Coldea, Andra (2021) The role of alpha oscillations in visual processing. PhD thesis.

The role of alpha oscillations in visual processing

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A thesis submitted in fulfilment of the requirements for the Degree of

Doctor of Philosophy

Institute of Neuroscience & Psychology

College of Science & Engineering

University of Glasgow

August 2021

Abstract

Alpha-band oscillatory activity over occipito-parietal areas is involved in shaping perceptual and cognitive processes. In this thesis, I have attempted to identify whether this alpha oscillatory activity is a neural predictor of subjective versus objective measures of task performance. Using electroencephalography (EEG), I demonstrate in the first experiment that pre-stimulus alpha power is inversely related to perceptual awareness, but is not linked to accuracy, indicating a double dissociation between the subjective and objective measures. In contrast, pre-stimulus alpha phase did not predict either behavioural measure. Following up from these findings, I have explored in the second experiment whether the relationship between pre-stimulus alpha power and perceptual awareness can be causally manipulated via entrainment. To do this, I have employed repetitive transcranial magnetic stimulation (rTMS) at alpha frequency. No evidence was found for an effect of active alpha-rTMS over parietal areas relative to control conditions. However, accuracy was positively correlated to resting individual alpha peak frequency of participants, indicating that alpha frequency modulates perceptual sensitivity. Finally, in the third experiment of the series, I continued to test the causal involvement of alpha oscillations in visual perception, while investigating the replicability of effects obtained using another technique, transcranial alternating current stimulation (tACS). To this end, I aimed to replicate the finding that alpha frequency tACS over parietal areas induces a change in attention bias away from the contra- towards the ipsilateral visual hemifield relative to the stimulated hemisphere. In contrast to several previous reports, I did not find an effect of alpha tACS stimulation on attention deployment as compared to sham. This negative result calls for a more systematic assessment of the factors that drive non-invasive brain stimulation effects, so that the full potential of these techniques is achieved.

The experiments presented in this thesis add to our current understanding of the role alpha oscillations have in processing visual input, and particularly in conscious awareness. At the same time, it addresses the effectiveness of neuromodulating brain

oscillations via non-invasive brain stimulation techniques and emphasizes the importance of replicability.

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Acknowledgement

I was able to complete my journey as a PhD student only because of the wonderful people in my life, to whom I could turn for support and guidance – both professional and personal.

I would like to express my deepest gratitude to Prof. Gregor Thut and Dr. Monika Harvey, for their excellent supervision. I am very thankful for the kindness and promptitude in your guidance and for creating a supportive environment throughout the years. Thank you also to the Economic and Social Research Council (ESRC) for financially supporting this work (grant number ES/P000681/1).

I would like to extend my sincere thanks to Chris, Mimma, and Stephanie. Your invaluable insights and expert advice have not only helped shape my projects but have made me a better researcher.

I am very grateful to all my academic collaborators, undergraduate students I had the pleasure of supervising, and participants who decided to participate in my experiments. This project would not have been the same without your input, and I have learned a lot from each one of you.

I would also like to thank my lab group, for your enthusiasm for science and thought-provoking discussions. Special thanks to the fellow PhD students who have shared this journey with me from the start. The cathartic chats had over a hot cup of tea often left me feeling motivated and reassured.

I am incredibly thankful to my friends, who helped me balance out work through dinners, hikes, concerts, volleyball, travel, to name a few. Susan, our weekly walks have helped keep me composed, and I am always grateful for our insightful and uplifting talks. Special thanks to Emilia, for being my mentor and caring friend for so many years and always believing in me.

I am deeply indebted to my loving family for always keeping me grounded. In particular, thank you to Dani, you never let me feel the physical distance between

us and are relentlessly showing your unconditional support for me. Thank you to Vlad, for making me smile and helping me put things in perspective.

My success would not have been possible without Adalberto. I could never even imagine having a more encouraging and thoughtful person by my side. The passion you put into everything you do, your kindness and generosity motivate me every day to become a better version of myself.

Lastly, I owe everything to my parents. This thesis is dedicated to them.

Mama și Tata, vă mulțumesc că ați avut întotdeauna încredere în mine și mi-ați dat libertatea de a-mi alege propriul drum, rămânând alături de mine la fiecare pas. Nu aș fi putut deveni persoana care sunt azi și nu aș fi putut realiza nimic fără dragostea necondiționată, susținerea și sacrificiile pe care le-ați făcut pentru mine. Lucrarea aceasta vă este dedicată vouă.

Author's Declaration

I declare that, except where explicit reference is made to the contributions of others, that this dissertation is the result of my own work and has not been submitted for any other degree at the University of Glasgow or any other institution.

Andra Coldea

Andra

Abbreviations

AFC	Alternative Forced Choice
ANCOVA	Analysis of Covariance
ANOVA	Analysis of Variance
CFC	Cross-Frequency Coupling
EEG	Electroencephalogram
ERP	Event Related Potentials
FEF	Frontal Eye Field
FFT	Fast Fourier Transform
fMRI	Functional Magnetic Resonance Imaging
IAF	Individual Alpha Frequency
IPS	Intraparietal Sulcus
MEG	Magnetoencephalogram
NIBS	Non-invasive Brain Stimulation
PAS	Perceptual Awareness Scale
PPC	Posterior Parietal Cortex
SDT	Signal Detection Theory
SSEP	Steady-State Evoked Potentials
SSVEP	Steady-State Visual Evoked Potentials
STG	Superior Temporal Gyrus
tACS	Transcranial Alternating Current Stimulation
tDCS	Transcranial Direct Current Stimulation
tES	Transcranial Electrical Stimulation
TMS	Transcranial Magnetic Stimulation
tRNS	Transcranial Random Noise Stimulation
VF	Visual Field

Previous dissemination of findings

Chapter 2:

- Published article: Benwell, C. S. Y.*, **Coldea, A.***, Harvey, M., & Thut, G. (2021). Low pre-stimulus EEG alpha power amplifies visual awareness but not visual sensitivity. The European Journal of Neuroscience. https://doi.org/10.1111/ejn.15166
- Poster presentation: “Pre-stimulus EEG alpha power and its relation with subjective perceptual awareness” at Annual Scientific Meeting of the British Association for Cognitive Neuroscience (BACN), 6th–7th September 2018, Glasgow, United Kingdom

Chapter 4:

- Published article: **Coldea, A.**, Morand, S., Veniero, D., Harvey, M., & Thut, G. (2021). Parietal alpha tACS shows inconsistent effects on visuospatial attention. PLOS ONE, 16(8), e0255424. https://doi.org/10.1371/journal.pone.0255424
- Poster presentation: “Using transcranial alternating current stimulation (tACS) at alpha frequency to modulate visual perception and attention: intermediary report of a replication study” at Transcranial Brain Stimulation in Cognitive Neuroscience Workshop, 6th-7th December 2018, Trento, Italy
- All relevant data are available on UK Data Service’s online repository Reshare at: https://reshare.ukdataservice.ac.uk/855052/

* Equally contributed to the manuscript

Chapter 1

General Introduction

1.1. Brain Oscillations in Perception

From the movement of atoms in molecules to the sounds produced by string instruments, oscillatory events are abundant in nature. In neuroscience, the term “brain oscillation” is used to describe rhythmic electrical activity occurring in the central nervous system across various temporal and spatial scales, either spontaneously or in response to external stimuli (Buzsáki, 2006). In humans, the first brain oscillation ever described was observed by Hans Berger (1929) at approximately ten waves per second (10 Hz). This became known as the alpha rhythm. Since their discovery, brain oscillations have become a focal point of the neuroscience literature and have been used as a tool for understanding cognitive processes (Karakaş & Barry, 2017).

1.1.1. Circuits and neuroanatomical characteristics of brain oscillations

Brain oscillations originate from the extracellular space outside neurons. A depolarizing event causes a flow of ions across the neuronal membrane, running from the extracellular space to the intracellular space and vice versa. If a certain threshold is reached, an action potential will be produced. Once initiated, the action potential travels along the axon to the axon terminal, where, at the synapse, it will release a chemical substance known as a neurotransmitter, signalling the postsynaptic neuron. The cerebral cortex consists mainly of pyramidal neurons that release excitatory neurotransmitters. Since excitation initiates more excitation, these connections can become unstable and are therefore embedded with inhibitory interneurons that suppress neuronal activity by releasing inhibitory neurotransmitters. It is worth noting that inhibitory interneurons target principal cells through feedforward or feedback inhibition. In a feedforward circuit, an external source sends excitatory signals to the interneurons, which in turn inhibit the principal cells, while in a feedback circuit, interneurons receive excitatory inputs from principal cells and proceed to inhibit these principal cells (Roux & Buzsáki, 2015). The balance between excitatory and inhibitory postsynaptic potentials is critical for the generation of oscillatory activity in the brain (Buzsáki, 2006). The simultaneous activation of spatially aligned groups of tens of thousands of neurons creates an electrophysiological signal detectable with electroencephalography (EEG) or magnetoencephalography (MEG). In what is now known as the communication-through-coherence hypothesis, Fries (2005) argues that different neuronal groups need to be phase-locked, creating temporal windows of opportunities for input and output that open simultaneously, facilitating the transmission of information and the neuronal communication required for cognitive dynamics.

Are brain oscillations functionally relevant, or are they a mere epiphenomenon? Singer (2018) argues that oscillations provide a precise temporal and spatial structure for neuronal activity. In addition to neural communication between networks (Fries, 2005, 2015), they have been shown to play an active role in exerting dynamic control over neuronal cell assemblies (Engel et al., 2001; Canolty et al., 2010; Palva & Palva, 2018), selection of sensory input (Schroeder & Lakatos, 2009), neural plasticity and memory (Fell & Axmacher, 2011), as well as in mediating cognitive processes such as attention (Clayton et al., 2015). In addition, disruptions in the temporal coordination of brain oscillations have been linked to neuropsychological disorders, for instance, in autism and schizophrenia (Uhlhaas & Singer, 2012).

1.1.2. Oscillatory components and their functional characteristics

Brain oscillations are characterized by three parameters: (1) *amplitude/power*, reflecting the number of neurons that fire synchronously (Pfurtscheller & Lopes da Silva, 1999), (2) *phase,* indicating the position of the oscillation in every given cycle and controlling the timing of neural signals (Jacobs et al., 2007; Buzsáki et al., 2012), and (3) *frequency*. Oscillations observed *in vivo* during wakefulness are typically divided into frequency bands, as follows:

1. *Theta oscillations* (~4-8 Hz) arise among other structures in the hippocampus (Buzsáki, 2002) and have been associated with spatial learning (Pu et al., 2017), working memory (Lee et al., 2005), top-down control of encoding and retrieval of episodic memory (Herweg et al., 2020; see also Hsieh & Ranganath, 2014), as well as cognitive control (Cavanagh & Frank, 2014).
2. *Alpha oscillations* (~8-14 Hz) are rhythms generated by thalamocortical loops (Lopes da Silva et al., 1973) and can be identified easily in EEG recordings even without any signal processing. Evidence suggests that the functional roles of alpha include modulation of working memory (Sauseng, Klimesch, Schabus, et al., 2005), emotion (Leuchter et al., 2015), creativity (Fink & Benedek, 2014), and perception by attention (Klimesch, 2012). Moreover, alpha oscillations have become one of the main targets for non-invasive brain stimulation (NIBS) techniques, such as transcranial magnetic stimulation (TMS; Thut et al., 2011) and transcranial alternating current stimulation (tACS; Zaehle et al., 2010) – both of which will be addressed in this thesis in chapters 3 and 4, respectively.
3. *Beta oscillations* (~14-30 Hz) have been traditionally linked to motor functions, with suppression in beta activity occurring during the preparation and execution of voluntary movements (Kilavik et al., 2013) and motor imagery (Lange et al., 2008). Beyond somatosensory processing, beta oscillations have been associated with numerous cognitive functions such as working memory and decision making (Spitzer & Haegens, 2017).
4. *Gamma oscillations* (~30-80 Hz) are involved in various cognitive functions, such as attentional selection, stimulus encoding, maintenance of working memory, and short- and long-term memory (see Jensen et al., 2007 for a review). They usually are stimulus-driven, as opposed to rhythms at slower frequencies (such as alpha) that can also be observed at baseline in the absence of sensory input (Marshall et al., 2015, see below).

The function of oscillatory components is consistent with their laminar organization. Animal research has shown that alpha and beta oscillations are prominently generated in deeper levels of the cortex and serve feedback signalling (Roopun et al., 2008; Buffalo et al., 2011; van Kerkoerle et al., 2014; Bastos et al., 2015; Jensen et al., 2015; Michalareas et al., 2016). Although they have different sub-functions, alpha/beta-oscillations are thought to reflect "top-down" signals from higher-order cortical regions, modulating integrative functions involving long-range interactions (e.g. attention, decision-making), which are reflected in the pre-stimulus period (Donner & Siegel, 2011; Bauer et al., 2014). On the other hand, gamma oscillations originate in superficial layers of the cortex and signal the response to stimuli in higher-level brain regions via feedforward connections (Roopun et al., 2008; Buffalo et al., 2011; van Kerkoerle et al., 2014; Bastos et al., 2015; Jensen et al., 2015; Michalareas et al., 2016). Gamma activity is local and determined by stimulus features (Hermes et al., 2015), therefore considered as "bottom-up" and its modulation is seen in the post-stimulus period (Bauer et al., 2014).

Since the time needed to complete one oscillatory cycle varies, frequency bands also differ in the temporal windows available for processing and are associated with distinct spatial scales, with small local neural networks oscillating at higher frequencies and large global neural networks oscillating at slower frequencies (von Stein & Sarnthein, 2000). However, brain oscillations do not act in isolation. In addition to the previously proposed hypothesis of communication-through-coherence (Fries, 2005, 2015), recent evidence shows that long-range brain communication is also facilitated through cross-frequency coupling (CFC; Canolty & Knight, 2010; Florin & Baillet, 2015; González et al., 2020). Cross-frequency interaction can occur as (i) amplitude-amplitude, (ii) phase-phase, (iii) phase-frequency, or (iv) phase-amplitude coupling (Jensen & Colgin, 2007; Engel et al., 2013), the latter being the most prevailing. In CFC, whenever an integrative process is needed, slow frequency bands are coupled with faster bands such as the gamma rhythm (Florin & Baillet, 2015). It has been proposed that CFC between alpha, beta, and gamma supports sensory and attentional functions (Palva & Palva, 2011; Siebenhühner et al., 2016; Hirvonen et al., 2018; Hirschmann et al., 2020) and is involved in selectively routing of sensory information (Bonnefond et al., 2017).

1.2. The alpha oscillation: a detailed account

1.2.1. General theories of alpha

The work in this thesis is primarily related to the parieto-occipital alpha rhythm. Alpha oscillations have been observed in cortical areas such as visual (Clayton, Yeung, & Cohen Kadosh, 2018), somatosensory (Haegens, Händel, et al., 2011), motor (Sauseng et al., 2009), auditory (Weisz et al., 2011), or prefrontal (Jensen & Bonnefond, 2013) regions, but also in subcortical structures such as the thalamus (Saalmann & Kastner, 2011) or basal ganglia (Hirschmann et al., 2011). In contrast to other frequency bands, alpha oscillations respond to task demands in two different ways: with a decrease (i.e. event-related desynchronization) or an increase (i.e. event-related synchronization) in amplitude/power. Initially, it was observed that alpha was most prominent over the posterior areas when eyes are closed but became suppressed when eyes were opened, leading to the conclusion that alpha reflects the "idling" brain (Pfurtscheller et al., 1996). However, evidence has accumulated against this initial belief and toward the hypothesis that alpha plays an active role in perceptual and cognitive processes.

Fluctuations in the baseline neural activity can occur unprompted, and then they are referred to as spontaneous. When measured immediately before the presentation of a sensory stimulus (pre-stimulus activity), the power, phase, and frequency of spontaneous alpha oscillations predict the outcome on perceptual tasks. More specifically, decreases in alpha power and certain alpha phase angles, as well as faster frequencies, have been linked with high cortical excitability and better detection and/or discrimination of near-threshold stimuli (Hanslmayr et al., 2007; Romei, Brodbeck, et al., 2008; van Dijk et al., 2008; Mathewson et al., 2009; Samaha & Postle, 2015). In addition, baseline alpha activity can be experimentally manipulated by endogenously shifting the focus of attention. In attentional cueing paradigms, contralateral decreases are paralleled by ipsilateral increases in alpha power relative to the attended visual field (Kelly et al., 2006; Thut et al., 2006) and research employing rhythmic TMS has found that stimulation in the alpha band leads to impairments in performance in contralateral space, establishing a causal link between alpha rhythms and perception (Romei et al., 2010; Ruzzoli & Soto-Faraco, 2014). Based on these findings, it has been proposed that synchronization of alpha oscillations reflects inhibitory processes (Klimesch et al., 2007; Jensen & Mazaheri, 2010; Foxe & Snyder, 2011; Payne & Sekuler, 2014; Clayton et al., 2018). Formally, this was initially postulated in the "inhibition-timing hypothesis": alpha power reflects changes in inhibition, while alpha phase reflects the time at which these rhythmic changes occur (Klimesch et al., 2007). These processes are under the control of top-down signals that trigger synchronization, which in turn facilitate the activation of target regions (Klimesch et al., 2007). Alternatively, under the "gating by inhibition" hypothesis (Jensen & Mazaheri, 2010), it has been suggested that alpha-band activity enables network communication by routing the information away from task-irrelevant pathways. The processing capabilities of task-irrelevant brain regions are inhibited through alpha activity which disrupts the ongoing gamma activity in a phasic manner and shortens the time allocated to processing the incoming information, filtering out distractors (Jensen & Mazaheri, 2010; Jensen et al., 2012). In line with these proposals, Mathewson et al. (2011) suggested that inhibitory processes are not monotonic but rather occur in a "pulsed" manner as a function of phase ("pulsed inhibition model"). In other words, when alpha activity becomes synchronized, inhibition occurs concurrently over large neural populations, and the signal representation becomes suppressed (Mathewson et al., 2009; 2011). In animal recordings, it has been shown that when alpha amplitude increases, the neuronal firing rates decrease, while neural firing rates fluctuate periodically with alpha phase, such that firing is lowest at the peak of the alpha cycle (Haegens, Nácher, et al., 2011). This supports the idea that perceptual processes occur discretely in a snapshot-like manner ("discrete sensory sampling hypothesis") (VanRullen & Koch, 2003; VanRullen, 2016a). While the view whereby alpha oscillations play an inhibitory role has been initially favoured, parts of this account might need to be reconsidered (Foster & Awh, 2019; Van Diepen et al., 2019). Studies manipulating distractor exclusion report alpha signatures associated with target expectation but not with distractor inhibition (Noonan et al., 2016), implying that alpha activity might support spatial attention through signal enhancement rather than distractor suppression, although the two mechanisms might not be mutually exclusive (Carrasco, 2011; Foster & Awh, 2019).

Many of the models described above imply that alpha oscillations mediate information processing at an early input stage. Recently, evidence has emerged suggesting that alpha activity might instead relate to late perceptual processing stages affecting the system's readout from sensory areas to higher-order cortical areas, rather than the input of information from the periphery into sensory areas (Chaumon & Busch, 2014). If alpha oscillations alter sensory gain, a co-modulation of pre-stimulus alpha and steady-state visual evoked potentials (SSVEP) is anticipated. Accordingly, in an attentional cueing paradigm, the decrease of contralateral pre-stimulus alpha activity should predict an increase in ipsilateral SSVEP responses with respect to the attended location. However, recent research has shown that the two processes are independent (Keitel et al., 2019; Antonov et al., 2020; Gundlach et al., 2020; Zhigalov & Jensen, 2020), with a distinct anatomical localization (Zhigalov & Jensen, 2020). This supports the role of alpha activity in modulating the readout of information rather than the input. In a complementing line of research, pre-stimulus alpha activity has been related to changes in response thresholds rather than stimulus sensitivity (Limbach & Corballis, 2016; Iemi et al., 2017) and to subjective measures of task performance (Benwell et al., 2017; Samaha, Iemi, et al., 2017).

Supporting the notion that alpha activity influences the flow of information from lower to higher cortical areas, Palva & Palva (2007) have proposed an "active-processing hypothesis". Here, the functional significance of alpha oscillations is defined by their phase dynamics rather than the amplitude. Since increases in alpha power have been associated with increases in the phase synchrony between cortical areas (Palva et al., 2010), the researchers argue that cross-frequency phase synchrony in multiple frequency bands is needed for processes such as attention, working memory, and consciousness to occur (Palva & Palva, 2007; Siebenhühner et al., 2016; Bonnefond et al., 2017). Nonetheless, the inhibition and active-processing hypotheses could be reconciled. One possibility is that inhibition occurring in sensory areas could be under the mechanistic control of top-down alpha phase interactions (Palva & Palva, 2011). In summary, it can be concluded that alpha oscillations play multiple functional roles in perceptual and cognitive processes and whilst evidence will be discussed in more detail in the next section, much remains to be understood about their roles.

1.2.2. Alpha oscillations and perception

1.2.2.1. Visual domain

Spontaneous fluctuations and perception

Perceptual experience depends on two factors: stimulus properties and the state of the sensory area at the time the input arrives. Numerous studies have been dedicated to finding a relationship between the amplitude of spontaneous oscillations and perception. In the visual domain, Ergenoglu et al. (2004) reported that pre-stimulus alpha power covaries with the detection probability of near-threshold stimuli, with low alpha power over the parieto-occipital areas leading to improved detection rates. Pre-stimulus alpha band power modulates discrimination ability when stimuli are presented at a central location (van Dijk et al., 2008) and can be used to distinguish between poor and proficient performers in visual task performance (Hanslmayr et al., 2005, 2007; Romei, Rihs, et al., 2008). Similar findings emerge when using non-invasive brain stimulation to probe visual cortex excitability. In blindfolded participants, TMS applied over the visual cortex induces visual percepts (i.e. sensations of light known as phosphenes) at moments of low alpha-band power, while high alpha-band power results in no such effects (Romei et al., 2008; replicated by Samaha et al., 2017).

The conscious perception of briefly presented stimuli is also partly influenced by the pre-stimulus alpha phase (Mathewson et al., 2009; Dugué et al., 2011; Hanslmayr et al., 2013). Mathewson et al. (2009) found that visual detection of a briefly presented stimulus is more likely when the stimulus is presented at the peak of the alpha cycle as opposed to its trough, increasing the likelihood of the stimulus reaching conscious awareness. Similarly, Busch and colleagues (2009) found that detection of near-threshold stimuli varies in time depending on the pre-stimulus alpha phase, which accounted for 16% of the variability in performance (see also Busch & VanRullen, 2010). Entrainment of alpha phase via visual stimulation (Mathewson et al., 2010; Spaak et al., 2014; Brüers & VanRullen, 2017; see also de Graaf et al., 2013), rhythmic TMS (Jaegle & Ro, 2014) and tACS (Helfrich et al., 2014; Herring et al., 2019) has further shown that detection and discrimination of upcoming visual targets are best when the stimuli are presented at a precise time/phase angle in the entraining sequence. Additionally, using TMS, it has been reported that the probability of phosphene perception is higher at the peak of the alpha cycle (Dugué et al., 2011; Samaha, Gosseries, et al., 2017). Altogether, pre-stimulus alpha power and phase are associated with high visual cortical excitability and better detection of targets.

The role of attention and alertness

One extensively studied aspect of top-down cognitive control that modulates neural activity is selective spatial attention. The voluntary deployment of visual attention toward a spatial location without making any eye or head movements can improve processing in the attended location and the selection of relevant stimuli (Carrasco, 2011). This is reflected in fluctuations in baseline alpha oscillations. When participants are asked to direct their attention to a spatial location where the stimulus is expected to appear, posterior pre-stimulus alpha power is decreased over the hemisphere contralateral to the attended location and/or increased over the hemisphere ipsilateral to that same location (Worden et al., 2000; Sauseng et al., 2005; Kelly et al., 2006; Thut et al., 2006; Rihs et al., 2007; see also Babiloni et al., 2006 for reverse results). More than reflecting which side of space is attended, pre-stimulus alpha power is topographically specific also when attention is oriented toward one out of multiple possible locations in the visual field (Rihs et al., 2007; Samaha et al., 2016; Voytek et al., 2017; Popov et al., 2019).

Brain stimulation techniques can be used to emulate the perceptually relevant alpha signatures activated by attentional processes. In a pioneering study, Romei et al. (2010) showed that the relationship between pre-stimulus alpha power and upcoming perception is causal. TMS delivery at alpha frequency over the parieto-occipital cortex elicited an enhancement of alpha power, resulting in an improvement in target visibility ipsilaterally to the stimulated hemisphere. At the same time, an impairment occurred in the contralateral hemisphere. Similar results have been reported using brain stimulation techniques such as tACS (Schuhmann et al., 2019; but see also de Graaf et al., 2020). One other method that can be used to infer causality is neurofeedback, where participants endogenously modulate their neural activity in real time (Sitaram et al., 2017). Recently, Bagherzadeh et al. (2020) trained participants to manipulate their ratio of hemispheric alpha power over the left versus the right parietal cortex. This led to corresponding alpha asymmetries over the visual cortex and to visual evoked responses, whereby reduced alpha was associated with better stimulus processing.

Altogether, these results support the proposal that pre-stimulus alpha power reflects inhibition of task-irrelevant visual information at an early input level (Klimesch et al., 2007; Jensen & Mazaheri, 2010; Foxe & Snyder, 2011; Payne & Sekuler, 2014). If improved perception occurred via mechanisms of suppression, pre-stimulus alpha power lateralization should be stronger when participants are presented with distractors contralateral to the target. However, this anticipated EEG signature was not found in studies that manipulated the distractors directly (Kelly et al., 2010; Noonan et al., 2016; Antonov et al., 2020), which could indicate that pre-stimulus alpha power may not be related to early sensory gain control but rather might operate at a later stage (Carrasco, 2011; Foster & Awh, 2019).

Apart from selective attention, another process of cognitive control engaged during task performance is alertness, which has been defined as a sustained general preparedness to respond to information (Sturm & Willmes, 2001). The prolonged readiness to respond to task demands has also been referred to as ‘sustained attention’ or ‘vigilance’ (Sarter et al., 2001). It is usually tested in tasks where participants are asked to be on alert for unpredictable changes in the stimuli for extended periods of time. Although the relationship between alpha oscillations and alertness has been less studied than spatial attention, some studies had suggested that performance in sustained attention tasks was better when alpha power was high (Dockree et al., 2007; Braboszcz & Delorme, 2011). Although this is in apparent contradiction to the link between alpha power and selective attention, Sadaghiani and Kleinschmidt (2016) have proposed that the cortical generators that control alpha oscillations can be dissociated. More specifically, it has been suggested that alertness is maintained through a widespread alpha power increase controlled by the cingulo-opercular/insular network. On the other hand, selective attention has been proposed to be implemented via a local decrease in alpha power that is under the influence of the dorsal attention network. This suggests that perception is shaped by multiple neural networks which exert top-down control of local and global information processing via alpha oscillations (Sadaghiani & Kleinschmidt, 2016).

Relationship to awareness

As described above, the outcome of a perceptual decision can be predicted by the amplitude and phase of spontaneous oscillations and is under the influence of endogenous factors, such as attention and alertness. Most of the abovementioned studies have used hit rates (trials when visual stimuli have been identified during detection tasks) or accuracy (the percentage of correct responses during discrimination tasks) as their primary metrics. However, an increasing number of recent studies had found links between trial-to-trial alpha variability and visual experience even when the input was missing or unreliable. For example, Lange et al. (2013) used suprathreshold stimuli in two tasks - the double-flash illusion and the fusion effect - where the perception of two stimuli as opposed to one can be either illusory or veridical, respectively. They found that low pre-stimulus alpha power predicted illusory and veridical perception, suggesting that alpha indexes enhanced cortical excitability without necessarily improving visual processing (Lange et al., 2013). Follow up results using the triple flash illusion have reported similar outcomes: pre-stimulus alpha phase and power can drive perception even when stimuli are not present (Gulbinaite et al., 2017).

The tendency to report a stimulus even when it is absent has been investigated systematically in the framework of signal detection theory (SDT; Green & Swets, 1966). SDT assumes that (1) internal signals that correspond to sensory noise have a Gaussian distribution to which a constant value is added when a stimulus is present, representing the signal, and (2) participants will set a threshold (or criterion) that the sensory activity needs to reach in order to elicit a response (Green & Swets, 1966). Moreover, this framework entails that performance can be assessed when false alarms (reports of the stimulus being present in stimulus-absent trials) are considered along with the hit rates (Green & Swets, 1966; Macmillan & Creelman, 2005). Replicating the experiment of Mathewson et al. (2009) while taking into account false alarm rates, it was found that lower alpha power was correlated with improved detection as well as a more liberal criterion, resulting in a tendency to report stimuli as seen (Limbach & Corballis, 2016). These findings contradict traditional views whereby excitability improves perceptual sensitivity (e.g. Ergenoglu et al., 2004). Iemi et al. (2017) further investigated this result by contrasting two models derived from SDT: a baseline model, based on the hypothesis that decreases in alpha power increase cortical excitability, which amplifies both signal and noise, and a precision model, relying on the assumption that attention leads to improved performance in signal-from-noise discrimination. If the first model is correct, low alpha power would change both the signal-plus-noise and noise distribution with respect to the criterion but would not improve precision in the task (see Figure 1). On the other hand, if the evidence points to a precision model, decreases in alpha power would result in improved sensitivity to the stimuli. Consistent with the findings using illusory perception described above, Iemi et al. (2017) observed that low alpha power was associated with a predisposition to report a stimulus even when there was none, thus providing support for the baseline model.

So, is this bias attributable to changes in participants' decision-making strategy or to their subjective perceptual experience? When Iemi & Busch (2018) contrasted performance on detection and discrimination tasks and found that low pre-stimulus alpha power predicted performance on detection, but not on discrimination tasks, they took this as evidence that strong cortical excitability biases participants' perceptual experience, rather than their decision strategy. This was confirmed in an innovative study conducted by Kloosterman et al. (2019), where participants were asked to adjust their criterion to either a liberal or a conservative one using stimulus-response reward contingencies. The researchers found that a liberal response-making strategy was reflected in a low pre-stimulus alpha power. In other words, participants' tendency to report a stimulus as being present caused a reduction in alpha power (Kloosterman et al., 2019). In further support of the predictions made by Iemi & Busch (2018), a number of studies using alternative forced-choice (AFC) paradigms have reported null results for pre-stimulus alpha-band activity on discrimination accuracy (Hanslmayr et al., 2007; Nelli et al., 2017; Benwell et al., 2018). In addition to this, recent experiments that dissociated between effects of pre-stimulus alpha on subjective and objective measures of performance have reported yet again that low pre-stimulus alpha power is not predictive of discrimination accuracy but instead is negatively correlated with subjective confidence (Samaha, Iemi, et al., 2017) and perceptual awareness (Benwell et al., 2017). These effects are now depicted in a new model, the "baseline sensory excitability model" (Samaha, Iemi, et al., 2020), which states that high pre-stimulus alpha power has a global inhibitory effect on the sensory evidence required to make a decision, changing conscious perception.

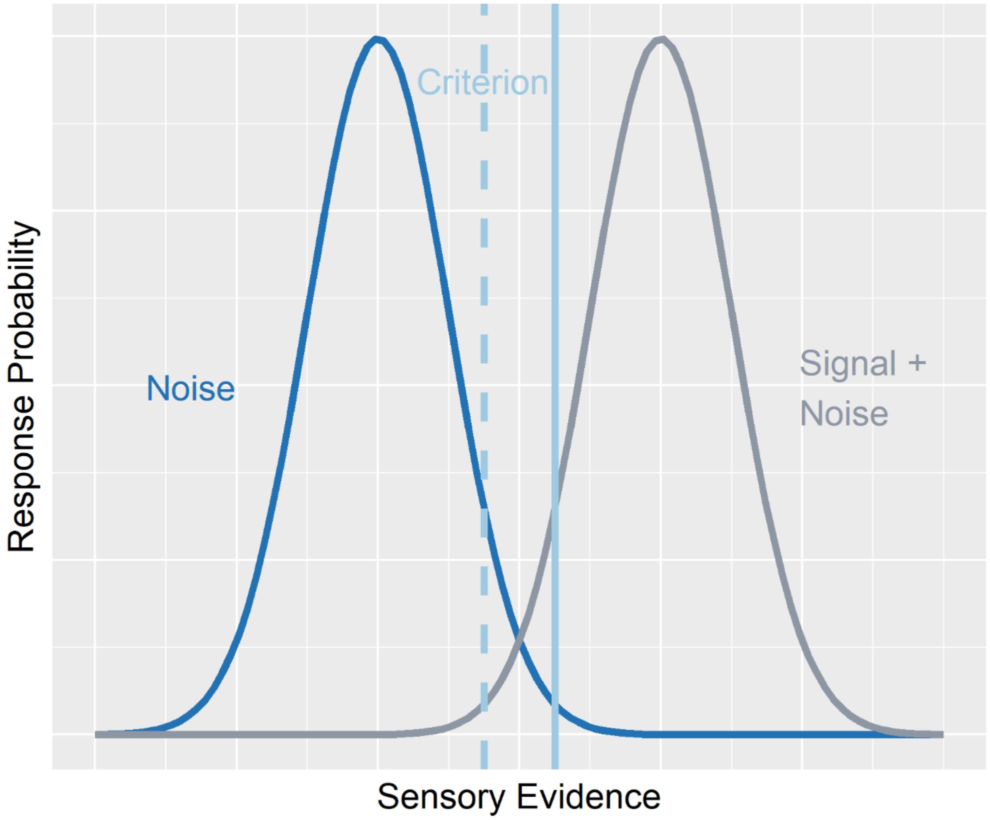


Figure 1: Criterion change within SDT framework (based on the model proposed by Iemi and colleagues, 2017). The noise and signal + noise distributions represent the internal representations of the internal sensory evidence. The decision criterion represents the decision bias. If it is shifted towards the noise distribution (dashed line), participants will have a more liberal criterion and thus an increased tendency to report having seen a stimulus. In contrast, if the decision criterion is located closer to the signal and noise distribution (solid line), participants will exhibit a more conservative decision bias. The change in criterion is illustrated by the blue arrow, a rightward change in criterion meaning a more liberal decision bias.

1.2.2.2. Tactile and auditory domain

While vision is undoubtedly the predominant modality depicted in the literature, spontaneous fluctuations in pre-stimulus alpha activity influence perception beyond the visual domain. However, the relationship between oscillatory activity and performance may be less clear.

In the somatosensory cortex, several studies have reported a negative linear relationship between pre-stimulus alpha power (also referred to as “mu alpha”) and tactile detection and discrimination for both near- and supra-threshold stimuli (Schubert et al., 2009; Jones et al., 2010; van Ede et al., 2012; Baumgarten et al., 2016; Frey et al., 2016). Manipulating somatosensory spatial attention leads to a similar electrophysiological response as in vision, with alpha oscillations becoming suppressed contralaterally (Jones et al., 2010; van Ede et al., 2011, 2014) and increased ipsilaterally (Haegens et al., 2012) to the upcoming tactile event, with lateralization stronger if the target stimulus is anticipated correctly (Haegens, Händel, et al., 2011). Consistent with recent reports emerging from the visual domain (for example, Limbach & Corballis, 2016), somatosensory alpha activity has been linked to subjective measures of performance. For instance, pre-stimulus alpha has been negatively correlated to self-reported ratings of attention (Whitmarsh et al., 2014, 2017). In macaque monkeys, high pre-stimulus alpha activity in the somatosensory cortex was linked to an increased probability of reporting a stimulus, regardless of its presence, reflecting a change in the monkey’s perceptual decision making on a vibrotactile detection task (Haegens et al., 2014). In human participants, pre-stimulus alpha states over somatosensory and occipital sites were negatively correlated with participants’ confidence in their reports of tactile simultaneity (i.e. the ability to perceive two tactile stimuli as being distinct rather than one stimulus) (Baumgarten et al., 2016). Notably, pre-stimulus alpha modulations over somatosensory regions have been reported in the absence of any external stimulus when participants erroneously report sensing touch. Craddock et al. (2017) found a negative linear relationship between alpha power and reports of both physical touch and tactile misperceptions. The effect was stronger for trials in which touch was absent, suggesting that alpha might lead to a shift in the decision criterion rather than somatosensory sensitivity alone (Craddock et al., 2017). By and large, these studies reporting a linear relationship between pre-stimulus alpha power and tactile perception are consistent with findings from the visual domain and suggest a common functional role of somatosensory and visual alpha.

In the auditory domain, alpha lateralization following the deployment of attention toward an anticipated auditory event follows the same pattern as in visual and somatosensory modalities, with alpha power decreases contralaterally to the attended side (Banerjee et al., 2011; Thorpe et al., 2012; Ahveninen et al., 2013; Frey et al., 2014; Wöstmann et al., 2016). Alpha power lateralization was shown to be stronger if the auditory stimulus was cued both spatially and temporally (Wöstmann et al., 2020) and can be successfully modulated using unihemispheric tACS (Wöstmann et al., 2018; Deng et al., 2019). If more complex stimuli are presented, alpha power fluctuations vary in synchrony with speech rate and lead to better stream comprehension (Wöstmann et al., 2016). When decoupling distractor suppression from target enhancement, specifically in a spatial pitch discrimination task, lateralization of alpha power was shown to be independent for these two processes, generated by partially distinct neural networks (Wöstmann, Alavash, et al., 2019). This finding is divergent from the recent evidence coming from the visual domain, where it has been suggested that alpha is not directly involved in distractor suppression (Foster & Awh, 2019; Antonov et al., 2020). Within the SDT framework, research coming from the auditory modality has linked pre-stimulus alpha oscillations with changes in decision criterion, where it was found that lower alpha predicted a more liberal detection criterion while sensitivity to the auditory stimulus was correlated to the theta band (Ho et al., 2017). Previously established links between pre-stimulus alpha and subjective measures of performance hold also in audition, as a negative correlation was found between spontaneous alpha and confidence in pitch discrimination of two identical tones (Wöstmann, Waschke, et al., 2019). Thus, findings from vision, somatosensory and auditory modalities converge and provide evidence for a unitary role of alpha at a late perceptual stage.

Although there is still conflicting evidence coming from different sensory modalities, and it is unclear whether alpha leads to target enhancement, stimulus suppression, or both, the research to date seems to indicate a supramodal role of alpha in attention that goes beyond simple input modulation.

1.3. Measurement and manipulation

1.3.1. M/EEG

Neural oscillations can be measured non-invasively using electroencephalography (EEG) – which records the electrical fields of the brain (Berger, 1929) - and magnetoencephalography (MEG) - which measures the magnetic fields of the brain (Cohen, 1972). These two powerful techniques are only partially independent, with both evolving from the same source signals, with high temporal precision and similar spatial resolution (Malmivuo, 2012). Using M/EEG, it is possible to relate electrophysiological dynamics to brain function and cognition in both healthy and diseased brains. For the purpose of this thesis, I will be largely focusing on EEG, but most of the points raised hereafter are valid to MEG as well.

In EEG, the neuronal signal is recorded through electrodes placed on the scalp. The signal is generated from summed postsynaptic potentials of large populations of geometrically aligned pyramidal neurons that are active simultaneously (Nunez & Srinivasan, 2006; Lopes da Silva, 2013). The signal then travels across multiple layers of tissue (e.g. cerebral spinal fluid, skull, muscles, skin etc.), causing it to be attenuated and distorted. The measured EEG signal is analogous to hearing a crowd cheering from outside the stadium (Biasiucci et al., 2019). Identifying the source of the EEG signal is formally known as the inverse problem of electroencephalography, whereby the active sources that produce a particular topography are estimated from voltage potentials recorded at scalp level (Grech et al., 2008). Although knowing the anatomical localization provides information regarding where the EEG signal comes from, it has been argued that to this day, very little is known about the interpretability of specific patterns in the signal (e.g. power- and phase-based analyses, cross-frequency coupling etc.) that have been linked to perception and cognition (Cohen, 2017).

The EEG signal can be decomposed into a series of sine waves that form the classification into frequency bands described in *Section 1.1.2*. This decomposition process has been valuable in quantifying two distinct classes of brain activity: *evoked activity*, which is time- and phase-locked to an event occurring during the experiment, and *induced activity* caused by cognitive events but not time-locked to such events. EEG features are not only effective in identifying the correlates of neuropsychological constructs but, as will be discussed in the next section, electrophysiological signatures can also be used to infer causality when combined with brain stimulation techniques in specific ways.

1.3.2. Entrainment

Brain oscillations reflect fluctuations in the excitability states of neural populations (Buzsáki & Draguhn, 2004). As introduced in *Section 1.2.2*, the level of excitability at any given time is predictive of the fate of upcoming perceptual stimuli across sensory modalities, such that stimuli presented during periods of high excitability are processed better than stimuli presented during times of low excitability. Hence, perception is not a continuous process but rather occurs in "snapshots" (VanRullen & Koch, 2003; VanRullen, 2016a). Moreover, the coordination of rhythmic activity between a physiological system and its surrounding environment is essential for the effective selection and integration of sensory inputs (Lakatos et al., 2019). This coordination can be achieved through entrainment, defined as a unidirectional process in which one (or more) self-sustained neural oscillator(s) become(s) synchronized to the frequency and phase of an external rhythmic (or quasi-rhythmic) input stream (Thut et al., 2011; Lakatos et al., 2019; Bauer et al., 2020). The degree of entrainment between an external and a neural oscillator depends on the intensity and the frequency of the external periodic force, defined by a concept known as Arnold tongue (Pikovsky et al., 2003). To be more specific, entrainment is more likely to occur when the frequencies of two oscillators are matched closely. However, if the intensity of the external driving force is increased, entrainment can occur at more frequencies adjacent to the intrinsic frequency.

Could the brain's rhythmic activity be driven *in vivo* using controlled entrainment with external forces? And if so, could this lead to behavioural benefits, which would indicate a causal role of brain rhythms in behaviour? In an attempt to answer these questions, it has been shown that entrainment of human brain oscillations can be achieved either via sensory stimulation or using NIBS techniques, particularly rhythmic TMS and tACS (Thut et al., 2011; Herrmann et al., 2016).

1.3.2.1. Sensory entrainment

Initial evidence of entrainment of the human brain came from research using sensory stimulation. When stimuli are presented rhythmically, neurons in sensory structures fire to the frequency of the flickering stimuli, eliciting a steady-state evoked potential (SSEP) in electrophysiological recordings (Regan, 1982; Picton et al., 2003). Evidence from the visual domain showed that SSVEPs were phase-locked to external stimulation up to frequencies of at least 50 Hz and, importantly, in line with the concept of Arnold tongues, presented an enhanced response when stimuli flickered in the range of the preferred frequencies (i.e. at 10, 20, 40, 80 Hz) (Herrmann, 2001). In the alpha range, the regularity of the entrainment sequence phase-locks the intrinsic oscillatory brain activity, inducing behavioural changes predictive of subjects' performance (Mathewson et al., 2012; Graaf et al., 2013). In further support of entrainment is the observation that oscillatory entrainment outlasts stimulation. Using rhythmic visual flickering, Spaak et al. (2014) found that the periodic modulation of the neural activity was observed a few cycles post-stimulation (see also Halbleib et al., 2012). This finding was also substantiated by results from the auditory modality when stimulation was in the delta frequency range (Lakatos et al., 2013). Furthermore, Notbohm et al. (2016) found that phase coupling between a visual flicker and alpha oscillations was stronger with increased intensities and at stimulation frequencies closer to participants' individual alpha frequency, with this relationship being found for rhythmic but not arrhythmic stimulation (Notbohm & Herrmann, 2016; Notbohm et al., 2016). Nonetheless, the view that SSEPs reflect entrainment has been debated (Keitel et al., 2014). The alternative explanation for the origin of SSEPs comes from the superposition of ERPs hypothesis, proposing that SSEPs can be predicted from the linear summation of transient ERP responses (Capilla et al., 2011). Moreover, Capilla et al. (2011) found no evidence that the induced oscillatory activity outlasted stimulation, suggesting that ERPs and SSEPs might have a common mechanism and function.

Although the evidence for entrainment can be disputed, sensory stimulation nonetheless alters perception (Mathewson et al., 2012; Graaf et al., 2013; Spaak et al., 2014). Initial behavioural work came from the auditory domain, with Jones et al. (2002) testing participants on a pitch discrimination task where stimuli occurred at expected versus unexpected times with respect to a rhythmic auditory tone sequence. They found performance to be best when the target stimulus appeared in-phase with the sequence. This result has since been replicated also in the visual modality, where near-threshold stimuli appearing in-phase with a rapid visual event increased the participants' sensitivity to a masked stimulus by as much as 55% (Mathewson et al., 2010). Similarly, Spaak et al. (2014) presented participants with one rhythmic and one arrhythmic visual stream in each hemifield and found that the detection performance of near-threshold stimuli followed a periodic pattern in performance in the entrained hemifield. Moreover, alpha activity in the visual cortex contralateral to periodic stimulation was increased, and this effect lasted several cycles beyond the end of stimulation (Spaak et al., 2014).

1.3.2.2. Entrainment with rhythmic neuromodulation

TMS

In contrast to sensory entrainment, NIBS techniques circumvent primary sensory areas and act upon the neuronal populations directly. One technique often employed in rhythmic neuromodulation is transcranial magnetic stimulation (TMS). Due to its effectiveness and high temporal precision, TMS has been used increasingly in research and clinical practice as an exploratory tool for cognitive neuroscience, a therapeutic and diagnostic tool. TMS relies on the principles of electromagnetic induction: a brief high-intensity electrical current stored in a capacitor is passed through a stimulation coil, generating a strong, rapidly changing magnetic field in the surrounding area of the coil. When placed on a participant's head, the magnetic field depolarizes the neuronal populations located directly below the coil. Stimulation parameters – such as frequency, intensity, duration, number of pulses, or duration of the interpulse interval – can be adjusted to create numerous potential TMS setups. The variability of the TMS modes results in three main types of stimulation: *single-pulse*, *paired-pulse*, and *repetitive TMS (rTMS)*. In single-pulse TMS, one pulse is applied at one time. In paired-pulse TMS, a variable interval separates two pulses, with both techniques being used to explore brain function (a more detailed account of these two modes of stimulation is beyond the scope of this thesis). In rTMS, a train of pulses is discharged that is expected to induce longer-lasting changes (i.e. offline effects) in brain activity (for a detailed description of TMS, see also Wagner et al., 2007; Rossi et al., 2009; Valero-Cabré et al., 2017). When the rTMS discharge frequency is < 1 Hz, it induces inhibition of excitability in the targeted cortical area (Romero et al., 2002; Valero-Cabré et al., 2007; Casula et al., 2014). However, if the frequency of the rTMS is high (> 1 Hz), the cortical excitability of the stimulated neural population is increased (Valero-Cabré et al., 2007).

In addition, the TMS-EEG combination provides further insights into the cortical networks and the oscillatory phenomena underlying cognitive functioning (Bortoletto et al., 2015; Taylor, 2018). Using this method, Herring et al. (2015) showed that TMS-locked local oscillatory activity resembled that of spontaneous oscillations after only one single pulse was applied. This suggests that the two have a common neural generator and that TMS directly manipulates brain oscillations, likely by phase-reset. Evidence for the direct manipulation of brain oscillations via entrainment through a TMS train (as opposed to a single pulse) first came from a pioneering study conducted by Thut, Veniero, et al. (2011). In the absence of an active task, the researchers observed that TMS stimulation over the posterior parietal cortex at individual alpha frequency resulted in an enhanced synchronization in the alpha band when TMS bursts were applied rhythmically (Thut, Veniero, et al., 2011). A similar increase in oscillatory synchronization was reported in the beta band but not in neighbouring frequencies when TMS was applied over the motor cortex at individual beta frequencies (Romei et al., 2016; see also Veniero et al., 2011). In addition, studies implementing TMS-EEG simultaneously during behavioural tasks have provided further confirmation of entrainment in the theta (Albouy et al., 2017), alpha (Herring et al., 2015), and beta bands (Hanslmayr et al., 2014).

Furthermore, research on the oscillatory signatures of cognition has provided evidence for a phase- and frequency-specificity of TMS-induced behavioural effects. In visual perception, TMS delivered at alpha frequency over the parietal cortex was shown to produce phase-dependent changes in subsequent discrimination performance when stimuli were presented centrally on the screen (Jaegle & Ro, 2014). Similarly, rhythmic alpha-rTMS applied over the occipital cortex impacted the temporal order perception of two distinct stimuli in a phase-dependent manner (Chota et al., 2020), supporting the notion of perception being a discrete process (VanRullen & Koch, 2003; VanRullen, 2016a). Romei et al. (2010) showed that when stimuli were presented lateralized, alpha-rTMS impaired detection contralaterally to the stimulated hemisphere while enhancing it ipsilaterally. This result was obtained when stimulation was delivered over the parietal and the occipital cortex. Rhythmic alpha TMS applied over the parietal cortex has also been found to play a role in increasing visual short-term memory capacity if the stimulation occurs at sites where distracting information is processed (Sauseng et al., 2009), to modulate local versus global visual attention (Romei et al., 2012), or induce spatially specific changes in tactile detection (Ruzzoli & Soto-Faraco, 2014).

TMS-induced entrainment of the beta oscillations has been associated with impairments in memory encoding (Hanslmayr et al., 2014) and facilitation of local but not global processing (Romei et al., 2011). Chanes et al. (2013) used rhythmic TMS to entrain brain oscillations at higher frequencies (in the high beta and gamma frequency, respectively). Using SDT, the researchers reported a dissociation in behavioural responses between the two frequencies, with high beta impacting perceptual sensitivity in a visual detection task, while gamma was related to changes in response criterion (Chanes et al., 2013).

tACS

Besides TMS, another way of stimulating the brain non-invasively is through transcranial electrical stimulation (tES), via three alternative methods: transcranial direct current stimulation (tDCS), random noise stimulation (tRNS), and alternating current stimulation (tACS) (Paulus, 2011). The latter is particularly relevant for observing neural entrainment. In tACS, the electrical current used for stimulation switches polarity between the anode and cathode. The electrical current used for tACS typically has a sinusoidal waveform bound to one single frequency, which alters the transmembrane potential of the active neurons, eliciting a change in their pattern of neuronal firing rate (Reato et al., 2013). The electrical current is delivered using a battery-driven stimulator through electrodes placed on the scalp, one over the region of interest, and one “return” electrode placed at a neutral location. The three main parameters of a tACS protocol that are usually manipulated are *frequency*, *intensity*, and *phase* of the stimulation (Antal & Paulus, 2013), although the montage and the type of electrodes used can shape the tACS-induced effect too.

The potential of using tACS to manipulate brain oscillations has been demonstrated in animal studies (Fröhlich & McCormick, 2010; Ozen et al., 2010; Ali et al., 2013; Krause et al., 2019). For example, in rats, low stimulation frequencies have been found to entrain neurons in widespread cortical areas, but the magnitude of the effect depended on stimulus intensity and whether the rats were awake or anaesthetized (Ozen et al., 2010). In nonhuman primates, single-unit recordings have shown that tACS entrains the spiking of individual neurons in a spatially localized and frequency-specific manner (Krause et al., 2019). Altogether, these studies suggest that tES can be effective in entraining the activity of neurons, but the extrapolation of results from animal models to humans should be done with caution and careful consideration of anatomical differences and the suitability of experimental parameters across species tested (Alekseichuk et al., 2019; Khatoun et al., 2019). In humans, demonstrating entrainment via EEG/MEG recordings while simultaneously applying tACS is problematic because tACS induces electrophysiological artefacts of the same frequency characteristics as the intrinsic oscillation of interest. As yet, these artefacts cannot be removed entirely with available techniques (for a review, see Kasten & Herrmann, 2019). Even if the removal of such artefacts was possible, it has been suggested that non-linear stimulation artefacts induced by the participant’s physiological state (i.e. heartbeat, respiration) still contaminate the data and can be misinterpreted as entrainment (Noury et al., 2016; also discussed by Neuling et al., 2017).

Nonetheless, attempts have been made to identify the electrophysiological signatures resulting from the application of tACS. Helfrich and colleagues (2014) have administered 10 Hz tACS to participants and have shown that stimulation causes an enhancement in alpha power over the parieto-occipital cortex. Furthermore, in sleeping participants, stimulation in higher frequencies, 25 Hz and 40 Hz, respectively, increased activity in the lower gamma frequency (Voss et al., 2014). One caveat of these concurrent tACS-EEG studies is that brain activity was measured before and after tACS stimulation (to circumvent the artefacts outlined above). Although artefact removal remains challenging, it has been suggested that MEG rather than EEG can be successfully used to separate the endogenous neural activity from the tACS signal even during stimulation (Neuling et al., 2015). Using tACS-MEG coregistration, evidence for entrainment has been reported at sites directly underneath the electrodes, as well as in their vicinity (Witkowski et al., 2016). tACS stimulation at individual alpha frequency elicited online event-related power modulations in the alpha band (Kasten et al., 2018) and increased phase coherence between tACS and brain oscillations in the visual cortex when participants were at rest with their eyes open (Ruhnau et al., 2016). All these results provide evidence for entrainment. In agreement with this, Fiene et al. (2020) paired tACS with rhythmic visual stimulation and found that steady-state responses are modulated by tACS in a phase-dependent manner in the parieto-occipital regions.

Although entrainment effects have been reported in the literature, tACS effectiveness remains controversial. Using in vivo recordings from rodents and human cadaver brains, it has been shown that the tissues passed by the electrical current (i.e. skin, soft tissue, and skull) attenuate approximately 75% of current entering the brain (Vöröslakos et al., 2018). While it has been reported that a voltage gradient of at least 1mV/mm is needed in order to change neuronal spiking (Vöröslakos et al., 2018), models based on intracranial recordings in epilepsy patients seem to indicate that this threshold is not reached with typical stimulation intensities used to date in human studies (Huang et al., 2017). Additionally, Lafon et al. (2017) found no evidence of entrainment with low frequencies during non-REM sleep and/or waking rest using intracranial recordings.

Despite the contradicting evidence regarding entrainment, an extensive body of research reports strong behavioural effects. Stimulation-induced effects have been found in brain oscillations (Zaehle et al., 2010; Vossen et al., 2015), or perception in the visual (Kanai et al., 2008; Laczó et al., 2012; Cabral-Calderin et al., 2015; Clayton et al., 2019; Schuhmann et al., 2019; Battaglini, Mena, et al., 2020; Hutchinson et al., 2020), auditory (Rufener et al., 2016; Wilsch et al., 2018; Wöstmann et al., 2018), and somatosensory domains (Feurra et al., 2011; Gundlach et al., 2016; Otsuru et al., 2019). tACS modulations have been reported in various aspects of motor function (Brittain et al., 2013; Pollok et al., 2015; Guerra et al., 2016), cognition (Kasten & Herrmann, 2017), or memory (Vosskuhl et al., 2015; Wolinski et al., 2018). Since the evidence supporting tACS entrainment is inconsistent, it has been suggested that behavioural effects could be driven by peripheral sensations induced by stimulation, such as phosphenes (Kar & Krekelberg, 2012) or transcutaneous stimulation inducing sensory entrainment (Asamoah et al., 2019b).

In fact, there has been a recent surge in studies reporting null effects (Brignani et al., 2013; Brauer et al., 2018; Wittenberg et al., 2019; Jones et al., 2019) and failed replications using tACS (Veniero et al., 2017; Bland et al., 2018; Fekete et al., 2018; Asamoah et al., 2019a). To assess the suitability of tACS for inducing reliable electrophysiological and behavioral effects, future work should optimize stimulation protocols, for example by taking into account inter-individual differences (Kasten et al., 2019), using M/EEG to guide interventions (Thut et al., 2017), or separating transcranial from sensory contributions (Asamoah et al., 2019b).

1.4. Motivation, controversies, and significance of the thesis

The current thesis can be divided into two parts. The first part capitalizes on the growing body of literature suggesting that pre-stimulus alpha relates to the perceptual experience of participants, rather than to the sensitivity of the presented stimulus, discussed in more detail in *Section 1.2.2.1* (Samaha, Iemi, et al., 2017; Iemi

& Busch, 2018; Kloosterman et al., 2019, etc.). In this regard, *Chapter 2* describes experimental work conducted to substantiate the dissociation between subjective and objective measures. It represents a conceptual replication of the study conducted by Benwell et al. (2017), in which low pre-stimulus alpha power was predictive of perceptual awareness. *Chapter 3* follows up this now confirmed finding by investigating whether the relationship between pre-stimulus alpha and subjective performance measures is merely correlational or whether causality can be established using entrainment. To the best of my knowledge, this is one of the first experimental attempts to date which uses TMS to evaluate this link.

The second part of the thesis, addressed in *Chapter 4*, relates more broadly to the efficacy of tACS as a tool for exploring brain oscillations. As neuro-enhancement via NIBS techniques is currently used extensively in research, clinical settings and even non-academically (Wexler, 2017), it is imperative that the mechanisms underlying these techniques and their effects are better understood. Generally, the field of psychology is amid a "replication crisis" (Maxwell et al., 2015) that must be overcome in order to preserve the credibility of psychological findings (Simmons et al., 2011). As described above in *Section 1.3.2.2*, the use of tACS, in particular, has been facing a lot of controversy over its potential to induce entrainment (e.g. Asamoah et al., 2019), the small effect sizes reported (e.g. Huang et al., 2017; Lafon et al., 2017), and the difficulty in replicating previous results (e.g. Veniero et al., 2017). Recently, multi-lab collaborations have started to tackle these issues, for example, the "tACS Challenge" (The TACS Challenge, 2020), the first multi-centre initiative that aims to test for online effects of tACS on behaviour arising from entrainment and not sensory confounds. Given these circumstances, in the last experimental chapter of my thesis, I will attempt to replicate the findings of another research group, namely the published study of Schuhmann et al. (2019), who found that alpha tACS applied over the left parietal cortex induces a shift in visuospatial attention.

1.5. Thesis at a glance (Abstracts)

1.5.1.1. Experiment 1: Low pre-stimulus EEG alpha power amplifies visual awareness but not visual sensitivity

Pre-stimulus oscillatory neural activity has been linked to the level of awareness of sensory stimuli. More specifically, the power of low-frequency oscillations (primarily in the alpha-band, i.e. 8-14 Hz) prior to stimulus-onset is inversely related to measures of subjective performance in visual tasks, such as confidence and visual awareness. Intriguingly, the same EEG signature does not seem to influence objective measures of task performance (i.e. accuracy). We examined whether this dissociation holds when stringent accuracy measures are used. Previous EEG studies have employed 2-alternative forced-choice (2-AFC) discrimination tasks to link pre-stimulus oscillatory activity to correct/incorrect responses as an index of accuracy/objective performance at the single-trial level. However, 2-AFC tasks do not provide a good estimate of single-trial accuracy, as many of the responses classified as correct will be contaminated by guesses (with the chance correct response rate being 50%). Here instead, we employed a 19-AFC letter identification task to measure accuracy and the subjectively reported level of perceptual awareness on each trial. As the correct guess rate is negligible (~5%), this task provides a purer measure of accuracy. These results replicate the inverse relationship between pre-stimulus alpha/beta-band power and perceptual awareness ratings in the absence of a link to discrimination accuracy. Pre-stimulus oscillatory phase did not predict either subjective awareness or accuracy. The present results hence confirm a dissociation of the pre-stimulus EEG power - task performance link for subjective versus objective measures of performance and further substantiate pre-stimulus alpha power as a neural predictor of visual awareness.

1.5.1.2. Experiment 2: Effects of alpha-band entrainment on perception - Evidence from TMS

Experiment 1 indicated that in the visual domain, pre-stimulus oscillatory neural activity is linked to measures of subjective awareness. More specifically, low pre-stimulus alpha power was negatively correlated to confidence and visual awareness, while objective performance on the task (i.e. accuracy) remained unaffected by the same EEG feature. Previous research has also indicated that repetitive transcranial magnetic stimulation (rTMS) at specific frequencies can be used to promote brain oscillations at the target frequency. To date, there are, however, no published reports exploring using rTMS whether alpha oscillations are causally involved in this double dissociation between subjective and objective measures of performance or are a mere epiphenomenon. In this experiment, 10Hz rTMS was administered over the right intraparietal sulcus (rIPS) prior to stimulus presentation in a visual discrimination task, while participants' subjective and objective performance was measured. Arrhythmic and 10 Hz sham TMS was used as control conditions. Based on prior literature, it was anticipated that 10Hz rTMS – but not the controls - induces changes in visual awareness ratings but not accuracy in the hemifield contralateral to stimulation. Contrary to this expectation, I did not observe any 10Hz-specific effect of rTMS on either measure overall. However, resting individual alpha frequency recorded using EEG was positively correlated with accuracy on task, and 10Hz rTMS effects on accuracy - but not awareness ratings – depended on individual alpha frequency, indicating that alpha frequency plays a functional role in perceptual sensitivity.

1.5.1.3. Experiment 3: Parietal alpha tACS shows inconsistent effects on visuospatial attention

Transcranial alternating current stimulation is a popular technique that has been used for manipulating brain oscillations and inferring causality regarding the brain-behaviour relationship.

Although it is a promising tool, the variability of tACS results has raised questions regarding the robustness and reproducibility of its effects. Building on recent research using tACS to modulate visuospatial attention, we here attempted to replicate findings of lateralized parietal tACS at alpha frequency to induce a change in attention bias away from the contra- towards the ipsilateral visual hemifield. 40 healthy participants underwent tACS in two separate sessions where either 10 Hz tACS or sham was applied via a high-density montage over the left parietal cortex at

1.5 mA for 20 min, while performance was assessed in an endogenous attention task. Task and tACS parameters were chosen to match those of previous studies reporting positive effects. Unlike these studies, we did not observe lateralized parietal alpha tACS to affect attention deployment or visual processing across the hemifields as compared to sham. Likewise, additional resting electroencephalography immediately offline to tACS did not reveal any notable effects on individual alpha power or frequency. This study emphasizes the need for more replication studies and systematic investigations of the factors that drive tACS effects.

Chapter 2

Low pre-stimulus EEG alpha power amplifies visual awareness but not visual sensitivity

2.1. Introduction

Discovering the neural mechanisms underlying perception remains a fundamental challenge for neuroscience. A growing body of evidence suggests that neural oscillations in specific frequency bands, as measured on the scalp using electroencephalography (EEG), may play a functional role in various perceptual processes (Salinas & Sejnowski, 2001; Varela et al., 2001; Siegel et al., 2012; Thut et al., 2012; Fries, 2015; Bonnefond et al., 2017; Gallotto et al., 2017; Keitel et al., 2018). For instance, alpha-band (8-14 Hz) power prior to stimulus onset has consistently been shown to predict the likelihood of reporting the presence of a stimulus during detection tasks, with detection reports more likely in states of low alpha-power preceding stimulus onset (Ergenoglu et al., 2004; Busch et al., 2009; Chaumon & Busch, 2014; Limbach & Corballis, 2016; Iemi et al., 2017; Iemi & Busch, 2018; Kloosterman et al., 2019; Ruzzoli et al., 2019). In order to establish a theoretical underpinning of how fluctuations in alpha-power relate to changes in perceptual performance, studies have recently started implementing psychophysical modelling techniques. One such formal framework comes from signal detection theory (SDT; Green & Swets, 1966; Macmillan & Creelman, 2005), whereby pre-stimulus alpha-power could affect performance in the task by either (i) changing perceptual sensitivity to the target stimulus (i.e. the ability to detect/discriminate the veridical target), and/or by (ii) changing the decision criterion of the participant (or the internal representation of the target stimulus) and subsequently biasing responses. Iemi and colleagues (2017) proposed that if decreases in alpha-power reflect an increase in global baseline excitability levels (see also evidence from TMS-EEG studies; Romei et al., 2008; Dugué et al., 2011; Samaha et al., 2017), then low alpha-power may lead to a more liberal decision criterion, leaving perceptual sensitivity unaffected. In line with this view, a number of recent studies have shown that pre-stimulus alpha-power influences the decision criterion and co-varies with subjective measures of task performance (i.e. confidence, perceptual awareness) but not objective measures such as accuracy (Lange et al., 2013; Limbach & Corballis, 2016; Craddock et al., 2017; Iemi et al., 2017; Iemi & Busch, 2018; Samaha, Iemi, et al., 2017; Benwell et al., 2017; Kloosterman et al., 2019; Wöstmann, Waschke, et al., 2019; Samaha, LaRocque, et al., 2020; Samaha, Iemi, et al., 2020). Moreover, it has recently been shown that a more liberal decision criterion can be induced experimentally by using different stimulus-response reward contingencies, which results in a suppression of pre-stimulus alpha-power (Kloosterman et al., 2019).

In line with these findings, our research group has recently shown that pre-stimulus EEG-power in the alpha/beta-bands over posterior sites inversely correlates with the level of subjective perceptual awareness of an upcoming threshold stimulus, but does not predict objective performance (accuracy) when a decision has to be made regarding visual stimulus features (Benwell et al., 2017). Furthermore, this relationship was found to be dependent on the stimulus being present and visible, consistent with a bias induced at the level of the perceptual experience rather than the decisional process *per se* (Chaumon & Busch, 2014; Iemi & Busch, 2018; Samaha, Iemi, et al., 2020). Here, we sought to replicate our lab's previous findings (Benwell et al., 2017) in a larger sample of participants and using a different task implemented to obtain a purer measure of objective task accuracy. In the previous experiment, a 2-alternative forced-choice (2-AFC) luminance discrimination task was employed (Benwell et al., 2017). However, 2-AFC tasks have a 50% correct guess rate by chance, meaning that many 'correct' responses will be contaminated by guesses when typical peri-threshold stimuli are used. As a consequence, a trial-by-trial relationship between true performance accuracy and EEG measures may be more difficult to detect. Here, we employed a masked letter identification task using 19 different letters, in combination with single-trial ratings of perceptual awareness (Ramsøy &

Overgaard, 2004). This 19-AFC task provides a purer measure of accuracy because contamination by guesses is rendered negligible (~5% correct responses expected by chance). By introducing a purer measure of accuracy, we sought to implement a more rigorous test for a dissociation between objective and subjective aspects of visual task performance.

Based on previous results, we hypothesized that pre-stimulus power would negatively predict subjective awareness ratings but not discrimination accuracy. Additionally, we investigated the relationship between pre-stimulus oscillatory phase and perception, for which current evidence is mixed. While many studies have linked the phase of oscillatory activity in specific frequency bands (before or during stimulus onset) to the likelihood of perception (Busch et al., 2009; Busch & VanRullen, 2010; Mathewson et al., 2009; Samaha et al., 2015), others have been unable to replicate these findings (van Diepen et al., 2015; Benwell et al., 2017; Ruzzoli et al., 2019; Vigué-Guix et al., 2020; see also Brüers & VanRullen, 2017). Together, our analyses aim to contribute to the understanding of the mechanisms by which baseline neural activity impacts visual perception.

2.2. Materials and Methods

2.2.1. Participants

22 participants (17 females, mean age = 22.9 years, min = 18, max = 29) were recruited for the study. All reported normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. Each participant gave written informed consent and received monetary compensation for their participation in the study. The study was approved by the Ethics Committee of the College of Science and Engineering at the University of Glasgow. The experimental sessions were carried out within the Institute of Neuroscience and Psychology at the University of Glasgow.

2.2.2. Task and Experimental Procedure

The task involved the identification of a briefly presented masked letter along with a subsequent rating of the level of awareness of the letter. The visual stimuli were presented on a CRT monitor (1280 x 1024 pixel resolution, 100 Hz refresh rate, viewing distance 57 cm) using E-Prime software (Version 2.0; Pittsburgh, Pennsylvania). Each trial (see Figure 2A) began with a white fixation cross presented on a grey background at the centre of the screen for a duration randomly varying between 2500ms and 3000ms. This was followed by the presentation of a white target letter (subtending 2.2° visual angle) for one of 5 possible exposure durations (10, 20, 30, 40 or 50ms). The letter was randomly selected on each trial from a set of 19 consonants (BCDFGHJKLNPQRSTVXYZ). The letter was immediately followed by a patterned mask which consisted of all letters superimposed for 200ms. After a delay period of 500ms during which a blank screen was presented, participants were asked to indicate which letter they had perceived by pressing the corresponding letter key on a standard keyboard using their right index finger. Participants were instructed to guess if they had not perceived any letter. Immediately following the response, participants were asked to rate the clarity of their experience of the letter using the Perceptual Awareness Scale (PAS; Ramsøy & Overgaard, 2004). The PAS scale consisted of the following categories: 1 – no experience, 2 – brief glimpse, 3 – almost clear experience, 4 – clear experience. Responses were given by pressing one of four different buttons on the keyboard (‘1’, ’2’, ’3’ and ’4’ on the numeric pad). Each of the two response prompts stayed on the screen until the participants made a button press. The whole experiment consisted of 475 trials, including 95 trials for each of the 5 presentation times (which were presented in a randomly intermixed order). A short break occurred every 95 trials. Participants completed a short block of practice trials prior to the main experiment to familiarise themselves with the task. The entire experimental session lasted approximately 2 hours.

2.2.3. Behavioural analysis

To evaluate the effectiveness of the experimental manipulation, statistical analyses were carried out separately for the proportion of correct responses and awareness ratings as the dependent variables and presentation time (10, 20, 30, 40 or 50ms) as the independent variable. One-way repeated-measures analyses of variance (ANOVA) were used. Additionally, effect sizes were calculated using partial η^2 and Cohen's d.

2.2.4. EEG recording

Continuous EEG was recorded with two BrainAmp MR Plus units (Brain Products GmbH, Munich, Germany) at a sampling rate of 1000 Hz through 61 Ag/AgCl pellet pin scalp electrodes placed according to the 10-10 International System. Two extra electrodes served as ground (TP9) and online reference (AFz). Electrode impedances were kept below 10 kΩ. Pre-processing steps were performed using custom scripts incorporating EEGLAB (Delorme & Makeig, 2004) and FieldTrip (Oostenveld et al., 2011) functions in Matlab (Mathworks, USA).

Offline, continuous data were filtered for power line noise using a notch filter centred at 50Hz. Additional low (100 Hz) and high-pass (0.1 Hz) filters were applied using a zero-phase second-order Butterworth filter. The data were then divided into epochs spanning -2.5:1.5s relative to stimulus onset on each trial. Subsequently, excessively noisy electrodes were removed without interpolation, the data were re-referenced to the average reference (excluding ocular channels), and trials with abnormal activity were rejected using a semi-automated artefact detection procedure, in which trials with potential artefacts are identified based on 1) extreme amplitudes (threshold of ± 75 microV), 2) joint probability of the recorded activity across electrodes at each time point (probability threshold limit of 3.5 and 3 standard deviations (SD) for single-channel limit and global limit, respectively; pop_jointprob; Delorme & Makeig, 2004) and 3) kurtosis (local limit of 5 SD, global limit of 3 SD; pop_rejkurt; Delorme & Makeig, 2004). An average of 0.14 electrodes (min = 0, max = 2) and 12.8 trials (2.7%; min = 0, max = 68) were rejected across participants. An independent component analysis (ICA) was then run using the 'runica' EEGLAB function (Delorme & Makeig, 2004) and components corresponding to blinks, eye movements and muscle artefacts were removed. Missing channels were then interpolated using a spherical spline method.

2.2.5. Spectral analysis

Fourier-based spectro-temporal decomposition of the artefact-free single-trial data was performed using the 'ft_freqanalysis' function (wavelet convolution method: 'mtmconvol') from the FieldTrip toolbox (Oostenveld et al., 2011), yielding complex-valued time-frequency planes for each trial. A temporal resolution was maintained by decomposing overlapping 0.5s segments of trial time series, consecutively shifted forward in time by 0.02s. Data segments were multiplied with a Hanning taper and then zero-padded to a length of 1s to achieve a frequency resolution of 1Hz across the range of 3:40Hz. The data were then re-epoched from -1s to 0.7s relative to stimulus onset. We sought to investigate spectral EEG predictors of both discrimination accuracy and visual awareness ratings. The two spectral measures investigated were power and phase.

2.2.6. EEG time-frequency power analysis

Single-trial power was obtained for all time-frequency points as follows:

$$EEG\ power\ (t, f)\ = |F\ (t, f)|^2$$

where F is the complex Fourier coefficient corresponding to time window t and frequency f. The absolute power values across trials were then rank scored to mitigate the influence of outlying trials. PAS ratings and letter presentation times were also rank transformed for the EEG power analyses. To test for systematic relationships between pre-stimulus power and behavioural measures, data were analyzed in the following steps:

Step 1: The *within-participant relationships* between single-trial power and both discrimination accuracy and visual awareness ratings were tested using separate models, in which EEG power and stimulus presentation time were entered as the predictors and the behavioural measure as the outcome variable. Stimulus presentation time was included as a predictor in the models in order to quantify the effect of EEG power independently of the effect of sensory evidence strength and to test for any interaction between the two. For PAS ratings, coefficients were estimated for the following linear model:

$$Ratings = a + b_{EEG} * EEG + b_{PresTime} * PresTime + \varepsilon$$

where ***Ratings*** represents the single-trial rank-transformed PAS ratings (1:4), ***EEG*** represents the single-trial rank-transformed power values, and ***PresTime*** represents the single-trial rank-transformed letter presentation times. The regression coefficient b_{EEG} indexes the direction and strength of the relationship between EEG power and PAS ratings that is independent of the relationship between letter presentation time and PAS ratings (indexed by $b_{PresTime}$). a is the model intercept and ε the error term. To test for an interaction between EEG power and letter presentation time, the following model was also run for each time electrode-time-frequency point:

$$Ratings = a + b_{int} * EEG * PresTime + \varepsilon$$

where the regression coefficient b_{int} indexes the extent to which the effects of each predictor (EEG Power and letter presentation time) on PAS Ratings are co-dependent. Both PAS Ratings models were implemented with the 'fitlm' function in Matlab R2020b (Mathworks, USA) using a least-squares solution.

For letter identification accuracy, a logistic regression was performed according to the following formula:

$$\log\left(\frac{P(Corr)}{1 - P(Corr)}\right) = a + b_{EEG} * EEG + \ b_{PresTime} * PresTime$$

where b_{EEG} indexes the direction and strength of the relationship between single-trial EEG-power and the probability of being correct ($P(Corr)$) independently of the relationship between letter presentation time and accuracy (indexed by $b_{PresTime}$). To test for an interaction between EEG power and letter presentation time, the following model was also run for each time electrode-time-frequency point:

$$\log\left(\frac{P(Corr)}{1 - P(Corr)}\right) = a + b_{int} * EEG * PresTime$$

where the regression coefficient b_{int} indexes the extent to which the effects of each predictor (EEG Power and letter presentation time) on letter identification accuracy are co-dependent. Both accuracy models were implemented with the 'fitglm' function in Matlab R2020b (Mathworks, USA).

Step 2: For all four of the models described in step 1, the regression coefficients were converted into z-statistics relative to participant-specific null hypothesis distributions built by repeatedly shuffling (500 times) the mapping between the PAS ratings/letter identification accuracy and the predictors and recalculating the coefficients each time. This resulted in a z-value for each participant, predictor and electrode-time-frequency point. Knowledge of the variability at the participant-level effects was thus incorporated into the group-level analyses.

Step 3: At the group level, z-scores were combined across participants for statistical analysis. More specifically, if at a given data point (electrode/frequency/time), EEG-power systematically co-varies linearly with the perceptual measure (discrimination accuracy or awareness rating), then z-scores should show a consistent directionality across participants. Alternatively, if there is no systematic linear relationship between EEG-power and the perceptual measure, then z-scores across participants should be random (centred around 0). Hence, for each EEG/behaviour relationship, two-tailed t-tests (test against 0) were performed on the z-score values across participants at all data points (i.e. all electrodes, frequencies, time points). Cluster-based permutation testing was employed in order to control the familywise error rate (FWER) across multiple comparisons (Maris & Oostenveld, 2007). Calculation of the test statistic involved the following: based on the initial t-tests, all t-values above a threshold corresponding to an uncorrected p-value of 0.05 were formed into clusters by grouping together adjacent significant time-frequency points and electrodes. This step was performed separately for samples with positive and negative t-values (two-tailed test). Note that for a significant sample to be included in a cluster, it was required to have at least 1 adjacent significant neighbouring sample. The spatial neighbourhood of each electrode was defined as all electrodes within approximately 5cm, resulting in a mean of 6.3 (min = 3, max = 8) and median of 7 neighbours per electrode. The t-values within each cluster were then summed to produce a cluster-level t-score (cluster statistic). Subsequently, this procedure was repeated across 2000 permutations of the data (z-scores from a random subset of participants were multiplied by -1, and the two-tailed t-test against 0 was calculated) with the largest cluster-level t-score on each iteration being retained in order to build a data-driven null hypothesis distribution. The location of the original real cluster-level t-scores within this null hypothesis distribution indicates how probable such an observation would be if the null hypothesis were true (no systematic difference from 0 in z-scores across participants). Hence, if a given negative/positive cluster had a cluster-level t-score lower than 2.5% or higher than 97.5% of the respective null distribution t-scores, then this was considered a significant effect (5% alpha level).

2.2.7. Bayes Factor (BF) analysis of EEG time-frequency power results

In order to estimate evidence for both the null hypothesis (no relationship between EEG power and behavioural measure) and the alternative hypothesis (significant relationship between EEG power and behavioural measure), Bayes Factor (BF) analyses were performed. A BF below 1/3 indicates evidence for the null hypothesis, above 3 indicates evidence for the alternative hypothesis and between 1/3 and 3 indicates that the evidence is inconclusive (potentially due to a lack of statistical power). For all data points included in the significant EEG power/PAS ratings cluster (detected in the regression analysis), the BF was calculated with a prior which followed a Cauchy distribution with a scale factor of 0.707 (Rouder et al., 2009). For each time-point, the percentage of electrode-frequency points showing evidence for the null and alternative hypotheses respectively were calculated. This analysis was performed separately for both the awareness and accuracy data.

2.2.8. Follow-up EEG power analysis

In our group's previous study, it was found that the negative relationship between pre-stimulus power and awareness ratings scaled with the strength of the stimulus, being present for higher but not for the lowest stimulus intensities (nor for catch trials in which no stimulus was presented) (Benwell et al., 2017). In order to replicate this finding, an additional analysis was performed to test for this effect in the current experiment, using the data from electrode-time-frequency points included in any significant clusters prior to stimulus onset and mirroring Benwell and colleagues' (2017) previous analysis approach. Single-trial, cluster-averaged, pre-stimulus power values were extracted for each participant and trials were split into 'above' and 'below' median power bins. The proportion of correct responses and mean PAS ratings were then calculated separately for each presentation time (10, 20, 30, 40, 50ms) in each pre-stimulus power bin ('above' and 'below' median). Subsequently, repeated measures ANOVAs with the factors pre-stimulus cluster power (high, low) and presentation time were performed on both the accuracy and awareness rating measures separately.

2.2.9. EEG time-frequency phase analysis

Step 1: To test for *within-participant relationships* between single-trial phase and both discrimination accuracy and visual awareness ratings, a measure of circular-linear association was employed, called "weighted intertrial phase clustering" (wITPC) (Cohen & Cavanagh, 2011; Cohen & Voytek, 2013). wITPC represents the resultant vector length (intertrial phase coherence) of single-trial phase angles once the length of each individual vector has been weighted by the single-trial behavioural outcome (i.e. PAS rating or accuracy). Under the null hypothesis of no EEG phase-behavior relationship, behavioural responses should be uniformly distributed across phase angles (and hence the average vector length would be close to zero). The magnitude of the average wITPC vector can be taken as a modulation of behaviour by phase angle.

wITPC was calculated for electrode-time-frequency point by multiplying the unit length complex-valued phase angle by the behavioural response on each trial, averaging those complex numbers across all trials, and taking the absolute value to obtain the average vector length. In order to quantify the effects of phase on behaviour independently of sensory evidence strength, and for the PAS ratings and accuracy main effect analyses separately, the residual variations were retrieved after regressing out the effect of letter presentation time on each behavioural measure. Hence, the wITPC was calculated here by multiplying the phase angle by the residual variation in behavioural responses, after regressing out the effect of letter presentation time, averaging those complex numbers across all trials, and taking the absolute value to obtain the average vector length. PAS ratings, accuracy (coded 0 (incorrect) or 1 (correct)), regression residuals, and letter presentation time were all rank transformed prior to calculation of the wITPC.

Step 2: Because the resulting magnitudes are not comparable across participants, and in order to control for possible non-uniformity of phase angles across trials (Cohen & Voytek, 2013), within-participant permutation testing was applied, in which a participant-specific null hypothesis distribution was built by shuffling the observed phase and behavioural values with respect to one another across 500 iterations. The standardized distance between the actual wITPC value and the null distribution was taken as a z-value corresponding to the probability of finding the observed behaviour-phase relationship by chance, given the observed data. The entire procedure was performed separately for the PAS ratings, accuracy and presentation time main effects, respectively.

Step 3: The group statistics on the single-participant wITPC z-scores then proceeded exactly as described in Step 3 of the EEG power analysis above.

2.2.10. Bayes Factor (BF) analysis of EEG time-frequency phase results

As with the power analyses, BFs were again calculated to quantify the evidence for both the null hypothesis (no relationship between phase and behavioural measure) and the alternative hypothesis (significant relationship between phase and behavioural measure). Again, the BF was calculated for all data points included in the significant pre-stimulus EEG power/PAS ratings cluster. For each time-point, the percentage of electrode-frequency points showing evidence for the null and alternative hypotheses respectively were calculated separately for both the awareness and accuracy data.

2.2.11. Phase Opposition Sum (POS) analysis

In order to replicate the method employed by Benwell et al. (2017) and hence to allow the current results to be directly comparable, a phase opposition sum (POS) analysis (VanRullen, 2016b) was employed. This approach tested whether trials associated with one perceptual outcome (i.e. correct letter identification or high subjective awareness) differed in terms of their distribution of oscillatory phases for a given time-frequency point compared to trials associated with the opposite perceptual outcome (i.e. incorrect identification or low subjective awareness). POS analysis involves the comparison of inter-trial phase coherence (ITPC) measured over all trials (serving as a baseline) with ITPC measured separately for the trials from each condition (i.e. correct versus incorrect identification and high versus low subjective awareness). If the ITPC from each condition is larger than the total ITPC, then this suggests that the two perceptual outcomes are phase-locked to different phase angles.

ITPC was calculated as follows:

$$ITPC\ (t,f) = \left| \frac{1}{n} \sum_{k=1}^{n} \frac{F_k\ (t,f)}{|F_k\ (t,f)|} \right|$$

where *F* is the complex Fourier coefficient corresponding to time window *t* and frequency *f*, *n* is the number of trials, and *k* is the individual trial index. The ITPC was calculated in this way over all trials and separately for those trials corresponding to correct identification, incorrect identification, high awareness ratings (‘3’ and ‘4’ PAS ratings) and low awareness ratings (‘1’ and ‘2’ PAS ratings) respectively.

Subsequently, the POS was calculated as follows:

$$POS = ITPC_A + ITPC_B - 2 * \ ITPC_{ALL}$$

where $ITPC_A$ and $ITPC_B$ are the ITPC calculated separately for the two trial-types to be compared (i.e. correct versus incorrect response trials or high versus low awareness rating trials) and $ITPC_{ALL}$ is the ITPC calculated across all trials regardless of condition. POS will be positive when the ITPC of each trial group exceeds the overall ITPC; the main situation of interest, which indicates significant phase opposition between the two conditions.

Statistical analysis was first performed at the level of individual participants using a permutation test. For each participant, the trial assignment to group A or B was randomly permuted 2000 times and the POS value calculated and stored on each iteration. For each electrode-time-frequency point, the p-value was calculated as the proportion of permutations that yielded a higher POS than the observed data. Hence, the p-value reflects the likelihood of observing the actual POS value if the null hypothesis (no phase opposition) was true. The individual participant p-values were subsequently combined using Fisher's combined probability test (Fisher, 1992), which yielded a single group-level p-value for each electrode-time-frequency point. In order to control for multiple comparisons, non-parametric False Discovery Rate (FDR) correction (Benjamini & Yekutieli, 2001) were employed across the pre-stimulus period with a threshold (q-value) of 0.05.

Additionally, 'correct' and 'incorrect' trials (for the accuracy analysis) and 'high awareness rating' and 'low awareness rating' trials (for the awareness analysis) were equalized by randomly selecting from the higher likelihood outcome the same number of trials present for the lower likelihood outcome. This resulted in an average equalized number of trials per outcome across participants of 166 (min = 83, max = 233) for visual awareness ('high awareness rating' versus 'low awareness rating') and 170 (min = 106, max = 231) for accuracy ('correct' and 'incorrect'). This analysis was implemented because the POS loses statistical power when trial numbers are not equal between conditions (VanRullen, 2016b).

The wITPC and POS measures provide similar information about EEG phase-behavior relationships. Whereas POS indexes whether there is a consistent difference in mean phase angle between binary behavioural outcomes (i.e. high versus low PAS ratings), the wITPC approach does not require a binary outcome measure (and hence no arbitrary binning of behavioural data) (Cohen & Cavanagh, 2011; Cohen & Voytek, 2013), and hence enabled a statistical approach that more closely approximates the

EEG power – behavior analyses, thereby facilitating comparison of the power and phase results.

2.2.12. Pre-stimulus FFT analysis

Due to the temporal smearing inherent in time-frequency decomposition, which can lead to pre-stimulus EEG effects being contaminated by post-stimulus activity (Zoefel & Heil, 2013; Brüers & VanRullen, 2017; van Diepen & Mazaheri, 2018), control analyses were employed for both power and phase which included only pre-stimulus EEG timepoints (-1: 0 s relative to stimulus onset) (see Samaha et al., 2017 for a similar approach*)*. Fast Fourier Transforms (FFT) was performed on the clean, single-trial pre-stimulus waveforms at each electrode within each participant, using the ‘mtmfft’ method in FieldTrip (Maris & Oostenveld, 2007). The pre-stimulus data segments were windowed using a Hanning taper and zero-padded to a length of 1s to achieve a frequency resolution of 1 Hz across the range of 3:40 Hz. The power- and phase-behaviour relationships were then tested using exactly the same 3 steps described above for the EEG-time-frequency analyses, but now with only the electrode and frequency dimensions: z-statistics were calculated for both regression coefficients (power-behaviour analyses) and wITPC (phase-behaviour analyses) by permuting the mapping between EEG data and behaviour 500 times within each participant. The group statistics on the z-scores proceeded exactly as described for the time-frequency analyses but with only 2 dimensions (electrodes and frequencies). Again, BFs were calculated to quantify the evidence for both the null and alternative hypotheses for each analysis. The BF was calculated for all electrode-frequency data points.

2.3. Results

2.3.1. Behavioural Results

The task involved the identification of one of 19 consonant letters that were displayed for 10-50ms (five exposure durations) before being masked by a 200ms letter compound stimulus (Figure 2A). Figure 2B plots the group-averaged proportion of correct responses as a function of presentation time, and Figure 2C plots the group-averaged awareness ratings. Both accuracy and awareness ratings increased as a function of presentation time. Mean proportions correct (Figure 2B) ranged from 0.1±0.04 (10ms) to 0.87±0.02 (50ms), whereby 0.053 represents chance-correct response rate (1/19 letters). Mean awareness ratings (Figure 2C) ranged from 1.3±0.1 (10ms) to 2.7±0.07 (50ms), hence from close to “no experience” (PAS 1) up to “almost clear experience” (PAS 3). The repeated measures ANOVA on the proportion of correct responses revealed a significant main effect of presentation time ($F(4,84) = 314.595$, $p<0.001$, $\eta_p^2 = .937$, linear contrast: $F(1,21) = 992.168$, $p<0.001$, $\eta_p^2 = .979$). Pairwise comparisons revealed significant increases in the proportion of correct responses across all presentation times (all p’s < .001, min t-value = 5.893, min Cohen’s *d* = 1.359). The repeated measures ANOVA on the PAS ratings (subjective awareness) also revealed a significant main effect of presentation time ($F(4,84) = 195.523$, $p<0.001$, $\eta_p^2 = .903$, linear contrast: $F(1,21) = 224.84$, $p<.001$, $\eta_p^2 = .915$). Pairwise comparisons revealed significant increases in PAS ratings across all presentation times (all p’s < .001, min t-value = 9.679, min Cohen’s *d* = 2.092). Hence, the experimental manipulation of presentation time led to the expected increases in both identification accuracy and awareness ratings.

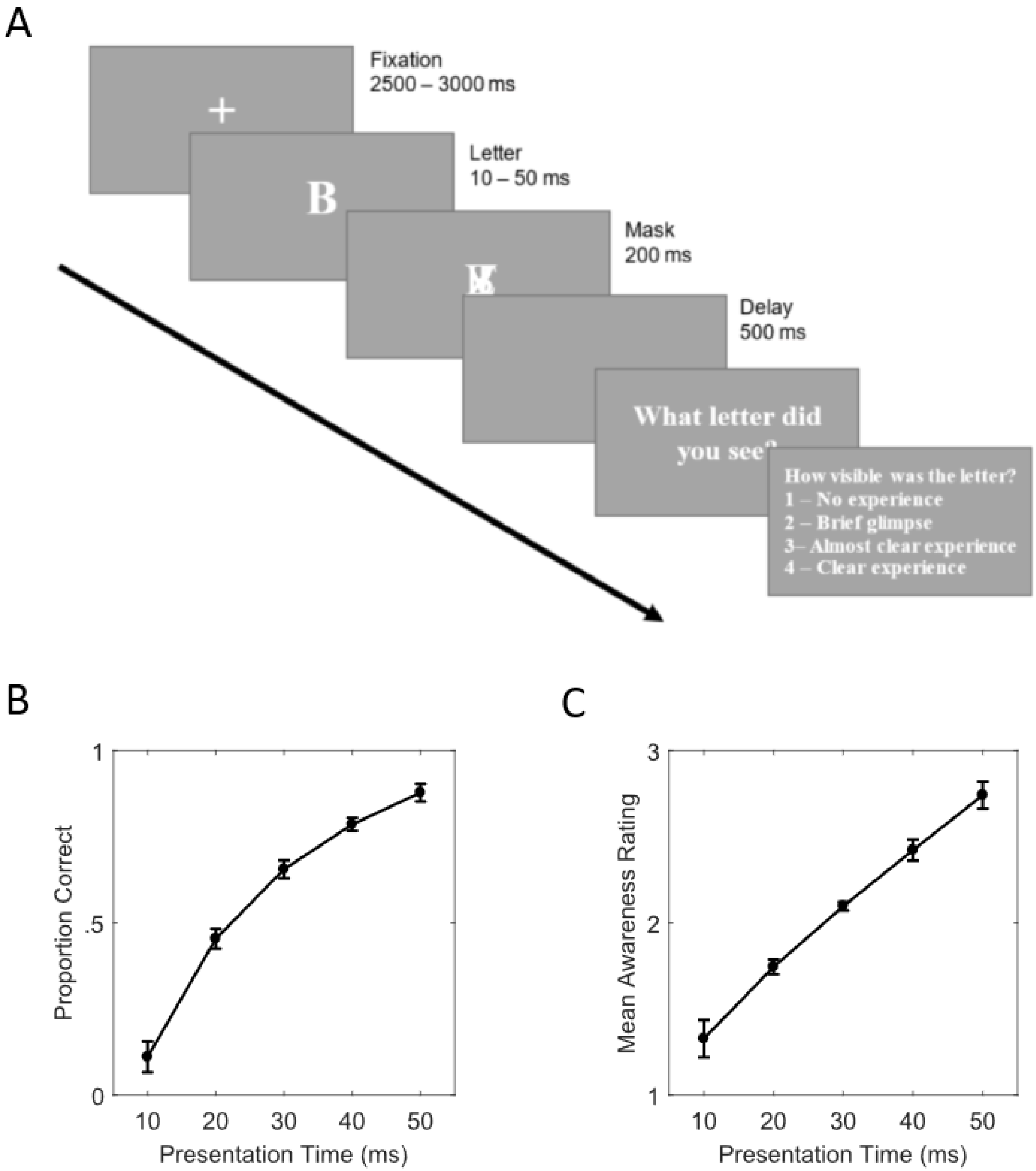


Figure 2: Task design and performance. (A) Each trial began with a white fixation cross presented for a jittered time between 2500 and 3000 ms, followed by the target stimulus – a consonant letter presented at 10, 20, 30, 40, or 50 ms, respectively. Immediately after, a mask appeared for 200 ms, followed by a blank screen for 500 ms. Then, a response prompt appeared, asking the participant which letter they saw. After the response, another prompt asked the participant to rate the quality of their perception on the four-point Perceptual Awareness Scale. **(B)** Group-averaged proportion of correct responses as a function of presentation time. **(C)** Group-averaged mean awareness ratings as a function of presentation time. Both accuracy and awareness rating increased as a function of presentation time. All error bars indicate within-subject ± standard error (SEM).

2.3.2. EEG Results

Pre-stimulus power predicts visual awareness ratings but not discrimination accuracy

Figure 3A plots t-values averaged across all electrodes at each time point (from -1 to +0.7s post-stimulus) denoting the strength of the EEG power - PAS rating relationship, whilst controlling for the influence of stimulus strength (letter presentation time) on PAS ratings, across frequencies of 3-40 Hz. These t-values represent group-level tests of whether regression coefficient (EEG power versus PAS rating) z-scores from the individual single-trial analyses showed a systematic linear relationship across participants. One significant negative cluster (i.e. low power was associated with high PAS ratings and high power with low PAS ratings) was found, which spanned across both pre- and post-stimulus timepoints (-0.84 – 0.7 s relative to stimulus onset, 3-31 Hz: cluster statistic = -24019, p = .0035). For Bayes Factors from those electrode-frequency points included in the significant negative cluster, the percentage of data points providing evidence for H_1 far outnumbered those providing evidence for H_0 (see Figure 3A, bottom inset). In the pre-stimulus period of interest, the effect was widely distributed over almost all electrodes but with a right posterior maximum (see Figure 3B, left map: data averaged over all electrode-time-frequency points included in the cluster from -1 to 0 s relative to stimulus onset). Figure 3B (right map) shows the topographical representations of the post-stimulus portion of the negative cluster. Figure 3C (left panel) plots the group averaged frequency spectra computed separately for high PAS rating trials (red lines) and low PAS rating trials (black lines) from the data point corresponding to the peak t-value in the pre-stimulus cluster (electrode POz, -0.54 s). Compared to low PAS rating trials, high PAS rating trials were associated with decreased pre-stimulus alpha power. This effect was highly consistent across participants, as shown by the scatterplot (Figure 3C, right panel) of the difference in mean 10 Hz power between high and low PAS rating trials for each participant.

In contrast, no relationship was found between EEG power and identification accuracy, whilst controlling for the influence of stimulus strength on accuracy, during either the pre-or post-stimulus time periods (Figure 3D). For Bayes Factors from those electrode-frequency points included in the significant negative cluster from the awareness analysis, the percentage of data points providing evidence for H_0 far outnumbered those providing evidence for H_1, during the pre-stimulus period, though this pattern tended to reverse post-stimulus (see Figure 3D, bottom inset). Figure 3F (left panel) plots the group averaged frequency spectra computed separately for correct (red lines) and incorrect trials (black lines) from the data point corresponding to the peak t-value in the visual awareness analysis (electrode POz, -0.54 s). No difference in power was observed between correct and incorrect trials (see also the scatterplot in Figure 3F (right panel) of the difference in mean 10 Hz power between correct and incorrect trials for each participant).

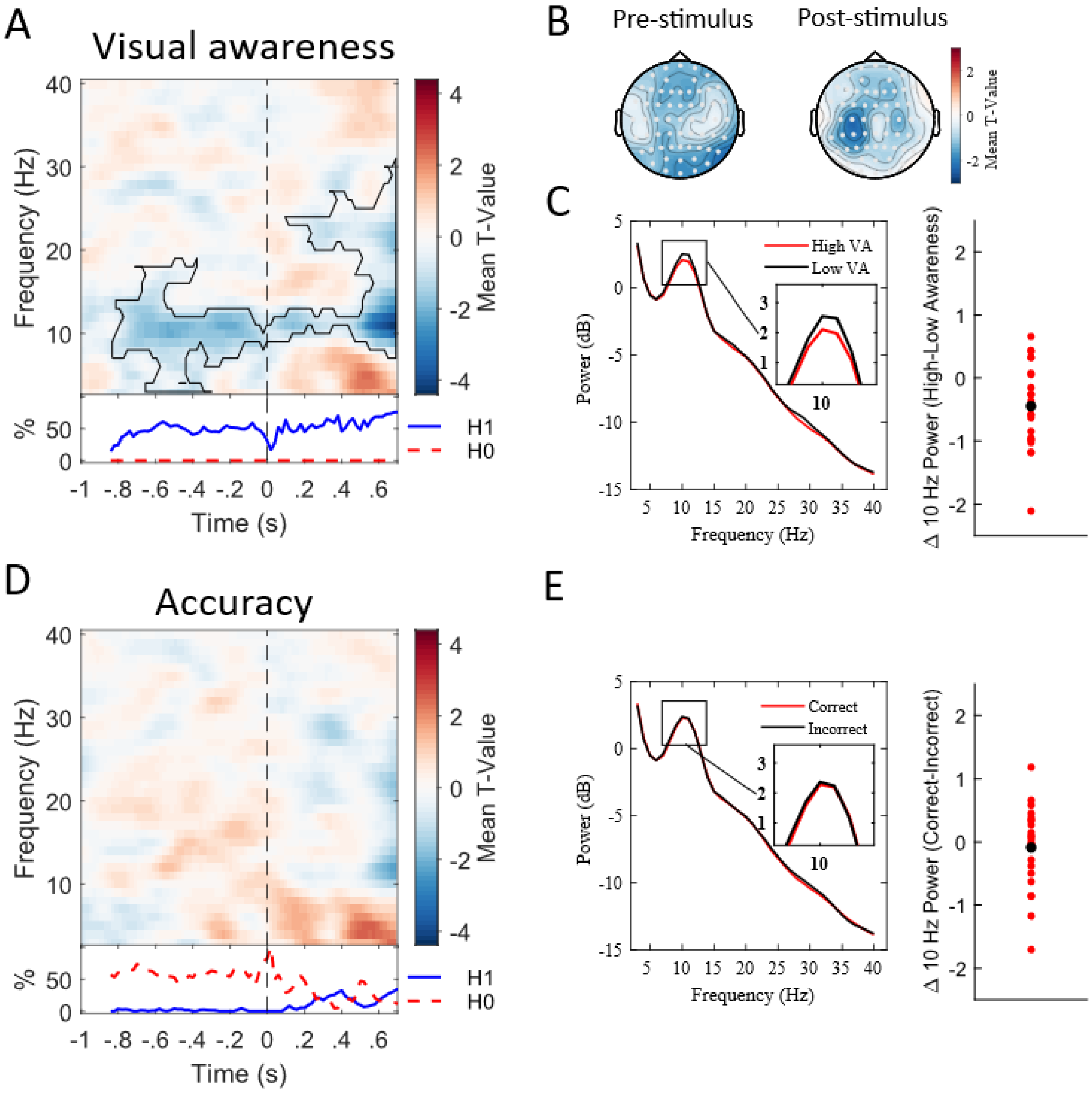


Figure 3: Relationship between oscillatory power and perception, controlling for letter presentation time. (A) The results of a single trial regression analysis revealed that pre-stimulus power was negatively correlated with visual awareness ratings (i.e. high power was associated with low PAS ratings and low power with high PAS ratings, black contour denotes significant cluster-corrected effects (p<0.05)). Stimulus onset is highlighted by a vertical black dashed line. The bottom inset plots the time-course of the percentage of electrode-frequency points within the significant cluster with Bayes Factors showing evidence for the null (H0: no EEG/awareness relationship (dashed red line)) and alternative hypotheses, respectively (H1: significant EEG/awareness relationship (solid blue line)). As expected, the percentage of data points providing evidence for H1 far outnumbered those providing evidence for H0. **(B)** Plots the scalp topographies of the group-averaged effect separately for the pre- and post-stimulus portions of the significant negative cluster. In the pre-

stimulus period of interest, the effect was widely distributed over almost all electrodes but with a posterior maximum (left map). Electrodes that were included in the significant cluster are highlighted in white. **(C)** Group-average frequency spectra computed separately for high PAS rating trials (red lines) and low PAS rating trials (black lines) in the pre-stimulus cluster. Compared to low PAS rating trials, high PAS rating trials were associated with decreased pre-stimulus alpha power. This effect was highly consistent across participants, as shown by the scatterplot (right panel: black dot represents the mean difference value) of the difference in mean 10 Hz power between high and low PAS rating trials for each participant. **(D)** No relationship was found between EEG power and discrimination accuracy in any of the time-frequency ranges examined. The bottom inset plots the time-course of the percentage of electrode-frequency points from the significant pre-stimulus EEG/awareness cluster with Bayes Factors showing evidence for the null (H0: no EEG/accuracy relationship (dashed red line)) and alternative hypotheses respectively (H1: significant EEG/accuracy relationship (solid blue line)). The percentage of data points providing evidence for H0 far outnumbers those providing evidence for H1 during the pre-stimulus period, though this pattern is reversed somewhat post-stimulus. **(E)** Group averaged frequency spectra computed separately for correct (red lines) and incorrect trials (black lines) within the pre-stimulus cluster that proved significant in the EEG/awareness analysis above. No difference in power was observed between correct and incorrect trials in this EEG/accuracy analysis. The right panel plots the difference in mean 10 Hz power between correct and incorrect trials for each participant (black dot represents the mean difference value).

Both the PAS rating and accuracy results were confirmed when only pre-stimulus data (-1-0 s relative to stimulus onset) were included in the single-trial FFT analyses. Figure 4A plots t-values averaged across all electrodes at each frequency (from 3 to 40) denoting the strength and direction of the EEG power - PAS rating relationship, whilst controlling for the influence of stimulus strength on PAS ratings. One significant negative cluster was found which spanned from 9 to 12 Hz (cluster statistic = -103.4, p = .0095). In contrast, no significant relationship was found between EEG power and identification accuracy at any frequency (see Figure 4B).

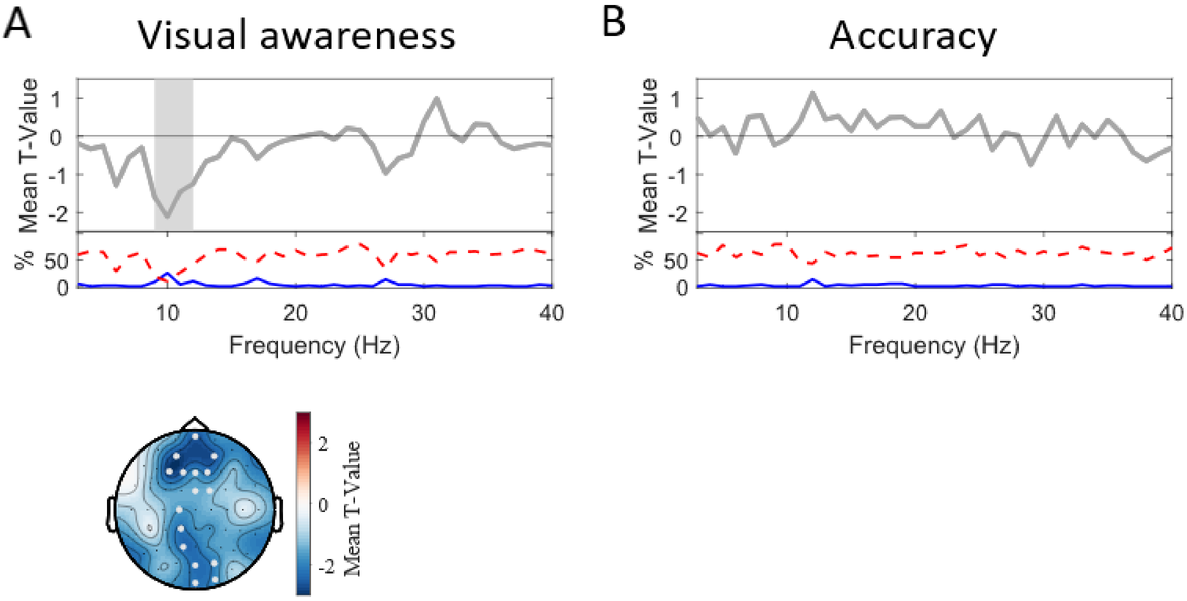


Figure 4: Single-trial Fast Fourier Transform analyses on pre-stimulus data confirm the relationship between pre-stimulus oscillatory power and perception. (A) Pre-stimulus power was negatively correlated with visual awareness ratings in the alpha (9-12Hz) band (i.e. high power was associated with low PAS ratings and low power with high PAS ratings, grey background fill denotes significant cluster-corrected effects ($p<0.05$)). The bottom inset plots the percentage of all electrodes with Bayes Factors showing evidence for the null (H0: no EEG/awareness relationship (dashed red line)) and alternative hypotheses respectively (H1: significant EEG/awareness relationship (solid blue line)) across frequencies. The topographical representation of the effect is shown below the line plot. Electrodes that were included in the significant cluster are highlighted in white. **(B)** In contrast, no relationship was found between pre-stimulus power and discrimination accuracy in any frequency band.

2.3.3. Follow-up EEG power analysis: No evidence that the pre-stimulus power-visual awareness relationship depends on stimulus strength

In order to test whether single-trial relationships between EEG power and the behavioural outcomes were dependent on the strength of the stimulus (letter presentation time), additional interaction analyses were performed. No significant interaction effects were found between EEG power and presentation time for either PAS ratings (Figure 5A) or identification accuracy (Figure 5B), when considering all electrode-time-frequency points or when considering only pre-stimulus timepoints in the FFT analysis (Figure 5C, 5D).

To directly replicate the analysis of Benwell et al. (2017), additional median power split repeated measures ANOVA analyses were performed, using the single-trial data only from the pre-stimulus (-1:0 s) portion of the significant EEG power-PAS ratings cluster. The proportion of correct responses and mean PAS ratings were calculated separately for each presentation time in each power bin and participant ('above' and 'below' median power). The corresponding group mean data are displayed for visual awareness ratings in Figure 5E and for proportion of correct responses in Figure 5F as a function of high (black dots/lines) and low power trials (red dots/lines) per presentation time.

The repeated measures ANOVA on the visual awareness ratings revealed a significant main effect of pre-stimulus power (F(1,21) = 9.946, p = .005, η_p^2 = .321), a significant main effect of presentation time (F(4,84) = 196.274, p<.001, η_p^2 = .903), but no significant pre-stimulus power x presentation time interaction (F(4,84) = 1.76, p = .145, η_p^2 = .077). Hence, while confirming that pre-stimulus power relates to awareness ratings as in our group's previous study (Benwell et al., 2017), no significant evidence was found that the pre-stimulus EEG power – PAS ratings relationship was dependent on stimulus strength (in contrast to Benwell et al., 2017).

The repeated measures ANOVA on the proportion of correct responses revealed a significant main effect of presentation time (F(4,84) = 311.97, p<0.001, η_p^2 = .937) but no significant main effect of pre-stimulus power (F(1,21) = .019, p = .892, η_p^2 < .001) and no significant pre-stimulus power x presentation time interaction (F(4,84) = 1.772, p = .142, η_p^2 = .078). Hence, there was also no evidence for an effect of pre-stimulus power on accuracy (or any interaction with letter presentation time), in line with the results of the regression analyses.

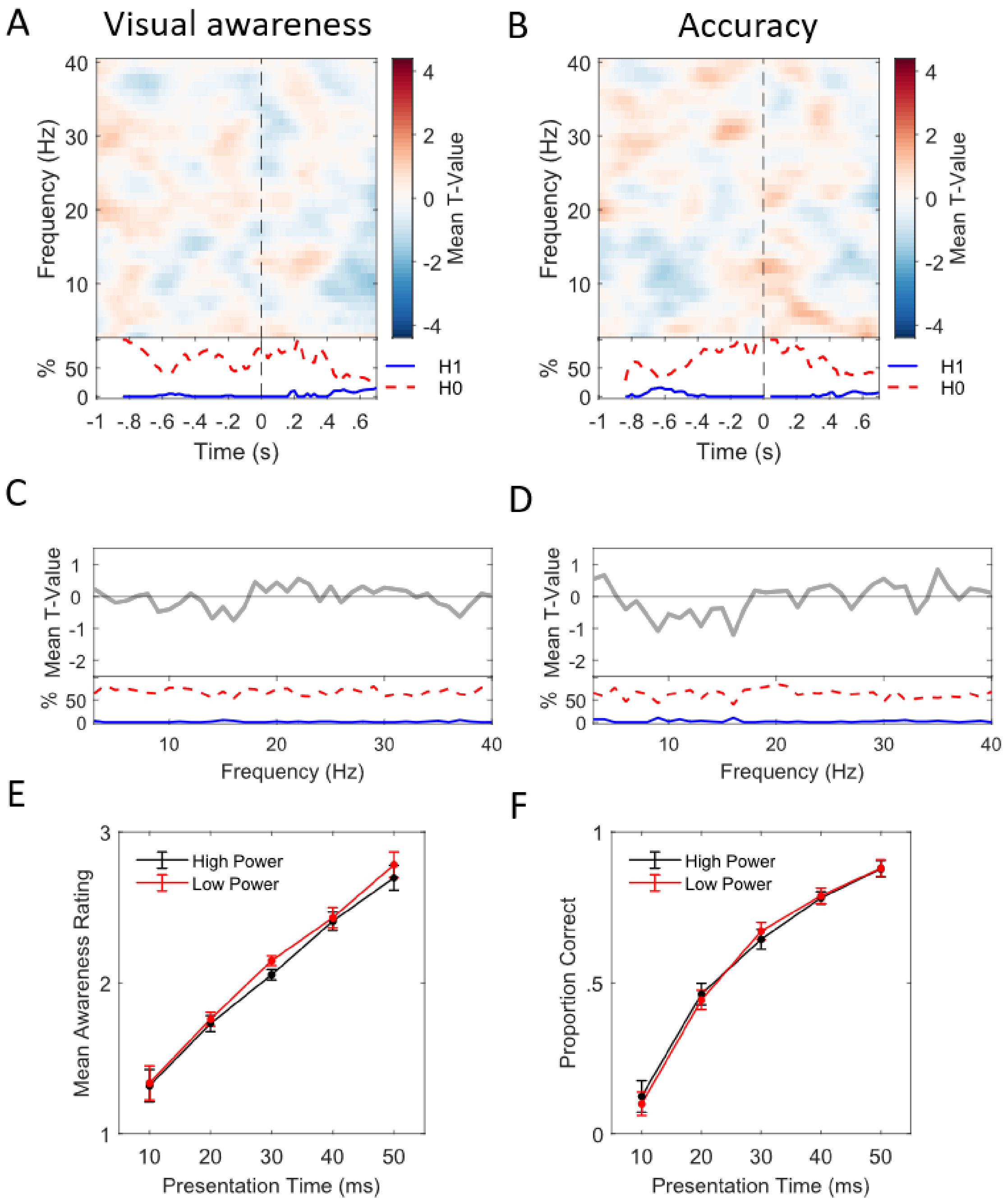


Figure 5: No interaction between oscillatory power and letter presentation time in predicting awareness ratings or accuracy. (A,B) The results of the single-trial regression analysis revealed that the relationship between pre-stimulus power and visual awareness ratings **(A)** or accuracy **(B)** was not dependent on letter presentation time (interaction terms shown). Stimulus onset is highlighted by a vertical black dashed line. The bottom insets plot the time-course of the percentage of electrode-frequency points from the significant pre-stimulus EEG/awareness cluster (of Figure 3A) with Bayes Factors showing evidence for the null (H0: no EEG/presentation time interaction (dashed red line))

and alternative hypotheses respectively (H1: significant EEG/presentation time interaction (solid blue line)). The percentage of data points providing evidence for H0 far outnumbers those providing evidence for H1 during the pre-stimulus period. **(C,D)** Single-trial Fast Fourier Transform analyses restricted to pre-stimulus data confirmed the lack of interaction effects between pre-stimulus EEG power and letter presentation time when predicting either PAS ratings **(C)** or accuracy **(D)**, respectively. The bottom insets plot the percentage of electrodes with Bayes Factors showing evidence for the null (H0: no EEG/presentation time interaction (dashed red line)) and alternative hypotheses respectively (H1: significant EEG/presentation time interaction (solid blue line)) across frequencies. **(E,F)** Task performance after a median power split using single-trial data from the pre-stimulus portion of the significant EEG power - visual awareness cluster presented in Figure 3A. Group-averaged mean awareness ratings **(E)** and group-averaged proportion of correct responses **(F)** are shown as a function of presentation time for low (red lines) and high (black lines) power. Both accuracy and awareness rating increased as a function of presentation time in both power conditions, but no significant interaction between EEG power and presentation time was found for either PAS ratings or proportion correct. All error bars indicate within-subject ± standard error (SEM).

2.3.4. No compelling evidence that pre-stimulus phase predicts visual awareness ratings or identification accuracy

Figure 6A plots t-values averaged across all electrodes at each time point for the wITPCz analysis denoting the strength of the EEG phase - PAS rating relationship, whilst controlling for the influence of stimulus strength (letter presentation time) on PAS ratings, across frequencies of 3-40 Hz. The t-values index group-level tests of whether weighting the single-trial phase vectors by their perceptual outcomes leads to an increase (positive values) or decrease (negative values) of the overall ITPC, relative to a participant-specific null distribution. Two significant positive clusters were found that were largely post-stimulus: a low frequency (3-13 Hz) cluster spanning -.14-.7 s relative to stimulus onset (cluster statistic = 9739.3, p = .0025), and a higher frequency (10-30 Hz) cluster spanning -.18-.46 s relative to stimulus onset (cluster statistic = 5363.4, p = .01). Figure 6B shows the topographical representations of the two clusters. Though both clusters included timepoints immediately preceding and including stimulus-onset, this likely reflects temporal smearing of primarily post-stimulus effects into the pre-stimulus period (Zoefel & Heil, 2013; Brüers & VanRullen, 2017; van Diepen & Mazaheri, 2018). Indeed, when only the pre-stimulus data (-1-0 s relative to stimulus onset) were included in the single-trial FFT analyses (thus ruling out any contamination from post-stimulus activity), no significant relationship was found between EEG phase and PAS ratings at any frequency (see Figure 6C).

For the relationship between EEG phase and identification accuracy (Figure 6D), one significant positive cluster was found that was largely post-stimulus (-0.06:0.7 s relative to stimulus onset, 3:24 Hz: cluster statistic = 19079, p < .001) (see map in Figure 6E for a topographic representation of the cluster). Again, when only pre-stimulus data were included in the single-trial FFT analyses, no significant relationship was found between the EEG phase and accuracy at any frequency (see Figure 6F).

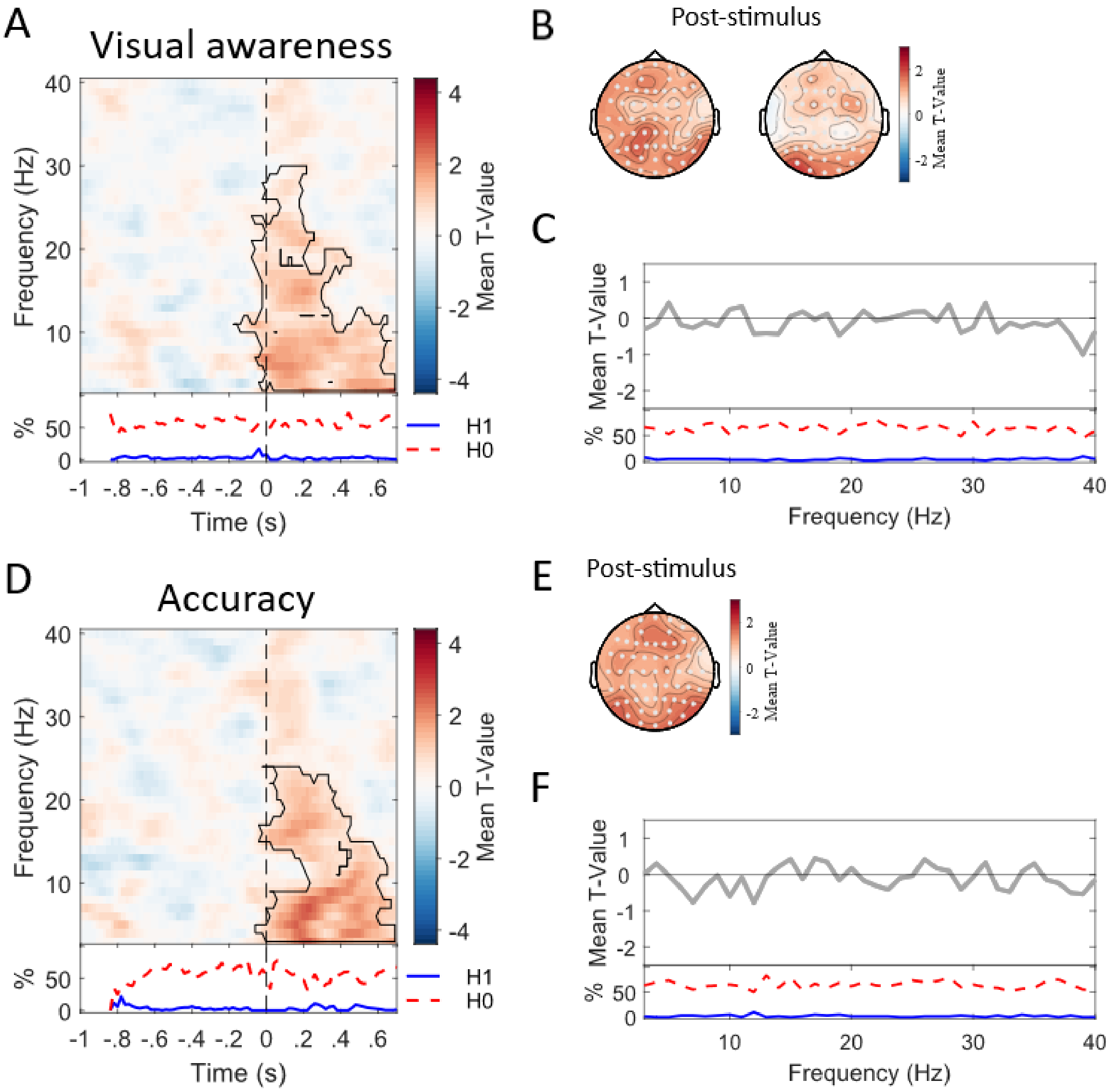


Figure 6: Relationship between oscillatory phase and perception, controlling for letter presentation time. (A) Time-frequency map of single-trial phase modulations by visual awareness rating residuals (with the effect of letter presentation time on awareness ratings regressed out) from a weighted inter-trial phase coherence z-score (wITPCz) analysis. These t-values index group-level tests of whether weighting the single-trial phase vectors by their perceptual outcomes leads to an increase (positive values) or decrease (negative values) of the overall ITPC, relative to a participant-specific null distribution. Black contour denotes significant cluster-corrected effects ($p<0.05$, significant clusters collapsed together). Stimulus onset is highlighted by a vertical black dashed line. The bottom inset plots the time-course of the percentage of electrode-time-frequency points from the significant pre-stimulus EEG power/awareness cluster with Bayes Factors showing evidence for the null (H0: no EEG phase/awareness relationship (dashed red line)) and alternative hypotheses

respectively (H1: significant EEG phase/awareness relationship (solid blue line)). **(B)** Plots the scalp topographies of the group-averaged effects separately for the two significant positive clusters. Electrodes that were included in the significant cluster are highlighted in white. **(C)** No relationship was found between pre-stimulus phase and awareness ratings when only pre-stimulus data (-1-0 s relative to stimulus onset) were included in the single-trial Fast Fourier Transform (FFT) analysis (thus ruling out any contamination from post-stimulus activity). The bottom inset plots the percentage of electrodes with Bayes Factors showing evidence for the null (H0: no EEG phase/awareness relationship (dashed red line)) and alternative hypotheses respectively (H1: significant EEG phase/awareness relationship (solid blue line)). **(D)** Time-frequency map of single-trial phase modulations by accuracy. These t-values index the group-level strength and direction of the phase-locking - accuracy relationship. The bottom inset plots the time-course of the percentage of electrode-time-frequency points from the significant pre-stimulus EEG power/awareness cluster with Bayes Factors showing evidence for the null (H0: no EEG phase/accuracy relationship (dashed red line)) and alternative hypotheses, respectively (H1: significant EEG phase/accuracy relationship (solid blue line)). **(E)** Plots the group-averaged scalp topography of the significant positive cluster. **(F)** Again, no relationship was found between pre-stimulus phase and accuracy when only pre-stimulus data were included in the single-trial FFT analysis.

Similar relationships were observed between the EEG phase and both PAS ratings and identification accuracy in two variants of the above analyses, with all relationships confined to the post-stimulus window (reported as Supplementary material). First, when letter presentation time was not controlled for, additional significant negative clusters were observed at early post-stimulus timepoints across low frequencies (see Supplementary Figure 1A&B, 1D&E). These negative clusters hence likely reflect the co-variation of letter presentation time with post-stimulus phase locking. Indeed, an additional analysis of the phase - presentation time main effect showed significant effects which largely overlapped in time, space and frequency (see Supplementary Figure 1G-H). Furthermore, no significant phase effects were observed for any of the single-trial FFT analyses when only pre-stimulus EEG data were included (Supplemental Figure 1C&F). Second, a Phase Opposition Sum (POS) analysis (replicating Benwell et al., 2017) also provided no evidence for a relationship between pre-stimulus phase and either PAS ratings or identification accuracy (see Supplementary Figure 2).

Overall, the data indicate that the observed significant EEG phase–behavior relationships originated entirely in stimulus-evoked neural activity (Cul et al., 2007; Brüers & VanRullen, 2017; van Diepen & Mazaheri, 2018; Tagliabue et al., 2019), and so no compelling evidence was found for an influence of spontaneous pre-stimulus oscillatory phase on perception in this data set.

2.4. Discussion

In this study, we implemented a letter discrimination task to examine the effects of pre-stimulus oscillatory activity on both discrimination accuracy and perceptual awareness ratings. Single-trial regression analyses revealed a negative correlation between pre-stimulus power (~9-12Hz, Figure 4) and subjective awareness ratings, but no relationship between pre-stimulus power and discrimination accuracy. In contrast, we did not find strong evidence that pre-stimulus oscillatory phase predicted subjective awareness ratings nor accuracy in any frequency band. These results largely replicate those reported by Benwell and colleagues (2017), but this time using an mAFC paradigm rather than a 2-AFC paradigm. Taken together, these experiments emphasize a dissociation between pre-stimulus neural predictors of subjective and objective measures of task performance and shed light on the processes by which pre-stimulus oscillatory activity influences visual perception.

Several recent studies employing formal psychophysical models (e.g. SDT; Green & Swets, 1966) have contributed to a better understanding of the relationship between baseline neural activity and visual perception. These studies have found correlations between pre-stimulus alpha suppression and a liberal decision criterion (Limbach & Corballis, 2016; Iemi et al., 2017). Furthermore, observers can exert deliberate control over fluctuations in pre-stimulus alpha activity when a more liberal decision criterion is experimentally induced (Kloosterman et al., 2019). Hence, baseline alpha-activity seems to relate to bias in perceptual reports rather than perceptual sensitivity, possibly because it reflects changes in global baseline excitability (Romei, Brodbeck, et al., 2008) that may affect both signal and noise (Iemi et al., 2017). This account is represented by the Baseline Sensory Excitability Model (BSEM) proposed by Samaha, Iemi, et al. (2020).

One question is then at what stage posterior baseline alpha activity/excitability interacts with information processing during perceptual tasks. In order to bias reports, increased baseline excitability could modulate the observers' decision-making strategy (i.e. induce a decision bias) and/or amplify their subjective perception (i.e. induce a perceptual bias) (Iemi et al., 2017; Samaha, Iemi, et al., 2020). Recently, Iemi and Busch (2018) have provided compelling evidence that pre-stimulus alpha-power induces changes in perceptual experience, rather than decision criterion alone, in an experiment involving a two-interval forced-choice (2IFC) task. Another line of research providing evidence that baseline alpha-power biases subjective perceptual experience comes from studies measuring subjective reports of performance. In 2-AFC discrimination tasks, pre-stimulus power is negatively correlated with perceptual awareness/subjective visibility ratings (Benwell et al., 2017; Samaha, LaRocque, et al., 2020) and decision confidence (Samaha, Iemi, et al., 2017; Wöstmann, Waschke, et al., 2019), but there is no effect of pre-stimulus power on accuracy, neither in visual nor auditory modalities. A similar dissociation has been reported for pre-stimulus alpha-power and idiosyncratic biases versus accuracy (Grabot & Kayser, 2019). In addition, Benwell et al. (2017) found the negative correlation between pre-stimulus alpha-power and awareness to be contingent on the stimulus being present (no such correlation in catch trials) and to depend on stimulus-intensity (see also Chaumon & Busch, 2014). This was taken as further evidence for the pre-stimulus alpha-perception link reflecting a perceptual rather than decisional bias. In the current experiment, catch trials were not implemented, as there was no stimulus-absent condition, and we were unable to fully replicate the aforementioned dependency of the alpha-perception relationship on stimulus-intensity (i.e. stimulus presentation times). However, a similar pattern as in Benwell et al. (2017) was observed (i.e. stronger influence of pre-stimulus alpha on awareness ratings at longer presentation times, see Figure 5E: 30&50ms vs. 10,20&40ms presentation times), although the relationship between pre-stimulus alpha power and awareness ratings did not significantly differ across letter presentation times. Overall, we therefore believe that the current results remain mostly in line with a model positing that baseline alpha-activity/excitability modulates perceptual experience directly rather than only modulating decision bias.

Mechanistically, changes in subjective perceptual experience as a function of alpha-band modulations may result from an effect on early sensory responses (Samaha, LaRocque, et al., 2020), a response gain mechanism at late perceptual stages (e.g. Benwell et al., 2017; Chaumon & Busch, 2014), or through a combination of both (see

Iemi et al., 2019). The evidence for either an early or a late perceptual account is inconclusive so far, and the present data cannot speak directly to this issue. More direct tests of the stage at which baseline alpha-activity interacts with stimulus processing may be obtained from the analysis of visual evoked potentials and their co-modulation with pre-stimulus alpha activity. Gundlach and colleagues (2020) measured ongoing alpha-band oscillations and steady-state visual evoked potentials (SSVEPs) simultaneously to establish whether alpha-band modulations relate to early sensory input gain. Using a spatial cueing paradigm, they showed that the amplitudes of both SSVEPs and alpha-band oscillations are modulated by spatial attention but that their modulations vary independently of each other and have different temporal dynamics (Gundlach et al., 2020; see also Keitel et al., 2019; Antonov et al., 2020). This is supportive of a role of alpha-band oscillations beyond early sensory processing. In line with these findings, Zhigalov and Jensen (2020) implemented a novel broadband frequency tagging technique and found that the sources of alpha oscillations were localized around the parieto-occipital sulcus rather than the primary visual cortex. By contrast, Iemi et al. (2019) found an early component of the visual evoked potential (C1) to co-modulate with spontaneous pre-stimulus alpha power, suggesting that alpha may have an inhibitory effect on early stages of sensory processing (see also Zazio et al., 2021). The source of these discrepancies in the literature is unclear. Further research is needed to disentangle the influence of pre-stimulus EEG power on different post-stimulus processing stages.

In addition to alpha power, the phase of low-frequency rhythms has been suggested to play an important role in visual perception (Mathewson et al., 2011; VanRullen, 2016a), although the evidence appears more mixed for the pre-stimulus phase- than the pre-stimulus power-perception link. The phase of pre-stimulus oscillations in the alpha-band has been associated with both the detection probability of near-threshold stimuli as well as discrimination accuracy between two rapidly presented visual stimuli (Busch et al., 2009; Mathewson et al., 2009; Samaha et al., 2015; Milton & Pleydell-Pearce, 2016; Ronconi et al., 2017). However, a recent registered report by Ruzzoli et al. (2019) failed to replicate the seminal finding that spontaneous pre-stimulus alpha-phase correlates with visual target detection. In the present experiment, we found no compelling evidence that the pre-stimulus oscillatory phase predicts either subjective awareness or accuracy in a letter identification task, replicating the results of Benwell et al. (2017). When only pre-stimulus EEG data were included in the single-trial analyses (thus ruling out any contamination from post-stimulus activity), no significant relationship was found between phase and either awareness ratings or accuracy at any frequency. The discrepancy with previous findings may be due to differences in experimental design. We presented the stimuli at varying time intervals from trial onset, which might have precluded phase from influencing perception. Samaha and colleagues (2015) found more phase consistency when participants expected the visual target onset, compared to when the visual stimuli were unexpected, while others have argued against a top-down modulation of alpha-phase even when the targets were temporally predictable (van Diepen et al., 2015). Additionally, in the present study, the visual stimuli were visible such that on average, identification accuracy was above threshold, while many previous studies reported a phase effect on perception when stimuli were near-threshold (see Busch et al., 2009; Mathewson et al., 2009). However, discrepancies found in the literature could also be due to contamination of the signal by target-locked, post-stimulus phase differences and temporal distortions of these phase effects towards pre-stimulus latencies (Brüers & VanRullen, 2017), a scenario that likely explains the pattern of results observed in the time-frequency wITPCz analyses here. Overall, our results add to a growing body of studies casting doubt on the effect of pre-stimulus phase on visual perception (van Diepen et al., 2015; Benwell et al., 2017; Ruzzoli et al., 2019; Vigué-Guix et al., 2020).

In conclusion, the present findings substantiate a growing body of evidence linking pre-stimulus EEG alpha power to subjective rather than objective psychophysical measures. Hence, pre-stimulus alpha power represents a neural predictor of the level of perceptual awareness, which is dissociated from perceptual sensitivity.

Chapter 3

Effects of alpha-band entrainment on perception: Evidence from TMS

3.1. Introduction

Our perception of the stimuli in the surrounding environment depends on their features but also on the influence of endogenous factors, such as underlying brain oscillations. As discussed in the previous chapter, pre-stimulus alpha activity (8 – 14 Hz) has been linked to a dissociation between the objective and subjective perception of sensory events. In the visual domain, it has been demonstrated that the amplitude of pre-stimulus alpha oscillations is negatively correlated with decision confidence (Samaha, Iemi, et al., 2017) and perceptual awareness (Benwell et al., 2017, 2021), but it is not related to task accuracy (Lange et al., 2013; Limbach & Corballis, 2016; Craddock et al., 2017; Iemi et al., 2017; Iemi & Busch, 2018; Kloosterman et al., 2019; see Samaha, Iemi, et al., 2020 for a review). Though most studies have demonstrated this relationship using low-level stimuli (e.g. Benwell et al., 2017; Samaha et al., 2017), Samaha et al. (2020) have recently shown that the effect is robust also when higher-level visual areas are engaged, i.e. low pre-stimulus alpha power was associated with increased visibility ratings when participants were asked to discriminate between houses and faces. Model-oriented experiments grounded in SDT (Signal Detection Theory; Green & Swets, 1966) have suggested that the relationship between spontaneous oscillations and subjective performance is due to the fact that a lowering of the pre-stimulus alpha activity leads to a more liberal criterion change, i.e. participants are more likely to report a stimulus as being present even when it is not, while their perceptual sensitivity to the target stimulus remains unchanged (Limbach & Corballis, 2016; Iemi et al., 2017).

On the other hand, the frequency of the alpha oscillations, and more specifically the peak of the alpha band, known as individual alpha frequency (IAF; Bazanova & Vernon, 2014), plays a role in the temporal integration of conscious perception (VanRullen & Koch, 2003; VanRullen, 2016a). Consequently, fluctuations in the alpha frequency should impact the temporal resolution of visual perception, i.e. slower alpha oscillations should cause two consecutive stimuli presented at short interstimulus intervals to fall within the same alpha cycle, and therefore to be more likely perceived as one stimulus (integration). In fact, Samaha & Postle (2015) found that participants with higher IAF, as recorded during eyes closed, were significantly less likely to perceive two flashes as one (segregation) than participants with lower IAF. Moreover, within participants, fluctuations in the trial-by-trial pre-stimulus alpha frequency predicted task accuracy (Samaha & Postle, 2015). In fact, pre-stimulus alpha frequency can be dynamically up or down-regulated depending on task demands. Wutz and colleagues (2018) reported that peak alpha frequency both pre- and during stimulus presentation decreased when participants were asked to perform a visual temporal integration task and increased when the task required temporal segregation of the stimuli. The timing of the change indicates that alpha frequency is under top-down control (Wutz et al., 2018). Using multi-sensory entrainment, Ronconi et al. (2018) have causally confirmed the link between pre-stimulus alpha frequency and the temporal window of perception, showing that faster entrainment improved segregation and led to faster fluctuations in behavioural performance on a visual task. In contrast, slower entrainment improved integration and reduced the fluctuations in performance.

Expanding on findings from the unisensory domain, a positive correlation between the IAF peak and the size of the temporal window of perception has been reported using judgments of simultaneity during an audiovisual illusion (Cecere et al., 2015) and a visuotactile task (Migliorati et al., 2020). Cecere et al. (2015) demonstrated the causality of this relationship by modulating alpha oscillations via occipital tACS, which resulted in a change in the size of the temporal window of illusion, such that if the IAF was driven towards slower or faster oscillations, the temporal window of the illusions lengthened or shortened, respectively (see also Minami & Amano, 2017; Battaglini et al., 2020, Ghiani et al., 2021 for tACS effects on the temporal resolution of visual perception). Since the frequency of alpha oscillations is associated with an improved perceptual experience, it has been hypothesized recently that this relationship could be generalized to perceptual accuracy more generally, and that the two characteristics of pre-stimulus alpha – its amplitude and frequency - should each map on subjective and objective measures of performance and hence predict their dissociation (Di Gregorio et al., in review – communication with authors).

While the link between IAF and temporal integration of visual perception has been repeatedly demonstrated using non-invasive brain stimulation techniques (Cecere et al., 2015; Battaglini, Mena, et al., 2020; Ghiani et al., 2021) and sensory entrainment (Ronconi et al., 2018), whether pre-stimulus alpha amplitude is indeed causally involved in subjective performance on visual tasks remains to be determined. To date, there are no published studies exploring this relationship using non-invasive brain stimulation methods. The relationship between a neural oscillator and behaviour is causal if (1) correlational evidence links a frequency F(x) and a behavioural function X and (2) non-invasive brain stimulation changes function X when applied at a frequency F(x), but not at a control frequency F(y) (Thut, Schyns & Gross, 2011).

Very recently, Di Gregorio and colleagues (in review) found that low EEG alpha amplitude was associated with higher confidence. In contrast, higher IAF was associated with increased accuracy in a detection task. The researchers then hypothesized that entraining the underlying alpha oscillations at a slower or faster frequency should result in a worsening or enhancement of accuracy on visual performance, respectively, while entraining at IAF would enhance alpha amplitude, lowering participants' confidence. Doing so using TMS, they were able to dissociate the perceptual sensitivity from the subjective interpretation of the sensory event (Di Gregorio et al., in review).

In the present study, we employed TMS while participants performed a 2AFC luminance discrimination task, followed by single-trial ratings using the Perceptual Awareness Scale (PAS; Ramsøy & Overgaard, 2004). . Based on the past literature (Samaha, Iemi, et al., 2017; Benwell et al., 2017) and the results of *Chapter 2*, it was hypothesized that applying 10 Hz repetitive TMS (rTMS) over the right intraparietal sulcus (rIPS) to enhance alpha amplitude (see Thut et al., 2011) should lead to a decrease in PAS ratings in the contralateral but not ipsilateral hemifield, while accuracy on the task should remain unaffected. Additionally, following the findings of Di Gregorio and colleagues (in review), it was anticipated that resting IAF would be positively correlated with accuracy on the task and that participants with IAF lower than the rTMS frequency (<10Hz) would profit from 10Hz rTMS in terms of task accuracy (as 10Hz rTMS should speed up their IAF). In contrast, the performance of participants with IAF higher than 10Hz (>10Hz) would be impaired (as 10Hz rTMS should slow down their IAF).

3.2. Materials and Methods

3.2.1. Participants

A total of 21 participants were recruited for the study. All reported normal or corrected-to-normal vision, no history of neurological or psychiatric disorders, and no contraindication to brain stimulation, according to the TMS screening questionnaire (Rossi et al., 2009). They all gave written informed consent before the start of the experiment. The study was approved by the Ethics Committee of the College of Science and Engineering at the University of Glasgow and was conducted in accordance with the latest revision of the Declaration of Helsinki. Data from 4 participants were excluded from the analysis because their individual alpha peak frequency could not be identified. Thus, 17 participants were included in the final sample (12 females, mean age = 23 years, age range: 19-36 years, right-handedness: 16/17).

3.2.2. Experimental procedure

The experiment consisted of two sessions of maximally two hours each, at least 48 hours apart. Participants sat in a dimly lit testing room in front of an LCD monitor (resolution 2560 x 1440, refresh rate 100 Hz, viewing distance 70 cm), with their heads stabilized in a chin rest. In the first session, participants underwent a threshold titration procedure and completed the first experimental block. The second session consisted of a threshold reassessment and performing the remaining blocks of the experimental task.

3.2.3. Stimuli

The task involved the discrimination of circular patches from the background. The patches were created with a Gaussian envelope (size = 1.3°) and were presented on a grey background (RGB: 127, 127, 127) in the lower left or right visual field (VF; =3.7° vertical and +/-4.1° horizontal eccentricity). Before the experimental task, the luminance of the Gaussian patches was individually adjusted to obtain four contrast levels (two lighter and two darker than the grey background, one for each side of the

VF) by using a threshold assessment procedure. The contrast of the stimuli presented varied from 0.011% to 0.05% of the maximal contrast of the grey patches.

3.2.4. Threshold titration

The aim of the titration session was to identify four contrast values (resulting in four luminance levels: lighter-than-background patch - left VF, lighter-than-background patch - right VF, darker-than-background patch - left VF, darker-than-background patch - right VF) that corresponded to a detection rate of 80%. The thresholds were identified using the method of constant stimuli (Urban, 1910). On the first day of testing, at the beginning of the session, ten evenly spaced contrast values ranging from 0.011% to 0.05% of the maximal contrast of the light/dark patches were presented in a randomized order, in the lower left or right visual field (see Stimuli for details). The first stage included a total of 120 trials per participant, with all contrast values being tested 12 times (3 trials per stimulus condition). On each trial, there was a brief (150 ms, 1000 Hz) warning tone followed by a 1000 ms interval, after which the stimulus appeared on the screen for 30 ms. Participants were asked to keep their eyes on a central fixation cross (size = 0.5°) and to judge the brightness of the stimulus relative to the grey background by pressing two buttons on the numeric keyboard (“1” for darker, “2” for lighter stimuli), using their right index and middle fingers. They were required to make a guess on the trials in which they did not see the stimulus. At the end of this block, a sigmoid function was fit to the data to identify the first contrast value at which participants´ performance was at ceiling (i.e. 100% accuracy). Participants were then tested again in four blocks but with stimulus contrasts now ranging from the lowest contrast value (i.e. 0.011%) to the newly identified contrast value of maximal performance below ceiling. These blocks included 10 trials for each contrast and stimulus type, resulting in a total number of 400 trials per participant. At the end of this block, sigmoid functions were again fit to the data for both light and dark stimuli for each visual field (i.e. left and right). Contrast values yielding detection thresholds of 80% were extracted for each participant for each of the four stimulus conditions for use in the experiment.

On the second day of testing, a shorter threshold re-assessment was performed to verify whether participants' performance was similar to that from the previous session. Ten evenly spaced contrasts ranging from previously identified contrast levels corresponding to 50% and 100% detection accuracy were tested in a total of 240 trials (10 contrasts x 4 stimulus conditions x 6 trials). Sigmoid functions were once again fit to the data for each of the stimulus conditions to ensure that the 80% detection threshold was confirmed and was consistent with that from the first session.

3.2.5. Discrimination task

The experimental task was a two-alternative forced choice discrimination task. Each trial (see Figure 7A) started with a black fixation cross for 10 s, followed by a warning tone (150 ms, 1000 Hz). After a randomized time interval that could range from 1.75 to 2.25 s, rTMS was applied for 400 ms (5 pulses). Stimulus onset was synchronized with the last TMS pulse. The stimulus, consisting of the light/dark grey Gaussian patch, appeared on the screen for 30 ms (3 frames) in the lower visual field, either to the left or to the right. A blank screen then followed for 1000 ms, after which participants were prompted to judge the brightness of the stimulus relative to the grey background, pressing with their right hand "1" on the numeric keyboard for stimuli darker than the background, and "2" for lighter stimuli. They were asked to make a guess on trials in which they did not perceive any stimulus. After the button press, another question appeared on the screen, prompting participants to rate the clarity of their perception on the four-point Perceptual Awareness Scale (PAS; Ramsoy & Overgaard, 2004). The four PAS categories were: (0) "no experience", (1) "brief glimpse", (2) "almost clear experience", and (3) "clear experience" of the stimulus. Responses were given by pressing four different buttons on the numeric pad of the keyboard ("0","1","2","3"). The experimental task was divided into 5 blocks. Each block was composed of 60 trials: 5 trials at the individually adjusted stimulus contrast for each of the four stimulus conditions, for each of the three TMS conditions (i.e. rhythmic TMS, arrhythmic TMS, sham TMS). This yielded a total of 300 trials per participant, with the order of the trials being randomized across each block. Participants had a self-paced break after 30 trials, and at the end of each block. The threshold assessment and the behavioural task were programmed and run in MATLAB (MathWorks Inc.), using the Psychophysics Toolbox Version 3 functions (Kleiner et al., 2007).

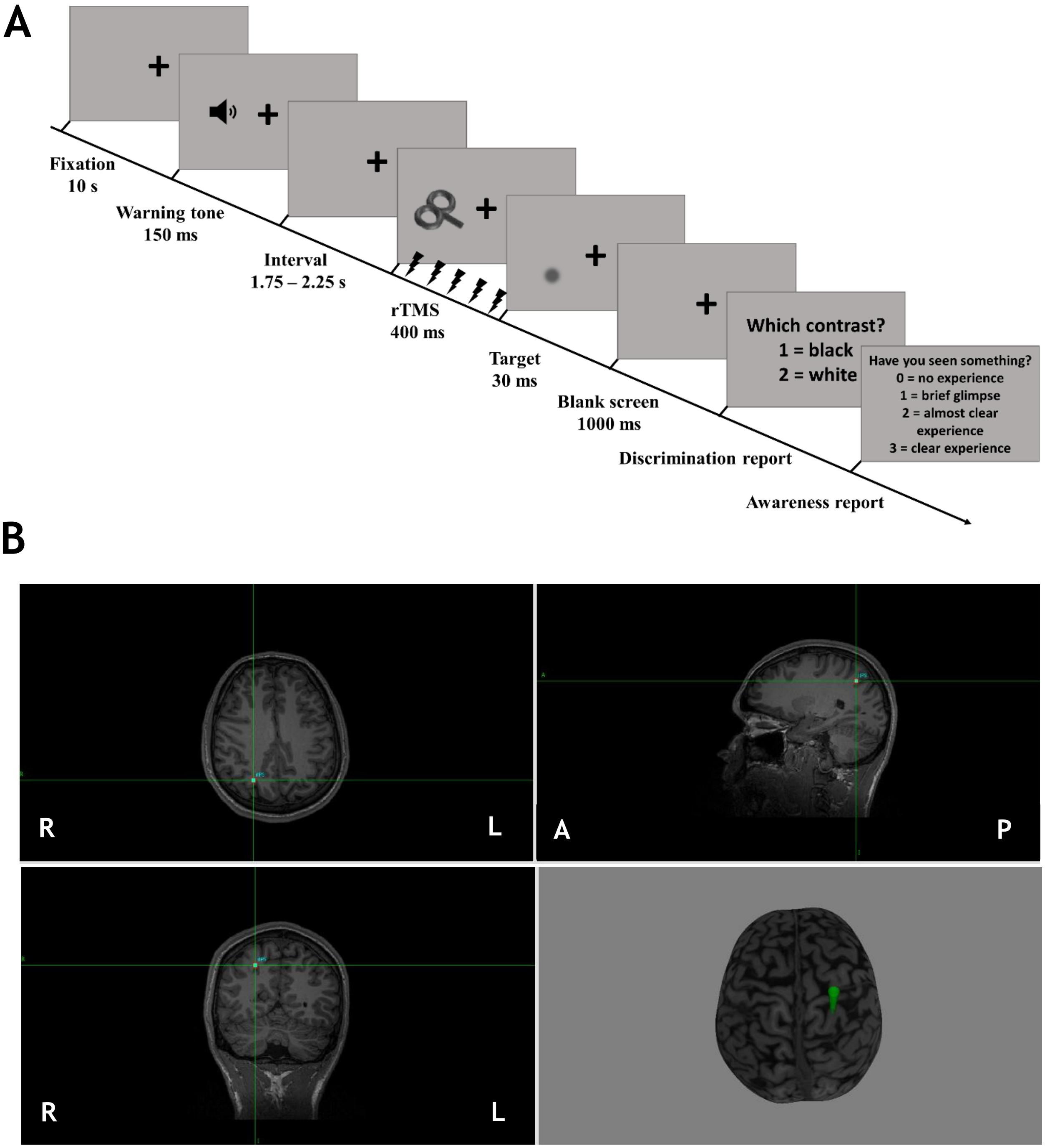


Figure 7: Task design. (A) Trial time course. The trials started with the presentation of a fixation cross for 10 seconds. A tone warned participants that the target stimulus would be presented shortly. After an interval ranging from 1.75 to 2.25 seconds, rTMS was applied in one of the three experimental

conditions (rhythmic, arrhythmic, or sham). The target stimulus was presented at the end of the last TMS pulse for 30 ms. Participants were then prompted to indicate the stimulus luminance of the target and rate their subjective perceptual experience on the PAS. **(B) TMS target.** This MR scan from a representative participant illustrates the target that was used for the neuronavigation, namely the right intraparietal cortex (rIPS). The TMS coil was oriented such that its handle was orientated upwards (R = Right; L = Left; A = Anterior; P = Posterior).

3.2.6. TMS

To be eligible for the study, all participants had to have an individual high-resolution T1-weighted anatomical MRI scans acquired at the Centre for Cognitive Neuroimaging (CCNi) at the University of Glasgow. The MRI scans were recorded in a 3T MR scanner (Magnetom Trio Siemens, Erlangen, Germany) using a 3D magnetization prepared rapid acquisition gradient echo sequence (ADNI- MPRAGE) (192 axial slices; voxel size = 1 x 1 x 1 mm; TR = 1900 ms; TE = 2.52 ms; inversion time = 900 ms; slice thickness = 1 mm; FoV = 256 mm; image resolution = 256 x 256; excitation angle = 9°). Due to its involvement in visual attention (fMRI-guided TMS study: Romei et al., 2011), the TMS target site was over the right intraparietal sulcus (rIPS; Talairach coordinates: 28, -51, 50). rIPS coordinates were first projected on each individual reconstructed 3D anatomical MRI scan using Brainsight (Rogue Research) (see Figure 7B for an example). The MRI scans were normalized into standard Tailairach space to identify the rIPS coordinates and then projected into native space. The anatomical MRI scans were co-registered with the participant's head, and the TMS coil was then neuronavigated to the target site. TMS was applied at a fixed intensity of 65% of the maximum stimulator output (MSO) using a Magstim Rapid2 Transcranial Magnetic Stimulator via a 70 mm figure-of-eight coil (Magstim Company).

Three TMS conditions were run per participant. In all conditions, the rIPS was stimulated with short TMS bursts (five pulses). For the active (rhythmic) TMS, the stimulation was set at an alpha frequency of 10 Hz (10Hz-TMS). The coil was oriented with the handle pointing upward (along the sagittal plane) so that the centre of the coil was overlaying the rIPS in each individual anatomical MRI scan with the TMS coil inducing currents perpendicular to the target gyrus in most participants, maximizing TMS efficacy (Thielscher et al., 2011; Thut et al., 2011). Additionally, two control conditions were run. In one control - arrhythmic TMS or ar-TMS - the same number of TMS pulses was applied as in the 10Hz-TMS (also within the same time window), but with randomized inter-pulse intervals of 70 ms, 80 ms, 120 ms, and 130 ms respectively. This control was intended to determine if a behavioural effect was due to alpha entrainment or a basic response to rapid-rate TMS bursts in general. Lastly, for the sham condition (10Hz-TMS sham), a second TMS coil (also a 70 mm figure-of-eight coil, 65% intensity of MSO) was turned perpendicular to the surface of the participant’s head over the main coil/target area. This emulated the sound clicks associated with the 10Hz-TMS, but the current was discharged away from the cortex, thus accounting for non-specific effects of TMS. The experimental trials were randomized, with participants receiving all three TMS conditions in every block.

3.2.7. EEG recording and alpha peak frequency identification

Resting-state EEG was recorded with a BrainAmp system (Brain Products, GmbH, Munich, Germany - BrainVision Recorder) using a cap with 3 Ag/AgCl pellet pin electrodes (EasyCap GmbH, Herrsching, Germany), placed according to the 10-10 International System at locations O1, Oz, and O2. Two extra electrodes served as ground (TP9) and online references (Cz). Electrode impedances were kept below 10 kΩ. Resting-state EEG was recorded for two minutes with eyes open and two minutes with eyes closed.

For each participant, the individual alpha peak was estimated from the occipital electrodes (O1, Oz, and O2) from the data recorded during eyes closed. It should be noted that no attempt has been made to differentiate between periodic and aperiodic (1/f-like) components in the electrophysiological signal, which could affect the accuracy of the estimated individual alpha peak frequencies (see Donoghue et al., 2020 for an algorithm which distinguishes the periodic and aperiodic components in the power spectral density). To determine the individual alpha peak frequency, an automated estimation process was adopted from (Corcoran et al., 2018). Pre-processing steps were performed using Brain Vision Analyzer 2.0 (Brain Products). The automated method of Corcoran and colleagues (2018) first extracts the power spectral density (PSD) of the pre-processed data and applies the Savitzky-Golay filter (SGF; Savitzky & Golay, 1964) to smooth the PSD function. Then, the first and second-order derivatives are calculated and analysed for a distinctive spectral peak in the alpha frequency band (8-14 Hz). To qualify as a valid peak, the largest peak detected has to be at least 20% higher than any other peak within the alpha band and to have the highest power value at least 1 standard deviation from the PSD mean. Overall, 17 out of 21 participants met these conditions and were included in the final analyses.

3.2.8. Statistical analysis

Trials with extreme reaction times were removed based on the median +/- 1.5 * interquartile range (IQR) criterion (Tukey, 1977). Participants had to have a minimum of 75 trials per TMS condition to be included in the final sample.

Main analyses: It was expected that a behavioural effect would be present during 10Hz-TMS in the visual field contralateral to the stimulation location for PAS ratings but not for accuracy. To test this, a within-subjects (repeated measures) analysis of variance (ANOVA) was conducted on the behavioural data with the factors TMS condition (10Hz-TMS vs ar-TMS vs 10Hz-TMSsham) x Target Location (left vs right visual field) x Stimulus Luminance (darker vs lighter than the background). Discrimination accuracy and awareness ratings were analysed separately. It was also expected that IAF positively correlates with task accuracy and that rhythmic TMS (as opposed to arrhythmic TMS) influences this relationship depending on IAF and hemifield. In contrast, no relationship of IAF with PAS was anticipated. To test this, multiple regression models were run, where the factors TMS condition, hemifield, stimulus luminance and IAF/alpha power were used as predictors of behavioural outcome. For further exploration, Pearson’s correlations were used to test the specificity of the 10Hz-TMS effects relative to ar-TMS in the hemifield contralateral to the stimulation site (in relation to individual factors such as IAF and power). Statistical analyses were performed using RStudio 3.4.1 (R Core Team, 2020).

3.3. Results

3.3.1. Overall task performance

Participants were presented with visual stimuli at threshold levels. After stimulus presentation, they had first to discriminate the stimulus from the background. Then, participants were asked to rate their subjective awareness of the stimulus (see Figure 7A). Figure 8A illustrates how participants used the PAS scale. On average, participants reported having “no experience” of the stimulus on 36.1% of all trials, “brief glimpse” on 29.8%, “almost clear experience” on 14.8%, and “clear experience” on 10.7% of trials. Accuracy was analysed as a function of the clarity of the subjective experience. This indicated that as the clarity of the target stimulus increased, so did accuracy, ranging from 70.9% accuracy when participants reported having “no experience” of the target stimulus, 76% when rating “brief glimpse”, 89.2% when rating “almost clear experience”, to 95% when the perceptual experience was “clear” (see Figure 8B).

Next, I checked whether the detection threshold manipulation had been successful and whether the performance across blocks in the 10Hz-TMS sham condition remained at the target levels (80% of the detection threshold of each participant, see Figure 8C). To this end, I conducted a repeated-measures ANOVA on the discrimination accuracy in the 10Hz-TMS sham condition in each experimental block. There was no significant difference between the accuracy levels in the five experimental blocks (F(4, 64)=.63, p=.63, η_G^2=.03), with the average detection threshold ranging from 74% to 80% across the experiment (see Figure 8C).

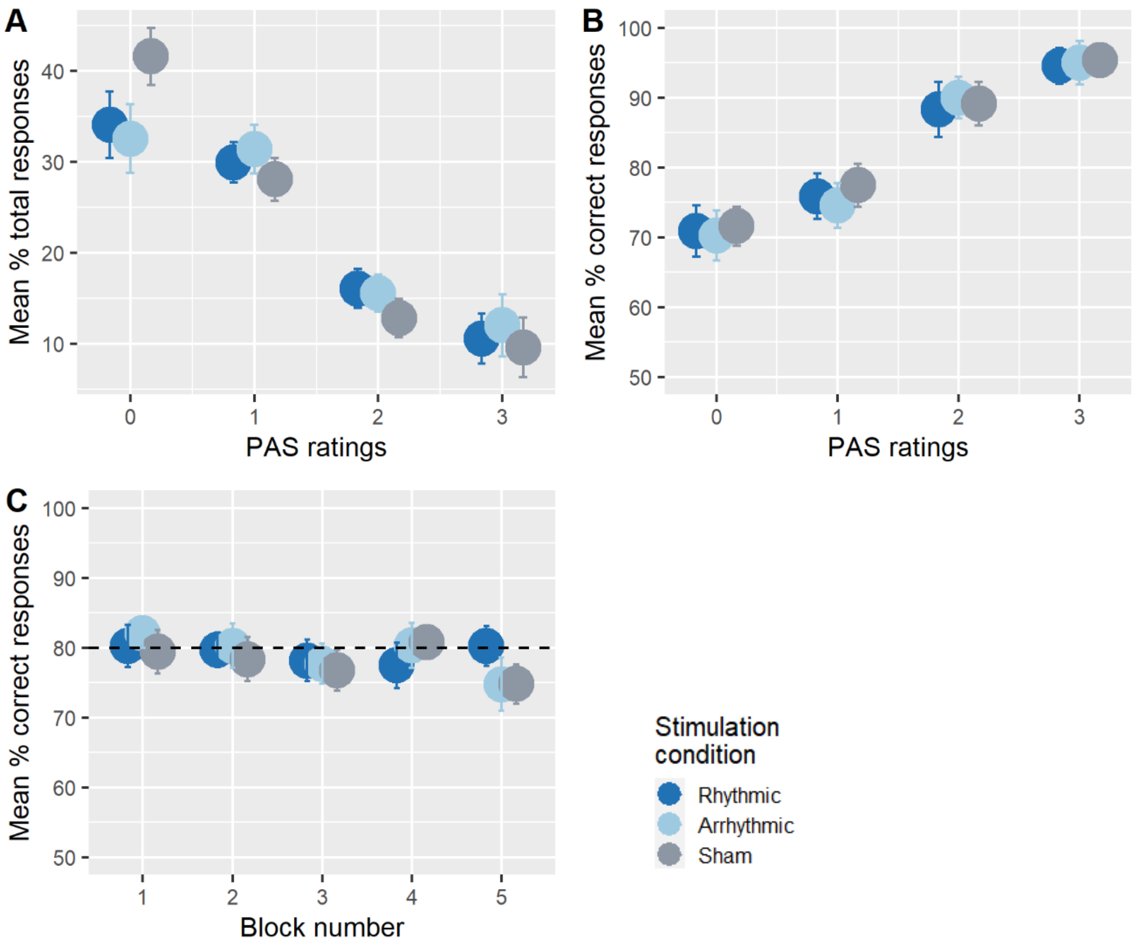


Figure 8: Overall task performance. (A) The use of the PAS ratings across the experiment. On average, participants reported having “no experience” [PAS=0] or “brief glimpse” [PAS=1] of the stimulus in over half of the total number of trials. **(B) Average percentage of correct responses as a function of the PAS ratings.** With increasing awareness, the accuracy of the participants increased. **(C) Accuracy of participants across experimental blocks.** There was no significant difference between accuracy across the blocks during the 10Hz-TMS sham condition. The performance of the participants was around 80% of their detection threshold throughout the entire experimental session indicating that stimulus-titration was successful.

3.3.2. Effects of rTMS

Accuracy

A three-way repeated-measures ANOVA was performed, with the factors TMS condition, target location, and stimulus luminance (see Figure 9). There were no significant main effects of stimulation (F(2, 32)=.72, p=.49, η_G^2=.002), hemifield (F(1,16)=1.8, p=.19, η_G^2=.009) or stimulus luminance (F(1,16)=3.07, p=.1, η_G^2=.08) on accuracy. However, the results of the rmANOVA revealed a significant interaction between hemifield and stimulus luminance (F(1,16)=7.4, p=.01, η_G^2=.04), TMS condition and stimulus luminance (F(2,32)=6.53, p=.004, η_G^2=.02) and between all three factors (F(2,32)=4.52, p=.02, η_G^2=.008), but no significant interaction of TMS condition and hemifield (F(2,32)=1.26, p=.29, η_G^2=.003).

First, follow-up analyses were conducted on the significant two-way interaction between TMS condition and stimulus luminance. To do this, the data were collapsed across hemifields, and a simple main effect analysis was conducted per luminance condition. There was a significant simple main effect of TMS condition for the darker luminance of the stimuli (F(2,32)=5.39, p=.01, η_G^2=.08), but not for the lighter contrast (F(2,32)=2.19, p=.128, η_G^2=.014). Simple pairwise comparisons were run on the TMS conditions with a Bonferroni adjustment applied, for the darker luminance condition. Accuracy was significantly different between 10Hz-TMS and 10Hz-TMSsham (p=.029), but not between 10Hz-TMS and ar-TMS (p=.375) or ar-TMS and 10Hz-TMSsham (p=.248).

Next, the significant three-way interaction was followed up with simple two-way interactions and simple main effects analyses. There was a statistically significant simple two-way interaction between TMS condition and stimulus luminance when the stimulus was presented in the right hemifield (F(2,32) = 11.2, p < .001, η_G^2=.05), but not for left hemifield trials (F(2,32)=1.85, p=.18, η_G^2=.013). For the trials in which stimuli were presented in the right hemifield, there was a statistically significant simple main effect of TMS condition on accuracy at a dark luminance (F(2,32) = 7.9, p = .002, η_G^2=.15), as opposed to a lighter luminance (F(2,32) = 2.95, p = .067, η_G^2=.01). All simple pairwise comparisons between the accuracy in these conditions were run with a Bonferroni adjustment applied. The average accuracy scores were significantly different between 10Hz-TMS and 10Hz-TMSsham (p = 0.012) and ar-TMS and 10Hz-TMSsham (p = 0.015), but not between 10Hz-TMS and ar-TMS (p = 1).

Overall, this indicates that rTMS had an effect on accuracy, but this is most likely explained by an unspecific effect of active TMS bursts in general (as opposed to sham), potentially reflecting an alerting effect due to the additional peripheral stimulation of active TMS relative to sham.

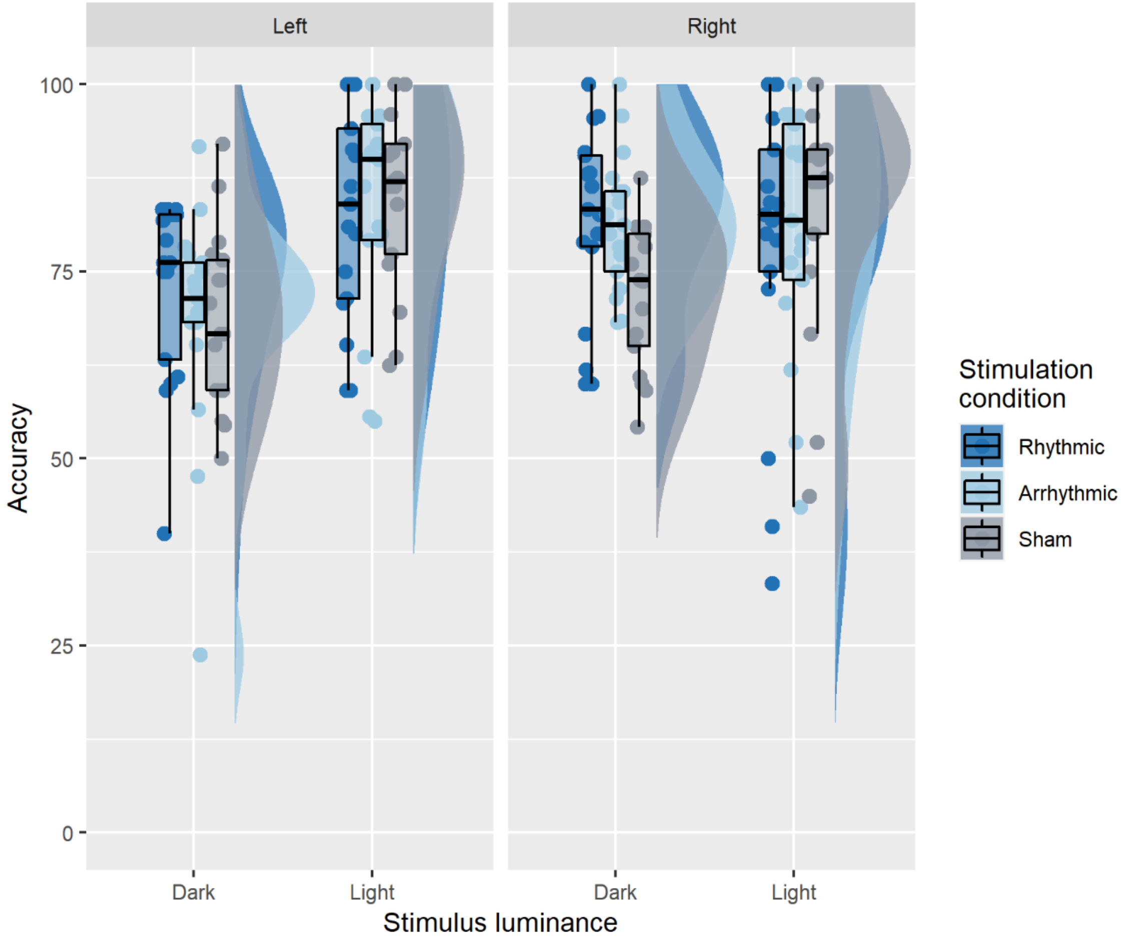


Figure 9: Accuracy across the experiment. The panels of the plots correspond to the left and right hemifield. The boxplots show a representation of the median and the first and third quartiles of the average accuracy per TMS condition, hemifield, and stimulus luminance. The whiskers of the boxplot can take a maximal value up to 1.5*interquartile range, with all the values exceeding the whiskers being outliers. The boxplots are superimposed with individual data points, while the clouds represent the probability distribution of the sample. TMS condition differentially affected accuracy (significant

interaction of TMS condition and stimulus luminance, and of TMS condition, stimulus luminance and hemifield), with active TMS (10Hz-TMS, ar-TMS) being different from 10Hz-TMSsham.

PAS Ratings

Likewise, a three-way repeated-measures ANOVA was performed on the PAS ratings, with the factors TMS condition, target location, and stimulus luminance (see Figure 10). This revealed a significant main effect of TMS condition (F(2,32)=18.8, p<.001, η_G^2=.01). PAS ratings during trials in the 10Hz-TMS condition (*M* = 0.979) were significantly higher than 10Hz-TMSsham ratings (*M* = 0.828) (t(16) = 4.27, p=.001, r^2=.46, Bonferroni corrected), as was the ar-TMS condition compared (*M* = 0.983) to the 10Hz-TMSsham condition (t(16) = 4.53, p=.001, r^2=.48, Bonferroni corrected). No significant difference was observed between the PAS ratings during 10Hz-TMS and ar-TMS (t(16) = -.37, p=1, r^2=.04, Bonferroni corrected). There was also a significant main effect of stimulus luminance (F(1,16)=18.16, p=<.001, η_G^2=.26), but not of hemifield (F(1,16)=.74, p=.4, η_G^2=.003). Additionally, there was a significant interaction between stimulus luminance and hemifield (F(1,16)=5.96, p=.02, η_G^2=.01) and TMS condition and stimulus luminance (F(2,32)=3.45, p=.043, η_G^2=.002), but not between TMS condition and hemifield (F(2,32)=.7, p=.5, η_G^2=.0004) nor between all three factors (F(2,32)=.43, p=.65, η_G^2=.0003).

The significant two-way interaction between TMS condition and stimulus luminance was then followed up with simple main effects. There was a statistically significant simple main effect of TMS condition on the PAS ratings for both luminance conditions, which was stronger for the trials in which the stimuli were presented in darker (F(2,32) = 18.5, p < .001, η_G^2=.026) than lighter (F(2,32) = 8.83, p < .001, η_G^2=.019) luminance. Bonferroni-corrected pairwise comparisons showed that there was a significant difference for the darker luminance between 10Hz-TMS and 10Hz-TMSsham (p<.001) and ar-TMS and 10Hz-TMSsham (p=.002). For the lighter luminance, there was a significant difference only between ar-TMS and 10Hz-TMSsham (p=.009).

The fact that there is no significant difference between 10Hz-TMS and ar-TMS indicates that as for accuracy, the effect of TMS on PAS ratings is not due to entrainment but rather reflects an unspecific response to the peripheral stimulation of active TMS bursts relative to sham.

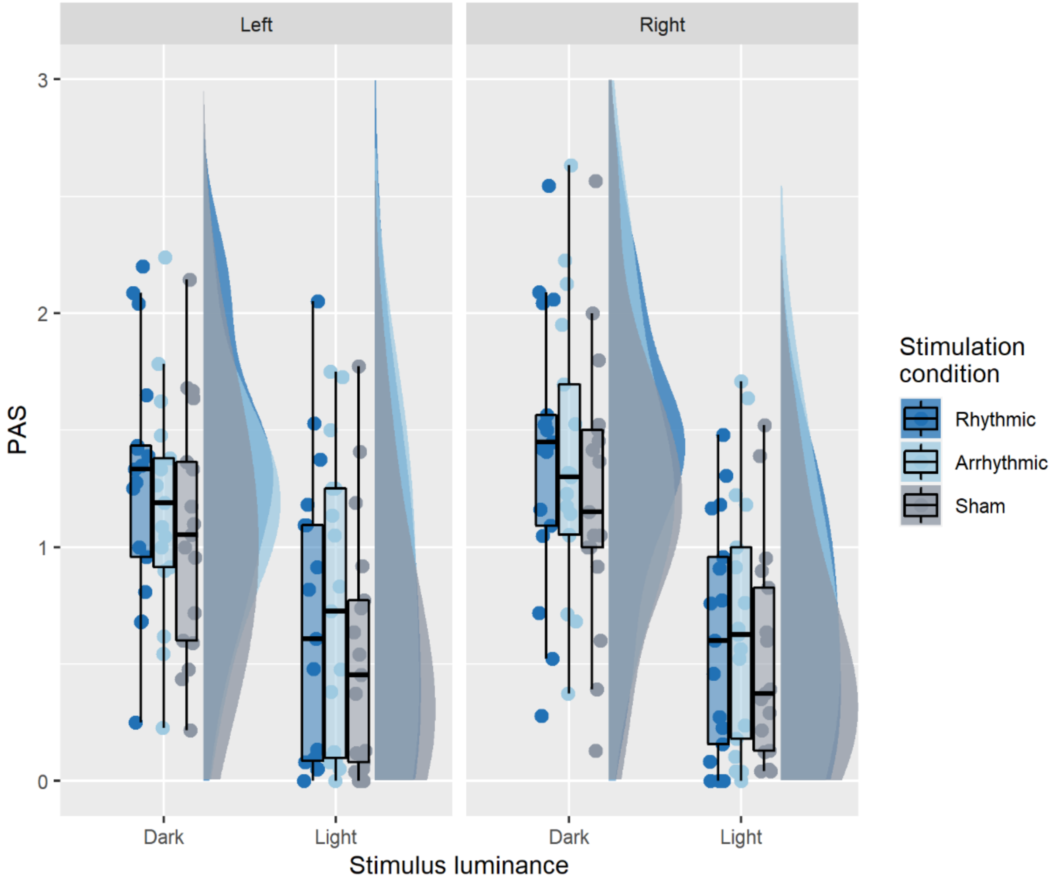


Figure 10: PAS ratings across the experiment. The panels of the plots correspond to the left and right hemifield. The boxplots show a representation of the median and the first and third quartiles of the average PAS ratings per TMS condition, hemifield, and stimulus luminance. The whiskers of the boxplot can take a maximal value up to 1.5*interquartile range, with all the values exceeding the whiskers being outliers. The boxplots are superimposed with individual data points, while the clouds represent the probability distribution of the sample. A significant main effect of TMS condition, as well as a significant interaction between TMS condition and stimulus luminance was found, explained by active TMS (10Hz-TMS, ar-TMS) improving PAS ratings relative to 10Hz-TMSsham.

3.3.3. Effects on accuracy and PAS ratings as a function of IAF

Resting EEG was recorded at the end of the experimental session, and the IAF was identified using an automated estimation process (Corcoran et al., 2018). To check whether the behavioural measures changed depending on the IAF (as recorded during the eyes closed condition), two multiple regression analyses were run to examine whether accuracy and/or PAS ratings, respectively, could be predicted by IAF, TMS condition, hemifield, and stimulus luminance.

For accuracy, the model was statistically significant ($F(5,198) = 6.251$, $p < .001$, $R^2 = .13$), with the variables IAF and stimulus luminance significantly adding to the prediction ($p<.01$). More specifically, the accuracy of the participants increased with increasing IAF (Figure 11A). To further explore whether rhythmic TMS (as opposed to arrhythmic TMS) may have influenced this relationship, I examined whether the effect of rTMS at 10Hz (relative to arrhythmic TMS) on accuracy depended on the offset of 10Hz from IAF. With entrainment, one would expect 10 Hz TMS to speed up the IAF and hence to increase accuracy in those participants in whom IAF is smaller than 10 Hz; or alternatively to slow down the IAF and hence to decrease accuracy in those participants in whom IAF is higher than 10 Hz. To explore this, the data was first collapsed across stimulus luminance. Then, spatially specific entrainment effects of 10Hz-TMS on accuracy were estimated by the following subtraction term:

$$\text{Accuracy}_{\text{Left Hemifield}}\ (\text{10Hz-TMS} - \text{ar-TMS}) - \text{Accuracy}_{\text{Right Hemifield}}\ (\text{10Hz-TMS} - \text{ar-TMS}),$$

where left/right hemifield is contra-/ipsilateral to the stimulation site, and entrainment effects are inferred by subtracting arrhythmic TMS from 10Hz-TMS. The relationship between this behavioural measure and IAF was then examined using the Pearson's correlation from the Robust Correlation Toolbox in Matlab (Pernet et al., 2013). This revealed a significant negative correlation (Pearson's $r = -.485$, $p = .048$, $CI = [-.75\ -.008]$), showing that as IAF increased, accuracy in the left hemifield decreased during 10Hz-TMS (as compared to the control conditions) (see Figure 11B). When running the robust correlation, two bivariate outliers were identified. In this case, Pernet et al. (2013) suggest that skipped-correlations are more suited for dealing with outliers, as they delete the outliers while preserving the structure of the data and accounting for the removal of the data points. However, the skipped correlation was not significant.

For the PAS ratings, the multiple regression model was also statistically significant ($F(5,198) = 14.52$, $p < .001$, $R^2=.26$), but with stimulus luminance being the only variable significantly adding to the prediction ($p<.01$). Since the variable IAF was not significant, the model was not further investigated.

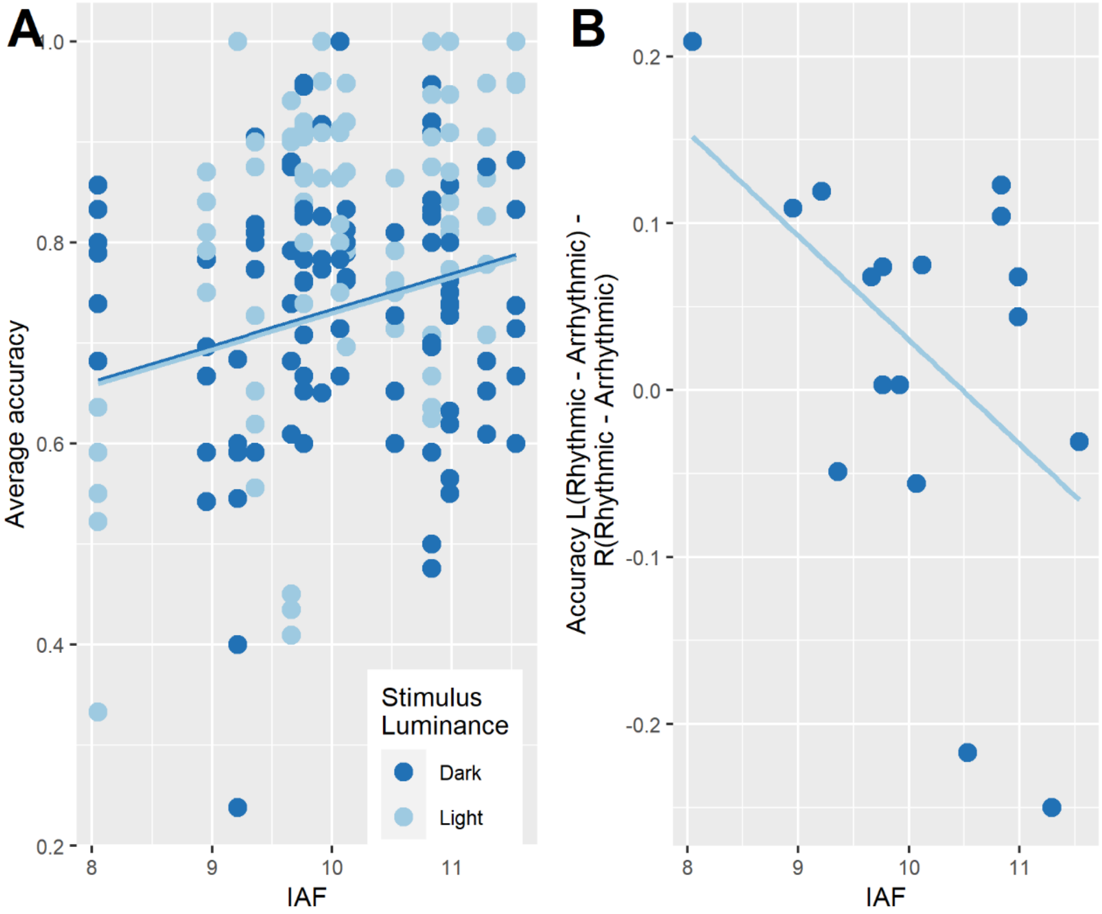


Figure 11: Change in accuracy as a function of IAF. **(A)** A multiple regression analysis showed that accuracy of the participants increased with increasing IAF measured at rest. (**B)** Spatially specific effects (LVF vs. RVF) of entrainment (10Hz-TMS minus ar-TMS) as a function of IAF. Participants with lower IAF had accuracy increased by 10Hz-TMS in the hemifield contralateral to the TMS site, hence benefitting from the 10Hz-TMS stimulation, while the opposite effect can be seen in participants with high IAF.

3.3.4. Effects of accuracy and PAS ratings as a function of alpha power

Similar to the IAF analysis, I checked whether the behavioural measures and effects of the TMS depended on the alpha power, as extracted from the resting state with eyes open. Multiple regression analyses were run to predict accuracy and PAS ratings, respectively, from alpha power, TMS condition, hemifield, and stimulus luminance.

For accuracy, the multiple regression model was statistically significant (F(5,198) = 14.52, $p < .01$, $R^2=.26$), with the variable stimulus luminance significantly adding to the prediction ($p<.01$). The variable alpha power did not significantly add to the model; hence, this was not further explored.

For PAS ratings, the model was statistically significant (F(5,198) = 15.08, $p < .001$, $R^2=.28$), with the variable stimulus luminance significantly adding to the prediction ($p<.01$). The variable alpha power did not significantly add to the model ($p = .09$), and therefore the effect was not explored further.

3.4. Discussion

In the present study, I aimed to test the causal relationship between the amplitude of alpha oscillations and subjective measures of performance, by using repetitive TMS in the alpha frequency to modulate perceptual awareness. Based on recent findings in the literature (Samaha, Iemi, et al., 2017; Benwell et al., 2017) and in *Chapter 2*, I expected 10Hz repetitive TMS over the rIPS to cause PAS ratings to decrease in the contralateral (i.e. left), but not ipsilateral (i.e. right) hemifield. This hypothesis was not confirmed, as there was no significant interaction between TMS condition and hemifield. Although I did find a statistically significant effect of the TMS stimulation on PAS ratings, with both 10Hz TMS and arrhythmic TMS leading to higher ratings than sham, there was no significant difference between the two active TMS conditions, thus indicating that the effect of the TMS stimulation was unspecific. This was further confirmed by the results on accuracy: here, it was anticipated that accuracy would remain unchanged following TMS stimulation. Instead, TMS stimulation had a statistically significant effect on accuracy for stimuli presented at a darker luminance in the right hemifield. Yet again, there were no significant differences between the two active TMS conditions - 10 Hz and arrhythmic - further suggesting that the behavioural effects seen following TMS were likely due to an alerting response to the TMS bursts generally rather than alpha entrainment.

It has been proposed that decreasing the pre-stimulus alpha amplitude leads to a more liberal decision criterion, while perceptual sensitivity is left unaffected (Iemi et al., 2017). While the causal evidence for the role of alpha oscillations in perceptual decisions is scarce, one study tested whether transcranial alternating current stimulation (tACS) changed perceptual sensitivity (i.e. ability to detect an existent target) or the decision criterion of the participants (i.e. the subjective internal representation of the target) when somatosensory stimuli were presented (Craddock et al., 2019). It was found that tACS increased the reports of a stimulus being present even when it was not there, consistent with the hypothesis that alpha oscillations lead to a more liberal decision criterion (Iemi et al., 2017). Additionally, if the proposal of Iemi and colleagues' (2017) is correct, prestimulus alpha activity should be related to the subjective awareness of participants, rather than to their ability to perceive stimulus features. Indeed, recent evidence has shown that prestimulus alpha power is negatively correlated with subjective measures of task performance such as confidence or visual awarness (Samaha, Iemi, et al., 2017; Samaha, LaRocque, et al., 2020; Benwell et al., 2017, 2021; Wöstmann, Waschke, et al., 2019) but not objective measures such as accuracy (Limbach & Corballis, 2016; Craddock et al., 2017; Iemi et al., 2017; Iemi & Busch, 2018). To my knowledge, only one other study has directly investigated the causal role of alpha amplitude in subjective confidence. Di Gregorio and colleagues (in review) applied 5 pulses of rTMS trains over the right occipital cortex at IAF and IAF ± 1, while participants performed a visual detection task and rated the confidence in their response. Identical to my design, they applied the TMS bursts immediately before the target onset. Similar to the present findings, it was reported that TMS stimulation did not affect confidence levels, even though evidence of entrainment was found in the EEG activity of participants.

To test whether the timing of TMS burst delivery - relative to the confidence rating - is key, Di Gregorio et al. (in review) then conducted a follow-up experiment, in which they delivered the TMS bursts before the confidence prompt, rather than pre-stimulus. This led to significant differences in confidence levels between rTMS and sham stimulation in the expected direction, such that higher alpha amplitudes prior to the prompt were associated with lower confidence, in keeping with recent correlational evidence from the literature (Samaha, Iemi, et al., 2017; Benwell et al., 2017, 2021; Wöstmann, Waschke, et al., 2019). This is in agreement with a recent study by Hobot et al. (2020), who demonstrated that perceptual awareness, but not accuracy, was successfully modulated via a single TMS pulse delivered to the primary motor cortex, when participants had to give the PAS ratings immediately after the stimulus presentation. Since entrainment lasts only a few cycles after the end of the TMS train (Thut, Veniero, et al., 2011; Lin et al., 2021) and participants' confidence responses in the present experiment were required more than one second after the TMS stimulation was applied, it is possible that the null results of the present experiment can be explained (in retrospect) by the suboptimal timing of the PAS rating prompt relative to TMS, rather than an absence of a causal relationship between alpha amplitude and confidence ratings. Future research should further explore this conjecture.

A second goal of this study was to investigate whether resting IAF is positively correlated with accuracy on task. It was hypothesized that active 10Hz TMS stimulation would benefit participants with a lower IAF than the applied rTMS frequency, resulting in improved accuracy due to 10Hz rTMS speeding up their IAF. In contrast, active 10 Hz TMS stimulation was expected to cause an impairment in the accuracy of participants with IAF higher than the applied rTMS frequency. I found that overall, participants were more accurate with increasing IAF and that this relationship is modulated by 10Hz rTMS, suggesting that the speed of the alpha oscillations modulates the sensitivity to a target stimulus. My results add to the work of Di Gregorio and colleagues (in review), who have reported that the trial-by-trial variability in pre-stimulus alpha frequency predicted task accuracy and that this relationship can be causally demonstrated using rTMS at IAF +/- 1Hz, improving/impairing accuracy respectively. This is also in line with findings in the visual domain where evidence suggests that IAF is correlated with the temporal sensitivity of participants (Samaha & Postle, 2015; Minami & Amano, 2017; Wutz et al., 2018; Ronconi et al., 2018; Battaglini, Mena, et al., 2020). Additionally, research has demonstrated the IAF plays a role in multisensory processing, such that a faster IAF is associated with a narrower temporal window of perception (Cecere et al., 2015; Migliorati et al., 2020), as well as in helping individuals to adjust to increasing task demands in cognitive (Haegens, Cousijn, et al., 2014; Maurer et al., 2015) and physical tasks (Gutmann et al., 2015; Hülsdünker et al., 2016). Together, these findings suggest that individual alpha peak frequency is functionally relevant to information processing (Mierau et al., 2017).

In conclusion, in this experiment, I applied TMS stimulation to investigate whether alpha oscillatory activity was causally influencing subjective and/or objective aspects of task performance. Although I did not find a significant effect of 10 Hz rTMS stimulation on accuracy nor on perceptual awareness ratings compared to arrhythmic and sham TMS, this study demonstrates the importance of causally manipulating alpha oscillations to better understand the dissociation between the predictors of conscious awareness and task performance. In line with previous research, I have found that individual alpha peak frequency as measured at rest is correlated with accuracy and that this relationship is modulated by 10Hz rTMS, pointing to a functional role of alpha frequency in perceptual sensitivity.

Chapter 4

Parietal alpha tACS shows inconsistent effects on visuospatial attention

4.1. Introduction

While the neural correlates of cognitive processes can be identified using brain imaging techniques, it is possible to obtain causal evidence on brain-behaviour relationships with the use of non-invasive (transcranial) brain stimulation methods. Transcranial alternating current stimulation (tACS), in particular, is of interest for probing causality between oscillatory activity of the brain and behaviour, as the sinusoidal tACS-currents hold promise to interact with intrinsic brain oscillations in a frequency-specific manner (Antal & Paulus, 2013; Fröhlich, 2015; Tavakoli & Yun, 2017; Vosskuhl et al., 2018). tACS has been gaining popularity in the last decade (Tavakoli & Yun, 2017; Polanía et al., 2018), yet many controversies remain unresolved (see Bland & Sale, 2019 for a review). For instance, it has been assumed that tACS-effects are caused by entrainment of brain oscillations and/or neuroplasticity (Ali et al., 2013; Vossen et al., 2015; Herrmann, Murray, et al., 2016). However, concurrent recordings of electrophysiological data is hindered by the presence of artefacts (Noury et al., 2016; Neuling et al., 2017), as a result of which the exact mechanisms of tACS-interaction with brain activity remain unclear. Likewise, it is unclear to what extent the low tACS-intensities that are in use can directly affect neuronal populations, given that much is being attenuated by the skin and skull (Huang et al., 2017; Lafon et al., 2017; Vöröslakos et al., 2018), or alternatively exert their effects indirectly through transcutaneous co-stimulation of peripheral nerves (Asamoah et al., 2019b). Others have questioned to what extent these effects can be reproduced (Héroux et al., 2017).

One domain that would seem ideal for testing the potential of tACS affecting performance through interacting with brain oscillations is visuospatial attention. Visuospatial attention refers to the ability of participants to allocate cognitive resources to a spatial location of interest in order to prioritise and improve the processing of relevant stimuli at that position (Posner, 1980). Numerous M/EEG studies have identified occipito-parietal alpha oscillations as correlates of visuospatial attention deployment, whereby alpha power is suppressed contralaterally to the attended hemispace and/or enhanced contralaterally to the unattended position (Worden et al., 2000; Sauseng, Klimesch, Stadler, et al., 2005; Thut et al., 2006; Rihs et al., 2007; Gould et al., 2011; Foxe & Snyder, 2011; Foster & Awh, 2019; Van Diepen et al., 2019). In addition, many M/EEG-studies have established a link between posterior alpha-power and specific behavioural outcomes in perceptual tasks, such as perceptual accuracy (Thut et al., 2006; van Dijk et al., 2008; Händel et al., 2010; Boncompte et al., 2016; Brüers & VanRullen, 2018) or subjective awareness of visual stimuli (Limbach & Corballis, 2016; Benwell et al., 2017; Iemi et al., 2017; Samaha, Iemi, et al., 2017; Benwell et al., 2018, 2021).

In the context of visuospatial attention, if occipito-parietal tACS at alpha-frequency were to bias behavioural performance in a spatially specific manner, this would be in (indirect) support of tACS causally interacting with underlying, perceptually relevant brain oscillations. Recently, Schuhmann and colleagues (2019) have shown that applying high-density (HD) alpha-tACS over the left parietal cortex at 10Hz but not sham induces a shift in visuospatial attention away from the contralateral right to the left hemifield. In analogy but adding concurrent EEG recordings, Kemmerer et al. (2020) revealed that left parietal tACS at IAF, but not at control frequencies (IAF±2 Hz) or sham, was associated with a left lateralization of alpha power, the magnitude of which predicted the right to leftward shift in visuospatial attention during endogenous shifts of attention. Similar results have been reported by Kasten and colleagues (2020), who stimulated both the left and right occipital cortex with alpha- and gamma-tACS, while presenting participants with endogenous and exogenous visuospatial cues. A significant effect of tACS on endogenous but not exogenous attention was found when stimulation was applied over the left hemisphere but not over the right (Kasten et al., 2020). Similarly, in the auditory domain, unihemispheric alpha-tACS caused a disruption in endogenous spatial attention contralaterally to the stimulated hemisphere (Deng et al., 2019; Wöstmann et al., 2018). Together, these studies suggest that tACS can be used to establish a causal link between alpha oscillations and spatial attention, as well as highlight the potential of the technique to interact with brain oscillations and behaviour for potential clinical purposes, e.g. rehabilitation treatment of pathological asymmetries in visuospatial attention.

In the present study, we sought to replicate the significant behavioural effects of alpha-tACS on spatial attention, consistently reported in the literature so far (summarised in Table 1), to contribute to the evaluation of its efficacy and replicability to modulate spatial attention. Therefore, we designed the study in accordance with this literature. We largely followed the study protocol and design of Schuhmann and colleagues (2019), including left parietal tACS at 10Hz using a high-density montage (central electrode at P3) with an assessment of the tACS-effects on spatial attention in the visual modality across the two visual fields (see Table 1). We tested a large sample of participants (n=40, at the upper end of previous studies with positive findings, see Table 1) using the exact same task as Schuhmann et al. (2019) measuring endogenous attention. We focused on task performance during tACS, as all previous studies reported consistent alpha-tACS effects on endogenous attention online to tACS (see Table 1). Finally, we applied tACS at 1.5mA for 20min (in the range of previous alpha-tACS studies with positive effects, see Table 1). We expected that with this design, that is 10 Hz tACS applied over the left posterior parietal cortex/P3, but not sham, we would induce a shift in attentional bias away from the contralateral right to the left hemispace. Additionally, resting EEG was recorded immediately after stimulation to examine potential effects of tACS on individual alpha frequency and power.

Table 1: Summary of studies using alpha tACS to modulate spatial attention

Study	Sensory modality tested	No.	Avg. age/Age range/ Gender	α-tACS frequency	Montage
Deng et al. (2019)	Auditory	N = 20	21.15; range 18-24; 13 F	10 Hz vs sham	HD-tACS; central electrode: P2; return electrodes: CP2, P4, Pz, PO4.
Kasten et al. (2020)	Visual	N = 20	25±2.7; 10 F	IAF vs gamma (47 Hz)	Two pairs of circular electrodes: O1-P3 and O2-P4
Kemmerer et al. (2020)	Visual	N = 21	45.38; range 19–72; 8 F	IAF vs IAF±2	HD-tACS; small circular electrode at P3 surrounded by a large ring electrode
Schuhmann et al. (2019)	Visual	N = 36	21.56; range 18-29; 18 F	10 Hz vs sham	HD-tACS: small circular electrode at P3 surrounded by a large ring electrode
Wöstmann et al. (2018)	Auditory	N = 20	Range 19-30; 10 F	10 Hz vs sham	Round electrodes placed over FC5 and TP7

Study	**Area stimulated**	**Intensity applied**	**Duration of stimulation**	**Behavioural probe & effect direction**
Deng et al. (2019)	R IPS	1.5 mA	20 min block	Online effects during tACS on endogenous attention; left hemispace affected
Kasten et al. (2020)	L and R occipital cortex	2 mA	8 min block	Online effects during tACS on endogenous (but not exogenous) attention in trials with invalid cues; leftward shift
Kemmerer et al. (2020)	L PPC	1.5 mA	35-40 min block	Online effects during tACS on endogenous attention (but not simple detection); leftward shift
Schuhmann et al. (2019)	L PPC	1 mA	35-40 min block	Online effects during tACS on endogenous attention (but not simple detection); leftward shift
Wöstmann et al. (2018)	L posterior STG, auditory and parietal regions	1 mA	25 min block	Online effects during tACS on endogenous attention; leftward shift

Abbreviations: IPS, intraparietal sulcus; PPC, posterior parietal cortex; STG, superior temporal gyrus.

4.2. Materials and Methods

4.4.1. Participants

Forty-two healthy volunteers (mean age 22.4, range 19 – 38, 22 female) completed this study. An *a priori* sample size calculation based on the effect size observed in Schuhmann et al. (2019) identified that a minimum of 38 participants was required for a repeated-measures ANOVA design (d = 0.6, α = 0.05, power = 0.95). We, therefore, decided on a final sample size of 40 participants (pre-determined), but we had to record 42 as two participants were excluded from the final analysis due to poor fixation during the experimental task or noisy EEG recording, respectively. Participants gave informed written consent and had no contraindication to tACS (i.e. neurological/psychiatric disorders, history or family history of seizures or epileptic seizures, metal or medical implants, pregnancy, headaches, intake of central nervous system medication or recreational substances). All participants were naïve to tACS, reported normal or corrected-to-normal vision, and were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). The procedures of the study were in line with the latest revision of the Declaration of Helsinki and were approved by the Ethics Committee of the College of Science and Engineering at the University of Glasgow.

4.4.2. Procedure and task

Each participant underwent two sessions of maximally 1.5 hours each, at least 2 days apart. During these sessions, participants received active 10 Hz or sham tACS over the left parietal cortex for 20 minutes (Figure 12A), while performing a visually cued target discrimination task (Figure 12B). The order of the two tACS sessions (10 Hz, sham) was counterbalanced across participants. Before the experiment, participants practised one block of the behavioural task. The experimental task measured performance on endogenous attention (see Figure 12B, identical replication from Schuhmann et al., 2019; stimulus material and script provided as a courtesy by these authors). Participants viewed stimuli on a computer screen (refresh rate, 60 frames/s) at a viewing distance of 57 cm. Each trial started with a fixation point presented for an interval ranging from 800 to 1200 ms, which turned into a bullseye for 500 ms. This was followed by a cue pointing either to the left (<< ● <<), right (>> ● >>), or both sides (<< ● >>), in anticipation of a forthcoming target. The cue was presented for 100ms and predicted with 80% accuracy the location of the target appearing after a 500 ms cue-target interval. The target stimulus was a Gabor patch tilted at 45° to either side (spatial frequency = 1.5 cycles per degree; envelope standard deviation = 0.75 degrees; Michelson contrast = 60%), appearing either in the left or right hemifield at 7° eccentricity (Figure 12B) and presented for 100 ms. Participants had to discriminate whether the Gabor patch was oriented clockwise or counterclockwise and were instructed to respond as fast and as accurately as possible once the target appeared on the screen, by pressing the left and right arrow keys on the keyboard, using the index and middle finger of their right hand, respectively. They were instructed to keep their eyes on the fixation point throughout the trial. The next trial started immediately after a response was made. One experimental session consisted of 336 trials containing 192 valid trials (i.e. target was presented in the cued hemifield), 48 invalid trials (i.e. target was presented opposite the cued hemifield), and 96 neutral trials (i.e. target was preceded by a neutral cue). The task duration was approximately 20 minutes, with self-paced breaks every 84 trials.

After task completion and tACS cessation, 4 minutes of resting EEG was recorded from three occipital electrodes to evaluate the amplitude and individual peak frequency in the alpha band (8-14Hz) across conditions (tACS and sham). At the end of each session, a questionnaire was administered to assess how well the participants tolerated the tACS stimulation. Furthermore, to assess whether participants were blinded to the stimulation protocol, an additional questionnaire was administered at the end of the second session, in which participants had to judge in which session they received real stimulation and in which session sham.

4.4.3. Transcranial alternating current stimulation

High-density tACS was delivered through a battery-driven, constant current stimulator (NeuroConn GmbH, Ilmenau, Germany) using a rubber ring tACS electrode with a small central, circular electrode (2.1 cm diameter, 3.5 cm^2; thickness: 2 mm) and a large outer ring (9 cm inner and 11 cm outer diameter, 31.5 cm^2; thickness: 2 mm) (as in Schuhmann et al., 2019). This montage was chosen to ensure a high spatial focality (Datta et al., 2008). The small circular electrode was positioned in accordance with the International 10-20 EEG montage over the left parietal cortex (P3), with the large electrode surrounding it (Figure 12A, again as in Schuhmann et al., 2019). The electrodes were applied on the scalp using conductive gel (ten20 paste, Weaver and Company, Aurora, CO, USA). Electrode impedance was kept below 10 kΩ. Stimulation frequency was 10Hz (as in Schuhmann et al., 2019), but the intensity was set slightly higher to 1.5 mA (peak-to-peak), yielding an average current density of 0.4 mA/cm^2 at the central electrode and 0.05 mA/cm^2 at the surround electrode. For a picture with the simulated voltage distribution, we refer to Schuhmann et al. (2019), their Figure 1A. tACS was administered in a within-subject design with one active condition and one sham condition. In the active condition, phase offset was set to 0 at the start, and 100 cycles were used for ramping up, with the stimulator being switched off after completion of the experimental task. The stimulation duration was approximately 20 minutes. In the sham condition, the stimulator was ramped up and then immediately ramped down, each within 100 cycles.

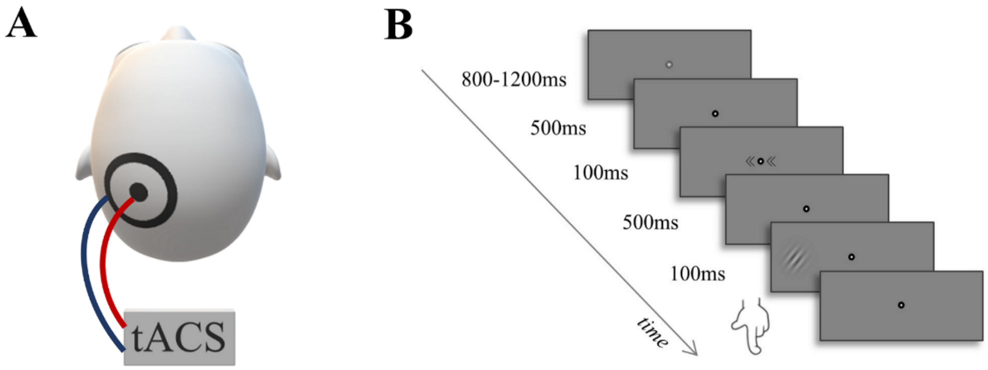


Figure 12: Experimental setup. (**A) tACS setup.** A small circular electrode was positioned over P3 and a large electrode was centring it. Figure adapted from Schuhmann et al. (2019) (**B) Stimulus schematics and trial time course.** The trial started with the presentation of a fixation point, followed by a cue (here: left). The target stimulus was a sinusoidal grating tilted at 45° to either left or right, presented on either side of the screen (here: presented right). Participants had to indicate the direction in which the grating was tilted. Figure adapted from Schuhmann et al. (2019).

4.4.4. Eye tracker

Eye-tracking (Eyelink 1000, SR Research, Mississauga, Ontario, Canada) was used during the experimental task to ensure fixation before stimulus presentation. A 9-point calibration and validation procedure was carried out before the start of the experimental task and then again before the start of each of the four blocks of trials. Data were acquired using monocular tracking of the right eye at a sampling rate of 1000 Hz.

4.4.5. Electrophysiological data recording

Immediately after completion of the experimental task and the tACS stimulation, Ag/AgCl electrodes were attached to the scalp of participants using conductive gel (ten20 paste, Weaver and Company, Aurora, CO, USA). A small number of electrodes was chosen to minimize the gap between the end of tACS and the start of EEG recording (~5min). Resting EEG was then recorded for a total of 4 minutes (2 minutes eyes closed; 2 minutes eyes open) from the occipital sites O1, Oz, and O2 (referenced to AFz), according to the international 10-20 Electrode Montage, using a BrainAmp MRPlus amplifier (BrainProducts GmbH, Munich, Germany). Electrode impedance was kept below 10 kΩ, and EEG data were acquired at a sampling rate of 1000 Hz.

4.4.6. Data analysis

Behavioural analysis

Pre-processing of the behavioural data was conducted in Matlab (MathWorks, Natick/USA). Following the procedure of Schuhmann et al. (2019), trials were removed *post-hoc* if the eye movements during a trial exceeded 2° of visual angle in the time window starting 100 ms before the cue until stimulus onset. On average, 1.7% of all trials were discarded per participant due to eye movements. Trials were also excluded if the reaction times (RTs) were extreme (i.e. < 120 ms, > 800 ms). For the analysis of reaction times, only correct trials were included.

For each participant, accuracy and median RTs were computed for each tACS condition (i.e. 10Hz tACS vs sham), type of cue (i.e. invalid, neutral, valid) and target location (i.e. left hemifield vs right hemifield), in analogy to Schuhmann et al. (2019). Because the RT distributions are usually skewed (Whelan, 2008), we also conducted the analyses using the log-transformed data. The results of the analyses remained qualitatively unchanged, not affecting the conclusions; hence these analyses are not reported here. Spatial bias was calculated by subtracting the RT/accuracy in the right hemifield from the RT/accuracy in the left hemifield ($\text{RT/Accuracy}_{\text{Left hemifield}} - \text{RT/Accuracy}_{\text{Right hemifield}}$).

EEG analysis

The EEG analysis was conducted in BrainVision Analyzer 2.0 (Brain Products) using a semi-automated approach. The post-tACS continuous EEG signal for both resting "eyes closed" and "eyes open" was segmented into 1 s epochs. A fast Fourier transform (FFT) was calculated for frequencies between 0.1 and 50 Hz using a Hanning window. For each participant, the resulting spectra of each tACS session were averaged across epochs. The frequency window for the analysis of the data was set between 8 and 12 Hz, within which the IAF peak and corresponding amplitude were identified.

Statistical analyses

Statistical analyses were performed using R 3.4.1 (R Core Team, 2020). To ensure that the attention manipulation was effective, we first performed a repeated-measures analysis of variance (rm-ANOVA) with the within-subject factor cue validity (invalid, neutral, valid) on the median RT of the sham data only (with the data collapsed across the target locations). To verify the presence of a hemifield/attentional bias as reported by Schuhmann et al. (2019) (RT left > right visual field), we also ran a rm-ANOVA with the within-subject factor hemifield (left, right) on the median RT of the sham data. The main analyses then followed the same steps as Schuhmann and colleagues (2019) and consisted of a rm-ANOVA with the factors tACS condition (10Hz, sham), and cue validity (invalid, neutral, valid) on the hemifield bias (median $RT_{\text{Left hemifield}}$ – median $RT_{\text{Right hemifield}}$). When sphericity was violated, Greenhouse-Geisser corrected values are reported. Where appropriate, t-statistics were employed to test simple effects.

Given the null results (see below), several additional exploratory analyses were run including on accuracy and using analyses of covariance (ANCOVA) to explore whether the effects of tACS may depend on specific individual (trait) factors. The ANCOVA analyses mirrored the main rm-ANOVA, such that two within-participant factors were included: tACS condition (10Hz, sham) and cue validity (invalid, neutral, valid), in addition to the covariates. We explored the influence of the following four covariates on tACS outcome (in four different ANCOVAs): an individual hemifield bias, IAF, deviation of IAF from 10 Hz (absolute difference), and alpha power; all inferred during the sham session to reflect individual trait factors unaffected by tACS. Because of the within-subjects design, covariates have been centred by subtracting the average covariate value from each covariate score to increase the precision of the analyses (Schneider et al., 2015). A significant effect of the covariate on tACS outcome would be reflected in a significant interaction either between the covariate and tACS condition and/or a significant triple interaction between the covariate, tACS condition, and cue validity. Additionally, we also analysed the potential effects of tACS on resting EEG and peripheral sensations.

4.5. Results

4.5.1. Main analyses

RTs

We first checked whether the experimental manipulation of spatial attention was effective by analysing RTs in the sham condition only. This was confirmed by a repeated-measures ANOVA on the median RTs (data averaged across hemifields, Figure 13A) revealing a significant main effect of cue validity (F(2,78) = 39.9, p <.001, η_G^2=.03). Responses in valid trials (M±SD: 450.7±70.5ms) were significantly faster than in neutral trials (464±76ms; t(39)=-5.2, p<.001, r^2=.38, Bonferroni corrected), and faster than in invalid trials (485.7±85.8ms; t(39)=-7.2, p<.001, r^2=.49, Bonferroni corrected), while responses in neutral trials were significantly faster than in invalid trials (t(39)=5.22, p<.001, r^2=.38, Bonferroni corrected).

We then tested whether there was a difference between the RTs in the left as compared to the right hemifield in the sham condition (RT left > right visual field), as reported by Schuhmann et al. (2019) employing the same paradigm. A t-test on median RTs (data averaged across cue validity, Figure 13B) indeed revealed a significant difference between hemifields (t(39)=3.13, p =.003, r^2=.24). Participants responded significantly faster when stimuli were presented in the right visual field (459.6±81.3ms) than the left visual field (474±75.4ms), replicating Schuhmann et al. (2019). This result suggests that, on average, participants had an overall rightward bias.

Before testing the main hypothesis that left parietal alpha-tACS but not sham affects this rightward bias, we wanted to check how consistent this measure of bias was within participants. To this end, a Pearson's product-moment correlation coefficient was calculated for the bias measures obtained in each session. There was a significant positive correlation between the rightward bias during stimulation versus sham (r=.73, p<.001; see Figure 13C), suggesting that this is a reliable, within-participant trait measure.

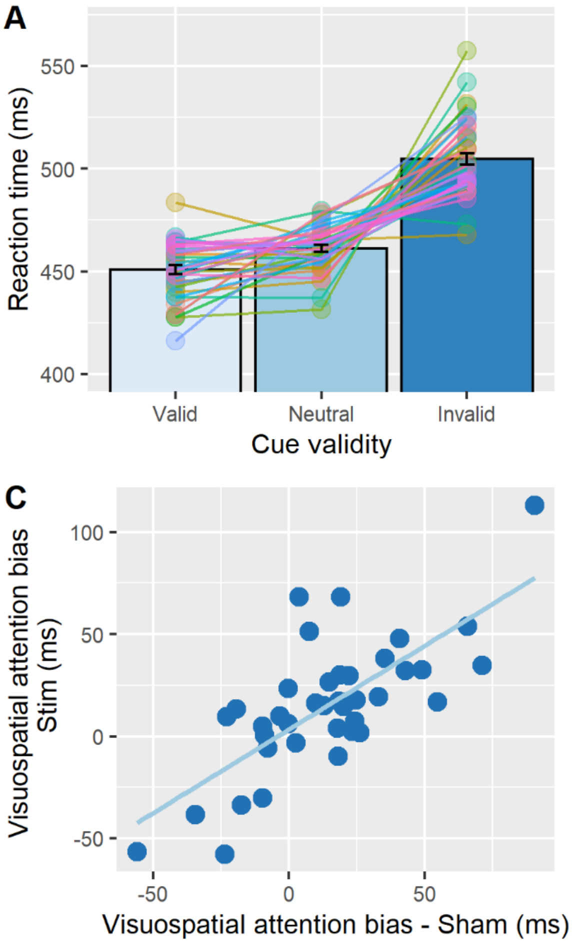


Figure 13: Experimental checks. (**A) Cueing effect:** RTs were averaged across target location for each type of cue (sham session only). Significantly faster RTs were found for valid trials, as compared to neutral and invalid trials. RTs in neutral trials were significantly faster than invalid trials. Error bars represent 95% confidence interval corrected for a within-subjects design (Cousineau, 2005). The bar plots have been superimposed with individual data points. (**B) Hemifield bias:** RTs were averaged across cue validity conditions for each target location (sham session only). Significantly faster RTs were found for trials in which the stimuli were presented in the right hemifield, as compared to the left. Error bars represent 95% confidence interval corrected for a within-subjects design (Cousineau, 2005). Similarly, the bar plots have been superimposed with individual data points. (**C) Correlation of measure of hemifield bias between the two experimental sessions**. Since the intercept is close to 0 (i.e. 3.3 ms) and the slope is close to 1 (i.e. 0.8), the model already indicates that the spatial bias in the two experimental sessions ($RT_{\text{Left hemifield}} - RT_{\text{Right hemifield}}$) is very similar and therefore a significant effect of stimulation is unlikely.

The main analysis then examined whether left parietal tACS induced a bias away from the right to the left hemifield when applied at 10Hz compared to sham, possibly as a function of cue condition (as reported by Schuhmann et al., 2019, see also Table 1). To this end, we ran a repeated-measures ANOVA with the factors tACS condition (i.e. 10 Hz tACS, sham) and cue validity (i.e. invalid, neutral, valid) on the spatial bias measure ($RT_{Left\ hemifield}$ – $RT_{Right\ hemifield}$) (see Figure 14A for the corresponding data). There was no significant main effect of tACS condition (F(1, 39)=.04, p=.83, η_G^2=.0001) and no significant interaction with cue validity (F(1, 78)=.52, p=.55, η_G^2=.001). These results show that left parietal tACS did not shift the bias to the left, as compared to sham, irrespective of cueing condition. However, we found a significant main effect of cue validity (F(1, 78)=5.78, p=.01, η_G^2=.02). Averaged across stimulation conditions, there was a greater rightward bias for neutrally cued trials (20±36.2ms) than valid (16.4±31.4ms) and invalid trials (7.8±40.2ms). Additionally, when computing the average spatial bias change per participant across session ($RT\ Bias_{10Hz\ tACS}$ – $RT\ Bias_{sham}$), we found that around 50% of all participants (n=21 out of 40) showed a greater leftward bias in the 10 Hz tACS condition, compared to sham (Figure 3B), which would be expected by chance. Given these null results obtained by employing the same analysis as Schuhmann et al. (2019), we ran several exploratory analyses reported below.

4.5.2. Exploratory analyses

Effect of stimulation on spatial bias (RT) across time

We first checked whether the effects of tACS on the spatial bias as measured by RT might have occurred only towards the end of the 20 min stimulation session. To this end, the data were split into blocks of ~5 min each (4 blocks of 84 trials), and average RTs were re-calculated for each participant and condition. Trials had to be collapsed across validity conditions because there was an insufficient number of invalid trials to allow calculation of the spatial bias measure per block. A repeated-measures ANOVA with the factors tACS condition (i.e. 10 Hz tACS, sham) and block (i.e. 1, 2, 3, 4) on the spatial bias measure ($RT_{Left\ hemifield}$ – $RT_{Right\ hemifield}$) (see Figure 14C) revealed no significant main effect of tACS condition (F(1, 39)=.6, p=.8, η_G^2=.0001), nor block (F(3,117)=1.31, p=.27, η_G^2=.005), and no significant interaction (F(3, 117)=1.94, p=.12, η_G^2=.005), which suggests that participants maintained a consistent level of spatial bias throughout the experiment for both stimulation conditions. Upon visual inspection, a difference between the two stimulation conditions seemed to appear in the last 5 minutes of stimulation. Yet, a t-test on the spatial bias during 10 Hz versus sham in block 4 was not significant (t(39) = -1.82, p =.07 r^2=.14). Please also note that the observed pattern would be against the predictions (more rightward bias with left parietal tACS compared to sham).

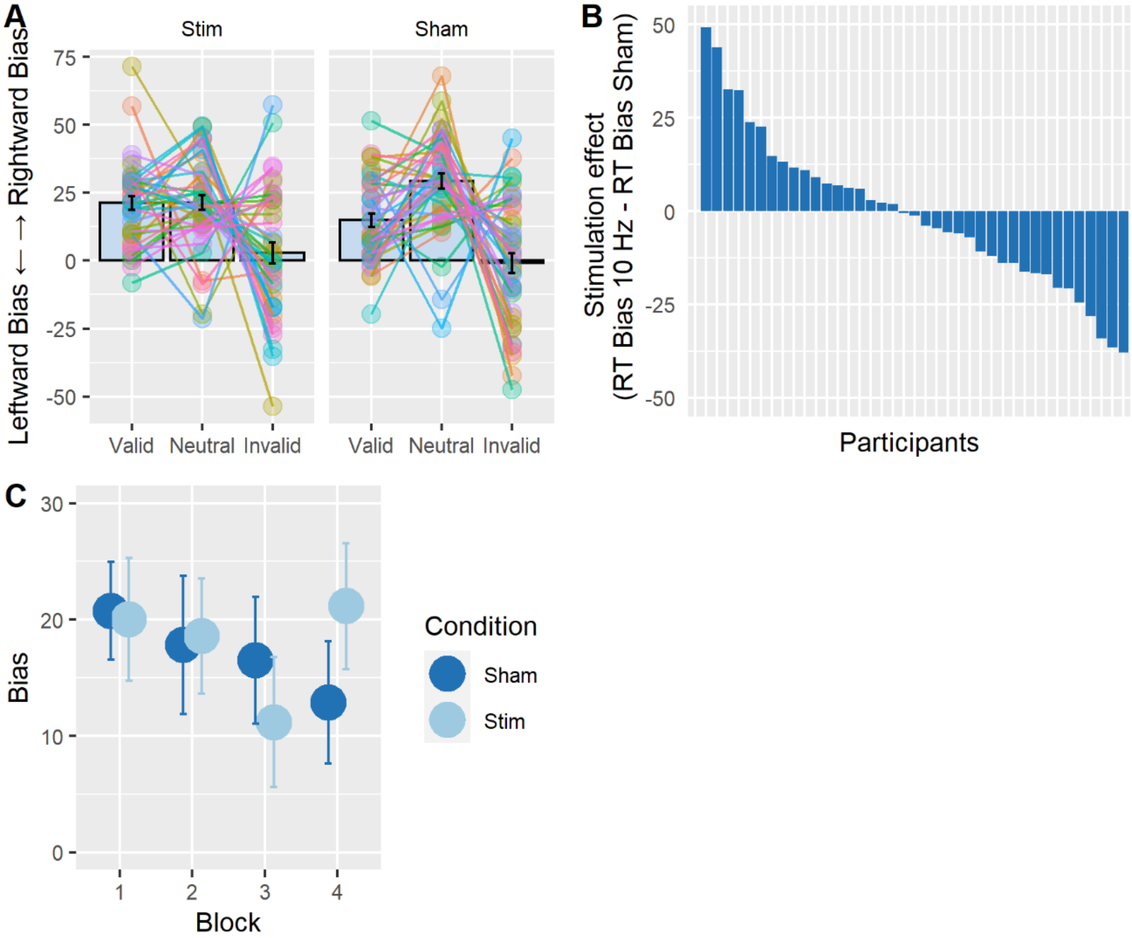


Figure 14: No tACS effects on hemifield bias. (A) Measure of spatial bias across simulation and validity conditions ($RT_{\text{Left hemifield}}$ -$RT_{\text{Right hemifield}}$). A positive value indicates a rightward bias (i.e. faster RTs in the right hemifield), whereas a negative value indicates a leftward bias (i.e. faster RTs in the left hemifield). The average values for each condition are superimposed with individual data points of

each participant. Error bars represent 95% confidence interval corrected for a within-subjects design (Cousineau, 2005). (**B**) Stimulation effect per participant on spatial bias ($\text{RTBias}_{10\text{Hz tACS}}$ -$\text{RTBias}_{\text{sham}}$). A negative value means that participants had a greater leftward (more negative) spatial bias with 10 Hz stimulation as compared to sham (expected direction). (**C**) Change in the measure of spatial bias across the 4 experimental blocks (~5 min). The plot displays the average spatial bias per block, and the lines represent the standard error, where a positive value of bias indicates a rightward bias. There was no significant difference between the stimulation conditions with time-on-task.

Dependency of tACS-effects (RT) on trait factors: Individual spatial bias and alpha-frequency/power

As previous studies using transcranial electrical stimulation have indicated, the effects may depend on the brain state and individual trait factors (Neuling et al., 2013; Krause & Cohen Kadosh, 2014). Therefore, we explored whether tACS outcome in the present study may have depended on four such factors.

First of all, we re-analysed the RT data as a function of the individual (trait) bias in visuospatial processing that we estimated from the sham data. To this end, we ran an ANCOVA mirroring the main rm-ANOVA analysis, with the factors tACS condition and cue validity on the dependent measure of hemifield bias, adding individual bias as a covariate. After controlling for the individual bias, the ANCOVA revealed a significant main effect of cue validity ($F(2,76) = 5.722$, $p = .005$) as before. However, the interaction between the covariate and tACS condition was not significant ($F(1,38)=2.127$, $p = .153$), nor was the triple interaction between the covariate, tACS condition and cue validity ($F(2,76) =.912$, $p = .406$), suggesting that the directionality of the individual bias as measured in the sham session did not impact the effect of tACS stimulation on the hemifield bias.

Next, we wanted to investigate whether tACS outcome depended on participants' brain oscillations as recorded in the sham session (based on the eye-closed data from the left electrode O1, see EEG below). To test this, we ran three ANCOVAs as above but with the covariates IAF, deviation of IAF from the 10Hz stimulation frequency (absolute difference), and alpha power. Interactions of tACS with underlying brain oscillations may be enhanced if tACS frequency (here 10Hz) matches IAF (e.g. Ali et al., 2013; Herrmann, Murray, et al., 2016). Additionally, previous studies have reported effects of alpha tACS to depend on alpha power at baseline (e.g. Neuling et al., 2013). There was a significant main effect of cue validity in all these analyses ($p<.05$), but no significant interactions were found in these analyses (interaction between the covariate and tACS condition: IAF $F(1,38) = .654$, $p = .423$, deviation of IAF from 10 Hz $F(1,38) = .023$, $p = .878$, alpha power $F(1,38) = .383$, $p = .539$; all triple interactions between the covariate, tACS condition and cue validity: IAF $F(2,76) = .8$, $p = .45$, deviation of IAF from 10 Hz $F(2, 76) = .159$, $p = .85$, alpha power $F(2,76) = .809$, $p = .448$). This indicates that the stimulation effect was not impacted by individual alpha frequency and/or alpha power.

We note though that the exploratory analyses of the impact of covariates was post-hoc, and the present design not optimal for inferring individual trait factors, as inferred during sham (counterbalanced with tACS), when these should have ideally been inferred before any experimental manipulation.

Effects of tACS on EEG

Resting EEG was recorded closely after tACS with both eyes open and eyes closed. Using the data recorded from O1, the test-retest reliability for identifying IAF was probed. A Pearson product-moment correlation coefficient was computed to assess the relationship between $IAF_{10Hz\ tACS}$ and IAF_{Sham}, revealing a weak positive correlation between the two variables in the eyes open condition ($r = .32$, $p = .03$) and a stronger correlation in the eyes closed condition ($r = .93$, $p < .001$, Figure 15A). Equivalent results were observed for alpha power, where a weak positive correlation was found between $\text{alpha-power}_{10Hz\ tACS}$ and $\text{alpha-power}_{Sham}$ during eyes open ($r = .47$, $p=.001$) and a stronger correlation during eyes closed ($r = .91$, $p < .001$, see Figure 15D). Due to the better test-retest reliability (SNR) of both IAF and power during eyes closed, we proceeded with the EEG analyses of the eyes-closed data only.

tACS-effects on alpha-frequency: To test whether tACS aligned IAF to the stimulation frequency, which would be in accordance with an entrainment effect of tACS (Antal & Paulus, 2013; Tavakoli & Yun, 2017; Thut, Schyns, et al., 2011), we ran a t-test on the difference IAF minus 10Hz (absolute difference) between 10Hz tACS and sham on data recorded from electrode O1, i.e. ipsilateral to the stimulation site. If entrainment occurred, the IAF of the participants should be closer to 10 Hz following active stimulation as compared to sham. No significant difference was found between the two conditions (t(39) = -1.93, p =.06, r^2=.15, Figure 15B). We also compared IAF peaks during the two tACS sessions (again using a t-test on the recordings from electrode O1) and found a significant difference between 10 Hz tACS and sham (t(39) = -3.83, p <.001, r^2=.28, Figure 15C). Similar results of small effect size were found for data recorded from electrode O2 (i.e. contralateral to the stimulation site) (t(39) = -2.29, p = .02, r^2=.17). Note that this significant tACS effect on IAF was very small in magnitude (an increase of 0.185Hz; from 9.98Hz for sham to 10.165Hz for alpha-tACS), and unexpected/unexplained, and is therefore not further discussed.

tACS-effects on alpha-power: Equivalent analyses were conducted on alpha power. T-test revealed no significant differences in power between sham and 10 Hz tACS, neither for electrode O1 (t(39) = -.06, p = .95, r^2=.004, Figure 15E) nor O2 (t(39) = -.73, p = .46, r^2=.05).

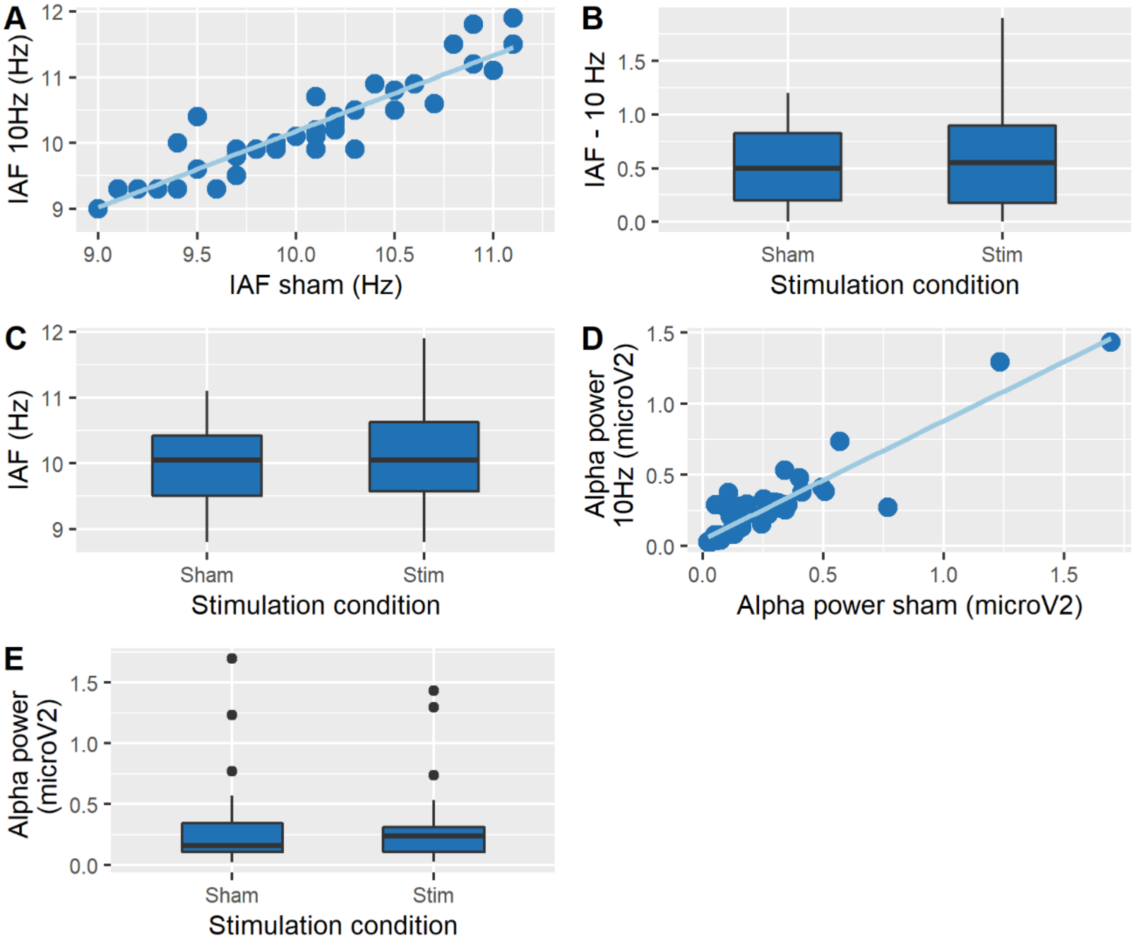


Figure 15: No tACS effects on EEG (eyes closed data). **(A)** Relationship between $IAF_{Stimulation}$ and IAF_{Sham} showing a good test-retest reliability. **(B)** Absolute difference between IAF and 10 Hz during sham and stimulation. There was no significant difference between the two stimulation conditions, indicating there is no evidence for entrainment in this sample (convergence of IAF to 10Hz tACS frequency = zero after tACS relative to sham). **(C)** IAF during sham and stimulation. IAF was slightly (by 0.185 Hz) but significantly increased after tACS relative to sham. **(D)** Relationship between alpha-$power_{Stimulation}$ and alpha-$power_{Sham}$. **(E)** Alpha power during sham versus stimulation, with no significant difference between the two conditions. All data shown are from electrode O1. The boxplots show a representation of the median and the first and third quartiles. The whiskers of the boxplot can take a maximal value up to 1.5*interquartile range, with all the values exceeding the whiskers being outliers.

Accuracy

The main analysis focused on RT, as this measure was shown to be affected by tACS in Schuhmann et al. (2019). Although the overall accuracy was 95% in my sample of participants (ranging from 73% to 100%) and hence close to ceiling (cf to 93% in

Schuhmann et al., 2019), we also checked for potential tACS effects on this measure. A repeated-measures ANOVA on the median accuracy in the sham condition (data averaged across hemifields) revealed a main effect of cue validity (F(2,78)=3.34, p=.04, η_G^2=.02). Participants were significantly more accurate in valid trials (95.9±4%) than in invalid trials (94.5±5.7%) (t(39)=2.33, p=.02, r^2=.18). There was no significant difference in accuracy between valid and neutral trials (95.1±4.7%) (t(39)=1.73, p=.09, r^2=.13), nor between neutral and invalid trials (t(39)=-1.06, p=.3, r^2=.08).

We also tested whether accuracy differed between the two hemifields during the sham condition but found no effect. The repeated measures ANOVA on median accuracy (data averaged across cue validity) was not significant (F(1,39) = .34, p = .56, η_G^2=.002), indicating that participants' accuracy was consistent regardless of stimulus location.

Next, we calculated a measure of hemifield bias based on accuracy ($\text{Accuracy}_{\text{Left hemifield}}$ – $\text{Accuracy}_{\text{Right hemifield}}$) per condition (Figure 16) and examined potential effects of tACS (10 Hz tACS, sham) on this bias measure as a function of cue validity (i.e. invalid, neutral, valid), using a repeated-measures ANOVA. In analogy to the analysis on RTs, this did not reveal any significant main effect of tACS condition (F(1,39) = 0.907, p = .346, η_G^2=0.003), nor an interaction with cue validity (F(2, 78) = .336, p = .70, η_G^2=.001), and also no main effect of type of cue (F(2,78) = 1.272, p =.28, η_G^2=.009).

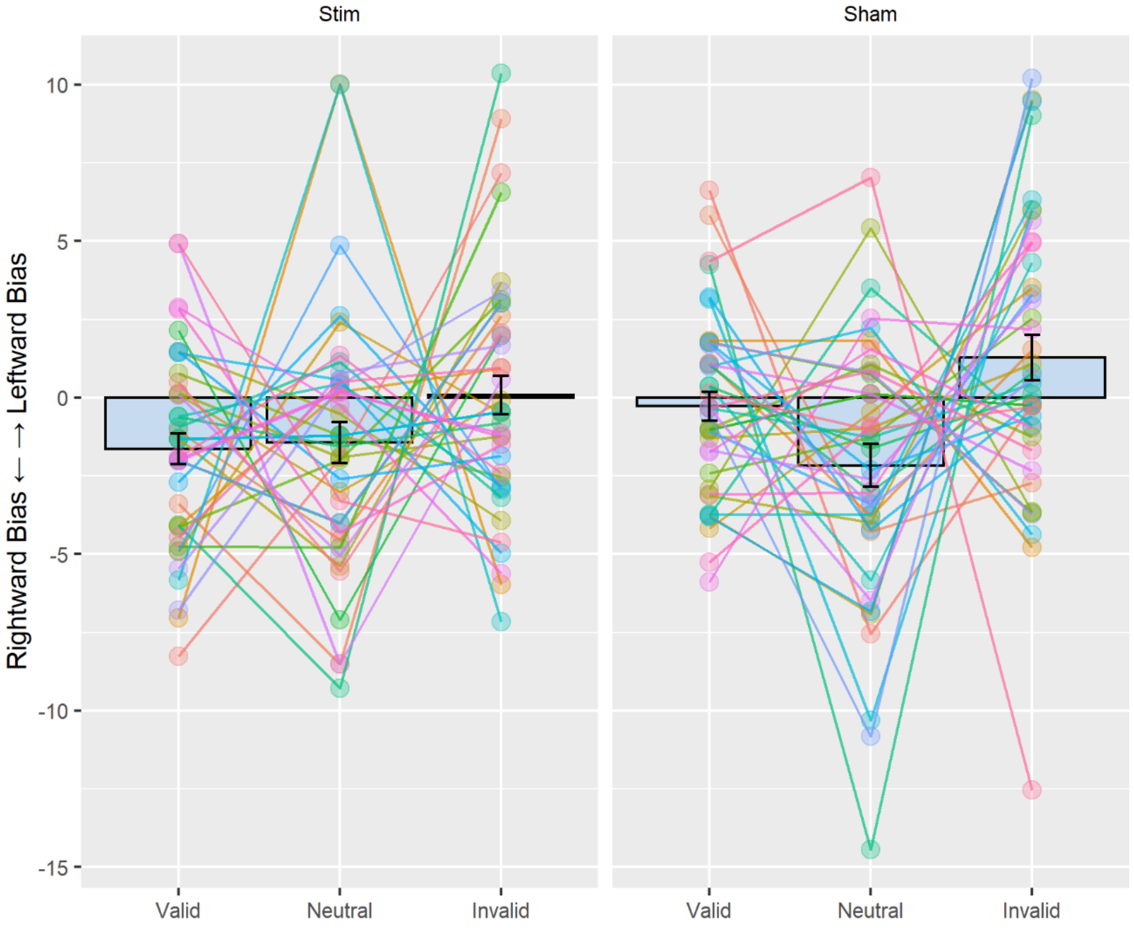


Figure 16: Accuracy. The average accuracy for each condition superimposed with individual data points of each participant. Error bars represent 95% confidence interval corrected for a within-subjects design (Cousineau, 2005). A positive value of the measure of bias in accuracy indicates a leftward bias (i.e. increased accuracy in the left hemifield), and a negative value indicates a rightward bias (i.e. increased accuracy in the right hemifield).

Effects of tACS on sensations and blinding

After each of the sessions, participants were asked to fill in a questionnaire regarding how well tACS was tolerated. A total of seven different sensations were rated on a scale from 1 (no sensations felt during the experiment) to 5 (strong sensations felt during the experiment). Table 2 shows the average ratings for each of these sensations. At the end of the second session, participants were asked to report in which session they thought they received real stimulation and in which sham. Of the

40 participants whose data was included in the analysis, 25 were able to correctly distinguish between 10 Hz tACS and sham sessions. A chi-square goodness of fit performed to compare the percentage of correct guesses (62.5% = 25/40) with the expected occurrence by chance (50%: 20/40) revealed no significant deviation from the expected value ($X^2(1) = 2.5$; p =0.12), thus confirming that the percentage of participants correctly identifying the sham condition was not different from chance.

We then tested whether there was an effect of 10 Hz tACS vs sham on the sensations reported by the participants. There were no significant differences between the two experimental conditions on the intensity of any of the seven sensations reported. The largest difference was found in the reports regarding burning (t(39) = -1.43, p = .16, uncorrected) and iron taste (t(39) = 1.43, p = .16, uncorrected).

Table 2: Average intensity of the sensations felt during the experiment as reported by participants on a scale from 1 (no sensations) to 5 (strong sensations)

Stimulation Condition	**Itchiness**	**Pain**	**Burning**	**Warmth/ Heat**	**Pinching**	**Iron taste**	**Fatigue**
10 Hz	1.43	1.28	1.3	1.48	1.45	1	1.43
Sham	1.3	1.23	1.15	1.4	1.33	1.05	1.53

4.6. Discussion

Several recent studies using alpha tACS have reported consistent effects on behavioural measures of spatial attention in both the visual and auditory modalities during tACS (Wöstmann et al., 2018; Deng et al., 2019; Schuhmann et al., 2019; Kasten et al., 2020; Kemmerer et al., 2020). Here, we tested this effect using the same endogenous attention task, stimulation site and high-density tACS setup as Schuhmann and colleagues (2019), as well as a tACS intensity and duration of similar magnitude to other groups reporting effects (Wöstmann et al., 2018; Deng et al., 2019; Kasten et al., 2020; Kemmerer et al., 2020). Based on this prior literature, we expected that 10 Hz tACS applied over the left posterior parietal cortex should induce a shift in bias away from the right and towards the left hemispace. In contrast with this prior literature, we failed to find a tACS effect using my parameter combinations, as there was no significant difference between 10 Hz tACS and sham.

Taking into account the evidence coming from EEG (Worden et al., 2000; Thut et al., 2006; Foxe & Snyder, 2011; Van Diepen et al., 2019) and the tACS literature (Wöstmann et al., 2018; Deng et al., 2019; Schuhmann et al., 2019; Kasten et al., 2020; Kemmerer et al., 2020) supporting a role of alpha oscillations in visuospatial attention, our results are unexpected. In our design, we got closest to the study of Schumann et al. (2019), implementing the exact same protocol, except for using higher intensity (1.5 mA instead of 1 mA) but shorter stimulation duration (20 min instead of 40 min). The present null results could therefore be attributed to the change in parameters that were implemented here as compared to Schuhmann and colleagues (2019). However, the efficacy of alpha tACS to shift spatial bias away from the contra- to the ipsilateral hemispace has been shown for a range of stimulation intensities (1-2 mA) and durations (8-40 minutes; see Table 1 for more details), suggesting that intensity and duration are poor predictors of outcomes of alpha-tACS on spatial perceptual bias. The current results are in line with other negative findings reported in the tACS literature. Hopfinger and colleagues (2017) showed that 10 Hz tACS had no effect on endogenous attention, although tACS was applied to the right not the left hemisphere. Similarly, Veniero and colleagues (2017) assessed the effect of right hemispheric alpha tACS on visuospatial attention, using a variant of the line bisection task. While their initial experiment yielded statistically significant effects of tACS, the results were not confirmed in a subsequent internal replication (Veniero et al., 2017). Even though we could not replicate the behavioural effect of tACS on task performance, we have conducted further exploratory analyses to determine whether the effect of tACS depended on the brain state and individual trait factors of the participants, namely the individual spatial bias, IAF, deviation from IAF, and alpha power, as recorded from the sham session. Although in the literature it is reported that the outcome of brain stimulation techniques is state/trait-dependent (see also Neuling et al., 2013; Krause & Cohen Kadosh, 2014; Feurra et al., 2013, 2019), we were unable to provide supportive evidence for such a dependency of alpha tACS effects for the dependent measure. However, the analyses were post-hoc and exploratory, so further evidence is needed to understand better the effects of these covariates on the effect of tACS as measured here.

An inconsistent picture also emerges when examining studies attempting to use transcranial direct current stimulation (tDCS) to shift attention bias. In an experimental paradigm similar to Schuhmann et al. (2019), Duecker et al. (2017) tested whether parietal tDCS could be used to induce an interhemispheric imbalance that would shift attention away from the right towards the left hemifield. They attempted to decrease cortical excitability through cathodal tDCS over the left hemisphere while increasing cortical excitability with anodal tDCS over the right. No effect of bihemispheric tDCS was found on the attentional bias, although it was reported that stimulation led to an impairment of attentional benefits (i.e. faster reaction times for trials when the cue was valid as opposed to neutral) in the right hemifield for endogenous orienting (Duecker et al., 2017). Similarly, Li and colleagues (2015) used oppositional parietal tDCS in a modified Posner task but found no effect of stimulation on spatial attention. However, shifts in visual attention following tDCS stimulation have been reported in perceptual line bisection paradigms (Giglia et al., 2011; Benwell et al., 2015; but see Veniero et al., 2017), as well as for visual localisation (Wright & Krekelberg, 2014), where a left-anodal right-cathodal montage has induced a rightward bias.

Here, we demonstrate the variable effects of tACS when targeting alpha oscillations for the purpose of modulating visuospatial attention in healthy participants. However, tACS has been successfully used for modulating alpha and beta oscillations in relation to other visual processes, such as temporal (Cecere et al., 2015; Minami & Amano, 2017; Battaglini, Mena, et al., 2020; Ronconi et al., 2020; Ghiani et al., 2021) and spatial binding (Battaglini, Ghiani, et al., 2020). The current study and negative results should hence not be taken to generalize to other relationships between brain oscillations and perceptual processes and their tests through non-invasive brain stimulation techniques. Also, this study in healthy participants may not be generalizable to patients. Alpha-tACS could be clinically relevant (Yavari et al., 2018; Elyamany et al., 2021; Learmonth et al., 2020), for example, in patients who have suffered right hemispheric damage following stroke and show attentional impairments (known as neglect; Corbetta & Shulman, 2011). One limitation of the present design in regards to a clinical implementation is the single session protocol. Recent experiments employing multi-session designs (Ahn et al., 2019; Alexander et al., 2019; Mellin et al., 2018) and/or stimulating at the individualized alpha frequency (Riddle, 2021) have demonstrated the potential of tACS as a therapeutic intervention for psychiatric disorders. The lack of these manipulations in my study and previous studies on spatial attention may explain some of the observed variability.

A survey on research practices targeting neuroscientists employing transcranial electrical stimulation techniques reported that only 45-50% of respondents were able to routinely replicate published effects (Héroux et al., 2017), although concerns regarding reproducibility have been extended to the whole scientific community (Collaboration, 2015; Baker, 2016; Bikson et al., 2018). In recent years, the tACS literature has seen a surge in studies reporting null effects (Brignani et al., 2013; Bland et al., 2018; Brauer et al., 2018; Clayton, Yeung, & Cohen Kadosh, 2018; Wittenberg et al., 2019; Jones et al., 2019) and failed replications (Veniero et al., 2017; Bland et al., 2018; Fekete et al., 2018; van Schouwenburg et al., 2018; Asamoah et al., 2019a). This calls for a more systematic investigation of the factors that are driving these inconsistencies. In this study, although coming close to

Schuhmann and colleagues (2019), we did unfortunately not fully mirror their design; hence inferences regarding the (in)effectivity of a particular parameter combination for shifting spatial attention are elusive. More direct replication studies of effects reported in the literature to better characterize the factors that determine the efficacy of tACS are needed.

Chapter 5

General Discussion

The purposes of this thesis were twofold: firstly, to identify the oscillatory correlates of the perceptual experience of participants and establish whether there is a double dissociation between subjective and objective measures of performance. Secondly, I wanted to contribute to the ongoing debate about the effectiveness of neuromodulating brain oscillations and the replicability of published results. To this end, a series of three experiments were carried out, involving electroencephalography and non-invasive brain stimulation methodology.

In the first experiment (presented in **Chapter 2**), using a multiple alternative forced-choice task in which the correct guess rate was negligible, I have found a negative correlation between pre-stimulus alpha power and perceptual awareness ratings. In line with previous studies, there was no link between pre-stimulus power and discrimination accuracy. This suggests that pre-stimulus alpha power is a neural predictor of visual awareness, which is indeed dissociated from perceptual sensitivity.

In the second experiment (presented in **Chapter 3**), a repetitive TMS protocol was implemented to demonstrate that the link between pre-stimulus alpha power and perceptual awareness can be causally manipulated. Experiment 2 failed to produce the expected results based on the literature. I have found that TMS stimulation had an unspecific effect on both visual awareness and accuracy. I argue that the successful neuromodulation of oscillatory activity and perceptual awareness is likely to be highly susceptible to complex experimental parameters, which would explain the null findings. However, I have found that individual differences in alpha frequency are related to accuracy, as evidenced through regression analysis. Taking into account the results of both experiments 1 and 2, it is possible that oscillatory power and frequency are distinct mechanisms related to subjective versus objective performance measures.

Finally, in the third experiment (presented in **Chapter 4**), I tried to replicate the finding that applying alpha tACS over the left parietal cortex induces a shift in visuospatial attention. This experiment failed to replicate the results of studies using similar conditions, which indicates that the effects of parietal alpha tACS on spatial bias are not very robust. Instead, they indicate that interindividual variability and small changes in the experimental parameters can lead to inconsistencies in results, which questions the potential of tACS to induce entrainment at an effect size that is of interest, for example, for clinical applications.

In this chapter, I will reflect on the theoretical implications of this set of studies and discuss the broader issues that contribute to the outcome of neuromodulation in these experiments and research more generally. I will also identify key questions that this thesis has brought up and how these questions can be explored effectively in future research avenues.

5.1. On the role of alpha oscillations in visual processing

5.1.1. Correlational evidence

One of the main goals of this thesis was to advance our current understanding of the contribution of oscillatory activity in how the visual sensory information is being processed. A long line of research demonstrates that alpha power prior to stimulus presentation predicts the perceptual outcome. Low pre-stimulus alpha power has been associated with increased accuracy in typical detection and discrimination paradigms (Ergenoglu et al., 2004; Hanslmayr et al., 2007; van Dijk et al., 2008; Busch et al., 2009) and with an increased likelihood of perceiving phosphenes following transcranial magnetic stimulation (Romei, Brodbeck, et al., 2008; Samaha, Gosseries, et al., 2017). In addition, it has been shown that pre-stimulus alpha phase also influences the fate of upcoming stimuli (Busch et al., 2009; Mathewson et al., 2009; Busch & VanRullen, 2010).

More recently, the functional role of pre-stimulus alpha activity has been explored in more depth by implementing psychophysical modelling techniques (Limbach & Corballis, 2016; Iemi et al., 2017). These studies have challenged the view that alpha activity modulates the perceptual precision of the observer to the upcoming stimuli (Chaumon & Busch, 2014; Samaha, Iemi, et al., 2020). Instead, it was suggested that pre-stimulus alpha power relates to perceptual decision making, i.e. states of high cortical excitability lead to a more liberal criterion making participants more likely to report seeing a stimulus regardless of whether or not it was presented, amplifying the representation of both signal and noise (Limbach & Corballis, 2016; Iemi et al., 2017). One established view is that cortical excitability is regulated via inhibitory mechanisms (Klimesch et al., 2007; Jensen & Mazaheri, 2010; Foxe & Snyder, 2011). At a physiological level, evidence coming from animal studies suggests that inhibition is modulated by the neuronal firing rate, such that lower alpha amplitude increase firing rate (Haegens, Nácher, et al., 2011).

One question follows from the result of Iemi and colleagues (2017): is the liberal decision criterion due to observers changing their decision-making strategies (i.e. decision bias), or is it due to an actual change in the observers' subjective experience (i.e. perceptual bias)? Iemi and Busch (2018) have provided evidence in support of the latter. Corroborating this point, a growing body of research has added a secondary metric, measuring subjective performance in addition to accuracy. EEG studies have found that pre-stimulus alpha power is negatively correlated with confidence (Samaha, Iemi, et al., 2017) and visibility ratings (Benwell et al., 2017; Samaha, LaRocque, et al., 2020). In contrast, the role the pre-stimulus alpha phase plays in subjective performance is still unclear.

In line with this work, **Chapters 2 and 3** bring additional evidence supporting the dissociation between objective and subjective measures of task performance. In experiment 1, I found that low pre-stimulus alpha power was correlated with high visual awareness ratings but not with accuracy. This supports the view that spontaneous alpha power is not related to an improvement in the perception of stimuli but instead influences the subjective experience of visual input (i.e. perceptual bias; in agreement with Iemi & Busch, 2018). Furthermore, in keeping with Benwell and colleagues' (2017) results, I have found no link between pre-stimulus alpha phase and perceptual awareness ratings or accuracy. Not only did I replicate previous findings in experiment 1, but this study demonstrates that the link between pre-stimulus alpha power and subjective performance can also be established in tasks of higher complexity beyond the two-choice alternatives. In experiment 2, I found a relationship between individual alpha frequency and accuracy but not perceptual awareness. Based on these results, I believe studies on the functional role of alpha oscillations could benefit from routinely incorporating subjective measures of performance.

In my study, I have looked at a linear relationship between spontaneous alpha power and measures of task performance. However, quadratic relationships between pre-stimulus alpha power and sensory perception have been reported. In the somatosensory domain, intermediate levels of alpha have been associated with higher detection rates for peri-threshold stimuli (Linkenkaer-Hansen et al., 2004; Zhang & Ding, 2010; Ai & Ro, 2013; Weisz et al., 2014; Wälti et al., 2019) and veridical perception during simultaneity judgment tasks (Lange et al., 2012). To explain the quadratic relationship, it has been suggested that spontaneous oscillatory activity acts as an intrinsic noise source (Linkenkaer-Hansen, 2004), or that only an intermediate level of pre-stimulus alpha can bring the neural populations to firing threshold, thereby inducing an optimal sensory-evoked response (Zhang & Ding, 2010). Based on this evidence, the existence of an inverted U-shaped relationship between pre-stimulus alpha and perception cannot be ruled out in the visual domain, and future studies should address this possibility.

Another potentially interesting line of future research would be to determine whether the change in the subjective experience takes place at an early sensory or a late perceptual stage, as this has not been clearly determined to date. More work is also required in identifying the mechanistic role of alpha oscillations. While the dominant account is that alpha oscillations regulate neural excitability, which consequently inhibits the irrelevant sensory information and facilitates the processing of stimuli that are relevant for behaviour (Klimesch et al., 2007; Jensen & Mazaheri, 2010; Foxe & Snyder, 2011), new studies have shown that activity in the alpha band has a role beyond early sensory processing (Gundlach et al., 2020). Therefore, future studies should elucidate the mechanism by which alpha oscillations interact with the subjective experience.

Finally, the results of **Chapter 2** led to one more question: can the role of pre-stimulus alpha power in perceptual decision making be studied using a causal approach?

5.1.2. Causal evidence

To establish causality, studies could probe the negative correlation between pre-stimulus alpha oscillations and subjective measures of performance using non-invasive brain stimulation techniques. This is what I attempted to do in **Chapter 3**, using repetitive TMS. Five pulses of 10 Hz rTMS were applied to the right intraparietal sulcus before the stimulus presentation, after which participants' accuracy and visual awareness were probed. Based on previous research and the findings of **Chapter 2**, I expected that 10 Hz rTMS - but not arrhythmic or sham TMS – would entrain the underlying alpha oscillations. As a result, an enhancement in alpha power should occur, consequently decreasing the visual awareness ratings in the hemifield contralateral to stimulation, leaving accuracy on task unaffected. In addition, based on the results of **Chapter 2,** where no relationship was found between pre-stimulus alpha phase and measures of task performance, I did not test for phase effects in this experiment. In disaccord with the expectations, I was unable to find specific TMS effects on visual awareness ratings.

At present, there are no published studies in which non-invasive brain stimulation techniques have been used to entrain pre-stimulus alpha with the purpose of modulating subjective performance. Thus, one can only speculate regarding the potential reasons why this experimental manipulation was not successful. First, one explanation for the null results may be related to the stimulation frequency. In the experiment presented in **Chapter 3**, I chose a fixed frequency of the rTMS train (of 10 Hz) rather than stimulating at the individual alpha frequency. From a theoretical standpoint, entrainment is more likely to occur the closer the frequency of the external oscillator is to the intrinsic frequency of each participant (Pikovsky et al., 2003). Accordingly, a better alignment of rTMS frequency with the underlying alpha oscillations of participants should be related to stronger enhancement in pre-stimulus alpha amplitude, which should have elicited stronger effects of active alpha rTMS stimulation relative to arrhythmic or sham stimulation.

Furthermore, another explanation for the null results in experiment 2 may be the stimulation site, which was the right intraparietal sulcus (rIPS). In **Chapter 2**, EEG results have indicated that the topography of the pre-stimulus activation in relation to visual awareness ratings is widespread in the occipito-parietal regions (see also Benwell et al., 2017). While the rIPS has been successfully targeted using rTMS before in studies of attention (e.g. Capotosto et al., 2012; Romei et al., 2012; Ahrens et al., 2019), only one other study has attempted to use TMS to interfere with measures of subjective performance. In this unpublished experiment, Di Gregorio and colleagues (under review; results taken from communication with authors) have modulated perceptual confidence by administering rTMS to the right occipital cortex. Therefore, it is possible that the choice of the parietal stimulation site was not optimal, and an occipital site would have conveyed better results.

In their study, Di Gregorio and colleagues (in review) applied rTMS before stimulus presentation. Participants were asked to perform a primary task measuring accuracy and then rate their confidence. Using this experimental setup, the researchers have observed no effect of IAF rTMS stimulation on confidence ratings. In a follow-up experiment, the timing of rTMS was changed to correspond with the onset of the confidence prompt, which elicited differences in confidence levels. Hence, another third possible explanation of the null results in **Chapter 3** is that the entrainment effect wore off by the time participants were prompted to respond to the perceptual awareness question. In hindsight, the attempt to explore a causal relationship between pre-stimulus alpha power and visual awareness ratings using a similar experimental structure as in **Chapter 2** may therefore have been suboptimal. Considering the abovementioned points, I believe my chosen experimental design could be improved. A critical design issue for future studies is to reverse the order of the questions such that participants need to complete the PAS scale first or to administer the rTMS pulses before the visual awareness prompt.

Although I could not demonstrate a causal link between pre-stimulus alpha activity and subjective performance using TMS, I have identified that resting-state individual alpha peak frequency correlates with accuracy on task but not with awareness ratings. In the present experiment, it was observed that inter-individual variability in IAF had an effect on task performance. However, an increasing number of studies have shown that fluctuations in IAF can occur moment-to-moment. Accelerations in IAF have been reported with increasing task demands in an N-back working memory paradigm (Haegens, Cousijn, et al., 2014;), as well as in a modified Sternberg task (Maurer et al., 2015). Furthermore, Jann and colleagues (2010) have found that subjects with higher IAF had an increased regional cerebral blood flow in areas associated with attention modulation and preparedness for external input. Identifying subtle changes in oscillatory frequency can have implications for determining the physiological mechanisms involved. For example, using computational models in real and artificial neural networks, Cohen (2014) has found that changes in IAF encode information about input intensity and play a role in spike timing variability, such that higher IAF will cause neurons to fire at higher input levels, thus enabling accurate responses. Furthermore, Mierau and colleagues (2017) have recently hypothesized that IAF fluctuations form an adaptive mechanism that mirrors the activation level of underlying neuronal populations, fast frequencies facilitating sensory sampling, neuronal computation, and communication between brain regions.

The result of **Chapter 3** that inter-individual variability in alpha peak frequency correlates with accuracy on task could further indicate, as suggested by Di Gregorio and colleagues (in review), that a double dissociation between subjective and objective measures of performance exists at both a behavioural and neural level. However, following from the studies reviewed above, future experiments should investigate how intra-individual pre-stimulus alpha frequency relate to task accuracy on a trial-to-trial basis and whether the changes in frequency are affected by increasing task demands in a visual discrimination task.

5.2. Improving the outcomes of tACS

In **Chapter 4**, I tried to replicate Schuhmann and colleagues (2019) finding that tACS stimulation can be successfully used to induce a shift in visuospatial attention. Since the research group have replicated their results internally (see Kemmerer et al., 2020), the null results I obtained were surprising.

5.2.1. Parameter choice

While generally, the parameter choice for tACS stimulation seems limitless, I have maintained the experimental setup as close as possible to the setup of Schuhmann and colleagues (2019). However, the small changes in parameters that were made may have abolished the effect. Although most parameters have been kept identical, two changes were made, one to the stimulation intensity (using 1.5 mA instead of 1 mA) and the other to duration (using 20 instead of 40 minutes). Since in the internal replication by Kemmerer and colleagues (2020), an intensity of 1.5 mA has been used with significant effects, it is possible that stimulation duration was too short in the present study. However, in the study of Kemmerer and colleagues (2020), stimulation frequency was IAF rather than 10 Hz, therefore adding more variability to the parameter space. In the context of my study, one straightforward way for future research to determine whether stimulation duration indeed affects the behavioural outcome would be to test the effects of 10 Hz tACS stimulation when the intensity is set at 1.5 mA, but the duration is extended to 40 minutes. It is worth noting that several previous studies reporting the effects of alpha tACS on spatial bias (see Table 1) used stimulation duration around or below 20 min (e.g. Wöstmann et al., 2018; Deng et al., 2019; Kasten et al., 2020).

5.2.2. Interindividual variability

Alternatively, the heterogeneity of tACS results may be influenced by factors beyond study design or methodological aspects, one of which is interindividual variability (Polanía et al., 2018; Krause & Cohen Kadosh, 2014). Differences in individual anatomy contribute to an attenuation of the standard stimulation intensities used in tES (Vöröslakos et al., 2018; Huang et al., 2017; Lafon et al., 2017), computational modelling studies reporting an inverse relationship between electric field strength within the brain and head volume, skull, skin, and cerebrospinal fluid volumes (Antonenko et al., 2021). Consequently, the variability of the resulting electric fields can be linked to inconsistencies in the outcomes of tACS stimulation (Kasten et al., 2019). Since I did not account for subject-specific anatomical differences, it is plausible that the stimulation targeting was not optimal for all participants. Therefore, considering individualised, a-priori estimations of the induced electrical field strength and distribution could help improve the effects of tACS stimulation (Kasten et al., 2019; Liu et al., 2018; Polanía et al., 2018).

Furthermore, the efficacy of tACS might also depend on brain states (Feurra et al., 2019, 2013; Neuling et al., 2013). While in **Chapter 4,** I tested for the dependency of stimulation effects on alpha frequency and power as recorded at rest, as well as of peripheral sensations, these were exploratory analyses, and a more systematic study of these factors might warrant different results.

5.3. The importance of null results and replicability

In this thesis, my two experiments using non-invasive brain stimulation techniques have yielded null results. In the context of prior research, this was somewhat unexpected. Encouragingly, the dissemination of null results has become more widespread in NIBS literature (e.g. special issue on “Positive lessons from negative findings”: Thut et al., 2018), and the value they add to the scientific community has been recognised (de Graaf & Sack, 2018).

Additionally, two of the three experimental chapters (**Chapter 2** and **4**) are conceptual replications, where I have tried to extend previous findings by making small changes to the experimental design, with mixed results. In **Chapter 2**, I have successfully replicated the findings that pre-stimulus alpha power is negatively correlated with measures of perceptual awareness. In **Chapter 4**, I was unable to replicate the result that tACS stimulation can be successfully used to induce a shift in visuospatial attention.

Replicability is one of the foundation stones of science. However, in the past decade, many scientific disciplines, including psychology and neuroscience, have found themselves in the middle of a "replication crisis". This issue became impossible to ignore when the Open Science Collaboration (2015) conducted a replication of 100 psychological studies, with only 35% of all replications being statistically significant and having a smaller magnitude of effect sizes than those originally reported. It follows from the widespread difficulty to replicate research findings that some of these results are false (Ioannidis, 2005), with estimations that the false report rate in the field of cognitive neuroscience most likely exceeds 50% (Szucs & Ioannidis, 2017). Similar numbers were reported in psychology, with the rate of positive results in registered reports – where the research question and methodology is peer-reviewed prior to data collection – being only 44%, as compared to 96% in the standard literature (Scheel et al., 2021).

Listed among the reasons that drove this current crisis are pressures to publish innovative and positive results (Nosek et al., 2012) that may lead in the worst case to dishonest research practices (John et al., 2012; Agnoli et al., 2017; Héroux et al., 2017; Janke et al., 2019; Paruzel-Czachura et al., 2021), inadequate completeness of scientific reporting (Héroux, 2018; Hensel, 2020), small sample and effect sizes (Szucs & Ioannidis, 2017; Algermissen & Mehler, 2018; Schäfer & Schwarz, 2019) and experimenter's vast flexibility in choosing analytical strategies (Hong et al., 2019; Hoffmann et al., 2021), also known as the "researcher degrees of freedom" (Simmons et al., 2011). For example, Botvinik-Nezer et al. (2020) asked 70 independent research teams to test 9 pre-established hypotheses based on a given fMRI dataset and found that each group chose a unique analysis pipeline to analyse the data, yielding different interpretations of the results (see also Silberzahn et al., 2018 for a similar study). In the field of cognitive neuroscience, researchers have the added difficulty of recruitment of participants often following strict eligibility criteria (Rossi et al., 2009), intraindividual variability in participants' behaviour during the experiment, as well as – specifically for non-invasive brain stimulation techniques - inter-individual variability of stimulation effects (López-Alonso et al., 2014).

Unfortunately, this list is not exhaustive. The abovementioned issues can have serious implications. A recent study has reported that 44% of researchers surveyed reported having lost confidence in at least one of their findings, with questionable research practices and not replicating findings being named as contributing reasons for their doubts (Rohrer et al., 2021). It seems that often this loss of confidence is kept private by the researchers, and attempts to self-correct are not yet common practice. Moreover, the limitations of the academic community can affect the credibility of science in the broader public (Pickett & Roche, 2018). However, for psychology, informing people about the replicability crisis does not change their trust in future research (Anvari & Lakens, 2018).

On a more optimistic note, the replication crisis has led to a visible shift in the cultural norms of the scientific community. Journals have started accepting articles and publishing special issues that have been dedicated to replicability and null results (e.g. Thut et al., 2018). Furthermore, researchers have been encouraged to make their work more transparent and reproducible via preregistration (Nosek et al., 2018), registered reports (Nosek & Lakens, 2014), and data and code sharing. It has been shown that in psychology, there is a very high rate of willingness to preregister studies (Lakens, 2017). Preregistration distinguishes clearly between confirmatory and exploratory analyses and requires that the analysis plan is established and documented in a verifiable registry prior to the start of the research (van’t Veer & Giner-Sorolla, 2016). As mentioned above, false positive findings are often published in our research field (Szucs & Ioannidis, 2017). This is often driven by selective reporting, or "p-hacking”: throughout the experiment, researchers may explore several alternatives regarding data collection, pre-processing, or statistical analysis, but only report the decisions that lead to a significant result – thereby causing biased published results and flawed conclusions (Head et al., 2015). By fully reporting the analysis steps, preregistration allows for more consideration of the experimental parameters and decisions made, and will help to correct effectively for multiple comparisons, and avoid false positive results (Nosek et al., 2018). A few concerns with pre-registration have been voiced by the research community. The main issue raised is that pre-registration limits exploratory data analysis and prevents scientific discovery. This is a common misconception, as pre-registration merely differentiates between planned and post-hoc analyses, and deviation is possible as long as it is reported. Other disadvantages include pre-registration being perceived as effortful and slowing down the research process, or that it negatively impact the scientific culture by perpetuating distrust (Simmons, Nelson & Simonsohn, 2021). A lot of these arguments represent technical and cultural barriers, but they do not invalidate the added value of pre-registration: it increases the credibility of published results and interpretability of statistical tests by reducing the rate of false positive results, and it promotes transparency.

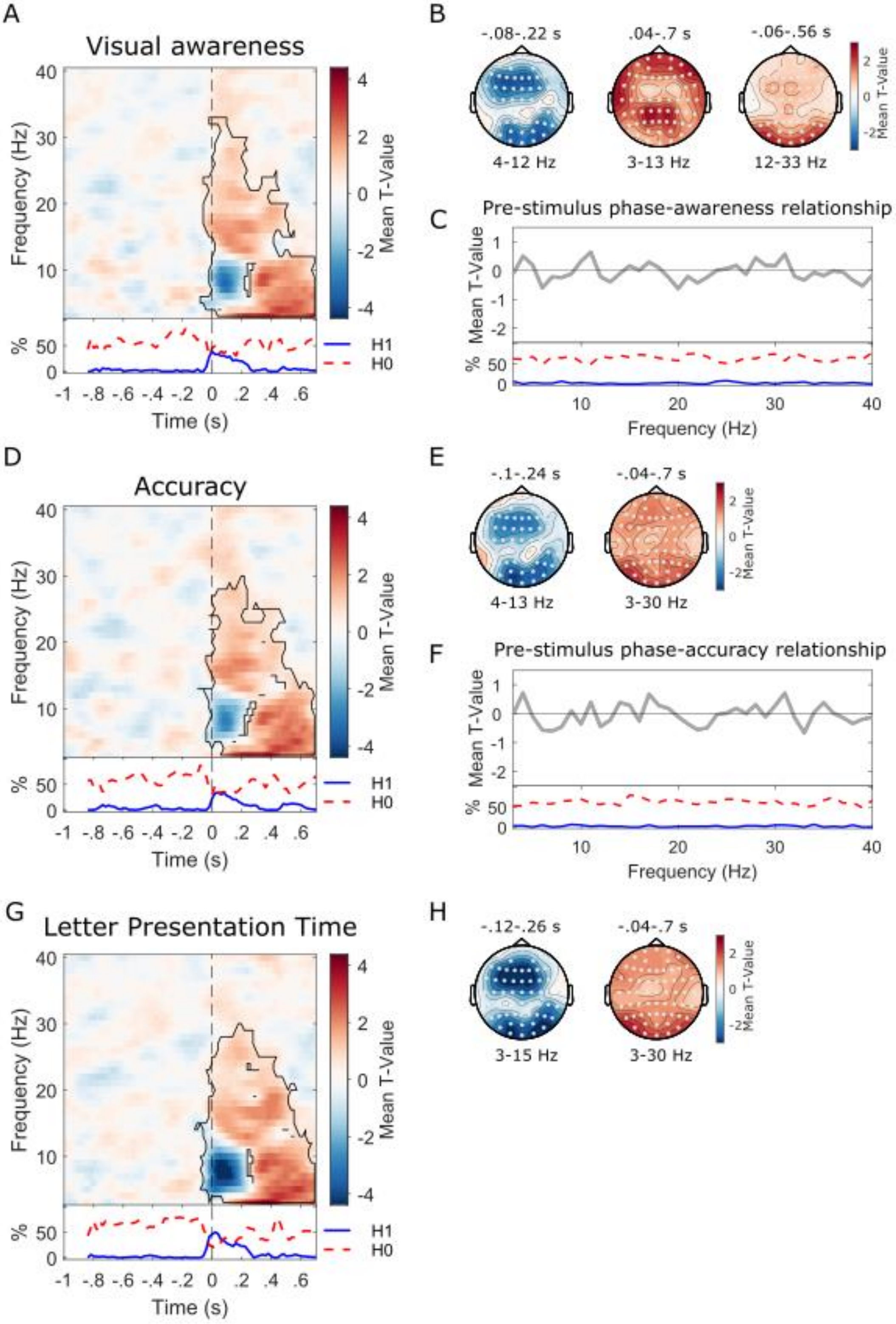
In addition, to avoid conducting underpowered studies, a series of "many labs" replication initiatives have emerged, where international research groups are crowdsourced with the goal of either attempting direct replications of seminal findings or testing novel research questions using a standardised protocol. This has been done so far in social psychology (Klein et al., 2014; Ebersole et al., 2016) and TMS (Corp et al., 2020, 2021) and is currently planned for EEG (Pavlov et al., 2021) and tACS (The TACS Challenge, 2020).

While bringing invaluable benefits for the scientific community, most of these initiatives require resources and a long-term commitment that might be limiting to early career researchers. In this thesis, I have attempted to contribute to previous findings in the literature while adhering to better research practices such as replication, dissemination of null results, collaboration with other research groups and data sharing.

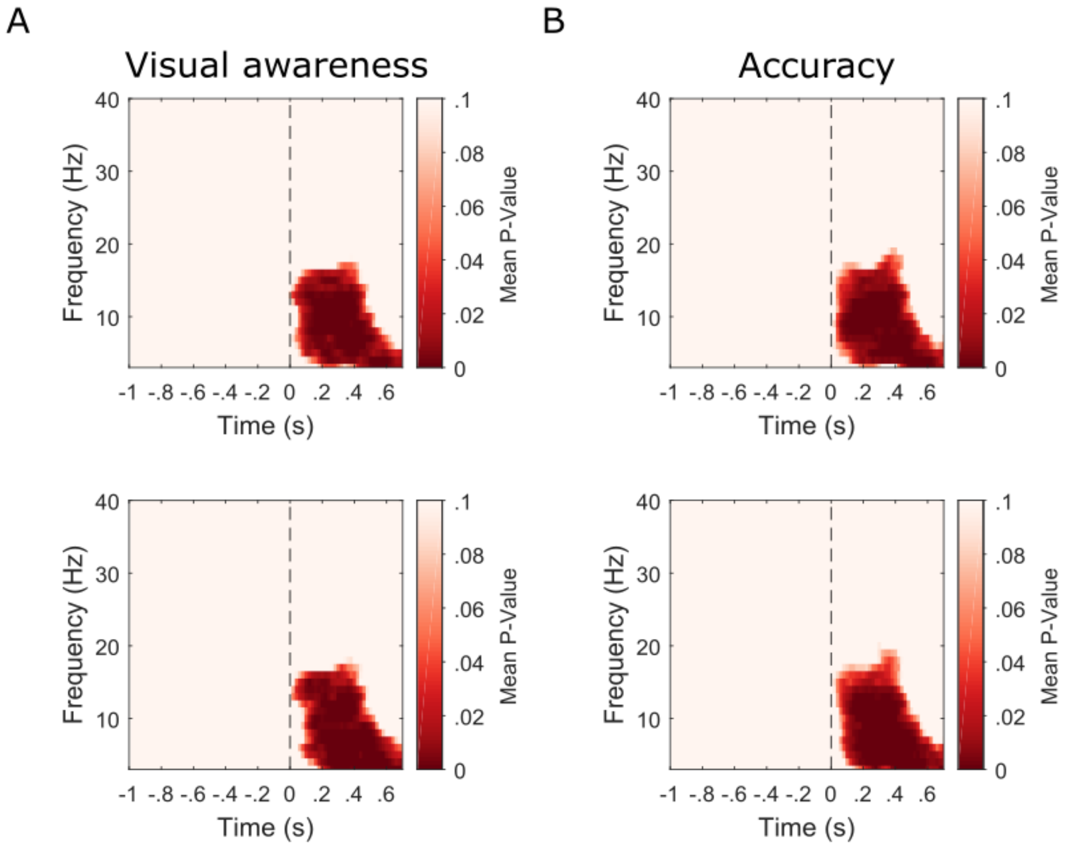
5.4. Conclusion

The collection of experiments presented in this thesis aimed to explore the functional role of alpha oscillations in visual perception. Replicating previous results from the literature, the EEG work in **Chapter 2** demonstrates that pre-stimulus alpha oscillations predict subjective perception and support the notion of a double dissociation between subjective and objective measures of task performance. In contrast, conclusions regarding the causal involvement of alpha oscillations in perception cannot be confidently drawn based on the corresponding NIBS experiments (**Chapter 3** and **4**), as the evidence for the neuromodulation of brain oscillations using TMS and tACS has been limited in my thesis. However, careful experimentation and planning, together with following open research practices, can provide promising avenues for a more in-depth understanding and improvement of the application of non-invasive brain stimulation techniques in research studies.

Supplemental material



Supplementary Figure 1: (A-C) plots t-values for the wITPCz analysis denoting the strength of the EEG phase - PAS rating relationship across frequencies of 3-40 Hz. In contrast to the phase analyses presented in Figure 5 in the main text, here letter presentation time was *not* controlled for. Relative to the analysis controlling for presentation times, we found one additional significant negative cluster (spanning -.08-.22 s relative to stimulus onset, 4-12 Hz: cluster statistic = -6264.6, p = .005; see S1A&B, left map). We also found two significant positive clusters: a low frequency (3-13 Hz) cluster spanning .04-.7 s post-stimulus onset (cluster statistic = 16388, p < .001) and a higher frequency (12-33 Hz) cluster spanning -.06-.56 s relative to stimulus onset (cluster statistic = 11154, p < .001, see S1A&B, middle and right maps). Due to the timing and topography of the low frequency positive cluster (middle map), this cluster is likely to represent a spectral representation of the P3 Event Related Potential (ERP) component previously linked to visual awareness ratings (Del Cul et al., 2007; Tagliabue et al., 2019). Although the negative clusters and the higher frequency positive cluster included timepoints immediately preceding and including stimulus-onset, when only pre-stimulus data (-1-0 s relative to stimulus onset) were included in the single-trial FFT analyses (thus ruling out any contamination from post-stimulus activity), no significant relationship was found between EEG phase and PAS ratings at any frequency (see S1C). **(D-F)** plots t-values for the wITPCz analysis denoting the strength of the EEG phase – identification accuracy relationship. We observed one negative cluster (-.1-.24 s relative to stimulus onset, 4-13 Hz: cluster statistic = -5627.4, p = .01) and one positive cluster (-.04-.7 s relative to stimulus onset, 3-30 Hz: cluster statistic = 27465, p < .001, see S1D&E). Again, when only pre-stimulus data were included in the single-trial FFT analyses, no significant relationship was found between EEG phase and accuracy, at any frequency (see S1F). (**G-H)** plots the EEG phase - letter presentation time (10, 20, 30, 40, 50 ms) relationship. One negative cluster (-.12-.26 s relative to stimulus onset, 3-15 Hz: cluster statistic = -14712, p < .001) and one positive cluster (-.04-.7 s relative to stimulus onset, 3-30 Hz: cluster statistic = 31103, p < .001) were found (see 1G&H). Note the similarity of the topographical representations of both the negative (left map) and positive (right map) clusters in S1H to the PAS ratings and accuracy cluster topographies in S1B and S1E.



Supplementary Figure 2 plots p-values (averaged over all electrodes) from the phase opposition sum (POS) analyses. These values represent group-level tests of whether high (3 and 4) versus low (1 and 2) PAS rating trials (S2A) or correct versus incorrect trials (S2B) tend to be phase locked to different (and hence preferred) phase angles. In the pre-stimulus period of interest, no p-values survived multiple comparison correction for either measure. However, post-stimulus clusters were found primarily in low frequencies for both visual awareness and accuracy. This was the case for the analyses with all trials included (S2A,B - top rows) and remained true also for the follow-up phase analyses in which relative trial numbers were equated between the two outcomes (S2A,B - bottom rows). It is likely that these post-stimulus phase effects represent differences in target-evoked ERPs to physically different (short versus long) presentation times that will, by design, be associated with different accuracy and awareness ratings. Hence, we did not find convincing evidence that pre-stimulus phase predicts either visual awareness ratings or identification accuracy.

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