Experimental Brain Research*, *240*(4), 991–1004. https://doi.org/10.1007/s00221-022-06308-8

Kasten, F. H., Wendeln, T., Stecher, H. I., & Herrmann, C. S. (2020). Hemisphere-specific, differential effects of lateralized, occipital–parietal α- versus γ-tACS on endogenous but not exogenous visual-spatial attention. *Scientific Reports*, *10*(1), 12270. https://doi.org/10.1038/s41598-020-68992-2

Kayser, J., & Tenke, C. E. (2015). On the benefits of using surface Laplacian (current source density) methodology in electrophysiology. *International Journal of Psychophysiology*, *97*(3), 171–173. https://doi.org/10.1016/j.ijpsycho.2015.06.001

Keil, J., Timm, J., SanMiguel, I., Schulz, H., Obleser, J., & Schönwiesner, M. (2014). Cortical brain states and corticospinal synchronization influence TMS-evoked motor potentials. *Journal of Neurophysiology*, *111*(3), 513–519. https://doi.org/10.1152/jn.00387.2013

Keitel, C., Quigley, C., & Ruhnau, P. (2014). Stimulus-Driven Brain Oscillations in the Alpha Range: Entrainment of Intrinsic Rhythms or Frequency-Following Response? *Journal of Neuroscience*, *34*(31), 10137–10140. https://doi.org/10.1523/JNEUROSCI.1904-14.2014

Keitel, C., Ruzzoli, M., Dugué, L., Busch, N. A., & Benwell, C. S. Y. (2022). Rhythms in cognition: The evidence revisited. *European Journal of Neuroscience*, *55*(11–12), 2991–3009. https://doi.org/10.1111/ejn.15740

Kelly, S. P., Lalor, E. C., Reilly, R. B., & Foxe, J. J. (2006). Increases in Alpha Oscillatory Power Reflect an Active Retinotopic Mechanism for Distracter Suppression During Sustained Visuospatial Attention. *Journal of Neurophysiology*, *95*(6), 3844–3851. https://doi.org/10.1152/jn.01234.2005

Khanna, P., & Carmena, J. M. (2015). Neural oscillations: Beta band activity across motor networks. *Current Opinion in Neurobiology*, *32*, 60–67. https://doi.org/10.1016/j.conb.2014.11.010

Kienitz, R., Schmid, M. C., & Dugué, L. (2022). Rhythmic sampling revisited: Experimental paradigms and neural mechanisms. *European Journal of Neuroscience*, *55*(11–12), 3010–3024. https://doi.org/10.1111/ejn.15489

Kilner, J. M., Paulignan, Y., & Boussaoud, D. (2004). Functional connectivity during real vs imagined visuomotor tasks: An EEG study: *NeuroReport*, *15*(4), 637–642. https://doi.org/10.1097/00001756-200403220-00013

Kim, N. Y., & Kastner, S. (2019). A biased competition theory for the developmental cognitive neuroscience of visuo-spatial attention. *Current Opinion in Psychology*, *29*, 219–228. https://doi.org/10.1016/j.copsyc.2019.03.017

King, J.-R., & Dehaene, S. (2014). Characterizing the dynamics of mental representations: The temporal generalization method. *Trends in Cognitive Sciences*, *18*(4), 203–210. https://doi.org/10.1016/j.tics.2014.01.002

Klein, R. M. (2005). On the Role of Endogenous Orienting in the Inhibitory Aftermath of Exogenous Orienting. In U. Mayr, E. Awh, & S. W. Keele (Eds.), *Developing individuality in the human brain: A tribute to Michael I. Posner.* (pp. 45–64). American Psychological Association. https://doi.org/10.1037/11108-003

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences*, *16*(12), 606–617. https://doi.org/10.1016/j.tics.2012.10.007

Klimesch, W., Fellinger, R., & Freunberger, R. (2011). Alpha Oscillations and Early Stages of Visual Encoding. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00118

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition–timing hypothesis. *Brain Research Reviews*, *53*(1), 63–88. https://doi.org/10.1016/j.brainresrev.2006.06.003

Klomjai, W., Katz, R., & Lackmy-Vallée, A. (2015). Basic principles of transcranial magnetic stimulation (TMS) and repetitive TMS (rTMS). *Annals of Physical and Rehabilitation Medicine*, *58*(4), 208–213. https://doi.org/10.1016/j.rehab.2015.05.005

Kloosterman, N. A., De Gee, J. W., Werkle-Bergner, M., Lindenberger, U., Garrett, D. D., & Fahrenfort, J. J. (2019). Humans strategically shift decision bias by flexibly adjusting sensory evidence accumulation. *eLife*, *8*, e37321. https://doi.org/10.7554/eLife.37321

Ko, L.-W., Komarov, O., Hairston, W. D., Jung, T.-P., & Lin, C.-T. (2017). Sustained Attention in Real Classroom Settings: An EEG Study. *Frontiers in Human Neuroscience*, *11*, 388. https://doi.org/10.3389/fnhum.2017.00388

Kobayashi, M., & Pascual-Leone, A. (2003). Transcranial magnetic stimulation in neurology. *The Lancet Neurology*, *2*(3), 145–156. https://doi.org/10.1016/S1474-4422(03)00321-1

Koevoet, D., Strauch, C., Naber, M., & Der Stigchel, S. V. (2023). The Costs of Paying Overt and Covert Attention Assessed With Pupillometry. *Psychological Science*, *34*(8), 887–898. https://doi.org/10.1177/09567976231179378

Kulke, L., Atkinson, J., & Braddick, O. (2020). Relation Between Event-Related Potential Latency and Saccade Latency in Overt Shifts of Attention. *Perception*, *49*(4), 468–483. https://doi.org/10.1177/0301006620911869

Lachaux, J.-P., Rodriguez, E., Martinerie, J., & Valera, F. J. (1999). Measuring phase synchrony in brain signals. *Human Brain Mapping*, *8*(4), 194–208.

Laffere, A., Dick, F., & Tierney, A. (2020). Effects of auditory selective attention on neural phase: Individual differences and short-term training. *NeuroImage*, *213*, 116717. https://doi.org/10.1016/j.neuroimage.2020.116717

Lakatos, P., Gross, J., & Thut, G. (2019). A New Unifying Account of the Roles of Neuronal Entrainment. *Current Biology*, *29*(18), R890–R905. https://doi.org/10.1016/j.cub.2019.07.075

Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of Neuronal Oscillations as a Mechanism of Attentional Selection. *Science*, *320*(5872), 110–113. https://doi.org/10.1126/science.1154735

Lakatos, P., Shah, A. S., Knuth, K. H., Ulbert, I., Karmos, G., & Schroeder, C. E. (2005). An Oscillatory Hierarchy Controlling Neuronal Excitability and Stimulus Processing in the Auditory Cortex. *Journal of Neurophysiology*, *94*(3), 1904–1911. https://doi.org/10.1152/jn.00263.2005

Landau, A. N., & Fries, P. (2012). Attention Samples Stimuli Rhythmically. *Current Biology*, *22*(11), 1000–1004. https://doi.org/10.1016/j.cub.2012.03.054

Lange, F. P., Rahnev, D. A., Donner, T. H., & Lau, H. (2013). Prestimulus Oscillatory Activity over Motor Cortex Reflects Perceptual Expectations. *The Journal of Neuroscience*, *33*(4), 1400–1410. https://doi.org/10.1523/JNEUROSCI.1094-12.2013

Lange, J., Keil, J., Schnitzler, A., Van Dijk, H., & Weisz, N. (2014). The role of alpha oscillations for illusory perception. *Behavioural Brain Research*, *271*, 294–301. https://doi.org/10.1016/j.bbr.2014.06.015

Lange, J., Oostenveld, R., & Fries, P. (2011). Perception of the touch-induced visual double-flash illusion correlates with changes of rhythmic neuronal activity in human visual and somatosensory areas. *NeuroImage*, *54*(2), 1395–1405. https://doi.org/10.1016/j.neuroimage.2010.09.031

Lange, J., Oostenveld, R., & Fries, P. (2013). Reduced Occipital Alpha Power Indexes Enhanced Excitability Rather than Improved Visual Perception. *The Journal of Neuroscience*, *33*(7), 3212–3220. https://doi.org/10.1523/JNEUROSCI.3755-12.2013

Laycock, R., Crewther, D. P., Fitzgerald, P. B., & Crewther, S. G. (2007). Evidence for Fast Signals and Later Processing in Human V1/V2 and V5/MT+: A TMS Study of Motion Perception. *Journal of Neurophysiology*, *98*(3), 1253–1262. https://doi.org/10.1152/jn.00416.2007

Lefaucheur, J.-P., Aleman, A., Baeken, C., Benninger, D. H., Brunelin, J., Di Lazzaro, V., Filipović, S. R., Grefkes, C., Hasan, A., Hummel, F. C., Jääskeläinen, S. K., Langguth, B., Leocani, L., Londero, A., Nardone, R., Nguyen, J.-P., Nyffeler, T., Oliveira-Maia, A. J., Oliviero, A., … Ziemann, U. (2020). Evidence-based guidelines on the therapeutic use of repetitive transcranial magnetic stimulation (rTMS): An update (2014–2018). *Clinical Neurophysiology*, *131*(2), 474–528. https://doi.org/10.1016/j.clinph.2019.11.002

Lefaucheur, J.-P., André-Obadia, N., Antal, A., Ayache, S. S., Baeken, C., Benninger, D. H., Cantello, R. M., Cincotta, M., De Carvalho, M., De Ridder, D., Devanne, H., Di Lazzaro, V., Filipović, S. R., Hummel, F. C., Jääskeläinen, S. K., Kimiskidis, V. K., Koch, G., Langguth, B., Nyffeler, T., … Garcia-Larrea, L. (2014). Evidence-based guidelines on the therapeutic use of repetitive transcranial magnetic stimulation (rTMS). *Clinical Neurophysiology*, *125*(11), 2150–2206. https://doi.org/10.1016/j.clinph.2014.05.021

León Ruiz, M., Sospedra, M., Arce Arce, S., Tejeiro-Martínez, J., & Benito-León, J. (2022). Current evidence on the potential therapeutic applications of transcranial magnetic stimulation in multiple sclerosis: A systematic review of the literature. *Neurología (English Edition)*, *37*(3), 199–215. https://doi.org/10.1016/j.nrleng.2020.05.004

Leon-Sarmiento, F. E., Bara-Jimenez, W., & Wassermann, E. M. (2005). Visual deprivation effects on human motor cortex excitability. *Neuroscience Letters*, *389*(1), 17–20. https://doi.org/10.1016/j.neulet.2005.06.061

Lepage, J.-F., Saint-Amour, D., & Théoret, H. (2008). EEG and neuronavigated single-pulse TMS in the study of the observation/execution matching system: Are both techniques measuring the same process? *Journal of Neuroscience Methods*, *175*(1), 17–24. https://doi.org/10.1016/j.jneumeth.2008.07.021

Li, Y., Lou, B., Gao, X., & Sajda, P. (2013). Post-stimulus endogenous and exogenous oscillations are differentially modulated by task difficulty. *Frontiers in Human Neuroscience*, *7*. https://doi.org/10.3389/fnhum.2013.00009

Limbach, K., & Corballis, P. M. (2016). Prestimulus alpha power influences response criterion in a detection task: Prestimulus alpha power influences response. *Psychophysiology*, *53*(8), 1154–1164. https://doi.org/10.1111/psyp.12666

Limbach, K., & Corballis, P. M. (2017). Alpha-power modulation reflects the balancing of task requirements in a selective attention task. *Psychophysiology*, *54*(2), 224–234. https://doi.org/10.1111/psyp.12774

Lin, Y.-J., Shukla, L., Dugué, L., Valero-Cabré, A., & Carrasco, M. (2021). Transcranial magnetic stimulation entrains alpha oscillatory activity in occipital cortex. *Scientific Reports*, *11*(1), 18562. https://doi.org/10.1038/s41598-021-96849-9

Lindsley, D. B. (1952). Psychological phenomena and the electroencephalogram. *Electroencephalography and Clinical Neurophysiology*, *4*(4), 443–456. https://doi.org/10.1016/0013-4694(52)90075-8

Ling, S., & Carrasco, M. (2006). Sustained and transient covert attention enhance the signal via different contrast response functions. *Vision Research*, *46*(8–9), 1210–1220. https://doi.org/10.1016/j.visres.2005.05.008

Linkenkaer-Hansen, K., Nikouline, V. V., Palva, J. M., & Ilmoniemi, R. J. (2001). Long-Range Temporal Correlations and Scaling Behavior in Human Brain Oscillations. *The Journal of Neuroscience*, *21*(4), 1370–1377. https://doi.org/10.1523/JNEUROSCI.21-04-01370.2001

Little, S., & Brown, P. (2014). The functional role of beta oscillations in Parkinson's disease. *Parkinsonism & Related Disorders*, *20*, S44–S48. https://doi.org/10.1016/S1353-8020(13)70013-0

Liu, B., Nobre, A. C., & Van Ede, F. (2022). Functional but not obligatory link between microsaccades and neural modulation by covert spatial attention. *Nature Communications*, *13*(1), 3503. https://doi.org/10.1038/s41467-022-31217-3

Livingstone, M., & Hubel, D. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *The Journal of Neuroscience*, *7*(11), 3416–3468. https://doi.org/10.1523/JNEUROSCI.07-11-03416.1987

Lo, S., & Andrews, S. (2015). To transform or not to transform: Using generalized linear mixed models to analyse reaction time data. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.01171

Lovinger, D. M. (2008). Communication networks in the brain: Neurons, receptors, neurotransmitters, and alcohol. *Alcohol Research & Health: The Journal of the National Institute on Alcohol Abuse and Alcoholism*, *31*(3), 196–214.

Lu, Z.-L., Lesmes, L. A., & Dosher, B. A. (2002). Spatial attention excludes external noise at the target location. *Journal of Vision*, *2*(4), 4. https://doi.org/10.1167/2.4.4

Luber, B., & Lisanby, S. H. (2014). Enhancement of human cognitive performance using transcranial magnetic stimulation (TMS). *NeuroImage*, *85*, 961–970. https://doi.org/10.1016/j.neuroimage.2013.06.007

Luck, S. J. (2014). *An introduction to the event-related potential technique* (2nd ed). MIT Press.

Lückmann, H. C., Jacobs, H. I. L., & Sack, A. T. (2014). The cross-functional role of frontoparietal regions in cognition: Internal attention as the overarching mechanism. *Progress in Neurobiology*, *116*, 66–86. https://doi.org/10.1016/j.pneurobio.2014.02.002

Lundqvist, M., Herman, P., Warden, M. R., Brincat, S. L., & Miller, E. K. (2018). Gamma and beta bursts during working memory readout suggest roles in its volitional control. *Nature Communications*, *9*(1), 394. https://doi.org/10.1038/s41467-017-02791-8

Lundqvist, M., Miller, E. K., Nordmark, J., Liljefors, J., & Herman, P. (2024). Beta: Bursts of cognition. *Trends in Cognitive Sciences*, *28*(7), 662–676. https://doi.org/10.1016/j.tics.2024.03.010

Luo, T. Z., & Maunsell, J. H. R. (2015). Neuronal Modulations in Visual Cortex Are Associated with Only One of Multiple Components of Attention. *Neuron*, *86*(5), 1182–1188. https://doi.org/10.1016/j.neuron.2015.05.007

Luo, T. Z., & Maunsell, J. H. R. (2018). Attentional Changes in Either Criterion or Sensitivity Are Associated with Robust Modulations in Lateral Prefrontal Cortex. *Neuron*, *97*(6), 1382-1393.e7. https://doi.org/10.1016/j.neuron.2018.02.007

Ly, J. Q. M., Gaggioni, G., Chellappa, S. L., Papachilleos, S., Brzozowski, A., Borsu, C., Rosanova, M., Sarasso, S., Middleton, B., Luxen, A., Archer, S. N., Phillips, C., Dijk, D.-J., Maquet, P., Massimini, M., & Vandewalle,

G. (2016). Circadian regulation of human cortical excitability. *Nature Communications*, *7*(1), 11828. https://doi.org/10.1038/ncomms11828

Macaluso, E., & Doricchi, F. (2013). Attention and predictions: Control of spatial attention beyond the endogenous-exogenous dichotomy. *Frontiers in Human Neuroscience*, *7*. https://doi.org/10.3389/fnhum.2013.00685

Macmillan, N. A. (2002). Signal Detection Theory. In H. Pashler (Ed.), *Stevens' Handbook of Experimental Psychology* (p. pas0402). John Wiley & Sons, Inc. https://doi.org/10.1002/0471214426.pas0402

Macmillan, N. A., & Kaplan, H. L. (1985). Detection theory analysis of group data: Estimating sensitivity from average hit and false-alarm rates. *Psychological Bulletin*, *98*(1), 185–199.

Macmillian, N. A., & Creelman, C. D. (1991). *Detection theory: A user's guide*. Cambridge University Press.

Madsen, K. H., Karabanov, A. N., Krohne, L. G., Safeldt, M. G., Tomasevic, L., & Siebner, H. R. (2019). No trace of phase: Corticomotor excitability is not tuned by phase of pericentral mu-rhythm. *Brain Stimulation*, *12*(5), 1261–1270. https://doi.org/10.1016/j.brs.2019.05.005

Mäki, H., & Ilmoniemi, R. J. (2010). EEG oscillations and magnetically evoked motor potentials reflect motor system excitability in overlapping neuronal populations. *Clinical Neurophysiology*, *121*(4), 492–501. https://doi.org/10.1016/j.clinph.2009.11.078

Marshall, T. R., O'Shea, J., Jensen, O., & Bergmann, T. O. (2015). Frontal Eye Fields Control Attentional Modulation of Alpha and Gamma Oscillations in Contralateral Occipitoparietal Cortex. *The Journal of Neuroscience*, *35*(4), 1638–1647. https://doi.org/10.1523/JNEUROSCI.3116-14.2015

Martinez-Trujillo, J. (2022). Visual Attention in the Prefrontal Cortex. *Annual Review of Vision Science*, *8*(1), 407–425. https://doi.org/10.1146/annurev-vision-100720-031711

Marzetti, L., Basti, A., Chella, F., D'Andrea, A., Syrjälä, J., & Pizzella, V. (2019). Brain Functional Connectivity Through Phase Coupling of Neuronal Oscillations: A Perspective From Magnetoencephalography. *Frontiers in Neuroscience*, *13*, 964. https://doi.org/10.3389/fnins.2019.00964

Mathewson, K. E., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To See or Not to See: Prestimulus α Phase Predicts Visual Awareness. *The Journal of Neuroscience*, *29*(9), 2725–2732. https://doi.org/10.1523/JNEUROSCI.3963-08.2009

Mathewson, K. E., Lleras, A., Beck, D. M., Fabiani, M., Ro, T., & Gratton, G. (2011). Pulsed Out of Awareness: EEG Alpha Oscillations Represent a Pulsed-Inhibition of Ongoing Cortical Processing. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00099

Maunsell, J. H. R., & Cook, E. P. (2002). The role of attention in visual processing. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1424), 1063–1072. https://doi.org/10.1098/rstb.2002.1107

Mazaheri, A. (2010). Rhythmic pulsing: Linking ongoing brain activity with evoked responses. *Frontiers in Human Neuroscience*, *4*. https://doi.org/10.3389/fnhum.2010.00177

McClintock, S. M., Reti, I. M., Carpenter, L. L., McDonald, W. M., Dubin, M., Taylor, S. F., Cook, I. A., O'Reardon, J., Husain, M. M., Wall, C., Krystal, A. D., Sampson, S. M., Morales, O., Nelson, B. G., Latoussakis, V., George, M. S., Lisanby, S. H., National Network of Depression Centers rTMS Task Group, & American Psychiatric Association Council on Research Task Force on Novel Biomarkers and Treatments. (2018). Consensus Recommendations for the Clinical Application of Repetitive Transcranial Magnetic Stimulation (rTMS) in the Treatment of Depression. *The Journal of Clinical Psychiatry*, *79*(1), 16cs10905. https://doi.org/10.4088/JCP.16cs10905

McCormick, D., & Mamassian, P. (2008). What does the illusory-flash look like? *Vision Research*, *48*(1), 63–69. https://doi.org/10.1016/j.visres.2007.10.010

McEvoy, L. K., Smith, M. E., & Gevins, A. (2000). Test–retest reliability of cognitive EEG. *Clinical Neurophysiology*, *111*(3), 457–463. https://doi.org/10.1016/S1388-2457(99)00258-8

Meehan, T. P., Bressler, S. L., Tang, W., Astafiev, S. V., Sylvester, C. M., Shulman, G. L., & Corbetta, M. (2017). Top-down cortical interactions in visuospatial attention. *Brain Structure and Function*, *222*(7), 3127–3145. https://doi.org/10.1007/s00429-017-1390-6

Mevorach, C., Humphreys, G. W., & Shalev, L. (2006). Opposite biases in salience-based selection for the left and right posterior parietal cortex. *Nature Neuroscience*, *9*(6), 740–742. https://doi.org/10.1038/nn1709

Meyyappan, S., Rajan, A., Mangun, G. R., & Ding, M. (2023). Top-down control of the left visual field bias in cued visual spatial attention. *Cerebral Cortex*, *33*(9), 5097–5107. https://doi.org/10.1093/cercor/bhac402

Michail, G., Toran Jenner, L., & Keil, J. (2022). Prestimulus alpha power but not phase influences visual discrimination of long-duration visual stimuli. *European Journal of Neuroscience*, *55*(11–12), 3141–3153. https://doi.org/10.1111/ejn.15169

Michalareas, G., Vezoli, J., van Pelt, S., Schoffelen, J.-M., Kennedy, H., & Fries, P. (2016). Alpha-Beta and Gamma Rhythms Subserve Feedback and Feedforward Influences among Human Visual Cortical Areas. *Neuron*, *89*(2), 384–397. https://doi.org/10.1016/j.neuron.2015.12.018

Michel, C. M., & Brunet, D. (2019). EEG Source Imaging: A Practical Review of the Analysis Steps. *Frontiers in Neurology*, *10*, 325. https://doi.org/10.3389/fneur.2019.00325

Millett, D. (2001). Hans Berger: From Psychic Energy to the EEG. *Perspectives in Biology and Medicine*, *44*(4), 522–542. https://doi.org/10.1353/pbm.2001.0070

Min, B.-K., Busch, N. A., Debener, S., Kranczioch, C., Hanslmayr, S., Engel, A. K., & Herrmann, C. S. (2007). The best of both worlds: Phase-reset of human EEG alpha activity and additive power contribute to ERP generation. *International Journal of Psychophysiology*, *65*(1), 58–68. https://doi.org/10.1016/j.ijpsycho.2007.03.002

Montemurro, M. A., Rasch, M. J., Murayama, Y., Logothetis, N. K., & Panzeri, S. (2008). Phase-of-Firing Coding of Natural Visual Stimuli in Primary Visual Cortex. *Current Biology*, *18*(5), 375–380. https://doi.org/10.1016/j.cub.2008.02.023

Moore, T., & Fallah, M. (2004). Microstimulation of the Frontal Eye Field and Its Effects on Covert Spatial Attention. *Journal of Neurophysiology*, *91*(1), 152–162. https://doi.org/10.1152/jn.00741.2002

Morillon, B., Arnal, L. H., Schroeder, C. E., & Keitel, A. (2019). Prominence of delta oscillatory rhythms in the motor cortex and their relevance for auditory and speech perception. *Neuroscience & Biobehavioral Reviews*, *107*, 136–142. https://doi.org/10.1016/j.neubiorev.2019.09.012

Mozer, M., C., Shettel, M., & Vecera, S., P. (2005). *Top-down control of visual attention: A rational account*. Advances in Neural Information Processing Systems 18, Vancover, British Columbia, Canada. https://www.researchgate.net/publication/220270100_Top-Down_Control_of_Visual_Attention_A_Rational_Account

Muggleton, N. G., Juan, C.-H., Cowey, A., & Walsh, V. (2003). Human Frontal Eye Fields and Visual Search. *Journal of Neurophysiology*, *89*(6), 3340–3343. https://doi.org/10.1152/jn.01086.2002

Myers, N. E., Stokes, M. G., Walther, L., & Nobre, A. C. (2014). Oscillatory Brain State Predicts Variability in Working Memory. *Journal of Neuroscience*, *34*(23), 7735–7743. https://doi.org/10.1523/JNEUROSCI.4741-13.2014

Myslobodsky, M. S., Coppola, R., & Weinberger, D. R. (1991). EEG laterality in the era of structural brain imaging. *Brain Topography*, *3*(3), 381–390. https://doi.org/10.1007/BF01129641

Nandi, B., Ostrand, A., Johnson, V., Ford, T. J., Gazzaley, A., & Zanto, T. P. (2023). Musical Training Facilitates Exogenous Temporal Attention via Delta Phase Entrainment within a Sensorimotor Network. *The Journal of Neuroscience*, *43*(18), 3365–3378. https://doi.org/10.1523/JNEUROSCI.0220-22.2023

Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, *9*(3), 353–383. https://doi.org/10.1016/0010-0285(77)90012-3

Nevler, N., & Ash, E. L. (2015). TMS as a Tool for Examining Cognitive Processing. *Current Neurology and Neuroscience Reports*, *15*(8), 52. https://doi.org/10.1007/s11910-015-0575-8

Ng, B. S. W., Logothetis, N. K., & Kayser, C. (2013). EEG Phase Patterns Reflect the Selectivity of Neural Firing. *Cerebral Cortex*, *23*(2), 389–398. https://doi.org/10.1093/cercor/bhs031

Nicholls, M. E. R. (1996). Temporal Processing Asymmetries Between the Cerebral Hemispheres: Evidence and Implications. *Laterality: Asymmetries of Body, Brain and Cognition*, *1*(2), 97–138. https://doi.org/10.1080/713754234

Noonan, M. P., Adamian, N., Pike, A., Printzlau, F., Crittenden, B. M., & Stokes, M. G. (2016). Distinct Mechanisms for Distractor Suppression and Target Facilitation. *The Journal of Neuroscience*, *36*(6), 1797–1807. https://doi.org/10.1523/JNEUROSCI.2133-15.2016

Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottereau, B. R., & Rossion, B. (2015). The steady-state visual evoked potential in vision research: A review. *Journal of Vision*, *15*(6), 4. https://doi.org/10.1167/15.6.4

Notbohm, A., Kurths, J., & Herrmann, C. S. (2016). Modification of Brain Oscillations via Rhythmic Light Stimulation Provides Evidence for Entrainment but Not for Superposition of Event-Related Responses. *Frontiers in Human Neuroscience*, *10*. https://doi.org/10.3389/fnhum.2016.00010

Nothdurft, H.-C., Pigarev, I. N., & Kastner, S. (2009). OVERT AND COVERT VISUAL SEARCH IN PRIMATES: REACTION TIMES AND GAZE SHIFT STRATEGIES. *Journal of Integrative Neuroscience*, *08*(02), 137–174. https://doi.org/10.1142/S0219635209002101

Nunez, P. L., & Srinivasan, R. (2006). *Electric fields of the brain: The neurophysics of EEG* (2nd ed). Oxford University Press.

Obleser, J., & Kayser, C. (2019). Neural Entrainment and Attentional Selection in the Listening Brain. *Trends in Cognitive Sciences*, *23*(11), 913–926. https://doi.org/10.1016/j.tics.2019.08.004

Ogata, K., Nakazono, H., Uehara, T., & Tobimatsu, S. (2019). Prestimulus cortical EEG oscillations can predict the excitability of the primary motor cortex. *Brain Stimulation*, *12*(6), 1508–1516. https://doi.org/10.1016/j.brs.2019.06.013

O'Keefe, J., & Recce, M. L. (1993). Phase relationship between hippocampal place units and the EEG theta rhythm. *Hippocampus*, *3*(3), 317–330. https://doi.org/10.1002/hipo.450030307

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Computational Intelligence and Neuroscience*, *2011*, 1–9. https://doi.org/10.1155/2011/156869

O'Sullivan, M. (2024). Localisation of function in the brain: A rethink. *Practical Neurology*, pn-2023-003773. https://doi.org/10.1136/pn-2023-003773

Palmigiano, A., Geisel, T., Wolf, F., & Battaglia, D. (2017). Flexible information routing by transient synchrony. *Nature Neuroscience*, *20*(7), 1014–1022. https://doi.org/10.1038/nn.4569

Palva, S., & Palva, J. M. (2011). Functional Roles of Alpha-Band Phase Synchronization in Local and Large-Scale Cortical Networks. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00204

Pascual-Leone, A., Gates, J. R., & Dhuna, A. (1991). Induction of speech arrest and counting errors with rapid-rate transcranial magnetic stimulation. *Neurology*, *41*(5), 697–702. https://doi.org/10.1212/WNL.41.5.697

Pavlidou, A., Schnitzler, A., & Lange, J. (2014). Beta oscillations and their functional role in movement perception. *Translational Neuroscience*, *5*(4). https://doi.org/10.2478/s13380-014-0236-4

Pavlov, Y. G., Adamian, N., Appelhoff, S., Arvaneh, M., Benwell, C. S. Y., Beste, C., Bland, A. R., Bradford, D. E., Bublatzky, F., Busch, N. A., Clayson, P. E., Cruse, D., Czeszumski, A., Dreber, A., Dumas, G., Ehinger, B., Ganis, G., He, X., Hinojosa, J. A., … Mushtaq, F. (2021). #EEGManyLabs: Investigating the replicability of influential EEG experiments. *Cortex*, *144*, 213–229. https://doi.org/10.1016/j.cortex.2021.03.013

Peirce, J., Gray, J. R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., Kastman, E., & Lindeløv, J. K. (2019). PsychoPy2: Experiments in behavior made easy. *Behavior Research Methods*, *51*(1), 195–203. https://doi.org/10.3758/s13428-018-01193-y

Peylo, C., Hilla, Y., & Sauseng, P. (2021). Cause or consequence? Alpha oscillations in visuospatial attention. *Trends in Neurosciences*, *44*(9), 705–713. https://doi.org/10.1016/j.tins.2021.05.004

Pfurtscheller, G. (2001). Functional brain imaging based on ERD/ERS. *Vision Research*, *41*(10–11), 1257–1260. https://doi.org/10.1016/S0042-6989(00)00235-2

Pfurtscheller, G., & Lopes Da Silva, F. H. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clinical Neurophysiology*, *110*(11), 1842–1857. https://doi.org/10.1016/S1388-2457(99)00141-8

Piantoni, G., Kline, K. A., & Eagleman, D. M. (2010). Beta oscillations correlate with the probability of perceiving rivalrous visual stimuli. *Journal of Vision*, *10*(13), 18–18. https://doi.org/10.1167/10.13.18

Picazio, S., Veniero, D., Ponzo, V., Caltagirone, C., Gross, J., Thut, G., & Koch, G. (2014). Prefrontal Control over Motor Cortex Cycles at Beta Frequency during Movement Inhibition. *Current Biology*, *24*(24), 2940–2945. https://doi.org/10.1016/j.cub.2014.10.043

Pikovskij, A., Rosenblum, M., & Kurths, J. (2003). *Synchronization: A universal concept in nonlinear sciences* (Repr., transferred to digital printing). Cambridge Univ. Press.

Polanía, R., Nitsche, M. A., & Ruff, C. C. (2018). Studying and modifying brain function with non-invasive brain stimulation. *Nature Neuroscience*, *21*(2), 174–187. https://doi.org/10.1038/s41593-017-0054-4

Pollen, D. A. (1999). On the Neural Correlates of Visual Perception. *Cerebral Cortex*, *9*(1), 4–19. https://doi.org/10.1093/cercor/9.1.4

Popov, T., Kastner, S., & Jensen, O. (2017). FEF-Controlled Alpha Delay Activity Precedes Stimulus-Induced Gamma-Band Activity in Visual Cortex. *The Journal of Neuroscience*, *37*(15), 4117–4127. https://doi.org/10.1523/JNEUROSCI.3015-16.2017

Posner, M. I. (1980). Orienting of Attention. *Quarterly Journal of Experimental Psychology*, *32*(1), 3–25. https://doi.org/10.1080/00335558008248231

Proekt, A. (2018). Brief Introduction to Electroencephalography. In *Methods in Enzymology* (Vol. 603, pp. 257–277). Elsevier. https://doi.org/10.1016/bs.mie.2018.02.009

Qin, Y., Menara, T., Bassett, D. S., & Pasqualetti, F. (2021). Phase-amplitude coupling in neuronal oscillator networks. *Physical Review Research*, *3*(2), 023218. https://doi.org/10.1103/PhysRevResearch.3.023218

Rahn, E., & Basar, E. (1993). Enhancement of Visual Evoked Potentials by Stimulation During Low Prestimulus Eeg Stages. *International Journal of Neuroscience*, *72*(1–2), 123–136. https://doi.org/10.3109/00207459308991629

Rahnev, D., Lau, H., & De Lange, F. P. (2011). Prior Expectation Modulates the Interaction between Sensory and Prefrontal Regions in the Human Brain. *Journal of Neuroscience*, *31*(29), 10741–10748. https://doi.org/10.1523/JNEUROSCI.1478-11.2011

Richter, C. G., Coppola, R., & Bressler, S. L. (2018). Top-down beta oscillatory signaling conveys behavioral context in early visual cortex. *Scientific Reports*, *8*(1), 6991. https://doi.org/10.1038/s41598-018-25267-1

Riddle, J., Hwang, K., Cellier, D., Dhanani, S., & D'Esposito, M. (2019). Causal Evidence for the Role of Neuronal Oscillations in Top–Down and Bottom–Up Attention. *Journal of Cognitive Neuroscience*, *31*(5), 768–779. https://doi.org/10.1162/jocn_a_01376

Rihs, T. A., Michel, C. M., & Thut, G. (2007). Mechanisms of selective inhibition in visual spatial attention are indexed by ?-band EEG synchronization. *European Journal of Neuroscience*, *25*(2), 603–610. https://doi.org/10.1111/j.1460-9568.2007.05278.x

Rihs, T., Michel, C., & Thut, G. (2009). A bias for posterior α-band power suppression versus enhancement during shifting versus maintenance of spatial attention. *NeuroImage*, *44*(1), 190–199. https://doi.org/10.1016/j.neuroimage.2008.08.022

Rizzolatti, G., Riggio, L., Dascola, I., & Umiltá, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, *25*(1), 31–40. https://doi.org/10.1016/0028-3932(87)90041-8

Ro, T. (2019). Alpha Oscillations and Feedback Processing in Visual Cortex for Conscious Perception. *Journal of Cognitive Neuroscience*, *31*(7), 948–960. https://doi.org/10.1162/jocn_a_01397

Roalf, D., Lowery, N., & Turetsky, B. I. (2006). Behavioral and physiological findings of gender differences in global-local visual processing. *Brain and Cognition*, *60*(1), 32–42. https://doi.org/10.1016/j.bandc.2005.09.008

Roberts, D. M., Fedota, J. R., Buzzell, G. A., Parasuraman, R., & McDonald, C. G. (2014). Prestimulus Oscillations in the Alpha Band of the EEG Are Modulated by the Difficulty of Feature Discrimination and Predict Activation of a Sensory Discrimination Process. *Journal of Cognitive Neuroscience*, *26*(8), 1615–1628. https://doi.org/10.1162/jocn_a_00569

Rogala, J., Kublik, E., Krauz, R., & Wróbel, A. (2020). Resting-state EEG activity predicts frontoparietal network reconfiguration and improved attentional performance. *Scientific Reports*, *10*(1), 5064. https://doi.org/10.1038/s41598-020-61866-7

Rogasch, N. C., & Fitzgerald, P. B. (2013). Assessing cortical network properties using TMS-EEG. *Human Brain Mapping*, *34*(7), 1652–1669. https://doi.org/10.1002/hbm.22016

Roijendijk, L., Farquhar, J., Van Gerven, M., Jensen, O., & Gielen, S. (2013). Exploring the Impact of Target Eccentricity and Task Difficulty on Covert Visual Spatial Attention and Its Implications for Brain Computer Interfacing. *PLoS ONE*, *8*(12), e80489. https://doi.org/10.1371/journal.pone.0080489

Romei, V., Brodbeck, V., Michel, C., Amedi, A., Pascual-Leone, A., & Thut, G. (2008). Spontaneous Fluctuations in Posterior -Band EEG Activity Reflect Variability in Excitability of Human Visual Areas. *Cerebral Cortex*, *18*(9), 2010–2018. https://doi.org/10.1093/cercor/bhm229

Romei, V., Driver, J., Schyns, P. G., & Thut, G. (2011). Rhythmic TMS over Parietal Cortex Links Distinct Brain Frequencies to Global versus Local Visual Processing. *Current Biology*, *21*(4), 334–337. https://doi.org/10.1016/j.cub.2011.01.035

Romei, V., Gross, J., & Thut, G. (2010). On the Role of Prestimulus Alpha Rhythms over Occipito-Parietal Areas in Visual Input Regulation: Correlation or Causation? *Journal of Neuroscience*, *30*(25), 8692–8697. https://doi.org/10.1523/JNEUROSCI.0160-10.2010

Romei, V., Rihs, T., Brodbeck, V., & Thut, G. (2008). Resting electroencephalogram alpha-power over posterior sites indexes baseline visual cortex excitability. *NeuroReport*, *19*(2), 203–208. https://doi.org/10.1097/WNR.0b013e3282f454c4

Rosanova, M., Casali, A., Bellina, V., Resta, F., Mariotti, M., & Massimini, M. (2009). Natural Frequencies of Human Corticothalamic Circuits. *Journal of Neuroscience*, *29*(24), 7679–7685. https://doi.org/10.1523/JNEUROSCI.0445-09.2009

Rosanova, M., Casarotto, S., Pigorini, A., Canali, P., Casali, A. G., & Massimini, M. (2011). Combining Transcranial Magnetic Stimulation with Electroencephalography to Study Human Cortical Excitability and Effective

Connectivity. In T. Fellin & M. Halassa (Eds.), *Neuronal Network Analysis* (Vol. 67, pp. 435–457). Humana Press. https://doi.org/10.1007/7657_2011_15

Rossi, S., Hallett, M., Rossini, P. M., & Pascual-Leone, A. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical Neurophysiology*, *120*(12), 2008–2039. https://doi.org/10.1016/j.clinph.2009.08.016

Rossini, P. M., Barker, A. T., Berardelli, A., Caramia, M. D., Caruso, G., Cracco, R. Q., Dimitrijević, M. R., Hallett, M., Katayama, Y., Lücking, C. H., Maertens de Noordhout, A. L., Marsden, C. D., Murray, N. M. F., Rothwell, J. C., Swash, M., & Tomberg, C. (1994). Non-invasive electrical and magnetic stimulation of the brain, spinal cord and roots: Basic principles and procedures for routine clinical application. Report of an IFCN committee. *Electroencephalography and Clinical Neurophysiology*, *91*(2), 79–92. https://doi.org/10.1016/0013-4694(94)90029-9

Rosso, C., Perlbarg, V., Valabregue, R., Obadia, M., Kemlin-Méchin, C., Moulton, E., Leder, S., Meunier, S., & Lamy, J.-C. (2017). Anatomical and functional correlates of cortical motor threshold of the dominant hand. *Brain Stimulation*, *10*(5), 952–958. https://doi.org/10.1016/j.brs.2017.05.005

Rotenberg, A., Horvath, J. C., & Pascual-Leone, A. (2014). The Transcranial Magnetic Stimulation (TMS) Device and Foundational Techniques. In A. Rotenberg, J. C. Horvath, & A. Pascual-Leone (Eds.), *Transcranial Magnetic Stimulation* (Vol. 89, pp. 3–13). Springer New York. https://doi.org/10.1007/978-1-4939-0879-0_1

Rugg, M. D. (2009). Event-Related Potentials (ERPs). In *Encyclopedia of Neuroscience* (pp. 7–12). Elsevier. https://doi.org/10.1016/B978-008045046-9.00752-X

Ruzzoli, M., & Soto-Faraco, S. (2014). Alpha Stimulation of the Human Parietal Cortex Attunes Tactile Perception to External Space. *Current Biology*, *24*(3), 329–332. https://doi.org/10.1016/j.cub.2013.12.029

Ruzzoli, M., Torralba Cuello, M., Molinaro, N., Benwell, C., Berkowitz, D. H., Brignani, D., Falciati, L., Greenwood, L.-M., Harris, A. M., Huber-Huber, C., Jack, B. N., Keitel, C., Kopčanová, M., Madan, C. R., Mathewson, K. E., Mishra, S., Mishra, S., Morucci, P., Myers, N., … Veniero, D. (2023). *An #EEGManyLabs study to test the role of the alpha phase on visual perception (a replication and new evidence)*. https://doi.org/10.31234/osf.io/3dhpx

Ruzzoli, M., Torralba, M., Morís Fernández, L., & Soto-Faraco, S. (2019). The relevance of alpha phase in human perception. *Cortex*, *120*, 249–268. https://doi.org/10.1016/j.cortex.2019.05.012

Saari, J., Kallioniemi, E., Tarvainen, M., & Julkunen, P. (2018). Oscillatory TMS-EEG-Responses as a Measure of the Cortical Excitability Threshold. *IEEE Transactions on Neural Systems and Rehabilitation Engineering*, *26*(2), 383–391. https://doi.org/10.1109/TNSRE.2017.2779135

Sack, A. T., Paneva, J., Küthe, T., Dijkstra, E., Zwienenberg, L., Arns, M., & Schuhmann, T. (2024). Target Engagement and Brain State Dependence of Transcranial Magnetic Stimulation: Implications for Clinical Practice. *Biological Psychiatry*, *95*(6), 536–544. https://doi.org/10.1016/j.biopsych.2023.09.011

Sadaghiani, S., & Kleinschmidt, A. (2016). Brain Networks and α-Oscillations: Structural and Functional Foundations of Cognitive Control. *Trends in Cognitive Sciences*, *20*(11), 805–817. https://doi.org/10.1016/j.tics.2016.09.004

Samaha, J., Bauer, P., Cimaroli, S., & Postle, B. R. (2015). Top-down control of the phase of alpha-band oscillations as a mechanism for temporal prediction. *Proceedings of the National Academy of Sciences*, *112*(27), 8439–8444. https://doi.org/10.1073/pnas.1503686112

Samaha, J., Iemi, L., Haegens, S., & Busch, N. A. (2020). Spontaneous Brain Oscillations and Perceptual Decision-Making. *Trends in Cognitive Sciences*, *24*(8), 639–653. https://doi.org/10.1016/j.tics.2020.05.004

Samaha, J., Iemi, L., & Postle, B. R. (2017). Prestimulus alpha-band power biases visual discrimination confidence, but not accuracy. *Consciousness and Cognition*, *54*, 47–55. https://doi.org/10.1016/j.concog.2017.02.005

Samaha, J., LaRocque, J. J., & Postle, B. R. (2022). Spontaneous alpha-band amplitude predicts subjective visibility but not discrimination accuracy during high-level perception. *Consciousness and Cognition*, *102*, 103337. https://doi.org/10.1016/j.concog.2022.103337

Samaha, J., & Postle, B. R. (2015). The Speed of Alpha-Band Oscillations Predicts the Temporal Resolution of Visual Perception. *Current Biology*, *25*(22), 2985–2990. https://doi.org/10.1016/j.cub.2015.10.007

Samaha, J., & Romei, V. (2024). Alpha-Band Frequency and Temporal Windows in Perception: A Review and Living Meta-analysis of 27 Experiments (and Counting). *Journal of Cognitive Neuroscience*, *36*(4), 640–654. https://doi.org/10.1162/jocn_a_02069

Sanei, S., & Chambers, J. A. (2013). *EEG Signal Processing*. Wiley.

Sauseng, P., Feldheim, J. F., Freunberger, R., & Hummel, F. C. (2011). Right Prefrontal TMS Disrupts Interregional Anticipatory EEG Alpha Activity during Shifting of Visuospatial Attention. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00241

Sauseng, P., & Klimesch, W. (2008). What does phase information of oscillatory brain activity tell us about cognitive processes? *Neuroscience & Biobehavioral Reviews*, *32*(5), 1001–1013. https://doi.org/10.1016/j.neubiorev.2008.03.014

Sauseng, P., Klimesch, W., Gerloff, C., & Hummel, F. C. (2009). Spontaneous locally restricted EEG alpha activity determines cortical excitability in the motor cortex. *Neuropsychologia*, *47*(1), 284–288. https://doi.org/10.1016/j.neuropsychologia.2008.07.021

Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., Gruber, W. R., & Birbaumer, N. (2005). A shift of visual spatial attention is selectively associated with human EEG alpha activity. *European Journal of Neuroscience*, *22*(11), 2917–2926. https://doi.org/10.1111/j.1460-9568.2005.04482.x

Schilberg, L., Ten Oever, S., Schuhmann, T., & Sack, A. T. (2021). Phase and power modulations on the amplitude of TMS-induced motor evoked potentials. *PLOS ONE*, *16*(9), e0255815. https://doi.org/10.1371/journal.pone.0255815

Schiller, P. H., & Chou, I. (1998). The effects of frontal eye field and dorsomedial frontal cortex lesions on visually guided eye movements. *Nature Neuroscience*, *1*(3), 248–253. https://doi.org/10.1038/693

Schneider, D., Herbst, S. K., Klatt, L., & Wöstmann, M. (2022). Target enhancement or distractor suppression? Functionally distinct alpha oscillations form the basis of attention. *European Journal of Neuroscience*, *55*(11–12), 3256–3265. https://doi.org/10.1111/ejn.15309

Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. *Trends in Neurosciences*, *32*(1), 9–18. https://doi.org/10.1016/j.tins.2008.09.012

Schröger, E., Kotz, S. A., & SanMiguel, I. (2015). Bridging prediction and attention in current research on perception and action. *Brain Research*, *1626*, 1–13. https://doi.org/10.1016/j.brainres.2015.08.037

Schuhmann, T., Kemmerer, S. K., Duecker, F., De Graaf, T. A., Ten Oever, S., De Weerd, P., & Sack, A. T. (2019). Left parietal tACS at alpha frequency induces a shift of visuospatial attention. *PLOS ONE*, *14*(11), e0217729. https://doi.org/10.1371/journal.pone.0217729

Schulz, H., Ubelacker, T., Keil, J., Muller, N., & Weisz, N. (2014). Now I am Ready--Now I am not: The Influence of Pre-TMS Oscillations and Corticomuscular Coherence on Motor-Evoked Potentials. *Cerebral Cortex*, *24*(7), 1708–1719. https://doi.org/10.1093/cercor/bht024

Schutter, D. J. L. G., & Hortensius, R. (2011). Brain oscillations and frequency-dependent modulation of cortical excitability. *Brain Stimulation*, *4*(2), 97–103. https://doi.org/10.1016/j.brs.2010.07.002

Scrivener, C. L., & Reader, A. T. (2022). Variability of EEG electrode positions and their underlying brain regions: Visualizing gel artifacts from a simultaneous EEG-fMRI dataset. *Brain and Behavior*, *12*(2), e2476. https://doi.org/10.1002/brb3.2476

Seguin, C., Sporns, O., & Zalesky, A. (2023). Brain network communication: Concepts, models and applications. *Nature Reviews Neuroscience*, *24*(9), 557–574. https://doi.org/10.1038/s41583-023-00718-5

Sekiguchi, H., Takeuchi, S., Kadota, H., Kohno, Y., & Nakajima, Y. (2011). TMS-induced artifacts on EEG can be reduced by rearrangement of the electrode's lead wire before recording. *Clinical Neurophysiology*, *122*(5), 984–990. https://doi.org/10.1016/j.clinph.2010.09.004

Semmlow, J. (2012). Fourier Transform. In *Signals and Systems for Bioengineers* (pp. 81–129). Elsevier. https://doi.org/10.1016/B978-0-12-384982-3.00003-1

Senkowski, D., & Herrmann, C. S. (2002). Effects of task difficulty on evoked gamma activity and ERPs in a visual discrimination task. *Clinical Neurophysiology*, *113*(11), 1742–1753. https://doi.org/10.1016/S1388-2457(02)00266-3

Shackman, A. J., McMenamin, B. W., Maxwell, J. S., Greischar, L. L., & Davidson, R. J. (2010). Identifying robust and sensitive frequency bands for interrogating neural oscillations. *NeuroImage*, *51*(4), 1319–1333. https://doi.org/10.1016/j.neuroimage.2010.03.037

Sherman, M. T., Kanai, R., Seth, A. K., & VanRullen, R. (2016). Rhythmic Influence of Top–Down Perceptual Priors in the Phase of Prestimulus Occipital Alpha Oscillations. *Journal of Cognitive Neuroscience*, *28*(9), 1318–1330. https://doi.org/10.1162/jocn_a_00973

Shirahige, L., Berenguer-Rocha, M., Mendonça, S., Rocha, S., Rodrigues, M. C., & Monte-Silva, K. (2020). Quantitative Electroencephalography Characteristics for Parkinson's Disease: A Systematic Review. *Journal of Parkinson's Disease*, *10*(2), 455–470. https://doi.org/10.3233/JPD-191840

Shirinpour, S., Alekseichuk, I., Mantell, K., & Opitz, A. (2020). Experimental evaluation of methods for real-time EEG phase-specific transcranial magnetic stimulation. *Journal of Neural Engineering*, *17*(4), 046002. https://doi.org/10.1088/1741-2552/ab9dba

Shulman, G. L., Pope, D. L. W., Astafiev, S. V., McAvoy, M. P., Snyder, A. Z., & Corbetta, M. (2010). Right Hemisphere Dominance during Spatial Selective Attention and Target Detection Occurs Outside the Dorsal Frontoparietal Network. *The Journal of Neuroscience*, *30*(10), 3640–3651. https://doi.org/10.1523/JNEUROSCI.4085-09.2010

Siddiqi, S. H., Kording, K. P., Parvizi, J., & Fox, M. D. (2022). Causal mapping of human brain function. *Nature Reviews Neuroscience*, *23*(6), 361–375. https://doi.org/10.1038/s41583-022-00583-8

Siebner, H. R., Funke, K., Aberra, A. S., Antal, A., Bestmann, S., Chen, R., Classen, J., Davare, M., Di Lazzaro, V., Fox, P. T., Hallett, M., Karabanov, A. N., Kesselheim, J., Beck, M. M., Koch, G., Liebetanz, D., Meunier, S., Miniussi, C., Paulus, W., … Ugawa, Y. (2022). Transcranial magnetic stimulation of the brain: What is stimulated? – A consensus and critical position paper. *Clinical Neurophysiology*, *140*, 59–97. https://doi.org/10.1016/j.clinph.2022.04.022

Siebner, H., & Rothwell, J. (2003). Transcranial magnetic stimulation: New insights into representational cortical plasticity. *Experimental Brain Research*, *148*(1), 1–16. https://doi.org/10.1007/s00221-002-1234-2

Siegel, M., Donner, T. H., & Engel, A. K. (2012). Spectral fingerprints of large-scale neuronal interactions. *Nature Reviews Neuroscience*, *13*(2), 121–134. https://doi.org/10.1038/nrn3137

Silvanto, J. (2013). Transcranial magnetic stimulation and vision. In *Handbook of Clinical Neurology* (Vol. 116, pp. 655–669). Elsevier. https://doi.org/10.1016/B978-0-444-53497-2.00052-8

Silvanto, J., Bona, S., Marelli, M., & Cattaneo, Z. (2018). On the Mechanisms of Transcranial Magnetic Stimulation (TMS): How Brain State and Baseline Performance Level Determine Behavioral Effects of TMS. *Frontiers in Psychology*, *9*, 741. https://doi.org/10.3389/fpsyg.2018.00741

Smith, D. T., & Schenk, T. (2012). The Premotor theory of attention: Time to move on? *Neuropsychologia*, *50*(6), 1104–1114. https://doi.org/10.1016/j.neuropsychologia.2012.01.025

Smith, M.-C., & Stinear, C. M. (2016). Transcranial magnetic stimulation (TMS) in stroke: Ready for clinical practice? *Journal of Clinical Neuroscience*, *31*, 10–14. https://doi.org/10.1016/j.jocn.2016.01.034

Smith, P. L., & Ratcliff, R. (2009). An integrated theory of attention and decision making in visual signal detection. *Psychological Review*, *116*(2), 283–317. https://doi.org/10.1037/a0015156

Smith, S., & Nichols, T. (2009). Threshold-free cluster enhancement: Addressing problems of smoothing, threshold dependence and localisation in cluster inference. *NeuroImage*, *44*(1), 83–98. https://doi.org/10.1016/j.neuroimage.2008.03.061

Spadone, S., Betti, V., Sestieri, C., Pizzella, V., Corbetta, M., & Della Penna, S. (2021). Spectral signature of attentional reorienting in the human brain. *NeuroImage*, *244*, 118616. https://doi.org/10.1016/j.neuroimage.2021.118616

Spadone, S., Wyczesany, M., Della Penna, S., Corbetta, M., & Capotosto, P. (2021). Directed Flow of Beta Band Communication During Reorienting of Attention Within the Dorsal Attention Network. *Brain Connectivity*, *11*(9), 717–724. https://doi.org/10.1089/brain.2020.0885

Spitzer, B., & Haegens, S. (2017). Beyond the Status Quo: A Role for Beta Oscillations in Endogenous Content (Re)Activation. *Eneuro*, *4*(4), ENEURO.0170-17.2017. https://doi.org/10.1523/ENEURO.0170-17.2017

Sridharan, D., Ramamurthy, D. L., Schwarz, J. S., & Knudsen, E. I. (2014). Visuospatial selective attention in chickens. *Proceedings of the National Academy of Sciences*, *111*(19). https://doi.org/10.1073/pnas.1316824111

Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior Research Methods, Instruments, & Computers*, *31*(1), 137–149. https://doi.org/10.3758/BF03207704

Stengel, C., Vernet, M., Amengual, J. L., & Valero-Cabré, A. (2021). Causal modulation of right hemisphere fronto-parietal phase synchrony with Transcranial Magnetic Stimulation during a conscious visual detection task. *Scientific Reports*, *11*(1), 3807. https://doi.org/10.1038/s41598-020-79812-y

Stinear, C. M., Barber, P. A., Smale, P. R., Coxon, J. P., Fleming, M. K., & Byblow, W. D. (2006). Functional potential in chronic stroke patients depends on corticospinal tract integrity. *Brain*, *130*(1), 170–180. https://doi.org/10.1093/brain/awl333

Stokes, M. G., Chambers, C. D., Gould, I. C., English, T., McNaught, E., McDonald, O., & Mattingley, J. B. (2007). Distance-adjusted motor threshold for transcranial magnetic stimulation. *Clinical Neurophysiology*, *118*(7), 1617–1625. https://doi.org/10.1016/j.clinph.2007.04.004

Stouffer, S. A., Suchman, E. A., DeVinney, L. C., Star, S. A., & Williams, R. M. J. (1949). *Studies in Social Psychology in World War II: The American Solider* (Vols 1, Adjustment During Army Life). Princeton University Press.

Suarez-Revelo, J. X., Ochoa-Gomez, J. F., Duque-Grajales, J., Montoya-Betancur, A., & Sanchez-Lopez, S. (2015). Test-retest reliability in electroencephalographic recordings. *2015 20th Symposium on Signal Processing, Images and Computer Vision (STSIVA)*, 1–5. https://doi.org/10.1109/STSIVA.2015.7330412

Szczepanski, S. M., & Kastner, S. (2013). Shifting Attentional Priorities: Control of Spatial Attention through Hemispheric Competition. *The Journal of Neuroscience*, *33*(12), 5411–5421. https://doi.org/10.1523/JNEUROSCI.4089-12.2013

Szucs, D., & Ioannidis, J. P. A. (2021). Correction: Empirical assessment of published effect sizes and power in the recent cognitive neuroscience and psychology literature. *PLOS Biology*, *19*(3), e3001151. https://doi.org/10.1371/journal.pbio.3001151

Talcott, T. N., & Gaspelin, N. (2021). Eye movements are not mandatorily preceded by the N2pc component. *Psychophysiology*, *58*(6), e13821. https://doi.org/10.1111/psyp.13821

Tallon-Baudry, C., Bertrand, O., Delpuech, C., & Pernier, J. (1996). Stimulus Specificity of Phase-Locked and Non-Phase-Locked 40 Hz Visual Responses in Human. *The Journal of Neuroscience*, *16*(13), 4240–4249. https://doi.org/10.1523/JNEUROSCI.16-13-04240.1996

Tamura, Y., Hoshiyama, M., Nakata, H., Hiroe, N., Inui, K., Kaneoke, Y., Inoue, K., & Kakigi, R. (2005). Functional relationship between human rolandic oscillations and motor cortical excitability: An MEG study. *European Journal of Neuroscience*, *21*(9), 2555–2562. https://doi.org/10.1111/j.1460-9568.2005.04096.x

Tarasi, L., & Romei, V. (2024). Individual Alpha Frequency Contributes to the Precision of Human Visual Processing. *Journal of Cognitive Neuroscience*, *36*(4), 602–613. https://doi.org/10.1162/jocn_a_02026

Tass, P., Rosenblum, M. G., Weule, J., Kurths, J., Pikovsky, A., Volkmann, J., Schnitzler, A., & Freund, H.-J. (1998). Detection of n: M Phase Locking from Noisy Data: Application to Magnetoencephalography. *Physical Review Letters*, *81*(15), 3291–3294. https://doi.org/10.1103/PhysRevLett.81.3291

Taylor, P. C. J., & Thut, G. (2012). Brain activity underlying visual perception and attention as inferred from TMS–EEG: A review. *Brain Stimulation*, *5*(2), 124–129. https://doi.org/10.1016/j.brs.2012.03.003

Thorpe, S., D'Zmura, M., & Srinivasan, R. (2012). Lateralization of Frequency-Specific Networks for Covert Spatial Attention to Auditory Stimuli. *Brain Topography*, *25*(1), 39–54. https://doi.org/10.1007/s10548-011-0186-x

Thut, G., & Miniussi, C. (2009). New insights into rhythmic brain activity from TMS–EEG studies. *Trends in Cognitive Sciences*, *13*(4), 182–189. https://doi.org/10.1016/j.tics.2009.01.004

Thut, G., Miniussi, C., & Gross, J. (2012). The Functional Importance of Rhythmic Activity in the Brain. *Current Biology*, *22*(16), R658–R663. https://doi.org/10.1016/j.cub.2012.06.061

Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). α-Band Electroencephalographic Activity over Occipital Cortex Indexes Visuospatial Attention Bias and Predicts Visual Target Detection. *The Journal of Neuroscience*, *26*(37), 9494–9502. https://doi.org/10.1523/JNEUROSCI.0875-06.2006

Thut, G., & Pascual-Leone, A. (2010). A Review of Combined TMS-EEG Studies to Characterize Lasting Effects of Repetitive TMS and Assess Their Usefulness in Cognitive and Clinical Neuroscience. *Brain Topography*, *22*(4), 219–232. https://doi.org/10.1007/s10548-009-0115-4

Thut, G., Schyns, P. G., & Gross, J. (2011). Entrainment of Perceptually Relevant Brain Oscillations by Non-Invasive Rhythmic Stimulation of the Human Brain. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00170

Thut, G., Veniero, D., Romei, V., Miniussi, C., Schyns, P., & Gross, J. (2011). Rhythmic TMS Causes Local Entrainment of Natural Oscillatory Signatures. *Current Biology*, *21*(14), 1176–1185. https://doi.org/10.1016/j.cub.2011.05.049

Tobimatsu, S., & Celesia, G. G. (2006). Studies of human visual pathophysiology with visual evoked potentials. *Clinical Neurophysiology*, *117*(7), 1414–1433. https://doi.org/10.1016/j.clinph.2006.01.004

Tort, A. B. L., Komorowski, R., Eichenbaum, H., & Kopell, N. (2010). Measuring Phase-Amplitude Coupling Between Neuronal Oscillations of Different Frequencies. *Journal of Neurophysiology*, *104*(2), 1195–1210. https://doi.org/10.1152/jn.00106.2010

Trajkovic, J., Sack, A. T., & Romei, V. (2024). EEG-based biomarkers predict individual differences in TMS-induced entrainment of intrinsic brain rhythms. *Brain Stimulation*, *17*(2), 224–232. https://doi.org/10.1016/j.brs.2024.02.016

Treder, M. S. (2020). MVPA-Light: A Classification and Regression Toolbox for Multi-Dimensional Data. *Frontiers in Neuroscience*, *14*, 289. https://doi.org/10.3389/fnins.2020.00289

Turi, Z., Lenz, M., Paulus, W., Mittner, M., & Vlachos, A. (2021). Selecting stimulation intensity in repetitive transcranial magnetic stimulation studies: A systematic review between 1991 and 2020. *European Journal of Neuroscience*, *53*(10), 3404–3415. https://doi.org/10.1111/ejn.15195

Ueno, S., & Sekino, M. (2021). Figure-Eight Coils for Magnetic Stimulation: From Focal Stimulation to Deep Stimulation. *Frontiers in Human Neuroscience*, *15*, 805971. https://doi.org/10.3389/fnhum.2021.805971

Van Der Stigchel, S., & Theeuwes, J. (2007). The relationship between covert and overt attention in endogenous cuing. *Perception & Psychophysics*, *69*(5), 719–731. https://doi.org/10.3758/BF03193774

Van Der Stigchel, S., Van Koningsbruggen, M., Nijboer, T. C. W., List, A., & Rafal, R. D. (2012). The role of the frontal eye fields in the oculomotor inhibition of reflexive saccades: Evidence from lesion patients. *Neuropsychologia*, *50*(1), 198–203. https://doi.org/10.1016/j.neuropsychologia.2011.11.020

Van Diepen, R. M., Cohen, M. X., Denys, D., & Mazaheri, A. (2015). Attention and Temporal Expectations Modulate Power, Not Phase, of Ongoing Alpha Oscillations. *Journal of Cognitive Neuroscience*, *27*(8), 1573–1586. https://doi.org/10.1162/jocn_a_00803

Van Dijk, H., Schoffelen, J.-M., Oostenveld, R., & Jensen, O. (2008). Prestimulus Oscillatory Activity in the Alpha Band Predicts Visual Discrimination Ability. *The Journal of Neuroscience*, *28*(8), 1816–1823. https://doi.org/10.1523/JNEUROSCI.1853-07.2008

Van Ede, F., De Lange, F., Jensen, O., & Maris, E. (2011). Orienting Attention to an Upcoming Tactile Event Involves a Spatially and Temporally Specific Modulation of Sensorimotor Alpha- and Beta-Band Oscillations. *The Journal of Neuroscience*, *31*(6), 2016–2024. https://doi.org/10.1523/JNEUROSCI.5630-10.2011

van Elswijk, G., Maij, F., Schoffelen, J.-M., Overeem, S., Stegeman, D. F., & Fries, P. (2010). Corticospinal Beta-Band Synchronization Entails Rhythmic Gain Modulation. *The Journal of Neuroscience*, *30*(12), 4481–4488. https://doi.org/10.1523/JNEUROSCI.2794-09.2010

Van Kerkoerle, T., Self, M. W., Dagnino, B., Gariel-Mathis, M.-A., Poort, J., Van Der Togt, C., & Roelfsema, P. R. (2014). Alpha and gamma oscillations characterize feedback and feedforward processing in monkey visual cortex. *Proceedings of the National Academy of Sciences*, *111*(40), 14332–14341. https://doi.org/10.1073/pnas.1402773111

VanRullen, R. (2016a). How to Evaluate Phase Differences between Trial Groups in Ongoing Electrophysiological Signals. *Frontiers in Neuroscience*, *10*. https://doi.org/10.3389/fnins.2016.00426

VanRullen, R. (2016b). Perceptual Cycles. *Trends in Cognitive Sciences*, *20*(10), 723–735. https://doi.org/10.1016/j.tics.2016.07.006

VanRullen, R., Carlson, T., & Cavanagh, P. (2007). The blinking spotlight of attention. *Proceedings of the National Academy of Sciences*, *104*(49), 19204–19209. https://doi.org/10.1073/pnas.0707316104

VanRullen, R., Zoefel, B., & Ilhan, B. (2014). On the cyclic nature of perception in vision versus audition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1641), 20130214. https://doi.org/10.1098/rstb.2013.0214

Vázquez Marrufo, M., Vaquero, E., Cardoso, M. J., & Gómez, C. M. (2001). Temporal evolution of α and β bands during visual spatial attention. *Cognitive Brain Research*, *12*(2), 315–320. https://doi.org/10.1016/S0926-6410(01)00025-8

Veniero, D., Gross, J., Morand, S., Duecker, F., Sack, A. T., & Thut, G. (2021). Top-down control of visual cortex by the frontal eye fields through oscillatory realignment. *Nature Communications*, *12*(1), 1757. https://doi.org/10.1038/s41467-021-21979-7

Vernet, M., Japee, S., Lokey, S., Ahmed, S., Zachariou, V., & Ungerleider, L. G. (2019). Endogenous visuospatial attention increases visual awareness independent of visual discrimination sensitivity. *Neuropsychologia*, *128*, 297–304. https://doi.org/10.1016/j.neuropsychologia.2017.08.015

Vinao-Carl, M., Gal-Shohet, Y., Rhodes, E., Li, J., Hampshire, A., Sharp, D., & Grossman, N. (2024). Just a phase? Causal probing reveals spurious phasic dependence of sustained attention. *NeuroImage*, *285*, 120477. https://doi.org/10.1016/j.neuroimage.2023.120477

Vinck, M., Van Wingerden, M., Womelsdorf, T., Fries, P., & Pennartz, C. M. A. (2010). The pairwise phase consistency: A bias-free measure of rhythmic neuronal synchronization. *NeuroImage*, *51*(1), 112–122. https://doi.org/10.1016/j.neuroimage.2010.01.073

Violentyev, A., Shimojo, S., & Shams, L. (2005). Touch-induced visual illusion: *NeuroReport*, *16*(10), 1107–1110. https://doi.org/10.1097/00001756-200507130-00015

Von Nicolai, C., Engler, G., Sharott, A., Engel, A. K., Moll, C. K., & Siegel, M. (2014). Corticostriatal Coordination through Coherent Phase-Amplitude Coupling. *The Journal of Neuroscience*, *34*(17), 5938–5948. https://doi.org/10.1523/JNEUROSCI.5007-13.2014

Wade, N. J., & Swanston, M. (2013). *Visual perception: An introduction* (3rd ed). Psychology Press.

Wahn, B., & König, P. (2017). Can Limitations of Visuospatial Attention Be Circumvented? A Review. *Frontiers in Psychology*, *8*, 1896. https://doi.org/10.3389/fpsyg.2017.01896

Walsh, V., & Pascual-Leone, A. (2003). *Transcranial magnetic stimulation: A neurochronometrics of mind*. MIT Press.

Wang, C., Rajagovindan, R., Han, S.-M., & Ding, M. (2016). Top-Down Control of Visual Alpha Oscillations: Sources of Control Signals and Their Mechanisms of Action. *Frontiers in Human Neuroscience*, *10*. https://doi.org/10.3389/fnhum.2016.00015

Wang, D. X., Schmitt, K., Seger, S., Davila, C. E., & Lega, B. C. (2021). Cross-regional phase amplitude coupling supports the encoding of episodic memories. *Hippocampus*, *31*(5), 481–492. https://doi.org/10.1002/hipo.23309

Wang, L., & Krauzlis, R. J. (2018). Visual Selective Attention in Mice. *Current Biology*, *28*(5), 676-685.e4. https://doi.org/10.1016/j.cub.2018.01.038

Wang, Q., Gong, A., Feng, Z., Bai, Y., & Ziemann, U. (2024). Interactions of transcranial magnetic stimulation with brain oscillations: A narrative review. *Frontiers in Systems Neuroscience*, *18*, 1489949. https://doi.org/10.3389/fnsys.2024.1489949

Wang, T., De Graaf, T., Tanner, L., Schuhmann, T., Duecker, F., & Sack, A. T. (2024). Hemispheric Asymmetry in TMS-Induced Effects on Spatial Attention: A Meta-Analysis. *Neuropsychology Review*, *34*(3), 838–849. https://doi.org/10.1007/s11065-023-09614-2

Ward, L. M. (2003). Synchronous neural oscillations and cognitive processes. *Trends in Cognitive Sciences*, *7*(12), 553–559. https://doi.org/10.1016/j.tics.2003.10.012

Wardak, C., Ibos, G., Duhamel, J.-R., & Olivier, E. (2006). Contribution of the Monkey Frontal Eye Field to Covert Visual Attention. *The Journal of Neuroscience*, *26*(16), 4228–4235. https://doi.org/10.1523/JNEUROSCI.3336-05.2006

Wardak, C., Olivier, E., & Duhamel, J. (2011). The relationship between spatial attention and saccades in the frontoparietal network of the monkey. *European Journal of Neuroscience*, *33*(11), 1973–1981. https://doi.org/10.1111/j.1460-9568.2011.07710.x

Wasserman, E., Epstein, C. M., & Ziemann, U. (Eds.). (2008). *The Oxford handbook of transcranial stimulation*. Oxford University Press.

Webster, K., & Ro, T. (2020). Visual Modulation of Resting State α Oscillations. *Eneuro*, *7*(1), ENEURO.0268-19.2019. https://doi.org/10.1523/ENEURO.0268-19.2019

Weiss, E., Kann, M., & Wang, Q. (2023). Neuromodulation of Neural Oscillations in Health and Disease. *Biology*, *12*(3), 371. https://doi.org/10.3390/biology12030371

Wen, H., & Liu, Z. (2016). Separating Fractal and Oscillatory Components in the Power Spectrum of Neurophysiological Signal. *Brain Topography*, *29*(1), 13–26. https://doi.org/10.1007/s10548-015-0448-0

Wickens, A. P. (2014). *A History of the Brain* (0 ed.). Psychology Press. https://doi.org/10.4324/9781315794549

Wiesman, A. I., Heinrichs-Graham, E., Proskovec, A. L., McDermott, T. J., & Wilson, T. W. (2017). Oscillations during observations: Dynamic oscillatory networks serving visuospatial attention. *Human Brain Mapping*, *38*(10), 5128–5140. https://doi.org/10.1002/hbm.23720

Wojciulik, E., & Kanwisher, N. (1999). The Generality of Parietal Involvement in Visual Attention. *Neuron*, *23*(4), 747–764. https://doi.org/10.1016/S0896-6273(01)80033-7

Wolpert, N., & Tallon-Baudry, C. (2021). Coupling between the phase of a neural oscillation or bodily rhythm with behavior: Evaluation of different statistical procedures. *NeuroImage*, *236*, 118050. https://doi.org/10.1016/j.neuroimage.2021.118050

Womelsdorf, T., Fries, P., Mitra, P. P., & Desimone, R. (2006). Gamma-band synchronization in visual cortex predicts speed of change detection. *Nature*, *439*(7077), 733–736. https://doi.org/10.1038/nature04258

Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory Biasing of Visuospatial Attention Indexed by Retinotopically Specific α-Bank Electroencephalography Increases over Occipital Cortex. *The Journal of Neuroscience*, *20*(6), RC63–RC63. https://doi.org/10.1523/JNEUROSCI.20-06-j0002.2000

Wöstmann, M., Alavash, M., & Obleser, J. (2019). Alpha Oscillations in the Human Brain Implement Distractor Suppression Independent of Target Selection. *The Journal of Neuroscience*, *39*(49), 9797–9805. https://doi.org/10.1523/JNEUROSCI.1954-19.2019

Wöstmann, M., Störmer, V. S., Obleser, J., Addleman, D. A., Andersen, S. K., Gaspelin, N., Geng, J. J., Luck, S. J., Noonan, M. P., Slagter, H. A., & Theeuwes, J. (2022). Ten simple rules to study distractor suppression. *Progress in Neurobiology*, *213*, 102269. https://doi.org/10.1016/j.pneurobio.2022.102269

Wróbel, A. (2000). Beta activity: A carrier for visual attention. *Acta Neurobiologiae Experimentalis*, *60*(2), 247–260. https://doi.org/10.55782/ane-2000-1344

Wróbel, A., Bekisz, M., Kublik, E., & Waleszczyk, W. (1994). 20 Hz bursting beta activity in the cortico-thalamic system of visually attending cats. *Acta Neurobiologiae Experimentalis*, *54*(2), 95–107.

Wróbel, A., Ghazaryan, A., Bekisz, M., Bogdan, W., & Kamiński, J. (2007). Two Streams of Attention-Dependent β Activity in the Striate Recipient Zone of Cat's Lateral Posterior–Pulvinar Complex. *The Journal of Neuroscience*, *27*(9), 2230–2240. https://doi.org/10.1523/JNEUROSCI.4004-06.2007

Wyart, V., & Tallon-Baudry, C. (2009). How Ongoing Fluctuations in Human Visual Cortex Predict Perceptual Awareness: Baseline Shift versus Decision Bias. *Journal of Neuroscience*, *29*(27), 8715–8725. https://doi.org/10.1523/JNEUROSCI.0962-09.2009

Yordanova, J., Kolev, V., Verleger, R., Heide, W., Grumbt, M., & Schürmann, M. (2017). Synchronization of fronto-parietal beta and theta networks as a signature of visual awareness in neglect. *NeuroImage*, *146*, 341–354. https://doi.org/10.1016/j.neuroimage.2016.11.013

Zagha, E., Erlich, J. C., Lee, S., Lur, G., O'Connor, D. H., Steinmetz, N. A., Stringer, C., & Yang, H. (2022). The Importance of Accounting for Movement When Relating Neuronal Activity to Sensory and Cognitive Processes. *The Journal of Neuroscience*, *42*(8), 1375–1382. https://doi.org/10.1523/JNEUROSCI.1919-21.2021

Zazio, A., Ruhnau, P., Weisz, N., & Wutz, A. (2022). Pre-stimulus alpha-band power and phase fluctuations originate from different neural sources and exert distinct impact on stimulus-evoked responses. *European Journal of Neuroscience*, *55*(11–12), 3178–3190. https://doi.org/10.1111/ejn.15138

Zeki, S. (2015). Area V5-a microcosm of the visual brain. *Frontiers in Integrative Neuroscience*, *9*, 21. https://doi.org/10.3389/fnint.2015.00021

Zhang, H., Morrone, M. C., & Alais, D. (2019). Behavioural oscillations in visual orientation discrimination reveal distinct modulation rates for both sensitivity and response bias. *Scientific Reports*, *9*(1), 1115. https://doi.org/10.1038/s41598-018-37918-4

Zhang, J. (2019). *Basic Neural Units of the Brain: Neurons, Synapses and Action Potential*. https://doi.org/10.48550/ARXIV.1906.01703

Zhang, Y., Chen, Y., Bressler, S. L., & Ding, M. (2008). Response preparation and inhibition: The role of the cortical sensorimotor beta rhythm. *Neuroscience*, *156*(1), 238–246. https://doi.org/10.1016/j.neuroscience.2008.06.061

Zhao, C., Kong, Y., Li, D., Huang, J., Kong, L., Li, X., Jensen, O., & Song, Y. (2023). Suppression of distracting inputs by visual-spatial cues is driven by anticipatory alpha activity. *PLOS Biology*, *21*(3), e3002014. https://doi.org/10.1371/journal.pbio.3002014

Zhigalov, A., & Jensen, O. (2020). Alpha oscillations do not implement gain control in early visual cortex but rather gating in parieto-occipital regions. *Human Brain Mapping*, *41*(18), 5176–5186. https://doi.org/10.1002/hbm.25183

Zhou, Y. J., Iemi, L., Schoffelen, J.-M., de Lange, F. P., & Haegens, S. (2021). Alpha Oscillations Shape Sensory Representation and Perceptual Sensitivity. *The Journal of Neuroscience*, *41*(46), 9581–9592. https://doi.org/10.1523/JNEUROSCI.1114-21.2021

Ziemann, U. (2017). Thirty years of transcranial magnetic stimulation: Where do we stand? *Experimental Brain Research*, *235*(4), 973–984. https://doi.org/10.1007/s00221-016-4865-4

Zmeykina, E., Mittner, M., Paulus, W., & Turi, Z. (2020). Weak rTMS-induced electric fields produce neural entrainment in humans. *Scientific Reports*, *10*(1), 11994. https://doi.org/10.1038/s41598-020-68687-8

Zoefel, B., Davis, M. H., Valente, G., & Riecke, L. (2019). How to test for phasic modulation of neural and behavioural responses. *NeuroImage*, *202*, 116175. https://doi.org/10.1016/j.neuroimage.2019.116175

Zoefel, B., Ten Oever, S., & Sack, A. T. (2018). The Involvement of Endogenous Neural Oscillations in the Processing of Rhythmic Input: More Than a Regular Repetition of Evoked Neural Responses. *Frontiers in Neuroscience*, *12*, 95. https://doi.org/10.3389/fnins.2018.00095

Zrenner, C., Kozák, G., Schaworonkow, N., Metsomaa, J., Baur, D., Vetter, D., Blumberger, D. M., Ziemann, U., & Belardinelli, P. (2023). Corticospinal excitability is highest at the early rising phase of sensorimotor μ-rhythm. *NeuroImage*, *266*, 119805. https://doi.org/10.1016/j.neuroimage.2022.119805

Zrenner, C., & Ziemann, U. (2024). Closed-Loop Brain Stimulation. *Biological Psychiatry*, *95*(6), 545–552. https://doi.org/10.1016/j.biopsych.2023.09.014

Zumer, J. M., Scheeringa, R., Schoffelen, J.-M., Norris, D. G., & Jensen, O. (2014). Occipital Alpha Activity during Stimulus Processing Gates the Information Flow to Object-Selective Cortex. *PLoS Biology*, *12*(10), e1001965. https://doi.org/10.1371/journal.pbio.1001965