The Role of Occipital Pre-stimulus Alpha Oscillations in Selective Attention

by

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Abstract

In everyday life relevant and distracting information often coincide and we rely on selective attention to efficiently discriminate between the pertinent information and the irrelevant noise. Existing research relates selective attention to neural oscillations in alpha frequency predominantly using spatial paradigms with one or no distractors, presented simultaneously with the target. In the current thesis the role of pre-stimulus alpha oscillations was investigated in the context of a visual search. First, the effect of visual stimulation on alpha oscillations and behavioural performance was investigated. No effects of stimulation were found and alpha oscillations were not successfully entrained. The relationship of spontaneous pre-stimulus alpha oscillations with performance was then explored. We demonstrated a negative correlation between the power of alpha oscillations and performance, indicating that high power is related to fast reaction times. Lastly, the effect of pre-stimulus alpha oscillations in the context of varying task demands was investigated. The results indicated that high alpha power is beneficial for performance when the target is presented simultaneously with multiple distractors, but not when presented with a singleton distractor. Moreover, the predictability of task demands resulted in modulation of pre-stimulus alpha oscillations, with higher power in anticipation of high task demands, as compared to low task demands.

To my parents Małgorzata and Andrzej.

I owe you everything.

"Niczego w życiu nie należy się bać, należy to tylko zrozumieć."

– M. Skłodowska-Curie

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Contributions

Publications and Presentations

The work presented here was designed, conducted, analysed and interpreted by myself, with the guidance and help from my doctoral project supervisors, Dr Simon Hanslmayr and Professor Kimron Shapiro. My supervisors advised on study design, data analysis and provided editorial guidance in the writing process. The following articles and conference proceedings are in preparation or were accepted for publication and/or presentation at conferences based on my doctoral project.

Papers in preparation for submission from this doctoral research

1. Pastuszak, A.; Hanslmayr S. Shapiro, K. The role of occipital pre-stimulus alpha oscillations in selective attention. (Chapters 4 and 5).

Conference abstracts from this doctoral research

1. Pastuszak, A.,Hanslmayr, S., Shapiro, K. (in press) The role of pre-stimulus alpha oscillations in distractor filtering during a visual search task. Journal of Vision. Paper presented at the Visual Sciences Society Conference, St Pete Beach, FL. (Chapter 5)
2. Pastuszak, A., Hanslmayr, S., Shapiro, K. (2016) Relationship between pre-stimulus individual alpha oscillations and reaction times in visual search. Program No. 115.13. 2016 Neuroscience Meeting Planner. San Diego, CA: Society for Neuroscience, 2016. Online. Paper presented at the Society for Neuroscience Conference, San Diego, CA. (Chapter 4)
3. Pastuszak, A., Hanslmayr, S., Shapiro, K. (2015) Modulation of behavioural measures of attention by visual entrainment in visual search. Paper presented at the Entrainment of Brain Oscillations Conference, University of Oldenburg, Delmenhorst, Germany (Chapter 3)
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Chapter 1

Introduction

In our everyday lives we are constantly exposed to a ceaseless stream of information about the environment we navigate in and the people we interact with. However, our information processing capacity is limited, and selective attentional mechanisms are needed to avoid information overload. It is widely accepted that these mechanisms are related to the underlying neural activity (cf. Buschman and Kastner, 2015). Specifically, brainwaves (oscillations) in the alpha band (defined by frequencies ranging between approximately 7Hz and 14 Hz; Linkenkaer-Hansen, 2004; Samaha and Postle, 2015) were demonstrated to affect the efficiency of target detection and shown to play a role in the inhibition of task-irrelevant information (Kizuk and Mathewson, 2017; Klimesch et al., 2007; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000). Research to date primarily focused on spatial attention, often presenting the target stimulus on its own, or with a singleton distractor. However, everyday situations are likely to resemble the popular “Where is Wally?” game, with things which we are looking for surrounded by many other distracting objects. These types of scenarios can be approximated by employing a visual search paradigm, in which the target is surrounded by distracting stimuli. Hence, the experiments presented in this thesis investigate the role of alpha oscillations in selective attention, using a visual search task.

In this chapter a relevant body of literature and the theoretical footing for the current project is presented. The focus will be on theories regarding selective attention and research concerning the relationship of selective attention with alpha oscillations.

1.1 Selective attention

1.1.1 The attentional filter

> *"The often-used phrase "pay attention" is apt: you dispose of a limited budget of attention that you can allocate to activities, and if you try to go beyond your budget, you will fail."* — Daniel Kahneman, Thinking, Fast and Slow

Attention is a crucial mechanism facilitating the processing of the relevant information. It is a finite resource (Broadbent, 1958) that can be applied to sift out the pertinent information from the irrelevant noise. The limited capacity of information processing has been remarked upon since the very early days of attention research. As early as in the 19th century Herman von Helmholtz (1867/1925, as in Mangun, 2012) laid the foundation for selective attention research, when in his experiments he provided evidence for the constraints of processing everything that is presented in the visual field. He proposed attention to be a process crucial to visual perception.

The seminal *early filter theory* (Broadbent, 1958) postulates a limited capacity of sensory information processing and suggests the necessity of a systematic attentional filter. Broadbent (1958) proposed an early processing stage bottleneck that would allow for efficient discarding of irrelevant and distracting information prior to conscious processing. This was supported by research which involved presenting participants with two separate channels of auditory information, and asking them to repeat ("shadow") only one of them (Cherry, 1953). The results demonstrated, that only one of the auditory streams was processed consciously, while the semantic information presented in the unattended stream was lost. This effect persisted even if both streams were identical, but presented at a delay to one another. Auditory research supporting Broadbent's early filter theory, had its visual equivalents. For example, a study by Rock and Guttman (1981) shows that when presented with two superimposed images and asked to attend to one of them, participants were unable to report what the second image represented.

However, Moray (1959) showed that participants asked to listen to two auditory streams, each presented to one of the ears, were able to report information from the unattended stream if it contained their name. This demonstrated that selective attention to specific information does not imply discarding of all of the unattended information. A similar effect was later found in the visual modality, where a well-established effect of attentional blink (Raymond et al., 1992) was eliminated if participant's own name was used as the second target. The interference of distracting features in processing of visual stimuli has also been evidenced in the seminal work by Stroop (1935). Here, names of colours were printed in coloured ink, either congruent or incongruent with the printed word. Participants, who were to report the colour of the ink and ignore the word itself, were significantly slower if the word and the ink were incongruent, demonstrating that the irrelevant semantic information was disruptive. This suggested that selection of relevant input may be occurring at a further processing stage than proposed by Broadbent. The *late processing theory* posits that such selection would occur following all of the sensory information has been analysed perceptually and semantically (Deutsch and Deutsch, 1963). Anne Treisman (1964) in the Attenuation Theory of Attention, compromised between the *early filter* (Broadbent, 1958) and the *late processing* (Deutsch and Deutsch, 1963) theories to extent. The early processing filter was proposed to attenuate the irrelevant or unattended information, rather than completely discard it. Thus, a weakened representation of unattended information would reach later stages of processing, allowing for highly salient stimuli (such as own name), to be perceived.

While the exact level at which filtering occurs can be deliberated on, there is a consensus that the limited capacity to process sensory input necessitates attentional selectivity. While the irrelevant information is inhibited, it is also crucial that the information pertinent to given situation or task is prioritised.

1.1.2 Selectiveness of attention

> *"My experience is what I agree to attend to. Only those items which I notice shape my mind - without selective interest, experience is an utter chaos."* — William James (1890)

Posner and Petersen (1990) proposed that the main functions of attention are orienting, detecting signals for conscious processing and maintaining alertness. *Exogenous* orienting is automatic and reflexive. Salient stimuli, such as our own name being spoken or a bright flash, can capture our attention very quickly and automatically. However, this manner of allocating the attentional resources would be highly imperfect on its own (Buzsaki, 2011). Hence, attention can also be allocated voluntarily (Jondies, 1981). *Endogenous* orienting represents intentional directing of attention towards a location or a feature of choice. It can be driven by task demands, allowing the focus of attention to be directed towards task-relevant information. It is the interplay between the endogenous (top-down) and the exogenous (bottom-up) fashion in which attention can be allocated (Posner, 1980), that results in successful navigation of our environment and optimal goal directed behaviour.

Selective attention has been demonstrated to affect the underlying neural activity (cf. Buschman and Kastner, 2015; Reynolds and Chelazzi, 2004). For instance, it has been shown that processing of task relevant stimuli is facilitated by increasing of *contrast gain*, resulting in an effective increase the target stimulus strength (Reynolds and Pasternak, 2000). The top-down influences which affect attentional processing (i.e. via a representation of the target to be detected, or a location to be attended) are an essential aspect of the 'biased competition model' introduced by Desimone and Duncan (1995). A fundamental assumption of this model is that perceptual resources are limited due to the inherent competitive nature of sensory processing by the attentional networks. Neurons in the visual cortex are fine-tuned to specific characteristics of the visual input, such as orientation and location, and will preferentially respond to favoured features, while other information will have a minimal effect on its activation (Reynolds and Desimone, 1999). Presenting preferred and non-preferred stimulus within one cell's receptive field, results in the activation output of the cell reflecting a combination of both signals (Reynolds et al., 1999). This activation output can be further modulated by attention. If attention is directed towards a specific characteristic of the signal, whether preferred or non-preferred by the particular cell, the output will be driven only by the feature attended to (Moran and Desimone, 1985). Guiding these competitive interactions to favour the task relevant information is one of the crucial roles of attention (Desimone and Duncan, 1995). This top-down biasing was further evidenced by studies using functional magnetic resonance (fMRI) in humans. Areas associated with specific, target related dimensions show increased brain activity (i.e. if attending to colour rather than motion of the target, the areas responsible for coding of colour would show higher levels of activation; Chawla et al., 1999). Similarly, using presentation of overlapping images of houses and faces (Baldauf and Desimone, 2014) show that depending on the category of objects which were attended to, the activity was observed in corresponding areas.

Importantly, these top-down influences have also been demonstrated in anticipation of the task, both in animal and human studies. Buschman and Miller (2007) have indicated that the signal related to bottom-up driven attention is conveyed from early sensory areas to the higher order frontal areas of the brain. While the top-down, memory based attention, was relayed from the frontal areas to the sensory areas. Moreover, neurons tuned to specific features of the target, or to the locations of interest, have been shown to have an increased baseline activity following the cue, which persisted throughout a delay period (Kastner et al., 1999; Luck et al., 1997). This preparatory activity allows for an increased sensitivity to the upcoming stimulus and could help resolve the competitive interactions in favour of task relevant stimuli (Sylvester et al., 2009). Thus, selective attention biases the neural competition via attentional templates: a feature or a set of features characterising the task relevant stimuli (eg. orientation, colour, location; Desimone and Duncan, 1995; Eimer, 2014; Nako et al., 2015). Working memory serves an important function by maintaining the attentional templates, and thus guiding the attention via top-down modulation. Both spatial and non-spatial information retained in the working memory facilitates performance on attentional tasks (Buschman and Miller, 2007; Desimone and Duncan, 1995; Luria and Vogel, 2011). Crucially, the defined target, generating the anticipatory bias in visual areas, does not itself depend on visual input. It can be created using arbitrary symbolic cues (Esterman and Yantis, 2010; Peelen and Kastner, 2011; Stokes et al., 2009). For instance, Giesbrecht et al. (2006) instructed participants to attend to either a location or a feature of the oncoming target. They demonstrated an increased activity in the areas of visual cortex corresponding to either the cued feature or location, respectively. Moreover, these modulations of activity were related to behavioural performance, with an increased activity related to improved target discrimination.

While, there is a consensus that selective attention operates on multiple levels of processing, allowing for analysing the information in a flexible and robust fashion, not all mechanisms underlying this process are yet fully elucidated. For instance, increasing evidence from electrophysiological studies indicates that attention is related to the neural oscillations, which reflect the synchrony of neuronal populations (Fries et al., 2001; Klimesch et al., 1999; Sauseng et al., 2005; van Ede et al., 2014), however the nature of this relationship is still being investigated.

1.2 Alpha oscillations and selective attention

First rhythmic oscillations of electrical potential recorded from human subjects, using electrodes placed on the scalp, were reported as early as 1929 (Buzsaki, 2011). These oscillations are a reasonably easily observable representation of the interactions between the neurons in the brain; they are a signature of rhythmic and simultaneous firing of neuronal populations (Buzsaki, 2011). Neural oscillations are characterised by frequency, amplitude and phase. Human electroencephalogram (EEG) signal spans a very wide range of frequencies, most pronounced of which is the alpha band frequency originating in the parieto occipital areas (7Hz and 14 Hz[1]; further referred to simply as *alpha oscillations* or *alpha*). Amplitude of an oscillation, often represented as power[2], represents the quantity of postsynaptic potentials elicited synchronously by neural populations. Phase determines the position of the wave at a given timepoint, indicating whether the neural populations are in the inhibitory or excitatory state (Hanslmayr et al., 2011).

Alpha oscillations, being the most prominent rhythm observed during wakeful rest (Romei et al., 2010), have been associated with modulation of perception (Busch et al., 2009; Hanslmayr et al., 2007; Milton and Pleydell-pearce, 2016; VanRullen and Dubois, 2011), attention (Haegens et al., 2011; Kizuk and Mathewson, 2017; Spaak et al., 2014; Worden et al., 2000), memory (Bonnefond and Jensen, 2012; de Vries et al., 2017; Jensen and Tesche, 2002; van Ede et al., 2017), as well as related to fMRI BOLD signal strength (Liu et al., 2016; Mayhew et al., 2013; Scheeringa et al., 2011).

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[1] The range of frequencies defined as alpha oscillations varies between publications, with some authors defining it, i.e. between 8-14 Hz (Samaha and Postle, 2015), 8 - 12Hz (Herring et al., 2015), 7 - 13Hz (Linkenkaer-Hansen, 2004; Mayhew et al., 2013). Thus, in this thesis alpha frequency is defined by a broad range between 7Hz - 14 Hz.

[2] Power is proportional to amplitude squared.

When allocating our attention to a stimulus, or a specified spatial location, target detection is facilitated in a conscious fashion, while potential distractors are being suppressed. The top-down modulation of early activity in visual areas by attention deployment, the suppression of unattended regions and the anticipation of the target stimulus, were associated with alpha oscillations (Händel and Jensen, 2014; Ikkai et al., 2016; Spaak et al., 2014; van Diepen et al., 2015; VanRullen and Dubois, 2011). Given the established importance of the alpha oscillation for selective attention, the following thesis focuses on this frequency band specifically.

1.2.1 Alpha power

Electroencephalography pioneer, Hans Berger (Buzsaki, 2011), demonstrated that the power of alpha oscillations was high at rest, and even higher when the subjects had their eyes closed. While the subjects were alert, and when attention was engaged, the oscillations were reported to disappear (Adrian and Matthews, 1934). Studies that followed, found that alpha signature did not solely reflect opening and closing of the eyes, but was also found to respond to visual and auditory stimulation. When the participant was presented with a sound or a flash of light, alpha oscillations have shown a short-lived decrease in power (desynchronisation), in areas respective to the type of stimulation (Pfurtscheller, 1977). This led to classifying the ongoing alpha oscillations as a signature of cortical idling. The desynchronisation of alpha oscillations, conversely, was thought to be indicative of active processing (Pfurtscheller and Lopes, 1999; Pfurtscheller et al., 1996).

Insofar, the alpha idling and desynchronisation effects could be observed across modalities (visual, auditory, movement preparation; Pfurtscheller, 1977), the same was expected to be found when presenting participants with a working memory task. Klimesch et al. (1999), however, found that with high task difficulty alpha oscillations showed an increase in power over occipital areas. Hence, alpha oscillations were proposed to act as an inhibitory mechanism, which, when the processing capacity is reached, suppresses the potentially interfering input. This was further supported by evidence showing that alpha power increases parametrically with the working memory load (Jensen and Tesche, 2002; Tuladhar et al., 2007).

More notably, considering alpha to be a reflection of attentional inhibition, indicated that it may be associated with behavioural performance. Ergenoglu et al. (2004) asked participants to report whether or not they have seen a brief light point (individually adjusted, near visual threshold stimulus). Power of occipito-parietal alpha (7.5-13 Hz) prior to onset of the stimulus, was found to be significantly lower for stimuli that were detected, as compared to stimuli that were missed. What is more, individual differences in alpha power were also associated with performance. Hanslmayr et al. (2007) used a target discrimination task, with a briefly presented singleton target. They demonstrate that participants who were unable to discriminate the target had significantly higher alpha power than participants, who performed successfully on the task. The relationship between low anticipatory (pre-stimulus) alpha power and improved performance was subsequently reproduced numerous times (Feng et al., 2017; Iemi et al., 2017; Marshall et al., 2016; Okazaki et al., 2015; van Dijk et al., 2008, but cf. Samaha et al., 2017). Hence, the ongoing alpha oscillations were proposed to be a reflection of continuous cortical inhibition, only released when relevant stimuli had to be attended and processed (Sauseng et al., 2005).

An important implication of continuous cortical inhibition mediated by the alpha oscillations, would be that activity in the regions ipsilateral to the cued location ought to remain approximately at baseline levels. Evidence to the contrary was provided by a number of studies presenting ipsilateral alpha increases as well as contralateral decreases, or exclusively the increases of alpha with the attention shift (Cosmelli et al., 2011; Haegens et al., 2012; Händel et al., 2011; Heuer et al., 2017; Rihs et al., 2009; Snyder and Foxe, 2010; Yamagishi et al., 2003), and demonstrating retinotopically mapped alpha increases in the unattended areas (Worden et al., 2000). For instance, Knakker et al. (2015) show that when participants were cued to attend to either, an image of a face, or a word, and presented an overlapping image of the two, alpha power increases were found over areas corresponding to the to-be-ignored category of the stimulus. Kelly et al. (2006) suggested that the disparities between the various paradigms used may be the reason for the inconsistent results. Rihs et al. (2009) observed that studies reporting alpha desynchronization in regions contralateral to the cued stimuli show a signal modulation between 400ms and 800 ms after the presentation of the cue. Meanwhile, reports of ipsilateral increase in power of the alpha frequency band had a longer SOA, requiring the attention to be sustained longer. Hence, they presented subjects with a cued spatial attention paradigm, where the SOA was varied (800ms or 1900 ms), while continous EEG was recorded. As anticipated, alpha power decreases occured under 700 ms of time from the cue in the region contralateral to the target location, while regions ipsilateral to attended location showed alpha band power increases at longer intervals during which the attention has to be sustained. This served to reconcile the conflicting reports, accentuating the role of differing paradigms; and revealed that both directionalities of alpha modulation play an active role in inhibition of the unattended locations.

While the assembled body of research demonstrates compelling evidence for anticipatory occipital alpha power as an underlying inhibitory mechanism for selective attention, the question of how said inhibition is expended remains. In an attempt to tackle this question Chaumon and Busch (2014) explored the two potential models of *contrast gain* and *response gain*, both of which would have yielded the same results with a near visual-threshold target in a classical cuing paradigm, and thus could not be resolved using previous research. Modulation of contrast gain by alpha oscillation, would indicate that there is a general visual improvement or deterioration, as if the stimulus physically changed in intensity. Modulation of response gain, would not affect stimulus intensity, but would rather modulate the peak performance, through affecting systems input/output transformation. Using brief presentation of stimulus varying in contrast they demonstrate that high alpha power is associated with low performance when stimuli were of highest contrast, which indicates a change in the response of the visual system and supports the response gain model. Correspondingly, Iemi et al. (2017) contrasted two models based on signal detection theory (Peterson et al., 1954; Stanislaw and Todorov, 1999) - *baseline excitability* and *response precision*. These models are associated respectively with the criterion, representing the likelihood of indicating target presence whether or not the target is indeed present; and the sensitivity, reflecting the difficulty of detecting the target. The researchers demonstrate that low alpha power is associated with low criterion, and thus an increase in hits and false alarms alike, but not with sensitivity suggesting no actual improvement in target detection. Similarly, Limbach and Corballis (2016) report that high alpha power is related to a more conservative criterion when detecting a target. Further evidence to this end, and an even closer association between alpha power desynchronisation and the probability of reporting the presence of the target has recently been put forward by Kloosterman et al. (2017). They present effects in line with Iemi et al. (2017) and Limbach and Corballis (2016), while also demonstrating that alpha power is modulated by experimentally manipulated criterion.

The premise, whereby alpha oscillation reflects general excitability and is a correlate of global neural excitability of the visual system, is in line with previous research examining the effect of alpha oscillation power fluctuations on illusory precepts (Gulbinaite et al., 2014). Using a cross-modal task, inducing a double flash illusion (i.e. perceiving an illusory second stimulus, when only one is presented) and a fusion effect (i.e. perceiving one stimulus when two were presented). Lange et al. (2013) investigated whether alpha desynchronisation reflects general increased cortical excitability or rather visual improvement. Low pre-stimulus occipital alpha resulted in perceiving double stimuli in both illusions, implying that visual cortex was more susceptible to input. The fluctuations of alpha oscillations seem to mirror the neural cortical excitability (Gulbinaite et al., 2014). Therefore, it is likely that alpha power modulation affects the decision pertaining to whether the target will be reported, more so than to the actual visibility of the target. Alpha power modulations can thus be understood as a reflection of the regulation of the neural populations excitability towards a state allowing for optimal performance.

1.2.2 Alpha phase

Further evidence of alpha oscillations playing an important role in visual perception and attention comes from studies investigating the relationship of the phase of the oscillations and target detection (Callaway, 1962; Callaway and Yeager, 1960; Dustman and Beck, 1965). Spontaneous fluctuations of alpha oscillations are reported to enhance processing of information if the stimulus onset coincides with the optimal phase and reflect of the fluctuations of attention

(Busch et al., 2009; Busch and VanRullen, 2010; Hanslmayr et al., 2013). In their study Mathewson et al. (2009) assessed the relationship of pre-stimulus alpha frequency phase and target detection with metacontrast masking. Participants were briefly presented a target, succeeded by a mask and were to indicate whether or not they have seen the target. The observed fluctuations in behavioural data were correlated with EEG signal recorded, whereby the decreases in target detectability were associated with alpha power increase. Moreover, when the alpha power was high the behavioural performance was demonstrated to be phase dependent. Rohenkohl and Nobre (2011) argued that the observed pre-stimulus alpha desynchronisation is a reflection of the anticipatory process, while phase fluctuations are predictive of the behaviour. Similarly Busch et al. (2009) find that approximately 16% of the variability in target detection is accounted for by the phase of the ongoing alpha oscillations. This suggests that alpha phase reflects periods, or “windows” of increased excitability (Jensen et al., 2012). Further evidence for the modulation of performance by alpha oscillations phase is provided by employing brain stimulation techniques, where the probability of reporting phosphenes induced by transcranial magnetic stimulation (TMS) was related to the pre-stimulus alpha phase, with 15% detectability difference between opposing phases (Dugué et al., 2011).

The implication of phasic modulation of behavioural performance, is that the target presented at an optimal phase, following rhythmic stimulation is more efficiently processed, and thus more readily detected (Mathewson et al., 2010). Arguably, the temporal predictability of the oncoming stimuli, whether task relevant or disruptive should allow alpha oscillation to adjust accordingly (eg. phase reset) in order to optimize the behavioural outcome. Phase adjustment to that effect has been demonstrated by Bonnefond and Jensen (2012) in a working memory task, with temporally and difficulty-wise predictable distractors. Notably, animal studies offer direct evidence associating the modulation of neuronal activity with alpha oscillations, indicating that while the spike firing rate is negatively affected by alpha power, the lowest firing rates are found at peaks of the oscillations (Bollimunta et al., 2008, 2011; Haegens et al., 2011; Mo et al., 2011).

It is important to note that the majority of research regarding the effects of alpha oscillations on attention employed paradigms in which a single, briefly presented, or near visual threshold stimulus was presented alone or with a singleton distractor. However, detection and discrimination of relevant information in real life is very likely to require searching through multiple irrelevant objects. While there is some indication that alpha oscillations play a role in tasks in which target and distractors are presented simultaneously, the effects of anticipatory alpha oscillations on behavioural performance on such tasks are not consistent; with some showing benefit associated with low (Van Den Berg et al., 2016), while others with high alpha power (Weaver et al., 2017). Hence, this thesis aims to elucidate the role of alpha oscillations in a visual search task, characterised by simultaneous presentation of the target and number of distractors.

1.2.3 Alpha entrainment

Henceforth, a vast body of research argues a pivotal role of modulation of the intrinsic brain rhythms in the alpha frequency range in the cognitive processes and perception (Henry and Obleser, 2012; Mathewson et al., 2009; VanRullen et al., 2011). The in depth investigation of the association of oscillations and cognition, with the possibility of establishing causality, can be performed through modulation of these oscillations by external rhythmic phenomena (Lakatos et al., 2008). The main characteristics of entrainment: increased oscillations power, increased phase synchrony and the resulting behavioural effects, can be achieved through using non-invasive brain stimulation (Capotosto et al., 2009), such as transcranial alternating current stimulation (tACS; Helfrich et al., 2014), rhythmic transcranial stimulation (rTMS; Thut and Miniussi, 2009; Thut et al., 2011), as well as through external sensory stimulation (Doelling and Poeppel, 2015; Kizuk and Mathewson, 2017; Notbohm et al., 2016).

For instance, using EEG in combination with TMS applied to the visual cortex, Romei et al. (2008) induced illusory percepts of a light flash (phosphene), intensity of which was adjusted to near-visibility threshold for each of the participants. The threshold of perceiving the phosphenes correlated with resting state alpha power, in that the higher the power of endogenous oscillations, the higher the perceptual threshold. In another study, applying rTMS, Romei et al. (2010) found a short lived impairment in perception of the near-threshold target, for alpha frequency stimulation condition, when the stimulation was located contralaterally to target presentation, and an enhancement if the target was presented ipsilaterally.

On the other hand, Mathewson et al. (2010) have explored whether a near-threshold stimuli detection can be modulated by behavioural rhythmic entrainment. They asked their subjects to indicate the detection of a visual target, each of which was preceded by a flickering stimulus (12.1 Hz) with varying SOAs between the entrainment offset and target onset. They show a temporary peak of perceptual sensitivity at about 82ms, when target detection improved significantly. Moreover, Kizuk and Mathewson (2017) demonstrate performance is likewise facilitated for the to-be-ignored areas, when targets are presented in phase with the entraining stimulus. This entrainment effect is assumed to be a result of a phase reset induced by the exogenous stimulus, and expected to last longer than the external stimulation (Calderone et al., 2014).

Recent studies suggest that this is indeed the case and provide further evidence of behavioural modulation associated with entrained oscillations (Graaf et al., 2013). For instance, Spaak et al. (2014) have used an uncued target detection task preceded by bilateral visual flickering stimuli, with one presented at 10 Hz and the other at jittered 10 Hz. They demonstrate evidence for alpha oscillations entrainment outlasting the visual stimulation by a few cycles, as well as entrainment related behavioural benefit.

The possibility of modulating the underlying oscillations via external stimulation provides a new, intriguing venue of investigating the neural underpinnings of attention. Thus, in the current project we employ visual stimulation to investigate the effects of pre-stimulus alpha oscillation on performance in an attentional task.

1.2.4 Thesis overview

The current thesis employed behavioural and electroencephalographic measures to investigate the pre-stimulus alpha oscillation as a mechanism underlying selective attention. In Chapter 2 the paradigm and methods used in the current project are presented. Following this, in Chapter 3 a set of behavioural experiments (Experiments 1-3) aiming to entrain the pre-stimulus alpha oscillations using visual stimulation and observe the effect of entrainment on behaviour, are presented. Furthermore, an EEG experiment (Experiment 4) is presented, in which the effect of visual stimulation on the underlying alpha oscillations is explored. In Chapter 4 the relationship between spontaneous pre-stimulus alpha oscillations and reaction times in a visual search task is explored using EEG. In Chapter 5 two electroencephalographic experiments (Experiments 6 and 7) are presented. Based on previous research, and the results presented in Chapter 4, it was proposed that the effects of pre-stimulus alpha oscillation on target detection will be dependent on task demands, as manipulated by means of set size. Moreover, it was proposed that if task demands are predictable, pre-stimulus alpha oscillation will be modulated in an anticipatory fashion. Chapter 7 provides a summary and a discussion of the reported results in the context of existing literature, as well as presents limitations and future directions.

Chapter 2

Methodology

2.1 Introduction

An overview of the behavioural and electrophysiological techniques, and the main analysis methods used to investigate the relationship between pre-stimulus alpha oscillation and attention will be presented in this chapter. Methods and procedures presented below will be referred to throughout this thesis and any deviations from the general procedures outlined in this chapter will be specified in the subsequent experimental chapters.

2.2 Participants

Participants were recruited from the pool of University of Birmingham students. All participants had normal or corrected to normal vision and were not colour-blind, which was assessed using Farnsworth-Munsell Dichotomous D15 test. Prior to commencing each experiment participants were asked to sign consent forms, screening questionnaires (if applicable), Edinburgh Handedness Inventory and a demographic information questionnaire (Experiments 5-7).

Ethics Statement All participants were treated in accordance with the ethical guidelines outlined by the British Psychological Society and the University of Birmingham. University of Birmingham Ethical committee approved all of the experiments. All of the participants signed a consent form and received a monetary reward or RPS credits for their participation. Subjects were naïve as to the purpose of the experiments.

2.3 Behavioural paradigm

While navigating the environment we have to be able to ignore the irrelevant and distracting aspects of our surroundings and efficiently identify and attend to the relevant information. This search and detection scenario can be studied by employing a well-established experimental paradigm of visual search (cf. Treisman and Gelade, 1980). Visual search provides predictable behavioural outcomes, and is an effective tool for investigation of underlying mechanisms of attention in our project. Hence, a modified version of a classical visual search paradigm was used for the purpose of investigating the relationship of underlying neural mechanisms and behavioural measures of attention.

2.3.1 Visual search

In a visual search paradigm, the participant searches for a target stimulus among a number of distractors (non-target stimuli). Traditionally the paradigm is separated into two types of search – a *feature search* and a *conjunction search* (Treisman and Gelade, 1980).

A *feature search* involves searching for a target with a distinct feature, such as colour or orientation, that distinguishes it from the distractors (e.g. red circle target among green circle distractors). The pattern of behavioural responses in this type of search, such as accuracy and reaction time is driven by the bottom-up salience of the target stimulus ("pop out" effect). In this condition the detectability of the target remains unaffected by the number of distractors surrounding the target. Hence, the function of reaction times plotted over the number of presented objects (set size) shows a flat, near to zero, slope (Wolfe and Horowitz, 2017, but cf. Moran et al., 2016).

If the target stimulus shares more than one feature with the surrounding distractors (e.g. red circle target among red square and green circle distractors) the reaction times show a linear increase as a function of set size. The efficiency of this *conjunction* type of search, and thus, the slope of the function, can be affected in various ways, i.e. by manipulating the similarity of the target and distractors, or by the choice of distinguishing features (Nordfang and Wolfe, 2014; Wolfe, 1998, 2001).

In the classical visual search task half of trials do not have the target within the display. In the target absent condition the reaction times of a conjunction search are approximately twice as long as when the target is present (Treisman and Gelade, 1980). This ratio of 2 : 1, or higher

(Liesefeld et al., 2016; Nordfang and Wolfe, 2014) indicates an exhaustive self-terminating search. On average, in target present trials, approximately half of the display is searched through (Horowitz and Wolfe, 1998). Meanwhile, in target absent trials, correct response requires searching through the whole display, potentially more than once; which yields longer reaction times (cf. Chun and Wolfe, 1996; Horowitz and Wolfe, 1998; Nordfang and Wolfe, 2014; Wolfe, 1998).

2.3.2 General Experimental Procedure

In all experiments in this thesis (with the exception of Experiment 4) a modified version of a classical visual search task is used. While the task remains the same, certain aspects of the paradigm are adapted in order to improve and optimise its utility in the context of the posed research questions. In this section an overview of the general procedure and paradigm employed, and a summary of the modifications will be presented (Table 2.1). Any changes to the main paradigm will be detailed in the respective method sections of following chapters.

2.3.2.1 Experimental design

All stimuli were programmed and presented in MATLAB® using the PsychToolbox software (Brainard, 1997) and presented on a 27-inch CRT display screen with a refresh rate of 60 Hz, and 1920 x 1080 resolution. The target stimuli were either a *red horizontal rectangle* (80 x 29 pixels), or a *green vertical rectangle* (29 x 80 pixels), with the exception of Experiments 1 and 2, where there was only one possible target (*red horizontal rectangle*). Distractors in all experiments were *red vertical* and *green horizontal rectangles* of the same sizes as targets. In the feature condition (included only in Experiment 1 and Experiment 2) the target appeared among either of the possible distractor groups. In the conjunction condition distractors were presented on the screen in a semi-randomized fashion, in that both types of distractors always appeared on the screen (Figure 2.1), but the numbers of each distractor type were not necessarily equal. The number of distractors presented on the display in each trial was dependent on the set size condition (either two or three possible set sizes, depending on the experiment). Our paradigm incorporated both target present (50%) and target absent (50%) trials. This aimed to avoid a response bias driven by the probability of target presence. Target absent trials were not used in the main analyses. Pilot experiments were conducted to ensure the visual search behavioural patterns and optimal ratios were found (see Appendix A). Participants were asked to indicate the detection or absence of the target on the display by pressing an appropriate key on the keyboard, and were instructed to do so as quickly and accurately as possible.

In Experiments 1 and 2 one target was used, which potentially allowed participants to ignore one group of distractors (i.e. looking for red horizontal target, they could focus on searching only through red distractors). This potential limitation was addressed in the subsequent experiments, by introducing an additional target. Firstly, because the number of each type of the distractor presentation was semi randomised, and ignoring one type would result in spurious adjustment of the set size. Secondly, not all participants would follow this strategy, allowing for potentially confounding differences in the set size modulation our paradigm necessitated.

Table 2.1: Visual search paradigm changes across experiments.

Experiment number	Visual Search conditions	Set sizes	Set Size design	Possible targets
1	Feature Conjunction	8, 16, 24	Mixed	1
2	Feature Conjunction	8, 16, 24	Mixed	1
3	Conjunction	16, 24	Mixed	2
5	Conjunction	16, 24	Mixed	2
6	Conjunction	2, 8, 16	Mixed	2
7	Conjunction	2, 8, 16	Blocked	2

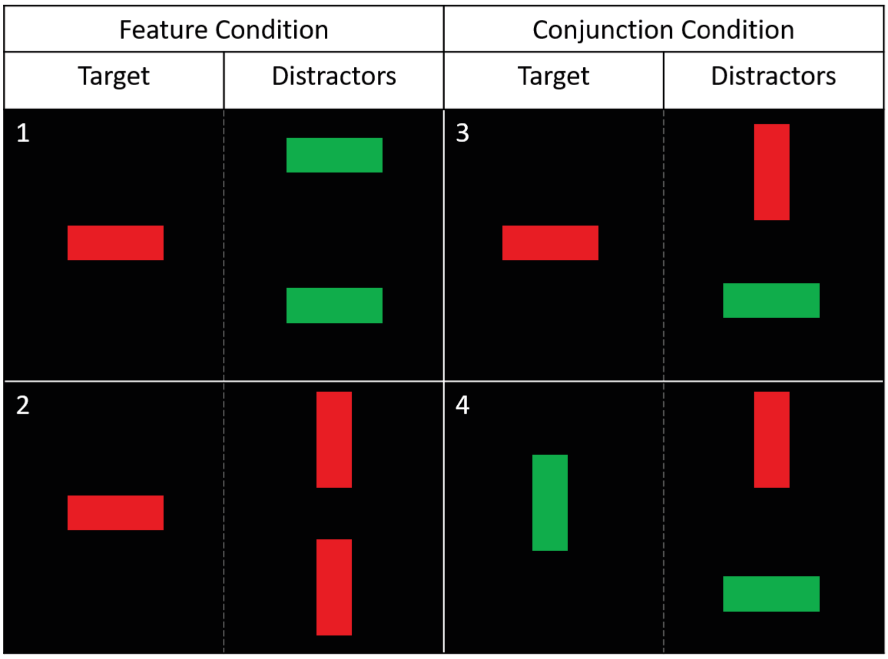

Figure 2.1: Types of targets and distractors per visual search condition. Combinations 1 and 2 were used only in Experiment 1 and 2. Condition 4 was used in Experiments 3, 5, 6 and 7.

2.3.2.2 Behavioural Analysis procedures

Outlier rejection Participants who consistently pressed random response buttons (demonstrating chance performance), as well as participants whose reaction times were greater than 3 standard deviations above the mean for hits, or false alarms were considered outliers and were not included in the final analyses.

Reaction time data trimming The raw reaction time data was trimmed using a low (200 ms) and high (RT mean ±2.5 SD) cut-off value. Data below the low cut-off, or above the high cut-off were removed from the analysis.

Statistical analysis All behavioural analyses were conducted using R computing environment (R Core Team, 2013) and SPSS (IBM Corp. Released 2013). In order to asses whether a speed accuracy trade-off occurred, correlations of reaction times and accuracy rates were calculated. Mean RTs and standard deviations were calculated for all experimental conditions. In order to statistically analyse the behavioural data appropriate Analyses of Variance (ANOVA) were performed. Repeated-measures ANOVAs were used in all experiments with the exception of Experiment 4, in which we did not collect behavioural data, and Experiment 5, where a paired-samples t-test was used. A mixed-design ANOVA was also used in Chapter 5, where an interaction between data from Experiments 6 and 7 was tested. If Mauchly's test of sphericity suggested heterogeneity of variance, Huynh-Feldt adjustment was employed (Huynh and Feldt, 1976).

Throughout this thesis the significance threshold of $\alpha = .05$ is used. Post-hoc tests were conducted when appropriate. Detailed designs are described in the methods sections of respective experiments, in the following chapters.

2.4 Electroencephalography

Inspired by the electrophysiological work of Luigi Galvani, showing the twitching of frogs legs induced by electrical stimulation of the nerves (Cajavilca et al., 2009), Richard Caton recorded the fluctuations of the neural signal from the surface of the brains and the scalps of animals using a galvanometer. Adolf Beck replicated his observations, and found that these oscillations were affected by external stimulation (Ahmed and Cash, 2013). First human recordings were conducted by Hans Berger (Fig 2; Buzsaki, 2011), who in his quest to find evidence of telepathy, recorded brain activity from the scalp of a participant using electrodes, an electrometer and a galvanometer. While he failed to prove the possibility of forging a telepathic connection between people, his invention, the Electroencephalogram (EEG) , proved to be pivotal for studying the neural underpinnings of cognition and behaviour.

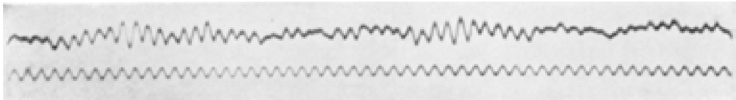

Figure 2.2: One of the first human EEG recordings (Berger and Gloor Pierre, 1969)

2.4.1 EEG signal generation

The EEG signal is the reflection of the electrical activity of the brain recorded by electrodes placed on the scalp. Neurons, the basic building blocks of the central and peripheral nervous system, transmitting signals within the brain as well as throughout the rest of the body, are the source of this signal. Their specialized cellular extensions allow rapid transmission of information: the dendrites receive the information from the neighbouring cells, while the axon passes the information on (Figure 2.3).

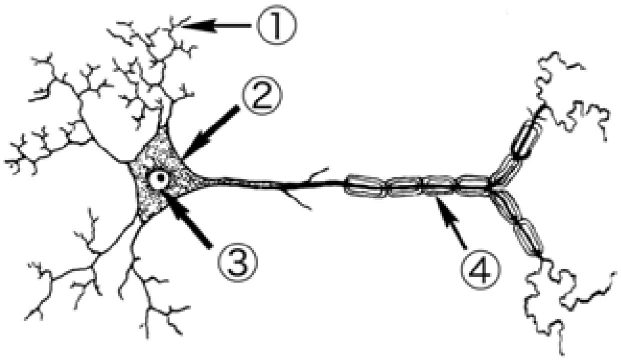

Figure 2.3: Schematic diagram of a neuron. 1) Dendrites, 2) cell body (soma), 3) nucleus, 4) axon covered in myelin sheath.

The communication between neurons takes place at the synapse, a junction separating the neural cells. It is most commonly facilitated by neurotransmitters (although there can also be electrical synapses, cf. Connors and Long, 2004), synthetized within the cell body (and sometimes within the dendrites; Lodish et al., 2000). Depending on whether the synapse is excitatory or inhibitory, the resting electrical potential of the neuron (approximately -60/-70 mV; Lodish et al., 2000; Ward, 2006) either increases or decreases. In a single neuron, many inhibitory and excitatory synapse activations may coincide and result in excitatory post-synaptic potentials (EPSPs) and inhibitory post synaptic potentials (IPSPs) which are summated. An above threshold increase of the membrane potential (approximately 10 to 15 mV) results in an action potential[1]

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[1] An action potential is a depolarisation of the membrane, followed by repolarisation, a refractory period and a return to resting levels (Lodish et al., 2000). This is an extremely rapid process, as the action potential can be propagated through a neuron even up to 100 meters per second, allowing the signal to be transmitted within milliseconds (Buzsaki, 2011).

(AP; Ward, 2006).

The EEG signal reflects the summated synchronous PSPs of neuronal populations, with negligible contribution of AP (with exceptions of synchronous events, e.g. epileptic activity; Olejniczak, 2006). While the AP of single neurons can be recorded using techniques such as single-unit recording, such signal is much too weak to be detected by electrodes placed on the scalp. Being very rapid, APs are not likely to occur at exactly the same time in vast numbers of neurons. PSPs, which have a longer duration, are more likely to co-occur[2]. Moreover, only the activity of neurons perpendicular to the surface, with their dipoles aligned (preventing cancelling out each other's potential), can be detected. While all neural cells can add to the EEG signal, the most prominent contributors are the apical dendrites of pyramidal cells located in the cortex. These are the most numerous cell type and most advantageously aligned (Buzsaki, 2011).

It is important to note that the same signature of EEG can be obtained from varying neuronal activity, and thus determining the anatomical sources can prove difficult. The recorded signal is affected by volume conduction[3] as well as the characteristics of the electrode itself (i.e. size, conductance, location). This results in a recorded signal, which is an adjusted impression of the actual potential generated by neurons (i.e. attenuated amplitude, spatially smeared; Burle et al., 2015).

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[2] Since AP is only evoked when a specific electrical potential threshold is met, APs are also less frequent than PSPs. Furthermore, the voltage changes induced by PSPs can be propagated further than that of AP, due to regional changes in conductivity resulting from simultaneous lowering of membrane resistances of neuronal populations (Paulus and Rothwell, 2016).

[3] The transmission of the potential through the extracellular liquid, cellular membranes, as well as tissues, such as bone and skin, that separate the electrode from the source.

2.5 Analysis of EEG signal

The raw EEG recording from a single electrode is a two dimensional representation (voltage over time) of a multidimensional signal (frequency, amplitude, phase, location and time; Cohen, 2014). There are multiple ways to analyse EEG, depending on the object of investigation.

2.5.1 Event Related Potentials

Event Related Potentials (ERPs) reflect the electrical activity in response to an external stimulus (cf. Luck and Kappenman, 2011). These voltage fluctuations are small on the scale of the recorded EEG signal. Hence, in order to observe them, trials with the same event or stimulus are repeated numerous times and the recorded signal is averaged (Cohen, 2014). This attenuates the spontaneous, non-event related activity and noise, and allows to tease out the activity that is consistently time-locked to the stimulus. ERPs are represented as a function of voltage difference in relation to baseline (activity prior to stimulus presentation) against time. While spatial resolution of other techniques (i.e. fMRI, PET) is superior, the ERPs are a valuable tool for investigating the functional mechanisms of cognition and perception with a very high temporal resolution (Woodman, 2010).

2.5.2 Time-Frequency Representation

Not all information contained in the EEG signal can be investigated using ERP analysis. In order to study the frequency of the signal, a Fast Fourier Transform (FFT) can be employed (Cooley and Tukey, 1965). The Fourier Theorem states that every periodic signal is comprised of weighted sums of sine and cosine functions (Freeman and Quiroga, 2013). FFT decomposes the EEG signal into sine waves, discarding the time dimension (assuming stationarity of the signal), allowing to determine the power (amplitude) and phase across respective frequencies (Figure 2.4a).

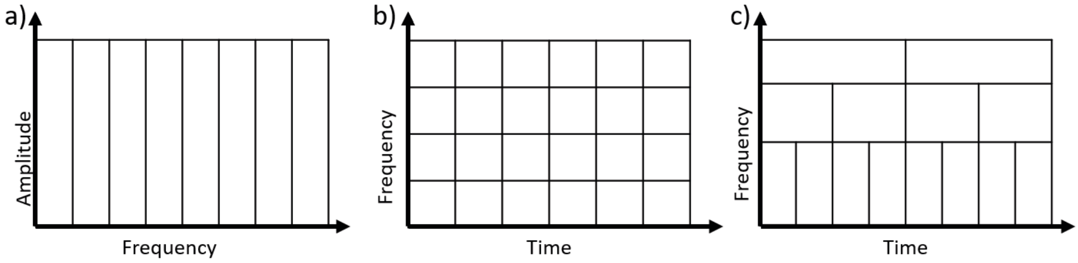

Figure 2.4: Signal represented in different domains. a) Fourier transform representation, b) Short Fourier transform representation, and c) Wavelet Transform representation.

In order to ascertain the changes in power (amplitude) across frequencies and time, a Time Frequency Representation (TFR) is used. The Short-Time Fourier Transform (STFT) returns the frequency content of the EEG in sliding windows over the time axes, thus producing a time dependent frequency representation of the signal. Because of the Heisenberg's Uncertainty Principle [4] , there is a trade-off between the time (width of the sliding window) and frequency resolution: increasing the time resolution will decrease the frequency resolution and vice versa (Figure 2.4b). One limitation of the STFT is that the time resolution (e.g., the width of the sliding window) is defined a priori and kept constant throughout the analysis, thus allowing the analysis of only specific frequencies. Wavelet Analysis (WA; cf. Cohen, 2014) addresses this limitation, as the sliding time window used in WA can vary according to the frequency of

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[4] Heisenberg's Uncertainty Principle describes the limitations of measuring the precise characteristics of complementary variables (eg. position and momentum, frequency and time), where the two characteristics cannot be precisely determined simultaneously (Ray and Maunsell, 2015)

interest (Figure 2.4c); hence providing a more efficient method for investigating non-stationary biological signals.

2.5.3 Source localisation

While the temporal resolution of EEG measurements is in the order of milliseconds, its spatial resolution is relatively poor (approximately in the order of centimetres). The poor spatial resolution results in a signal between different electrodes being correlated. Thus the same topography could represent different combinations of neural sources. Estimation of these sources requires the use of said noisy, correlated EEG signal, resulting in an ill-posed problem (inverse problem; cf. Kabanikhin, 2008; Srinivasan et al., 2007). Techniques that could overcome these limitation, providing a good estimate of neural sources include the use of spatial filters such as Laplacian, or beamforming (cf. Cohen, 2014).

2.6 General EEG Procedures

2.6.1 Apparatus

2.6.1.1 EEG System

The EEG recordings (Experiments 4-7) have been acquired using multi-channel ActiveTwo BioSemi (BioSemi, Amsterdam, Netherlands) electrode system with 128 scalp electrodes (Figure 2.5; ABC system partially overlaping with classical 10-20; Klem et al., 1958) and ActiView acquisition software (BioSemi, opensource program in LabView).

The silver/silver-chloride (Ag/AgCl) electrodes in the ActiveTwo system are active electrodes, which allow attenuation of artifacts introduced by high impedances and electronic noise (Metting van Rijn et al., 1990). This eliminates the need for preparatory skin exfoliation. Output impedances are below 1kΩ for an active electrode, which reduces the effect related to cable and connector intterference on the signal.

The EEG system uses the CMS/DRL reference approach. Comon Mode Sense (CMS) active electrode and a Driven Right Leg (DRL) passive electrode form a feedback loop driving the average voltage of the participant as close as possible to analog-to-digital converter voltage (which can be considdered the amplifier zero value), which is a substitute for ground electrodes used in other EEG systems. Signal recorded by the system is the potential difference between recording electrodes and the CMS electrode.

2.6.1.2 Electrode Coordinate Digitizer

Polhemus Fastrack magnetic digitizer (Polhemus, Colchester, VT, USA) and an opensource Brainstorm software (Tadel et al., 2011) for MATLAB®were used to collect the exact three dimensional coordinates of each electrode for every participant (Experiments 6 and 7). The participant was seated on a wooden chair within the range of electromagnetic dipole field emitted by the transmitter placed behind the chair. One sensor was placed on the cap as a reference to control for movements and shifts.The fiducial landmark positions (nasion, left and tight preauricular points) were collected using the second sensor (stylus). The stylus was then placed into each

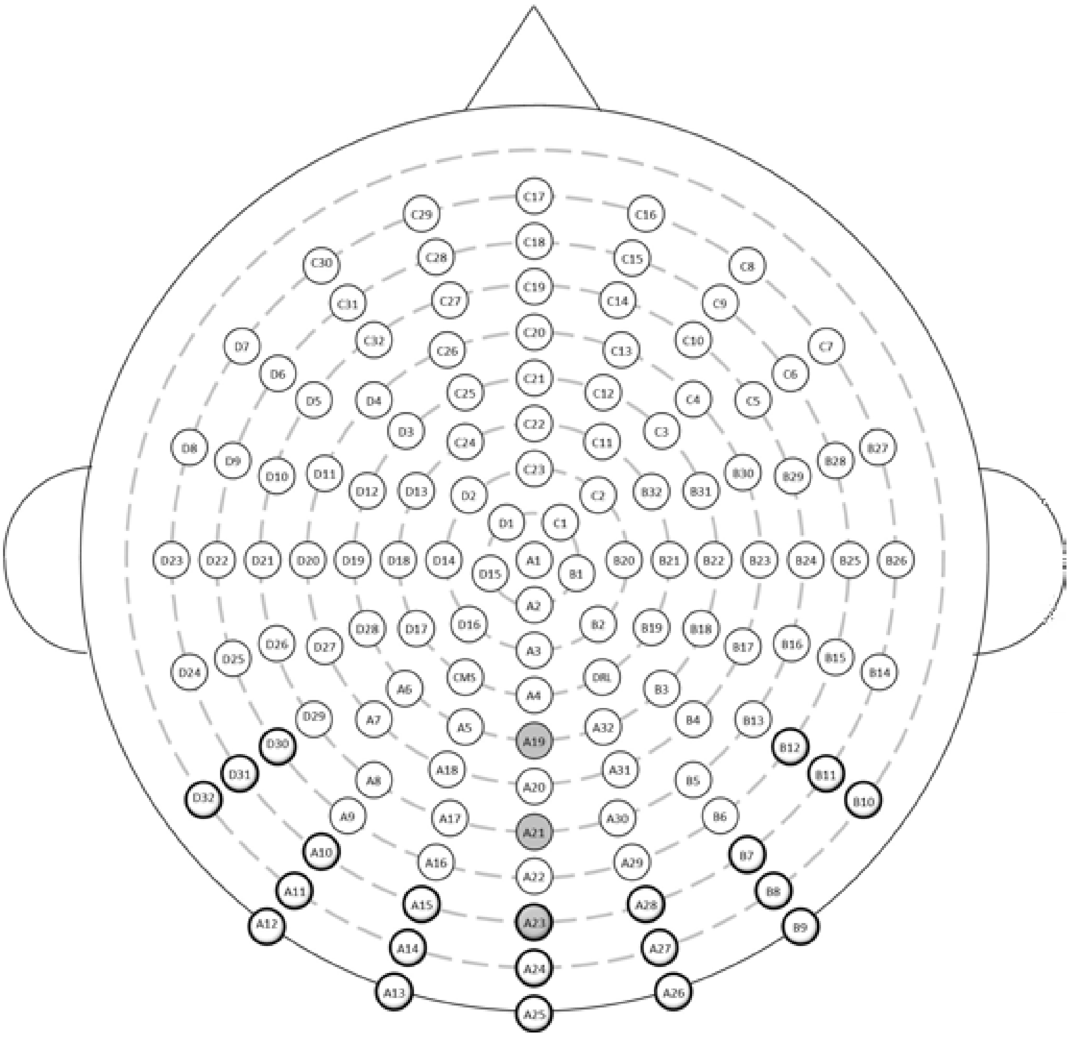

Figure 2.5: BioSemi 128-electrode layout. Greyed out electrodes were used for IAF estimation. Bold framed electrodes represent ROI used for main analyses.

electrode placeholder on the cap and x, y and z coordinates of its position were recorded, creating a three dimensional 'spatial map' of electrode layout. The data was later exported and used to create individual electrode layouts.

2.6.2 General Experimental Procedure

All subjects participating in EEG experiments (Experiments 4-7) were requested to fill in an EEG screening form in addition to a consent form. All participants were fully informed regarding the criteria of participating in an EEG study in advance, either via the advertisement on the recruitment website, or via email. On entering the EEG lab the whole procedure was once more clearly explained.

Preparation for the EEG recording session included wiping participants skin with alcohol wipes, measuring the circumference of the head and specifying the distances between nasion and the inion, as well as both left and right preauricular fiducials, in order to accurately place the cap. In the Experiments 6 and 7, following cap placement, the coordinates of all electrode placeholders were recorded using Polhemus Fastrack Digitizer. The electrode placeholders where then filled with saline based, highly conductive SIGNAGEL®, using plastic nib syringes. After placing the CMS and DRL and 128 recording electrodes onto the cap, the quality of the EEG signal was inspected, and the setup was adjusted accordingly, if necessary. Once the cap setup was completed, participants were asked to relax and the resting state signal (eyes open, eyes closed) was recorded. The EEG was recorded with a 1024 Hz sampling rate, with the experimenter continously monitoring the quality of the signal, triggers as well as the ongoing experiment presentation.

2.6.3 EEG Analysis procedures

2.6.3.1 Preprocessing procedure

The recorded signal was pre-processed and analysed using Fieldtrip toolbox for MATLAB®(Oostenveld et al., 2011). Continuously recorded data was downsampled to 512 Hz and segmented into 4 second epochs (from 2 seconds pre-stimulus onset, to 2 seconds post-stimulus onset). Long time windows were chosen in order to avoid the edge artefacts that can result from applying temporal filters when performing a time frequency analysis (Cohen, 2014)

The data was re-referenced to average reference. In high density montages the enclosed volume is uniformly sampled and average reference results in a good approximation of zero voltage (true zero would be obtained if the montage covered the whole sphere of the skull; Bertrand et al., 1985; Trejo, 1998).

Human EEG suffers contamination by several physiological artefacts (e.g., muscle and eye artefact) and non-physiological (power line noise, ect.; Figure 2.6). Hence, we applied a 48 Hz low-pass filter to attenuate the effect of high frequency muscle activity and line noise effects on the data, removed the linear trend, and demeaned the data, which alleviates potential DC component artefacts. Additionally, artefact rejection of trials and channels was performed under visual inspection. The rejection process was restricted in order to retain as much data as possible (maximum 20% of trials). In Experiments 5, 6 and 7 incorrect and trimmed trials, based on behavioural data, were rejected. Channels characterised by continuous or repetitive artefacts were also removed (maximum 10% channels). We use Independent Component Analysis (ICA;

cf. Hyvärinen et al., 2010), using 'runica' function, as implemented in FieldTrip software (Oostenveld et al., 2011), to remove eye blink and horizontal eye movement artefacts. On average 2 components, and not more than 3, were rejected per participant. We have then interpolated the deleted channels, using the plain average of neighbouring channels (as implemented in FieldTrip; cf. Oostenveld et al., 2011). Pre-processed data was then once more re-referenced to average reference and sorted into experimental conditions.

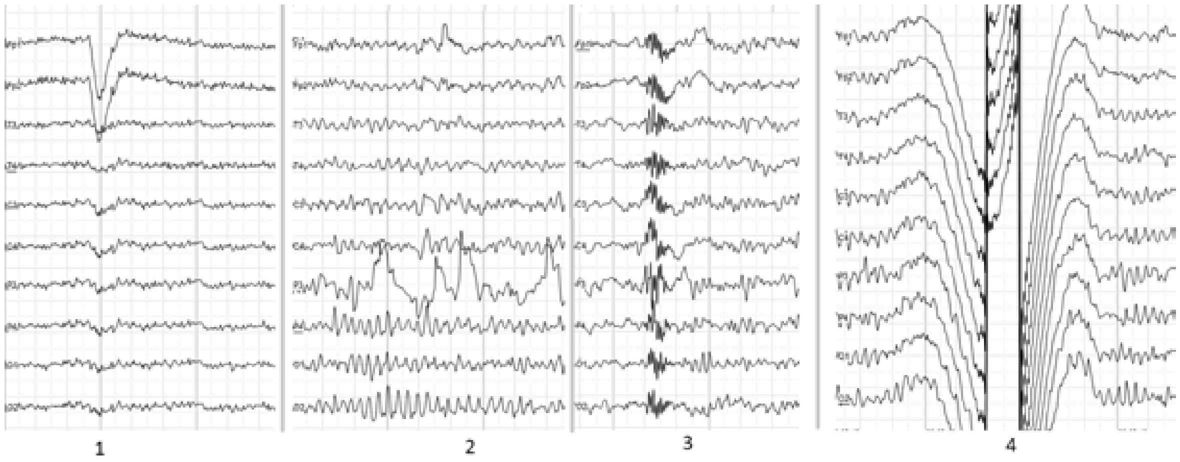

Figure 2.6: Examples of EEG artefacts. 1) Electrooculographic artefact (blink), 2) electrode artefact resulting from bad contact between electrode and the scalp, 3) swallowing artefact, 4) artefact resulting from bad contact common reference electrode and scalp. By Andrii Cherninskyi - Own work, CC BY-SA 4.0

2.6.3.2 Individual alpha frequency estimation

In order to investigate the relationship between alpha oscillation and attention *individual alpha frequency* (IAF) was estimated for each subject (Expriments 5-6). Alpha is the most prominent oscillation, and is typically characterised by an easily detectable peak frequency. The individual differences within alpha frequency band are age related (Aurlien et al., 2004; Doppelmayr et al., 1998), influenced by genetic factors and highly hereditable (Bodenmann et al., 2009; Smit et al., 2006). IAF remains reasonably stable over time in a neurotypical subject (Grandy et al., 2013), although when engaged in a cognitive task slight decreases ($\approx$ 0.2 Hz per hour) have been observed (Benwell et al., 2017). IAF has been shown to be more sensitive to detecting subtle effects than analyses conducted using the broad alpha oscillation range; with IAF variations associated with performance on cognitive tasks (i.e. working memroy and attention; Angelakis et al., 2004a,b; Clark et al., 2007; Klimesch et al., 1999). Using IAF has been suggested to be more appropriate than using a fixed alpha band, or sub-bands (Doppelmayr et al., 1998; Gulbinaite et al., 2017).

Peak frequency method was used to determine the IAF for each participant (Experiments 5-7). The power spectrum was calculated (FFT of 1s of EEG, in steps of 0.2 Hz, Hanning window; cf. Freeman and Quiroga, 2013) using eyes-closed resting state recording from 3 posterior electrodes: A19(Pz) ,A21 and A23(Oz) (Figure 2.5; Doppelmayr et al., 1998; Grandy et al., 2013; Hanslmayr et al., 2005). The IAF was estimated as the peak frequency in the broad alpha frequency range between 7 and 14 Hz.

2.6.3.3 Time-frequency analysis

A time-frequency decomposition was computed using a 3 cycle Morlet wavelet for IAF$\pm$1Hz (in steps of .25Hz). It is a common practice to use wavelet of 5 or 7 cycles for frequency analyses (Forschack et al., 2017; Sauseng et al., 2005; Vissers et al., 2017). However, since the pre-determined frequency band was specific and narrow, and high temporal resolution was of interest, a 3 cycle wavelet was specified (Cohen, 2014).

2.6.3.4 Correlation analysis

The power output of the time-frequency analysis and reaction times were correlated, across all participants, using Spearman's rank correlation. This correlation method was used as power data tend to be non-normally distributed and may contain outliers (Cohen and Steel, 2014). This was done for every channel and every frequency within the narrow individual alpha band (IAF ±1Hz) and at every time point of the pre-stimulus period.

2.6.3.5 Source localisation analysis

The sources of neural activity as well as the power—reaction time correlation effects were estimated using a linearly constrained minimum variable beamforming method (LCMV; Van Veen et al., 1997). Standard MRI and boundary element models (FieldTrip Oostenveld et al., 2011), and individual electrode positions were used (with exception of Experiment 5, where adapted 128 BioSemi layout was used for all participants. The pre-processed data was time-locked and moved into source space, onto the virtual electrodes. This data was then analysed in an identical fashion as the sensor-level data. The time windows chosen for the source reconstruction analysis were based on the time-windows of significant effects found in the sensor-level analysis.

2.6.3.6 Region of interest

Region of interest (ROI) of 21 occipital electrodes (Figure 2.5, bold-framed electrode locations) was chosen for the purposes of analysis, based on previous research showing perceptually relevant alpha activity in posterior areas (Cecere et al., 2015; Goldman et al., 2002; Hanslmayr et al., 2007), and positing involvement of the occipital cortex in generation of alpha oscillations (Makeig et al., 2002).

2.6.3.7 Statistical analysis

Cluster-based permutation tests (further reffered to as cluster permutation tests), using Montecarlo simulation were used to determine the statistical significance. This method allows for controlling for the problem of multiple comparisons and increases the specificity of the test (Maris and Oostenveld, 2007). Randomized t-statistic distributions for each data point (i.e. data point for every channel, time and frequency) were computed by shuffling the data across the conditions 5000 times. The observed t-statistics were then compared against these randomised distributions to identify the significant clusters. The significant clusters were determined by summing all the observed neighbouring t-statistics which exceeded a cluster-threshold (α=0.05 for one-tailed tests, and α=0.025 for two-tailed tests), with a minimum cluster size of 2 channels. The T-statistics reported throughout this thesis represent the maximum of the cluster-level statistics, which are the sum of sample-specific t-statistics within the given cluster. Unless otherwise specified, the electrodes within the region of interest, and frequencies within the narrow individual alpha band (IAF ± 1Hz) were averaged for the purposes of the statistical analysis.

Chapter 3

The effect of visual entrainment of alpha oscillations on target detection

3.1 Introduction

Previous research provides considerable support for the importance of alpha oscillations in visual attention (cf. Chapter 1). Low alpha power has been associated with facilitation of target detection, while high alpha power with inhibition of external stimuli (Janssens et al., 2017; Mayhew et al., 2013; Okazaki et al., 2015). In order to ascertain the causality of this relationship neural brain stimulation methods can be used (Thut, 2014). Techniques such as transcranial magnetic stimulation (TMS) have been shown to successfully entrain the underlying oscillations (Herring et al., 2015), resulting in an increased phase coherence effect (i.e. phase locked to rhythmic TMS impulses), as well as increased power of alpha oscillations (Jaegle and Ro, 2014; Thut et al., 2011; Vossen et al., 2015; Zaehle et al., 2010). Furthermore, rhythmic TMS and transcranial alternating current stimulation (tACS) have been shown to modulate performance on perceptual tasks when applied in alpha frequency (Romei et al., 2010). It has also been proposed that endogenous oscillations can be entrained using sensory stimulation. Frequency tagging, whereby stimuli are presented at differing frequencies (flickered), is an established method used for discerning the processing of specific stimuli (Mora-Cortes et al., 2017). As stimuli flicker at certain frequencies the neural signal reflects the same temporal dynamic (steady state evoked potential, SSVEP). It has been suggested that this effect is a result of the entrainment of the underlying oscillations (Herrmann et al., 2016; Notbohm and Herrmann, 2016; Notbohm et al., 2016; Thut et al., 2011, but cf. Capilla et al., 2011).

Such visual stimulation in alpha frequency has been shown to affect the power and phase of alpha oscillation, as well as the behavioural measures on attentional tasks (Kizuk and Mathewson, 2017; Mathewson et al., 2010, 2012; Spaak et al., 2014). The majority of previous research investigated the effects of entrainment of alpha oscillations with regards to singular, near visual threshold stimulus detection. However, in everyday life, we are likely to engage in searches for objects surrounded by other, often distracting, things (i.e. looking for a stapler on a messy desk). There is evidence that alpha oscillations are also related to performance on target detection tasks with multiple, above visual threshold stimuli. Spaak et al. (2016) used brief and repeated exposure of a visual search display to show that inhibition of the power of alpha oscillations contralateral to the target location is related to fast reaction times, while high alpha power is detrimental to performance. However, evidence regarding the effect of entrainment of alpha oscillations on performance in a visual search task is contradictory. Gonzalez-Rosa et al. (2015), using static magnetic stimulation[1], observed a power increase in the individual alpha frequency, associated with longer reaction times in difficult conditions (conjunction) of the visual search task. Müller et al. (2015), on the other hand, reported improved performance in a conjunction visual search, as measured by d' (sensitivity index), following 5 sessions of tACS alpha entrainment. However, they do not find any effect of tACS entrainment on reaction times. What is more, since EEG was not used, no direct evidence of neural entrainment is provided. It is likely that the differences in stimulation procedure, such as continuous stimulation throughout the experiment (Gonzalez-Rosa et al., 2015), as compared to tACS stimulation over consecutive days, with behavioural testing on a different day (Müller et al., 2015) result in divergent outcomes.

In the following experiments the efficacy of entrainment using visual stimulation, and its effect on behavioural performance in a visual search task (Treisman and Gelade, 1980), were explored, aiming to resolve the conflicting evidence. Specifically, visual stimulation (a flickering stimulus) was used to modulate endogenous oscillations by increasing (using a flickering stimulus with 10 Hz frequency) or decreasing alpha power (using an arrhythmic flickering stimulus, with a mean of 10 Hz). This effect was expected to persist for several cycles after the visual stimulation ends (Spaak et al., 2014) and thus affect the performance on the upcoming visual search task.

In Experiments 1-3 a flickering stimulus was presented prior to visual search onset. In experiment 1 the flickering stimulus was a filled in rectangle covering the whole area in which the visual search would be presented, while in Experiment 2 a peripheral frame was used. In both

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[1] Oliviero et al. (2011) propose using static magnetic fields, by placing potent magnets on the participants scalp, as a non-invasive method of cortex stimulation. They provide evidence for reduced excitability of the motor cortex following such stimulation. Gonzalez-Rosa et al. (2015) used a cylindrical nickel-plated neodymium magnet, with a nominal strength of 120kg and a magnetic field intensity of .45T, which at 2-3 cm from the magnet surface (the approximate distance of the visual cortex from the scalp) results in 120 – 200mT of magnetic field strength. They provide evidence for focal increase in power of alpha oscillations following static magnetic stimulation over occipital areas.

experiments, a non-flickering stimulus was used as a control. Previous research indicates that high power of alpha oscillations is detrimental to target detection (Romei et al., 2010; Thut et al., 2012). Thus, in Experiments 1 and 2, flickering stimulus in alpha oscillation, presented prior to visual search task, was expected to result in longer reaction times, as compared to reaction times in non-alpha flickering and non-flickering stimulus conditions. In Experiment 3 two flickering stimuli were presented simultaneously in two hemifields, the stimulus flickering in alpha frequency on one side and arrhythmic flickering stimulus on the other. This manipulation was introduced to induce an alpha lateralisation effect (Spaak et al., 2016) and observe whether reaction times will be affected by target location with respect to the flickering stimulus type. We expected that reaction times would be faster when the target is presented in the hemifield opposite to the alpha flickering stimulus (contralaterally), while slower if the target was presented in the same hemifield (ipsilaterally). Experiment 4 was conducted to assess the efficacy of the visual stimulation used in behavioural experiments. The EEG signal was recorded while participants were presented with the flickering stimulus, identical to the one used in Experiment 2, to investigate the effects of this manipulation on the underlying alpha oscillation. There was no behavioural task in Experiment 4. An increased synchrony in alpha condition, represented by higher inter-trial phase coherence (ITPC) and an increased power of the underlying oscillations at approximately 10Hz was expected. The entrainment effect was expected to persist after the offset of visual stimulation (Spaak et al., 2014).

3.2 Experiment 1

Experiment 1 investigated the influence of a flickering visual stimulus on reaction times (RTs) of target detection in a visual search (VS) task. Here, the flickering stimulus was a filled-in rectangle covering the whole area where the visual search display would subsequently be presented. The frequency of the flickering stimulus was expected to affect the reaction times, in that a stimulation in the alpha frequency (10Hz) would result in longer RTs, as compared to non-alpha stimulation, as well as non-flickering control. Non-alpha flickering stimulus was expected to result in shortest RTs across the three conditions.

3.2.1 Methods

3.2.1.1 Participants

A sample of 24 University of Birmingham students (17 females, 7 males) with a mean age of 21.7 years (19-29)[2] participated in Experiment 1. Participants were recruited following the sampling procedure described in Chapter 2. All subjects were included in the analysis.

3.2.1.2 Materials

Flickering stimuli: Two types of visual rhythmic stimuli were used to modulate the endogenous alpha oscillation. In the alpha condition, the stimulus preceding the visual search display was flickered at 10 Hz. In the non-alpha condition, a frequency randomly distributed between

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[2] Due to a technical error the age information has only been recorded from 13 participants.

5Hz and 15 Hz (mean value of 10 Hz) was used. Each flash of the flickering stimulus lasted for approximately 33ms (2 refresh frames of the monitor). Both stimulation conditions (alpha and non-alpha) had an equal number of flashes within one flickering stimulation sequence. The timing of trial onset, and thus the first flash, was kept constant in both conditions. The control condition consisted of a non-flickering stimulus, which was displayed on the screen for the same amount of time as the flickering stimuli (Figure 3.1). The flickering stimulus was a filled-in rectangle (45 x 25.5 cm, centred on the screen) covering the whole area where the visual search display would subsequently be presented.

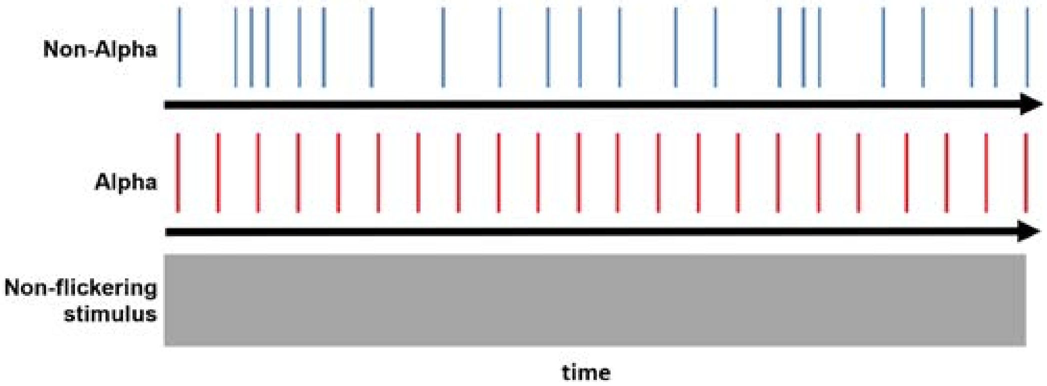

Figure 3.1: Schematic representation of the stimulation sequences.Top: Non-alpha - arrhythmic flicker with a mean of 10 Hz; Middle: Alpha - rhythmic flickering in 10Hz; Bottom: Non-flickering stimulus.

Visual search task: A modified visual search (VS) paradigm as described in Chapter 2 was employed (Treisman and Gelade, 1980). A feature and a conjunction search type (Chapter 2), with three set sizes, and one target type were used. Participants responded by pressing either “a” (absent) or “p” (present) keys on the keyboard to indicate the presence or absence of the target on the display and were instructed to do so as quickly and accurately as possible.

3.2.1.3 Design

A within-subjects 3 x 2 x 3 repeated-measures design (Table 3.1) was used. The independent variables were stimulation condition (alpha, non-alpha and non-flickering control), VS condition (feature and conjunction) and set size (8, 16 and 24). The dependent variable was reaction time (RT) for target-present trials. Stimulation conditions were manipulated between 3 blocks (each consisting of 192 trials): each block consisted of 4 sub-blocks (48 trials), 2 per visual search type condition, while set size conditions were manipulated randomly within each sub-block (16 trials per each condition combination within sub-block).

Table 3.1: Summary of the experimental design used in Experiments 1 and 2.

Conditions	Design	Levels
Flicker	Blocked	Alpha Non-alpha Non-flickering
Visual Search	Blocked	Feature Conjunction
Set Size	Mixed	8 16 24
Target	Mixed	Present *Absent*

Note: Level in grey was excluded from the final analysis.

3.2.1.4 Procedure

Participants were seated in a dark room, 55 cm from the display screen (22° x 13° visual angle of the flickering stimulus/visual search display in relation to the centre of the screen), Figure 3.2 shows the trial sequence. At the trial onset, subjects fixated on a cross in the centre of the screen for 1000ms, followed by a flickering stimulus which lasted for 2800ms. Participants

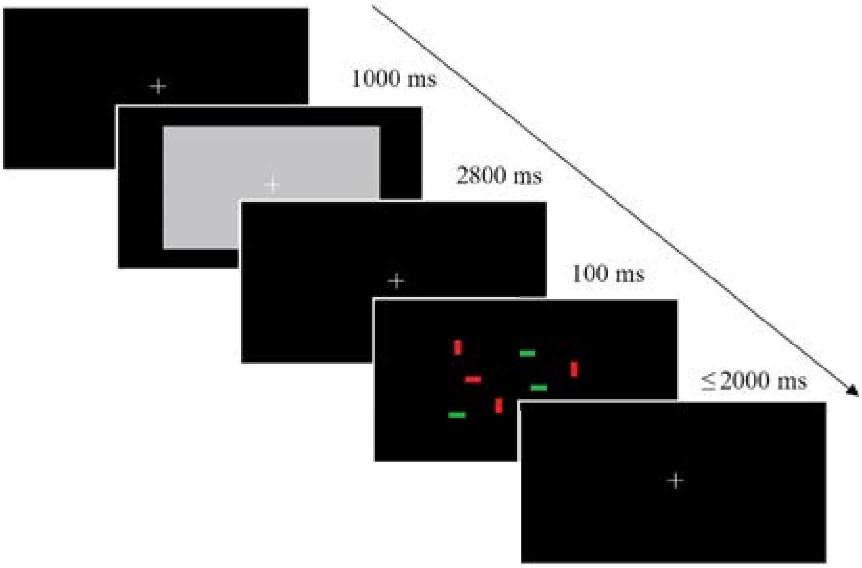

Figure 3.2: Example of a trial sequence in Experiment 1.

were instructed not to blink during this period. The visual search display appeared 100ms after the offset of the flickering stimulus and remained on the screen for a maximum of 2000ms, or until the response was given. Blocks were separated by breaks, self-paced by the participant. Participants completed 4 blocks of practice trials and 12 experimental blocks (controlled for order effects using a Latin square design between participants). Each experimental session lasted approximately 40 minutes.

3.2.2 Results

RT means and standard deviations (SDs) were calculated for target present trials across all conditions. Data were trimmed as detailed in Chapter 2. Box-plots presenting raw RTs for correct trials across all experimental conditions are presented in Figure 3.3. A descriptive summary of trimmed data is reported in Table 3.2.

Table 3.2: Mean reaction times [ms] for all experimental conditions in Experiment 1.

VS Type	Stimulus Type	Set Size 8		Set Size 16		Set Size 24	
Feature	Non-flickering	544.48	(145.08)	537.52	(132.49)	544.57	(147.71)
	Alpha	542.22	(160.84)	542.02	(154.21)	537.67	(149.42)
	Non-alpha	569.54	(177.82)	573.05	(184.35)	577.28	(189.89)
Conjunction	Non-flickering	737.33	(204.29)	873.42	(276.86)	945.23	(301.19)
	Alpha	752.54	(204.94)	881.3	(275.82)	944.15	(300.53)
	Non-alpha	797.01	(241.14)	911.05	(307.77)	978.81	(313.5)

Note: The standard deviations are reported in parenthesis.

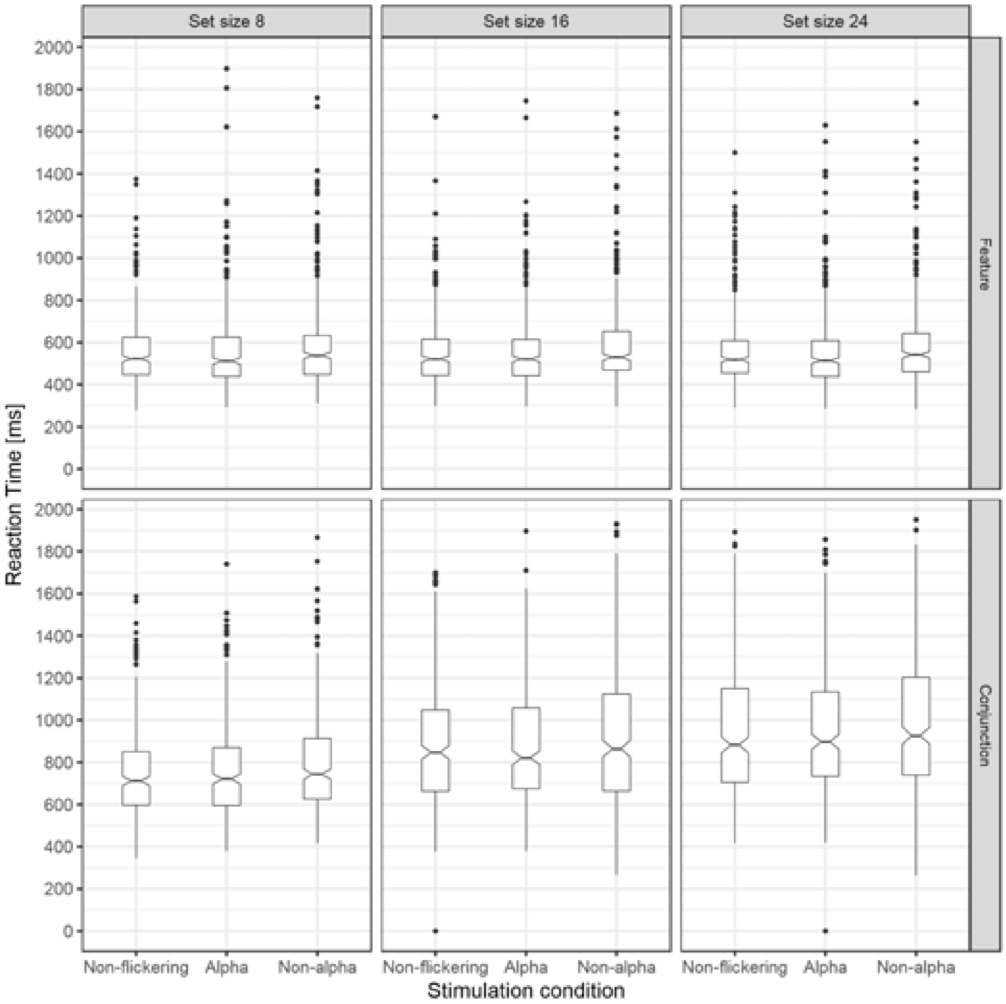

Figure 3.3: Raw reaction times for correct responses across all experimental conditions in Experiment 1.

The overall average accuracy was 95.37% (SD = 2.96%). The condition means plotted as a function of set size are shown in Figure 3.4. Data were analysed using a repeated measures analysis of variance (ANOVA) with independent variables of stimulation condition (3), visual search type (2) and set size (3). Significant main effects of visual search type (F (1, 23) = 524.66, p < .0001, η_G^2 = .669) and set size (F (2, 46) = 222.48, p < .0001, η_G^2 = .164) were found. No significant main effect of stimulation condition was found (F (2, 46) = 1.633, *p* = .206, η_G^2 = .007). A significant interaction between visual search type and set size (F (2, 46) = 267.285, p < .0001, η_G^2 = .17) was found . There were no other significant interactions (visual search type x stimulation condition x set size (F (4, 92) = .923, *p* = .455, η_G^2 = .0008); stimulation condition x set size (F (4, 92) = 1.745, *p* = .147, η_G^2 = .002; visual search type x stimulation condition (F (2, 46) = .406, *p* = .669, η_G^2 = .0006). The RTs per stimulation condition and visual search type were correlated with corresponding accuracy rates to assess whether a speed-accuracy trade-off occurred. Significant positive correlations indicated the presence of a speed-accuracy trade-off for feature search with alpha stimulus type and non-flickering and alpha stimulus in conjunction condition (for correlation coefficients and associated p-values see Appendix B.1). These correlations were driven by 2 participants one of which had the highest miss rate, and the other the highest false alarm rate. However, since they did not meet the exclusion criteria, their data was included in the final analysis.

3.2.3 Experiment summary

Summarising, the results of Experiment 1 did not support the hypothesis, showing no modulation of reaction times by the stimulation condition, in either, the alpha or non-alpha conditions.

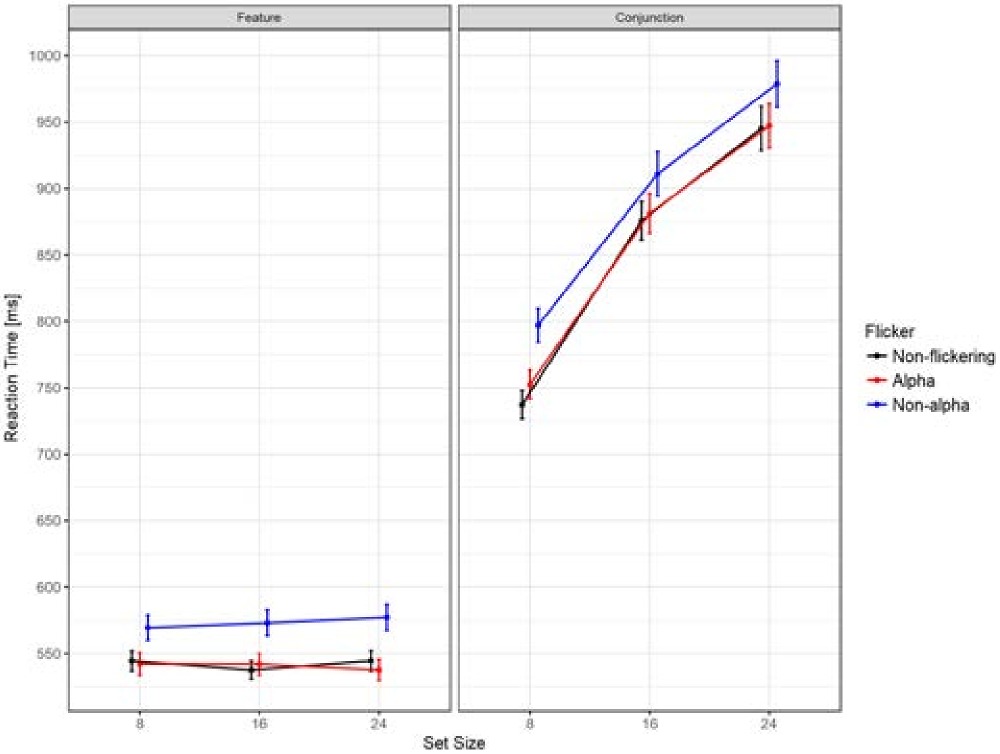

Figure 3.4: Mean reaction times, for every condition of visual search and stimulation type as a function of set size in Experiment 1. Error bars indicate standard error of the mean.

However, this may have been be due to the potential limitations of the flickering stimulus design. Participants commonly reported the flickering stimulus to be very distracting, uncomfortable and, in some cases, reported experiencing illusory perceptual effects. These limitations are addressed in Experiment 2.

3.3 Experiment 2

Experiment 2 explored the effect of the visual flickering stimulus on reaction times in a visual search task and addressed the design limitation of Experiment 1 regarding the flickering stimulus saliency. Here, the visual flickering stimulus was a frame encompassing the whole area where the visual search display would appear. The frequency of the flickering stimulus was expected to affect the reaction times, in that a flickering stimulus in the alpha frequency (10Hz) would result in longer RTs, as compared to non-flickering control, as well as non-alpha flickering stimulus. Non-alpha flickering stimulus was expected to result in shortest RTs across the three conditions.

3.3.1 Methods

3.3.1.1 Participants

29 participants, (27 women, 2 men) with a mean age of 24.3 (18-28)[3], were recruited in accordance with the procedure detailed in Chapter 2 . Two participants withdrew, while two other participants were excluded due to responding with random button presses throughout the experiment. Furthermore, two participants were identified as outliers (as specified in Chapter 2), and were therefore removed from the analysis. Thus, 23 participants were included the final analysis.

3.3.1.2 Materials

Flickering stimuli: As in Experiment 1, visual repetitive stimuli were used to modulate the endogenous alpha oscillation. Stimulation conditions were identical to those in Experiment 1 (alpha, non-alpha and non-flickering conditions). In Experiment 2, the flickering stimulus was a grey frame 20 pixels wide (45 x 25.5 cm, centred) surrounding the area in which the visual

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[3] Due to a technical error the age information has only been recorded from 15 participants.

search display would subsequently appear. All other characteristics of the stimulus were kept identical to Experiment 1.

Visual search task: A modified visual search (VS) paradigm was employed (Treisman and Gelade, 1980), identical to visual search task used in Experiment 1.

3.3.1.3 Design

In accordance with Experiment 1, a within-subjects design was used, with independent variables of flickering stimulation (alpha, non-alpha and non-flickering conditions), set size (8, 16 and 24) and VS condition (feature, conjunction). A repeated-measures GLM analysis (2 x 3 x 3) was used to assess the differences in the target present RTs (dependent variable) across conditions. The block and trial design were identical to Experiment 1 (Table 3.1).

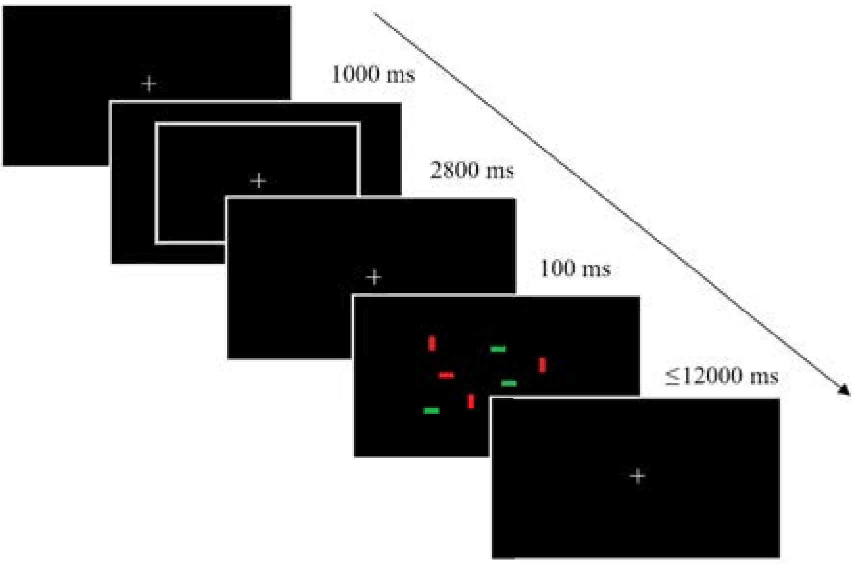

Figure 3.5: Example of a trial sequence in Experiment 2.

3.3.1.4 Procedure

The trial sequence is shown in Figure 3.5. The procedure was identical to Experiment 1, with the exception of the maximum time of visual search display presentation, which here was 12 seconds.

3.3.2 Results

Mean RTs and SDs were calculated for each experimental condition, for target present trials only. The raw reaction time data (Figure 3.6) were trimmed as described in Chapter 2 . A descriptive summary of trimmed data is presented in Table 3.3.

Table 3.3: Mean reaction times [ms] for all experimental conditions in Experiment 2.

VS type	Stimulus type	Set size 8		Set size 16		Set size 24	
Feature	Non-flickering	514.27	(117.06)	523.55	(134.37)	512.44	(118.06)
	Alpha	497.24	(126.69)	507.01	(152)	518.64	(154.3)
	Non-alpha	496.5	(117.84)	487.31	(125.41)	507.96	(104.15)
Conjunction	Non-flickering	733.48	(202.2)	875.52	(303.71)	992.6	(335.83)
	Alpha	721.58	(241.93)	848.73	(299.7)	957.05	(379.95)
	Non-alpha	706.57	(188.29)	811.11	(228.74)	912.37	(312.45)

Note: The standard deviations are reported in parenthesis.

The overall average accuracy was 94.35% (SD = 3.92%). The condition means plotted as a function of set size are shown in Figure 3.7. A repeated measures ANOVA was used, with stimulation condition (3), visual search type (2) an set size (3) as independent variables. Statistically significant interactions were followed up with a planned post hoc analysis. The results show main effects of visual search type (F(1,22) = 236.495), $p < .0001$, $\eta^2_G = .633$) and set size (F(2,44) = 103.129, $p < .0001$, $\eta^2_G = .13$), as well as a main effect of stimulation condition:

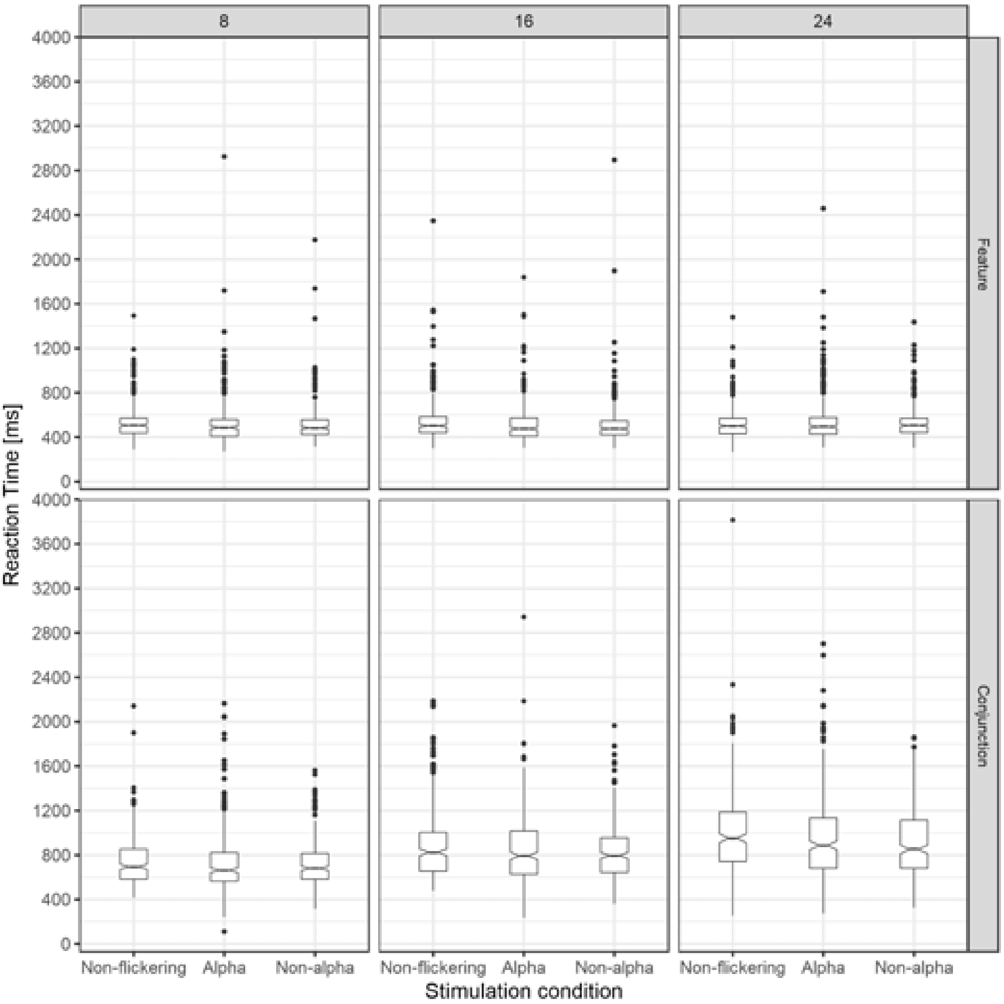

Figure 3.6: Raw reaction times for correct responses across all experimental conditions in Experiment 2.

F(2,44) = 3.404, p = .042, η^2_G = .014, whereby the non-alpha flickering stimulus results in significantly faster RTs than a the non-flickering control (Δ M = 36.83, p = .01 with 95% CI [9.72, 63.95]). A significant interaction is reported between visual search type and set size (F (2, 44) = 86.978, p < .001, η^2_G = .113). No other interactions were significant (stimulation condition and set size (F (4,88) = 1.157, p = .335, η^2_G = .002); stimulation condition and visual search type (F (2,44) = 0.983, p = .382, η^2_G = .003); visual search type x stimulation condition x set size (F (4,88) = 1.003, p = .41, η^2_G = .002). To ensure that this benefit stimulation condition upon RTs was not at the expense of accuracy, a speed-accuracy trade-off analysis was conducted. None of the correlations were significant suggesting there was no speed-accuracy trade-off (for correlation coefficients and associated p-values see Appendix B.2).

3.3.3 Experiment summary

Summarising, the results of Experiment 2 show that visual stimulation affected the reaction times. Non-alpha flickering stimulation showed significantly faster reaction times as opposed to the non-flickering condition. However, the expected longer reaction times in alpha condition in comparison to either non-alpha or non-flickering conditions were not observed. This lack of an

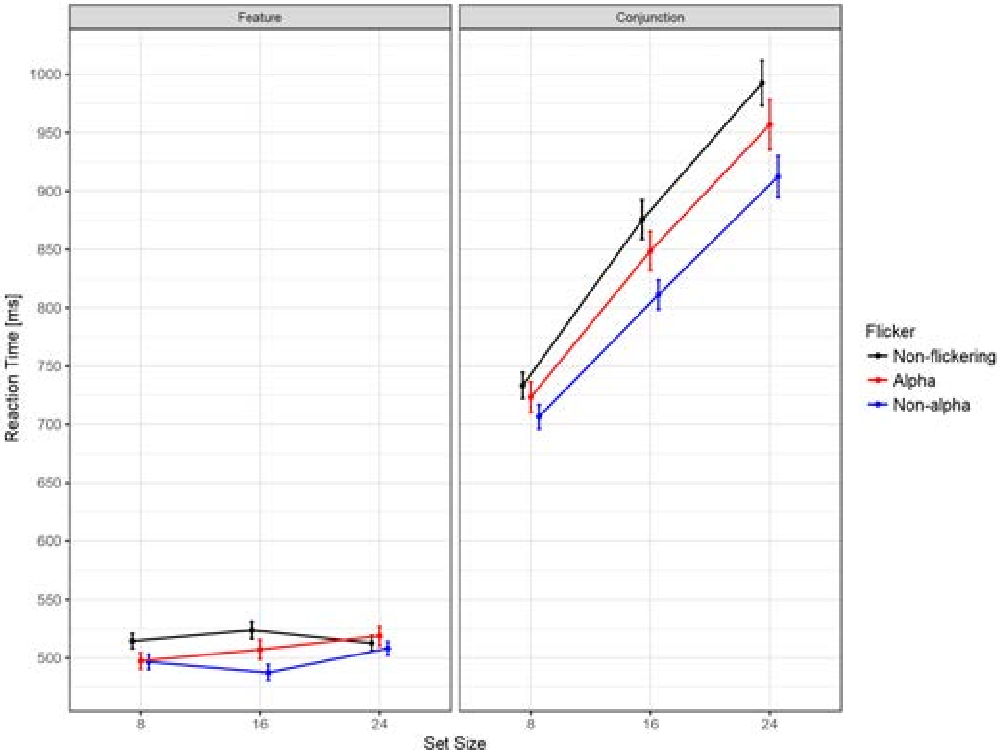

Figure 3.7: Mean reaction times for every condition of visual search and stimulation type as a function of set size in Experiment 2. Error bars indicate standard error of the mean.

effect may be related to the design of the study, since the full visual field was stimulated, while alpha entrainment effects have been shown to be pronounced in lateralized designs (Okazaki et al., 2015; Spaak et al., 2014). Thus, in Experiment 3 a lateralised stimulation design was used.

3.4 Experiment 3

To investigate the effect of a lateralized flickering stimulus, Experiment 3 was conducted using two flickering stimuli. Alpha and non-alpha flickering stimuli were presented simultaneously in the period prior to visual search onset. Drawing from previous research (Boncompte et al., 2016; Okazaki et al., 2015; Spaak et al., 2014) it was hypothesized that the two types of stimulation presented simultaneously, one in each hemifield will affect alpha oscillations in a lateralized fashion. Power of alpha oscillations was expected to increase contralateral to alpha flickering stimulus presentation and decrease contralateral to non-alpha flickering stimulus presentation. Thus, it was hypothesised that reaction times to targets appearing in the hemifield congruent to the alpha flickering stimulus will be longer than reaction times to targets presented incongruently.

3.4.1 Methods

3.4.1.1 Participants

12 University of Birmingham students were recruited (Chapter 2). 9 females and 2 males, with a mean age of 19.5 years (18-23). All subjects were included in the analysis.

3.4.1.2 Materials

Flickering stimulus: As in Experiments 1 and 2 visual repetitive stimuli were used to modulate endogenous alpha oscillation. Here, the flickering stimulus comprised of two frames (approximately 31 x 14.75 cm each, separated by a horizontal space of 1.5 cm in the centre of the screen) encompassing the whole area where the visual search display would subsequently be presented. Due to the design of this experiment only alpha and non-alpha flickering stimuli were used. Presenting flickering and non-flickering stimulus simultaneously may have biased the attention of the participants and thus confounded the results. Unlike the previous experiments stimulation duration in Experiment 3 was varied (either 700, 1400 or 2100ms). This variation was introduced to avoid participants' habituation to the rhythm of the trials across the block while preserving the phase of the entrainment fixed as in previous experiments. A fixation cross was presented in the centre of the display, and participants were asked to fixate on it for the whole duration of the flickering stimulus.

Visual Search Task: Visual search task used in this experiment was a modified version of the paradigm used in the previous experiments. Only conjunction condition was used. Set size conditions were reduced to 16 and 24. This was done to allow for the highest variability in behavioural measures. The distractor stimuli remained identical to Experiments 1 and 2. An additional potential target was introduced. Thus, the target could be, as in previous experiments, a red horizontal rectangle, or a green vertical rectangle. The rationale for introducing an additional target stimulus is provided in Chapter 2. As in previous experiments, the participants were asked to indicate the presence or absence of the target by responding with either 'a' (absent) or ‘p’ (present) key, as quickly and accurately as possible.

3.4.1.3 Design

A 2 x 2 within-subjects design was used (Table 3.4), with independent variables of congruency between the stimulation condition and target position (congruent: target in the same hemifield as alpha flickering stimulus; incongruent: target in the same hemifield as non-alpha flickering stimulus) and set size (16 and 24).

Table 3.4: Summary of the experimental design used in Experiment 3.

Conditions	Design	Levels
Congruency	Mixed	Congruent Incongruent
Set Size	Mixed	16 24
Target	Mixed	Present *Absent*

Note: Level in grey was excluded from the final analysis.

Stimulation conditions were manipulated in a randomised fashion, as were the target position, flickering stimulus duration and set size conditions, across 6 experimental blocks (fully counterbalanced, 64 trials per each block, a total of 384; 50% with target present).

3.4.1.4 Procedure

Participants were seated approximately 65 cm from the display screen, which gave approximately 13.4° visual angle of the flickering stimulus and visual search display in relation to the fixation cross in the centre of the screen. The trial sequence is presented in Figure 3.8.

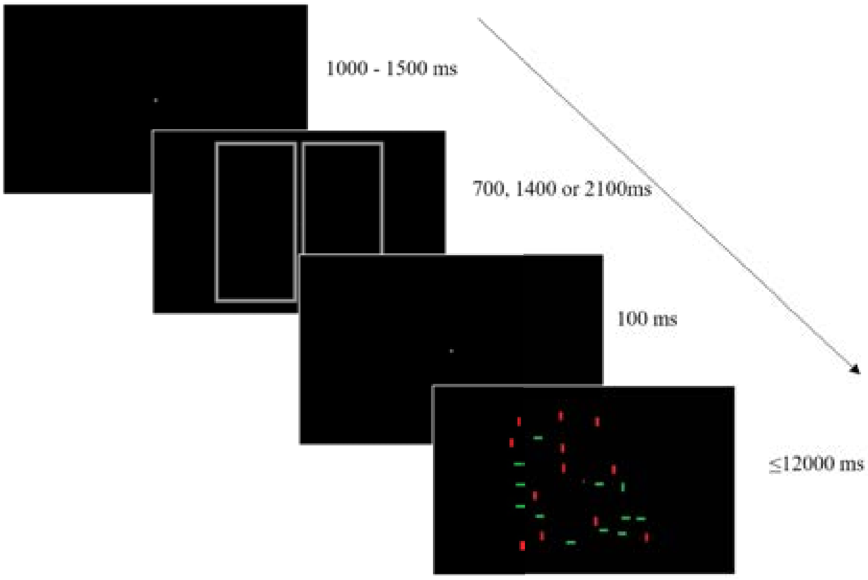

Figure 3.8: Example of a trial sequence in Experiment 3.

Each trial started with a centred cross (1000-1500ms), on which participants were required to maintain fixation. This was followed by the onset of the simultaneous presentation of two flickering stimuli, which lasted either 700ms, 1400ms or 2100ms. The visual search display was presented 100ms after the flickering stimulus offset and remained on the screen for a maximum of 12 seconds, or until a response was made. Each block of trials (6 blocks, 384 trials in total) was separated by a one minute break. The experimental session lasted approximately 30 minutes.

3.4.2 Results

RT means and SDs were calculated for target present trials for all conditions. The raw reaction time data (Figure 3.9) was trimmed as described in Chapter 2 . A descriptive summary of the data can be seen in Table 3.5.

The overall average accuracy was 89.32% (SD = 4.91%). The condition means plotted as a function of set size are shown in Figure 3.10. A statistical analysis was conducted using a repeated measures ANOVA, with independent variables of congruency (2) and set size (2). Significant main effect of set size (F (1, 11) = 26.2), p < .0001, η^2_G =.15) was found. No significant main effect of congruency (F (1, 11) = .318, p = .58, η^2_G =.001) was found. No significant interaction between set size and congruency (F (1,11) = .431, p = .52, η^2_G =.002) was found.

Table 3.5: Mean reaction times [ms] for all experimental conditions in Experiment 3.

Congruency	Set Size 16		Set Size 24	
Congruent	1732.64	(673.17)	1949.44	(748.75)
Incongruent	1728.16	(629.61)	1974.68	(865.47)

Note: The standard deviations are reported in parenthesis.

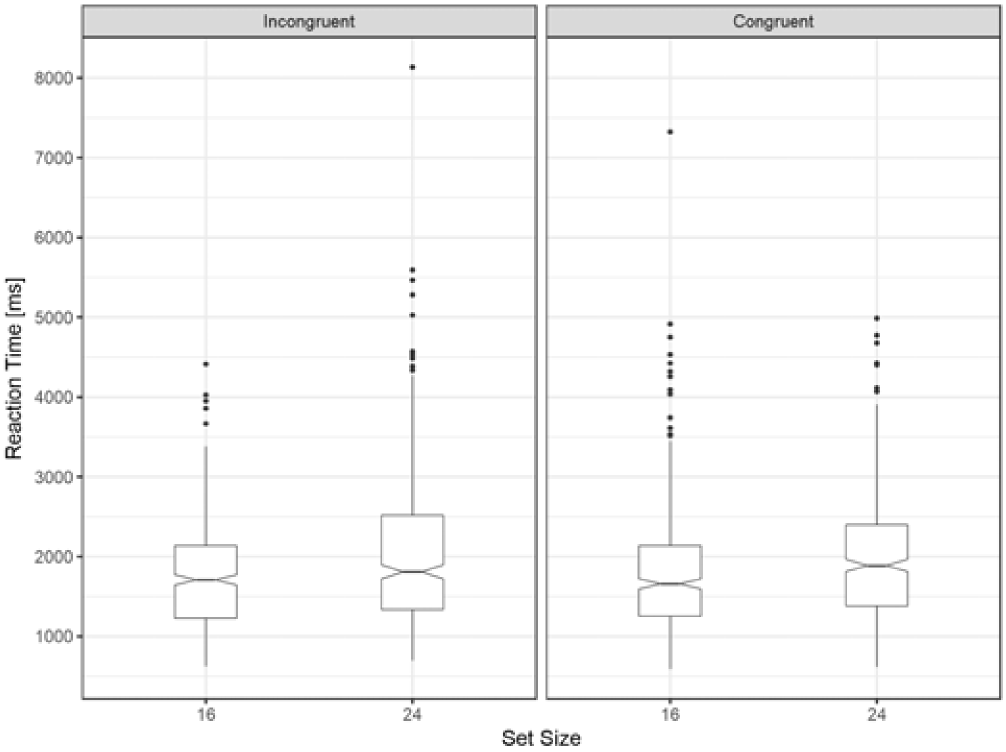

Figure 3.9: Raw reaction times for correct responses across all experimental conditions in Experiment 3.

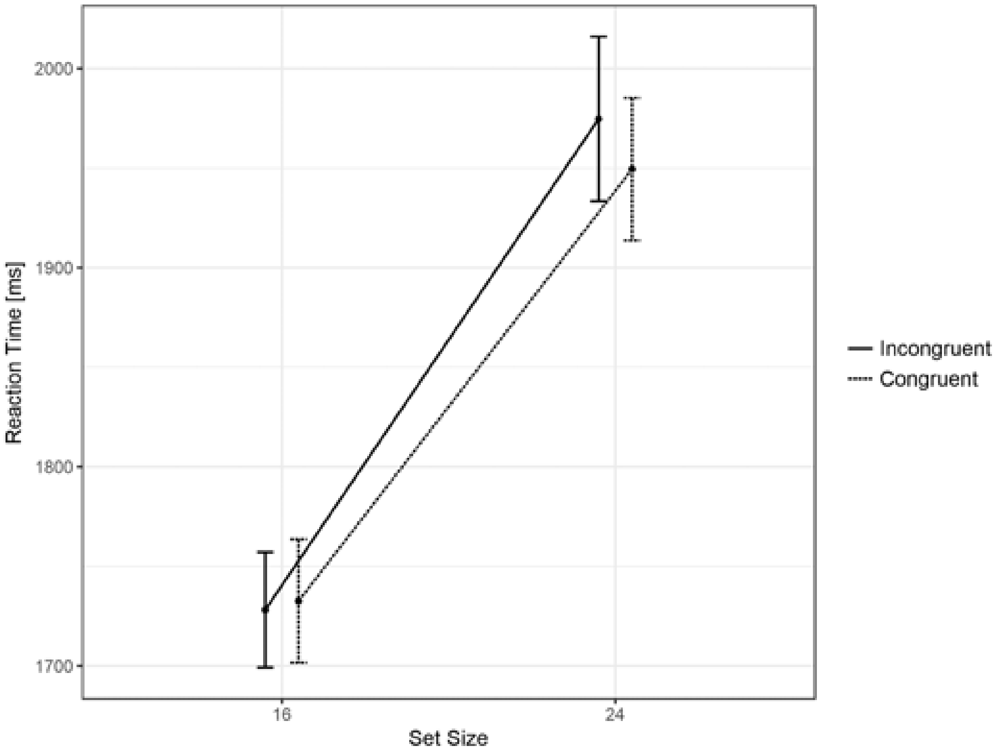

Figure 3.10: Mean reaction times for congruent and incongruent conditions as a function of set size in Experiment 3. Error bars indicate standard error of the mean.

3.4.3 Experiment summary

In summary, the hypothesised effects of flickering stimulus congruency with target position were not found. The inconsistent effects found across Experiments 1, 2 and 3, may suggest that the visual stimulation has little impact on performance in visual search. It is also plausible that the stimulation used in Experiments 1-3 may not have had the anticipated effects on subjects' underlying alpha oscillation. Hence, in Experiment 4 participants were presented with the flickering stimulus while continuous EEG signal was recorded, to assess whether the underlying alpha oscillations were affected by the visual stimulation.

3.5 Experiment 4

In Experiment 4 the efficacy of the visual flickering stimulation, used in previous behavioural experiments (specifically Experiment 2) was assessed using EEG. All three visual stimulation conditions were presented (non-flickering, alpha and non-alpha) while EEG was continuously recorded. This was done to investigate whether the anticipated entrainment of endogenous oscillations via visual flickering stimulus occurs and whether it differs between the stimulation conditions. The alpha flickering stimulus was anticipated to result in higher inter-trial phase coherence (ITPC) and an increased endogenous alpha power at approximately 10Hz indicating effective entrainment, as opposed to the non-alpha and the non-flickering condition. Furthermore, the entrainment effect was expected to persist after the offset of the flickering stimulus (Spaak et al., 2014). Participants did not have to perform any behavioural tasks.

3.5.1 Methods

3.5.1.1 Participants

6 University of Birmingham students (5 females, 1 male) with a mean age of 23 years (19-31), were recruited (Chapter 2). All subjects were included in the analysis.

3.5.1.2 Materials

Flickering stimulus: Flickering stimuli used in Experiment 2 were adapted for Experiment 4. As in experiment 3, flickering stimulus duration was varied to avoid habituation (either

700ms, 1400ms or 2100ms). The fixation cross was presented in the centre of the display, and participants were asked to fixate on it for the whole duration of the flickering stimulus.

3.5.1.3 Design

Stimulation conditions were manipulated by block, with 3 experimental blocks (72 trials per each block, a total of 216), counterbalanced across the participants using Latin square.

3.5.1.4 Procedure

Participants were seated approximately 65 cm from the display screen, which gave approximately 22° x 13° visual angle of the flickering stimulus in relation to the fixation cross in the centre of the screen. The trial sequence is shown in Figure 3.11. At the start of every trial, a white fixation cross was presented at the centre of the screen for 2000ms to avoid post-stimulus contamination. This was followed by a red fixation cross (1000ms) when participants were allowed to blink. Once the cross turned to white again it remained on the screen for 500MS to 1000ms and participants were not allowed to blink or move their eyes away from the fixation for the remainder of the trial. This was followed by the onset of the flickering stimulus which lasted either 700, 1400 or 2100ms. EEG signal was recorded continuously during the experiment. The experimental session, excluding the EEG set up, lasted approximately 15 minutes.

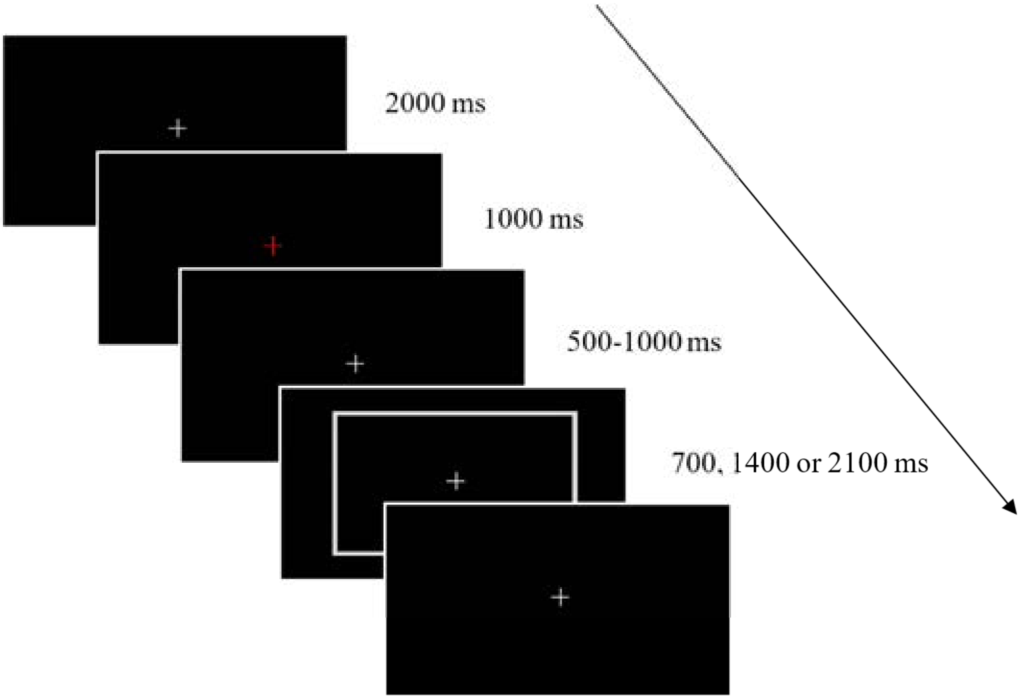

Figure 3.11: Example of a trial sequence in Experiment 4.

3.5.1.5 EEG Recording and Analysis

ERP waveforms, as well as the inter-trial phase coherence (ITPC) and power of alpha oscillations were analysed to ascertain the effect of the visual stimulation. EEG recording and pre-processing were conducted as described in Chapter 2, with epochs cut into 6-second trials (-3s to 3s). For the analysis of ERP waveforms, the epochs were locked to the onset of the stimulation. For the analysis of ITPC and alpha power, epochs were locked to the offset of the stimulation. Epochs longer than specified in Chapter 2 were chosen due to the experimental design (stimulation duration between 700ms - 2100ms). All epochs were baseline corrected to 200ms window prior to flickering stimulus onset.

Analysis of ERPs Prior to ERP averaging, data were high-pass (0.1 Hz) and low-pass (30 Hz) filtered using a finite impulse response filter, with mirror padding of 10 seconds on the epochs.

Analysis of ITPC For inter-trial phase coherence analysis, the number of artefact free trials per subject, per condition were equalized (random draw of a minimum number of trials, 51). Complex Fourier spectrum was obtained using a multi-taper-method convolution ('mtmconvol' method for ft_freqanalysis, as in FieldTrip software), with Hanning taper, on frequencies between 2 and 30 Hz in steps of 1 Hz, and a sliding time window set to 4 cycles per frequency. The inter-trial phase coherence is an estimation of event-related synchronisation of activity, as measured by phase angle clustering (Delorme and Makeig, 2004). ITPC was calculated by taking the absolute value of a complex mean of normalised Fourier values:

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

Differences between experimental conditions were quantified, as specified in Chapter 2, using a cluster permutation test, and the pre-specified region of interest encompassing occipital electrodes (Figure 2.5). The time windows used for analyses were 1 second from the stimulation onset for the analysis of ERPs, and a 1-second pre-, to 1-second post-stimulation offset time window for the analysis of ITPC and power.

Analysis of alpha power Time-frequency spectrum for the analysis of alpha power was calculated as described in Chapter 2, using a 2 second time window (-1 to 1 second, locked to stimulation offset) and a narrow alpha frequency band (9 to 11 Hz). The frequency band of interest was chosen as the alpha flickering stimulus frequency ±1Hz. For the purposes of statistical analysis data were averaged across frequency only.

3.5.2 Results

Analysis of the ERPs

No amplitude modulation of event-related potentials, driven by the flickering stimulation, was observed in alpha condition as compared to other conditions. No statistically significant differences were found between the ERP waveforms following a cluster-based permutation test. The ERP waveforms for all conditions are presented in Figure 3.12.

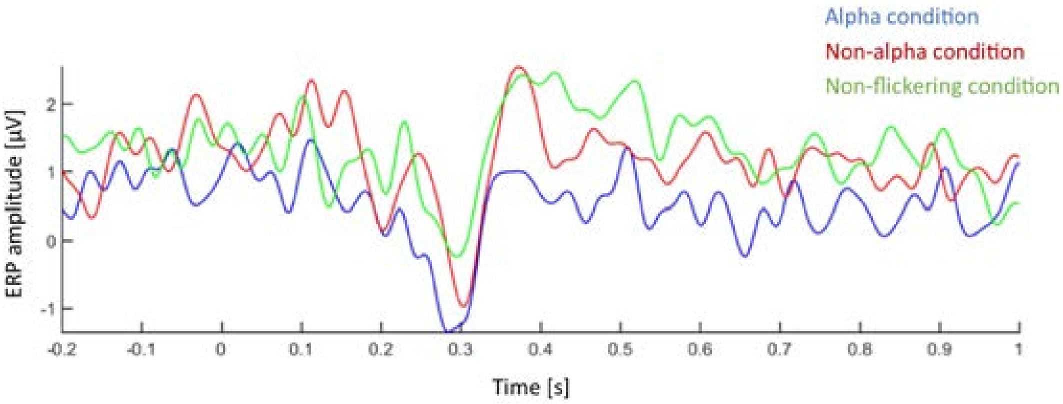

Figure 3.12: Grand averaged ERP waveforms of non-flickering (green), alpha (blue) and non-alpha (red) stimulation conditions, during visual stimulation. Time = 0 indicates the onset of the flickering stimulus.

Analysis of ITPC

No significant differences between the conditions were found in the ITPC during stimulation period. A significant difference was found between non-flickering and non-alpha flickering stimulation conditions post stimulation offset (from approximately -19ms to 270ms), with non-flickering condition showing significantly higher ITPC than non-alpha condition ($p < 0.001$, $T = -716.39$). This effect corresponded to the timespan of an ERP component resulting from the offset of the non-flickering stimulus (Figure 3.13).

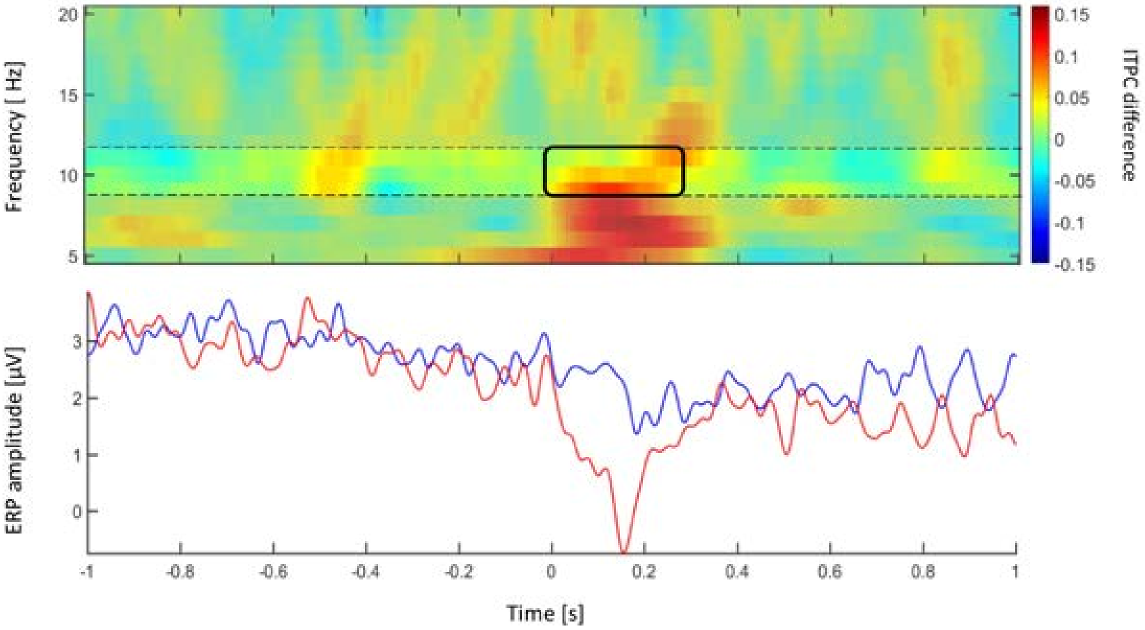

Figure 3.13: Top: Inter-trial phase coherence difference plot between non-flickering and non-alpha conditions, with an indicated frequency band of interest. Black outline indicates the significant difference between conditions. Bottom: Grand averaged ERP waveform of non-flickering (red) and non-alpha (blue) conditions. Time = 0 indicates the offset of the flickering stimulus.

Analysis of alpha power

No differences between alpha and non-alpha conditions, or alpha and non-flickering conditions were found in power of alpha oscillations. A comparison of non-flickering and non-alpha flickering stimulation conditions resulted in a significant cluster ($p < 0.001$, T = -62.57, Figure 3.14), whereby the non-flickering condition was found to be higher in power over a 150ms period during visual stimulation (-249ms to 101ms, Figure 3.15).

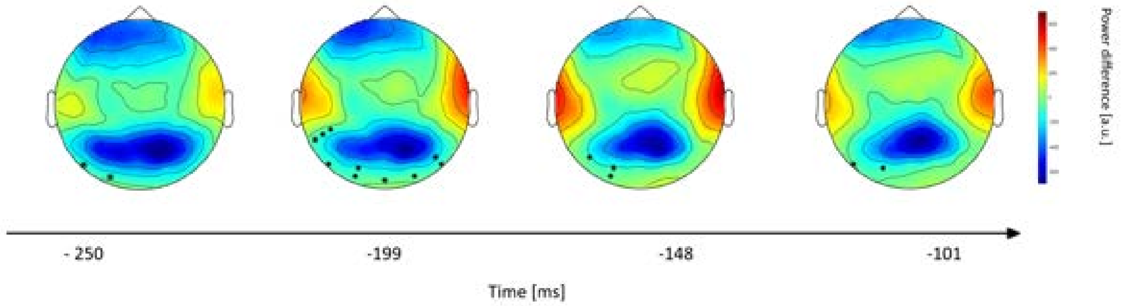

Figure 3.14: Topographical power difference plots between non-flickering and non-alpha conditions, with significant clusters marked. Time indicates the period prior to flickering stimulus offset.

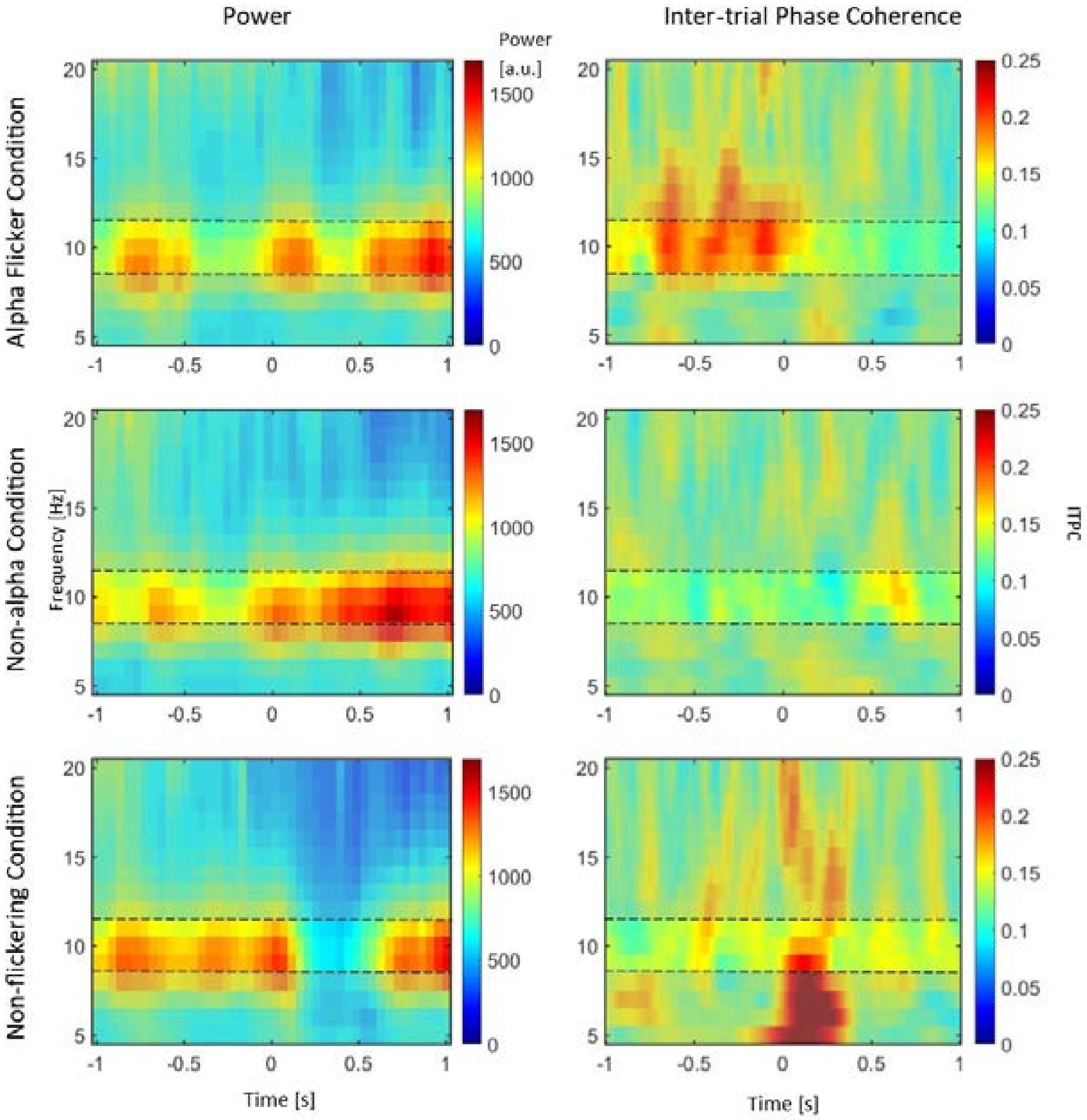

Figure 3.15: Time-frequency plots of power (right) and ITPC (left) for all stimulation conditions: alpha (top), non-alpha (middle) and non-flickering (bottom); with an indicated frequency of interest.

3.5.3 Experiment summary

Summarising, the results of Experiment 4 suggest that visual stimulation used to entrain the endogenous alpha oscillations did not result in the anticipated neural response. Neither power nor ITPC of alpha oscillations were increased during or post-stimulation offset in the alpha stimulation condition, as compared to non-alpha or non-flickering conditions.

3.6 Discussion

The experiments presented in this chapter aimed to clarify and expand the understanding of the effect of rhythmic visual stimulation on attention. The association between alpha power decrease and processing facilitation, as well as alpha power increase and the inhibition of visual stimuli, is widely accepted (Boncompte et al., 2016; Haegens et al., 2011). Previous studies, investigating the effects of repetitive visual stimulation, typically used singular, near visibility threshold stimuli (Graaf et al., 2013; Mathewson et al., 2012; Spaak et al., 2014; Worden et al., 2000). However, in everyday life, target detection tends to involve scanning through multiple irrelevant or distracting objects. Here, a visual search task (cf. Chapter 2) which mirrors such situations, was used.

Using a salient flickering stimulus (Experiment 1), covering the whole area of the upcoming visual search display, was predicted to result in faster (following non-alpha condition) or slower (following alpha condition) target detection. This hypothesis was not supported, as no differences were found between the stimulation conditions. These null results may be due to the saliency of the flickering stimulus covering approximately 70% of the whole screen. Indeed, it has been demonstrated that flickering stimuli below the critical flicker frequency[4] induce visual fatigue (Zhu et al., 2010). Previous research reports participants to subjectively describe a whole display flickering at lower frequencies (<60 Hz) as 'uncomfortable' or even 'intolerable' (Collins and Hopkinson, 1957). Following the completion of Experiment 1, some participants reported having experienced illusory precepts while the flickering stimulus was being presented. These potential motion illusions, induced with stroboscopic stimuli, have been previously reported in the literature (Mathewson et al., 2009, 2012). The effects of fatigue, combined with potential motion illusions may have had a detrimental effect on performance, and thus confounded and mitigated the effect of visual stimulation on target detection.

Hence, in Experiment 2 a less salient stimulus, a peripheral frame, was used. Here, the significant effects of the flickering stimulus in non-alpha condition as compared to non-flickering condition were observed. Non-alpha flickering stimulus was used to inhibit alpha power, which in turn, was expected to induce an advantageous anticipatory state and result in faster target detection. Results show that with non-alpha flickering stimulus participants were on average 31-76ms (depending on set size) faster in the conjunction condition as compared to non-flickering stimulus control (between 4.5ms and 36ms in feature condition).

However, the results do not support the hypothesis with respect to the anticipated RT disadvantage in alpha condition as compared to other stimulation conditions. No significant differences between alpha and non-alpha conditions, nor between alpha and non-flickering control conditions were found. Arguably, this result could be due to the task type, where participants grow tired and, therefore, endogenous alpha levels may already be high. This could have mitigated

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[4] Critical flicker frequency: frequency threshold above which flickering stimulus is seems indistinguishable from non-flickering stimulus (Wells et al., 2001)

any effect of the visual stimulation on the power of alpha oscillations. However, the power of alpha oscillations observed in Experiment 4 seemed to be lower in alpha condition compared to the non-flickering condition. Although this difference was not significant, it indicates that a ceiling effect is not a likely explanation. Mathewson et al. (2009, 2012) show that targets presented in-phase with the visual stimulation are more readily detected when the power of alpha oscillations is high, while low alpha power attenuates the phase effect. This may potentially affect the results presented here, as the visual search display onset in all experiments (1-3) was always presented in phase with the offset of the flickering stimulus. Thus, the results of Experiment 2, may indicate a combination of the in-phase presentation effect (alpha condition) and inhibition of alpha power (non-alpha condition). The null result of alpha stimulation condition could also be explained by the continuous cortical inhibition hypothesis, whereby only a power decrease of alpha oscillations would effectively affect target detection. Meanwhile, a power increase would not have a significant effect, as baseline levels of alpha oscillations represent a continuous suppression of stimuli (Sauseng et al., 2005). However, this hypothesis has been disputed by a significant number of studies showing inhibitory effects of alpha power increases (Rihs et al., 2009).

An alternative explanation may be that the results observed are an effect of general, non-frequency specific ‘awakening’ (Ariga and Yokosawa, 2008). The flickering stimulus, irrespective of the frequency, maintains continuous alertness of the system, thus resulting in quicker responses as compared to the non-flickering condition. Some support for this explanation is provided by Experiment 4 results, where non-flickering control condition results in the highest power of alpha oscillations across all conditions, and significantly higher than in non-alpha condition specifically. Moreover, the effect of flickering stimulation in Experiment 2 could be speculated to result from the rhythmicity of the experimental procedure. The periodicity of the trial sequence in the non-flickering and alpha conditions may result in habituation to the rhythm of the task block, as opposed to the non-alpha stimulation. Despite the consistent 100ms of inter-stimulus interval separating stimulation offset and visual search onset, the apparent temporal predictability of the oncoming visual search task is lower. Increased vigilance may, therefore, result in faster reaction times in the non-alpha condition.

The potential effect of visual flickering stimulation on target detection was further explored in Experiment 3, by presenting the flickering alpha and non-alpha stimuli simultaneously in two respective hemifields of the display. This modulation was expected to result in alpha lateralisation (Boncompte et al., 2016; Okazaki et al., 2015; Spaak et al., 2014). Power of alpha oscillations contralateral to the alpha flickering stimulus was expected to increase, while a decrease was expected ipsilateral to alpha stimulus presentation. Detection of the target presented congruently to the alpha stimulus was expected to be slower, as compared to detection of the target presented in the incongruent hemifield. This hypothesis was not supported by the results. Arguably, both flickering stimuli were presented very close to the fixation cross potentially negating each other's effects. Moreover, the results of Experiment 4 indicate that visual stimulation may not have resulted in the anticipated modulation of the underlying alpha oscillation.

To address the inconsistent results of Experiments 1, 2 and 3, in Experiment 4, EEG was used to assess whether the flickering stimulus does affect the endogenous alpha oscillation. It was anticipated that alpha stimulation will result in a pronounced entrainment, observable in an ERP waveform during flickering stimulus presentation. Alpha stimulation condition was also expected to be characterised by higher power and inter-trial phase coherence as compared to non-alpha stimulation and non-flickering condition. Entrainment effects were expected to persist after the flickering stimulus offset (Spaak et al., 2014), and thus affect the performance on the visual search task (in Experiments 1-3). However, neither an increase in ERP amplitude nor a periodicity of the waveform resulting from alpha stimulation was observed. The only significant difference in power of alpha oscillations was found between non-flickering and non-alpha conditions in a 150ms time window during stimulation. However, no anticipated power difference between the conditions was found post stimulation offset. This suggests that the period when the visual search was presented in Experiments 1-3 was likely not affected in an expected manner. Similarly, no significant difference was found in the inter-trial phase coherence measure between the conditions during the visual stimulation. In was concluded that flickering stimuli, used in the behavioural experiments did not effectively entrain the underlying oscillation. This may be due to the design of the flickering stimulus used. It has been shown that the effect of flickering stimulus diminishes with increasing visual angle of presentation (Parks et al., 2013). It may be, that the wide visual angle of the stimulus could not result in a strong enough entrainment of the underlying alpha oscillations for performance to be affected. Moreover it has been recently demonstrated that the effects of visual entrainment may be dependent on the frequency of the individual alpha oscillation. It has been proposed that the closer the stimulation frequency to the individual alpha frequency, the stronger the effect (Gulbinaite et al., 2017). It is likely that the effects of 10 Hz stimulation used in Experiments 1-4 were attenuated.

3.6.1 Chapter conclusions

Four experiments presented in Chapter 3 aimed to explore the relationship between alpha oscillations and performance on a visual search task. The effect of visual stimulation on endogenous alpha oscillations and reaction times was investigated. It was anticipated that visual stimulation in alpha condition will result in higher power and an increased ITPC of alpha oscillations as opposed to non-alpha and non-flickering conditions. Experiments 1-3 used behavioural measures, while Experiment 4 used EEG to assess the effects of stimulation conditions. No differences between alpha and non-alpha, nor alpha and non-flickering conditions, were found. The results of Experiment 4 indicate that the flickering stimulation did not result in entrainment of alpha oscillations.

Chapter 4

Exploring the relationship between alpha oscillations and target detection in a visual search task

4.1 Introduction

The experiments presented in Chapter 3 aimed to investigate the effects of entrainment of alpha oscillations, via visual stimulation, on performance in a visual search task. To this end, a flickering stimulus was used, presented either in alpha (10 Hz) or non-alpha (arrhythmic flickering, with a mean of 10Hz) frequency. No difference was found in reaction times between the two stimulation conditions in the behavioural experiments (1-3). Furthermore, no differences in the power or the inter-trial phase coherence of the underlying alpha oscillations were found between the stimulation conditions in Experiment 4. Thus, it was concluded that the intended entrainment of the alpha oscillations was not successful.

Experiments 1 to 3 were conducted under the assumption that the power of pre-stimulus alpha oscillations would affect the performance on the visual search task. This was inferred from previous research associating alpha oscillations with modulation of performance on attentional tasks (Feng et al., 2017; Händel et al., 2011; Hanslmayr et al., 2007; Okazaki et al., 2015; van Diepen et al., 2016). Decreases of alpha oscillatory activity were related to facilitation of processing, while increased activity was demonstrated to reflect inhibition of unattended locations, and/or distracting information (Feng et al., 2017; Jensen and Tesche, 2002; Kizuk and Mathewson, 2017; Klimesch et al., 2007; Thut et al., 2006). Likewise, studies employing lateralization paradigms provide evidence showing an effect of alpha oscillations on performance. High alpha power lateralization in response to a predictive cue was demonstrated to show improved reaction times and accuracy, while the lack of lateralisation, or it's opposite pattern (i.e. induced by an invalid cue) results in impaired performance (Boncompte et al., 2016; Haegens et al., 2011; van Diepen et al., 2016). It has been proposed that alpha oscillations reflect fluctuations of cortical excitability (Lange et al., 2013). In their study, Haegens et al. (2011) demonstrated that increases in alpha power were associated with improved performance, as well as decreases in neuronal spiking in monkey sensory cortices. Recently a number of studies indicated that, while alpha power affects target detection rates, it also affects the false alarm rates, in that high alpha power was associated with lower hit rates and lower false alarm rates, as compared to low alpha power. Thus it was proposed that alpha oscillations affect the criterion (the likelihood of reporting the target whether or not it is actually presented on the screen) rather than the sensitivity index (the actual detectability of the target stimulus; Iemi et al., 2017; Limbach and Corballis, 2016).

The phase of pre-stimulus alpha oscillations was also shown to predict performance on attentional tasks (Hanslmayr et al., 2007, 2013; VanRullen and Dubois, 2011). Numerous studies report perceptual effects mediated by alpha phase, where certain phases are optimal for perception, while others are disadvantageous to performance (Dugué et al., 2011; Gulbinaite et al., 2017; Mathewson et al., 2009). Hanslmayr et al. (2013) investigated the effects of low alpha (7Hz) phase on perception in a combined EEG-fMRI study. Researchers have asked the participants to detect a contour of aligned Gabor patches among non-aligned stimuli. They report that trials with correct detections and trials on which the target was missed show clustering in opposite phases (π for hits and 0 for misses). Similarly, Busch et al. (2009), have demonstrated increased phase locking for perceived and for undetected near threshold flashes of light. Furthermore, adjustment of pre-stimulus phase in preparation for an oncoming distractor resulted in faster reaction times in working memory tasks (Bonnefond and Jensen, 2012), further supporting the role of alpha oscillations in inhibition of task-irrelevant stimuli.

The existing research predominantly employs target detection tasks with cued, near visual threshold target presentation, with either single distractor or no distractors at all. This, thus, cannot be directly related to a typical visual search task, where the target and multiple distractors, all above the visual threshold, are presented concurrently. Previously described studies investigating the effects of alpha oscillations in a visual search task (Chapter 3), did not investigate the period directly prior to visual search onset, but report effects of alpha modulation during visual search task (Gonzalez-Rosa et al., 2015), alpha entrainment on preceding days

(Müller et al., 2015), or with regards to a modified version of visual search task with preview benefit[1] (Spaak et al., 2016).

However, recently Van Den Berg et al. (2016) investigated performance on a visual search task in the context of preparatory neural mechanisms. Participants engaged in a feature search task ("pop-out"; cf. Chapter 2) over 5 sessions. They were asked to discriminate the orientation of the target, which was presented simultaneously with neutral placeholders and a single distractor. Researchers demonstrate a significant improvement in task performance over time in an experimental session, as well as over consecutive sessions. They propose this behavioural improvement to be related to optimization of preparatory attention, as reflected by pre-stimulus alpha oscillations. Van Den Berg et al. (2016) show a significantly lower pre-stimulus alpha power for trials with fast reaction times, as opposed to trials with slow reaction times. This finding follows the premise that low pre-stimulus alpha power results in the facilitation of target detection and discrimination. On the other hand, Mazaheri et al. (2011) show posterior alpha power increase prior to a successful execution of a saccade to the target, in presence of a salient distractor. They conclude that increased pre-saccadic parietal alpha oscillations play a role in inhibiting intruding bottom-up information.

In this chapter, an exploratory electroencephalographic (EEG) study extending this line of research is presented. In Experiment 5 the role of spontaneous pre-stimulus alpha oscillations, with regards to performance on a conjunction visual search (VS) task, was investigated. There was no experimental modulation during the pre-stimulus period, therefore the participants were

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[1] Preview benefit represents a decreased competition of a subset of distractors, resulting from presentation of said distractors prior to presentation of the entire visual search display (Meinhardt, 2015).

naïve as to which of the two possible targets will be presented during the subsequent trial. Likewise, they were not aware of where on the display the target might appear, nor of the number of objects that will be presented on the screen. The power of pre-stimulus individual alpha frequency (±1 Hz; IAF) was related to reaction times (RTs) in a number of analyses:

1. A correlation analysis between IAF power and RTs was conducted, followed by alpha power comparison between fast and slow RT bins. The existing research associated alpha power increases with inhibition of visual stimuli, and alpha power decreases with facilitation of target detection (Feng et al., 2017; Jensen and Tesche, 2002; Kizuk and Mathewson, 2017; Klimesch et al., 2007; Thut et al., 2006). Consequently, one of two potential outcomes could be anticipated. A positive relationship could be observed, with low alpha power related to fast RTs, and high alpha power related to slow RTs. This would be in line with research wherein decreased alpha power was shown to be beneficial for single stimulus detection, while high alpha power was associated with worse target detection performance (Van Den Berg et al., 2016). Alternatively, a negative relationship could be found, with high IAF power related to improved performance, indicating that alpha oscillations affect distractor inhibition (Klimesch et al., 2007; Mazaheri et al., 2011).

2. Considering the recent evidence suggesting that alpha oscillations reflect a criterion modulation rather than increased sensitivity index, the behavioural measures of criterion and sensitivity index for fast and slow RT bins were investigated.

3. Previous research shows performance improvement in VS task over the time of the experimental session and associates these effects with pre-stimulus alpha power changes over

time (Van Den Berg et al., 2016). Thus, the effect of time in experimental session was explored with regards to alpha power, as well as performance.

4. The relationship between IAF phase and RTs was investigated. Phase of alpha oscillations was expected to correlate with reaction times, in line with the body of research showing phase related modulation of performance on attentional tasks (Hanslmayr et al., 2007, 2013; VanRullen and Dubois, 2011).

4.2 Experiment 5

In Experiment 5, EEG was recorded during a conjunction visual search task to explore the relationship between pre-stimulus alpha oscillations and performance. Participants were naïve as to the time of the onset of visual search display, number of object that would be presented, the type of target used in a given trial, or where it may be located within the display. Visual search comprised of above visual threshold objects, the number of which was determined by set size condition. Spontaneous alpha oscillations prior to visual search onset were analysed with respect to reaction times. Two possible outcomes could have been anticipated: a positive relationship, with high alpha power being detrimental to performance, and low alpha power facilitating fast target detection; alternatively, a negative relationship, with high alpha power reflecting successful inhibition of distractors, and resulting in improved performance. Furthermore, pre-stimulus alpha phase was expected to correlate with performance on the task.

4.2.1 Method

4.2.1.1 Participants

21 University of Birmingham students (6 males and 15 females) were recruited for the study according to the sampling procedure described in Chapter 2. Two participants withdrew during the recording session, data from one participant were discarded due to chance level performance (random button presses), and one participant was excluded, due to being identified as a behavioural outlier (determined as described in Chapter 2). Data from 17 subjects (5 males) with a mean age of 23 (19-31) were used in the analysis.

4.2.1.2 Materials

Visual search task A conjunction visual search paradigm with two set size conditions, target present and target absent trials, and two potential targets types, was used in Experiment 3.

4.2.1.3 Design

Behavioural differences between set size conditions A within-subjects design was used, with the independent variable of set size (16 and 24), and dependent variable of RT in target present condition for correct trials. The experimental design summary is presented in Table 4.1.

Table 4.1: Summary of the experimental design used in Experiment 5.

Conditions	Design	Levels
Visual Search	Blocked	Conjunction
Set Size	Mixed	16 24
Target	Mixed	Present *Absent*

Note: Level in grey was excluded from the final analysis.

Signal detection behavioural analysis Signal detection theory (Peterson et al., 1954) is used to examine decision making in presence of uncertainty (i.e. in the case when a stimulus is near the visibility threshold, or ambiguous stimuli are being presented), when the responses are binary (i.e. “yes” vs. “no”, or “present” vs. “absent”). The sensitivity index (*d’*) indicates the difficulty of discriminating the signal from the noise; while the criterion (β) indicates how likely it is that the signal will be classified as noise, and vice versa. Here, the uncertainty related to whether the target stimulus was present on a given trial. The sensitivity index measured the difficulty of correctly detecting the target stimulus, with higher values reflecting better performance. The criterion reflected the likelihood of reporting the target as present, whether the target was actually presented on the screen or not, with lower values (a more liberal criterion) reflecting an increased likelihood of responding “target present”, and higher values (a conservative criterion) indicating a tendency to respond with “target absent”.

To perform this behavioural analysis correct and incorrect responses were included in the data, for both target present and target absent conditions. Data was trimmed (cf. Chapter 2) and binned into fast and slow conditions across both set sizes, with fast bin encompassing the third of fastest trials for each subject, and slow bin a third of trials characterised by slowest reaction times. Sensitivity index and criterion were determined using normalised hit rate (proportion of hits in all target present trials) and false alarm rate (proportion of false alarms in target absent trials), as follows:

$$d' = Z_{HR} - Z_{FA}$$

$$\beta = \frac{Z_{HR} + Z_{FA}}{(-2)}$$

In circumstances where hit rate or false alarm rate were equal to 0 or to 1, a correction was used (Macmillan and Kaplan, 1985; Stanislaw and Todorov, 1999), whereby rates equal to 0 were replaced with *0.5* $\div$ *n* (where n is the total number of target present or target absent trials accordingly), while rates which were equal to 1 were replaced with *(n – 0.5)* $\div$ *n*.

A 2 x 2 within-subjects design, with independent variables of set size (16 and 24) and reaction time bin (fast and slow) was used. The dependent variables were the sensitivity index and the criterion.

Time-in-session behavioural analysis A 2 x 2 within-subjects design was used. The independent variables were set size (16 and 24) and time in session bin (beginning and end), while the dependent variable was RT in target present condition for correct trials.

4.2.1.4 Procedure

Participants were seated approximately 65 cm in front of the display screen. The trial sequence with the time window of interest is presented in Figure 4.1. At the onset of each trial a fixation cross was presented in centre of the screen for 2000ms - 3000ms. A long inter-trial time was used to control for post stimulus contamination of the analysed time window. Participants were instructed not to blink or make eye movements during that period. Visual search display followed and remained on the screen until a response was given, or for a maximum of 12 seconds. All participants completed 2 practice and 13 experimental blocks (with a total of 832 trials, with 208 in each condition). All blocks were separated by breaks, duration of which was self-paced by the participant. EEG signal was recorded continuously during the experiment. Each experimental session, excluding EEG setup, lasted approximately 1.5 hours.

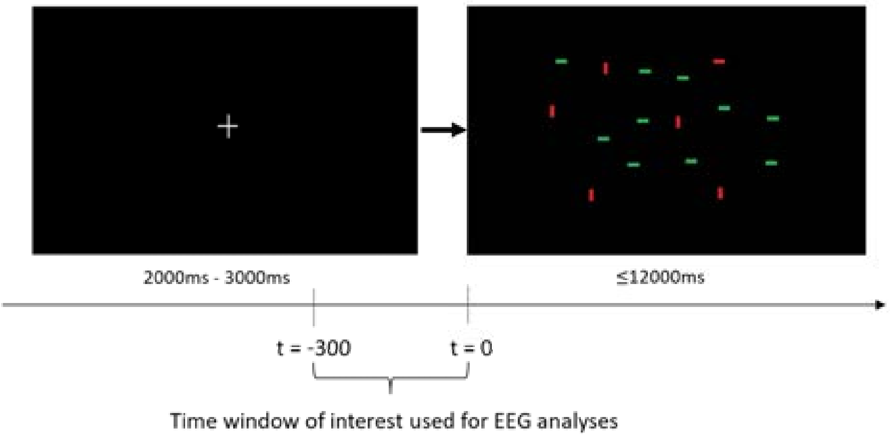

Figure 4.1: Example of a trial sequence in Experiment 5.

4.2.1.5 EEG recording and analysis

A series of EEG analyses were conducted to explore the relationship between pre-stimulus individual alpha oscillations and performance on a visual search task. Pre-processing was performed as described in Chapter 2. The time-frequency decompositions (TFR; -1000ms to 1000ms, locked to the onset of visual search) and statistical analyses were conducted as described in Chapter 2, unless otherwise specified. A 300ms time window of pre-stimulus period was used in all statistical analyses (Figure 4.1). Individual alpha frequencies per participant are shown in Table 4.2

Table 4.2: Individual alpha frequency per participant in Experiment 5.

Subject Number	IAF [Hz]
1	8.4
2	12.6
3	12
4	8
5	8.6
6	8
7	10.4
8	9
9	10.8
10	8.8
11	10.2
12	10.2
13	9.2
14	10.2
15	11
16	10.6
17	10

Comparison of IAF power between the set size conditions An analysis comparing IAF power between set size conditions was carried out. A difference between set size conditions was not anticipated as there was no modulation in the pre-stimulus period.

IAF power – RT correlation A correlation analysis was performed as described in Chapter 2. Power output for each time point (111, -1000ms to 100ms, in steps of approximately 9.8ms), frequency bin (9, in steps of 0.25 Hz) and channel (128) was correlated with RTs for each participant. Furthermore, the IAF power – RT correlations were also carried out in source-space in an analogous manner to the sensor - space analysis. To estimate the sources of the correlation effects, an LCMV beamforming method was used (see Chapter 2). Template volume conduction and source models as provided in FieldTrip (Oostenveld et al., 2011), with adapted BioSemi 128-channel layout, were used.

Power binned by RTs An analysis comparing alpha power of the slow and fast RT bins was carried out for both set size conditions. Data bins were determined by separating trials into bins based on two RT quantiles, where fast condition comprised of the fastest 3rd of the reaction times, while the slow condition of the slowest 3rd of reaction times, per condition, per subject.

Power binned by time-in-session The changes in IAF power and RTs over the duration of the experiment (time-in-session) were evaluated, using a third of trials from the beginning of the experiment, and a third of trials from the end of the session.

IAF phase - RT correlation A phase – RT correlation analysis was carried out. Uneven trial numbers are known to bias the results of phase analyses (Cohen and Steel, 2014; Hanslmayr et al., 2013). Thus, prior to calculating the correlation coefficients, trial numbers were equalized across conditions and participants using a random selection (94 trials per condition). Complex Fourier spectra were obtained using a Morlet wavelet-based TFR (3 cycles). Those values were subsequently transformed into phase angles (radians), and correlated with RTs using circular-to-linear correlation function (Berens, 2009). To assess the significance of the correlations, a permutation test was carried out. Randomized correlations, using shuffled reaction time values, were computed 50 times per participant. Subsequently, a 1000 grand-averages of randomized data were created. P-values of the observed correlations grand-average were then estimated per each time point and corrected for multiple comparisons using Benjamini-Hochberg correction (Benjamini and Hochberg, 1995).

Phase bifurcation index Due to the design of the study (no time-locked event in pre-stimulus period and a variable trial onset) the phase of pre-stimulus alpha oscillations should be randomly distributed across trials. Thus, an inter-trial phase coherence (ITPC) analysis could not have been used to explore the difference between trials with fast and slow reaction times. To investigate whether the fast and slow reaction time trials demonstrate specific phase concentration, the phase bifurcation index (PBI), was analysed. Busch et al. (2009) proposed PBI, as determined by comparing ITPC for fast and slow RT bins against ITPC for all trials, as a measure of phase opposition. If PBI is a positive value, the two conditions of interest exhibit a degree of phase locking (PBI of 1 suggests perfect phase locking), with opposite mean phase directions. If PBI is a negative value, it indicates phase locking of only one of the conditions. Here, PBI was calculated as follows:

$$\mathrm{PBI}_{(t,f)} = (ITPC_{fast(t,f)} - ITPC_{all(t,f)}) \times (ITPC_{slow(t,f)} - ITPC_{all(t,f)})$$

ITPC was calculated as described in Experiment 4, Chapter 3. The fast condition (*ITPCfast*) included a 3rd of trials with shortest reaction times, while the slow condition (*ITPCslow*) included a 3rd of trials with the longest reaction times, with the number of trials equalized per condition, for each subject. ITPCall contained the same number of trials as fast and slow conditions, drawn from ITPCfast and ITPCslow in a pseudorandomised fashion (half of the trials from each of the subsets; mean number of trials per condition = 44). To determine whether the PBI values differed significantly from zero, a permutation procedure analogous to the one employed in the correlation analysis was used. Trials were randomly assigned to the slow and fast condition. The phase bifurcation index was then calculated for these randomised conditions. This procedure was repeated 100 times for each subject. Subsequently a 1000 grand-averages were calculated. Based on the obtained random distribution, p-values were calculated for every time point and corrected for multiple comparisons using Benjamini-Hochberg correction (Benjamini and Hochberg, 1995).

4.2.2 Results

4.2.2.1 Behavioural analyses

Behavioural differences between set size conditions

The means and SDs of recorded reaction times (Table 4.3) were calculated for correct, target present trials in the two set size conditions. The raw data for correct responses across conditions is presented in Figure 4.2. Data was trimmed as determined in Chapter 2. Speed accuracy trade-off was found, with r = .52, p = .03, driven by one participant. However since they did not meet the exclusion criteria, their data was included in the final analyses[2].

Table 4.3: Trimmed mean reaction times [ms] per set size condition in Experiment 5.

Set Size 16		Set Size 24	
1773.54	(731.86)	2048.34	(894.52)

Note: The standard deviations are reported in parenthesis

Differences between set size conditions were evaluated by means of a paired-samples t-test (Figure 4.3). Set size 16 and set size 24 differed significantly (t (16) = 10.647, $p < .0001$, Δ M

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[2] After excluding subject 5 no speed accuracy trade-off was found (r = 0.43, p = .097). None of the effects of subsequent analyses differ when performed excluding subject 5.

= 266.03, with 95% CI [213.05, 318.99]), with set size 24 showing longer RTs as compared to set size 16.

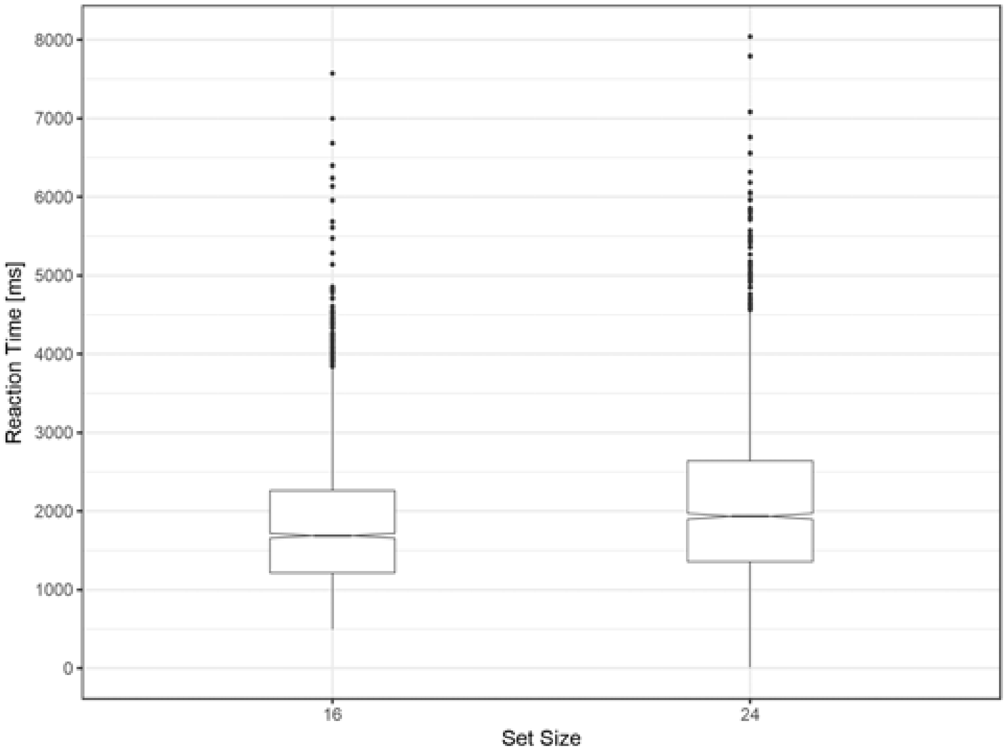

Figure 4.2: Raw reaction times for correct responses per set size condition in Experiment 5.

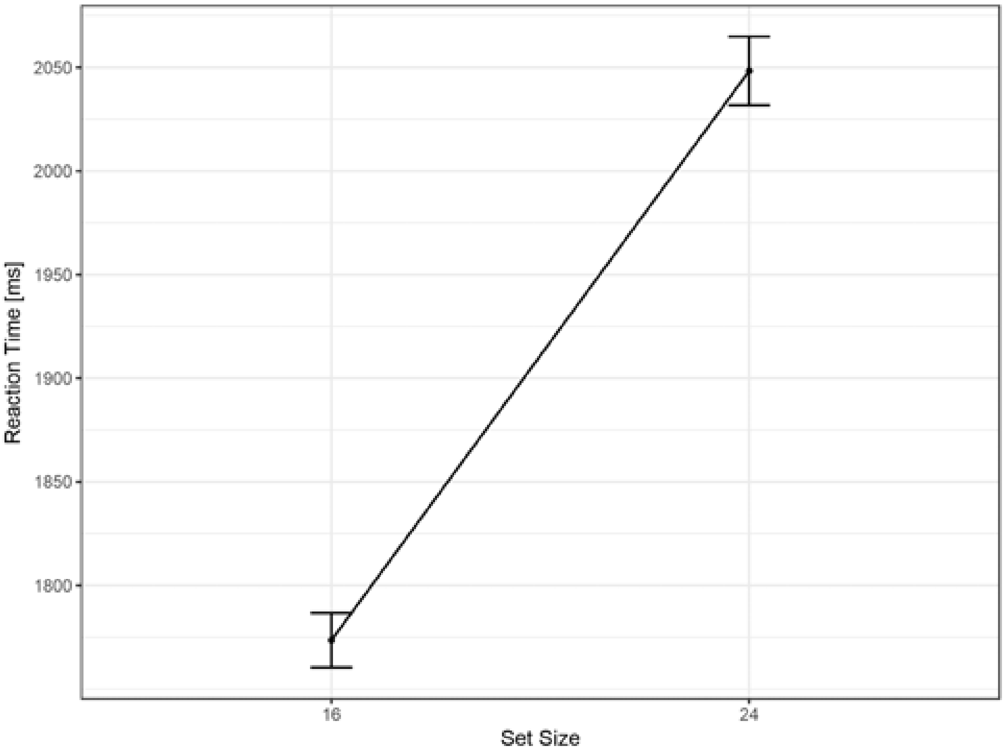

Figure 4.3: Mean reaction times as a function of set size in Experiment 5. Error bars indicate the standard error of the mean.

Signal detection behavioural analysis

The means and SDs of the sensitivity index and criterion for fast and slow RT bins were calculated for two set size conditions (Table 4.4). Differences between conditions were evaluated by means of a 2 x 2 repeated measures analysis of variance (ANOVA).

Table 4.4: Signal detection theory measures for all experimental conditions in Experiment 5.

SDT measure	Set Size 16				Set Size 24			
	Fast		Slow		Fast		Slow	
Sensitivity (d’)	4.316	(0.561)	3.271	(0.409)	4.286	(0.542)	2.929	(0.417)
Criterion (β)	0.124	(0.254)	0.735	(0.216)	0.005	(0.298)	0.892	(0.179)

Note: The standard deviations are reported in parenthesis.

Sensitivity index

Significant main effects of set size (F (1, 16) =5.67), $p < .03$, $\eta^2_G = .094$) and RT bin (F (1, 16) =147.14, $p < .0001$, $\eta^2_G = .812$) were found. A significant interaction between set size and RT bins (F (1, 16) = 4.94, $p = .041$, $\eta^2_G = .068$) was also found (Figure 4.4). Follow-up pairwise comparisons (Bonferroni corrected), revealed significantly higher sensitivity index for fast RT bin as compared to slow RT bin in both, set size 16 (t (16) = 8.543 , $p < .0001$, Δ M = 1.045, with 95% CI [.786, 1.304]) and set size 24 (t (16) = 11.267 , $p < .0001$, Δ M = 1.367, with 95% CI [1.102, 1.612]). Furthermore, there was a significant difference between set size 16 and 24 in the slow RT bin (t (16) = 4.414, $p = .002$, Δ M = .343, with 95% CI [.178, .507]), whereby set size 16 was characterised by higher sensitivity index than set size 24. No significant

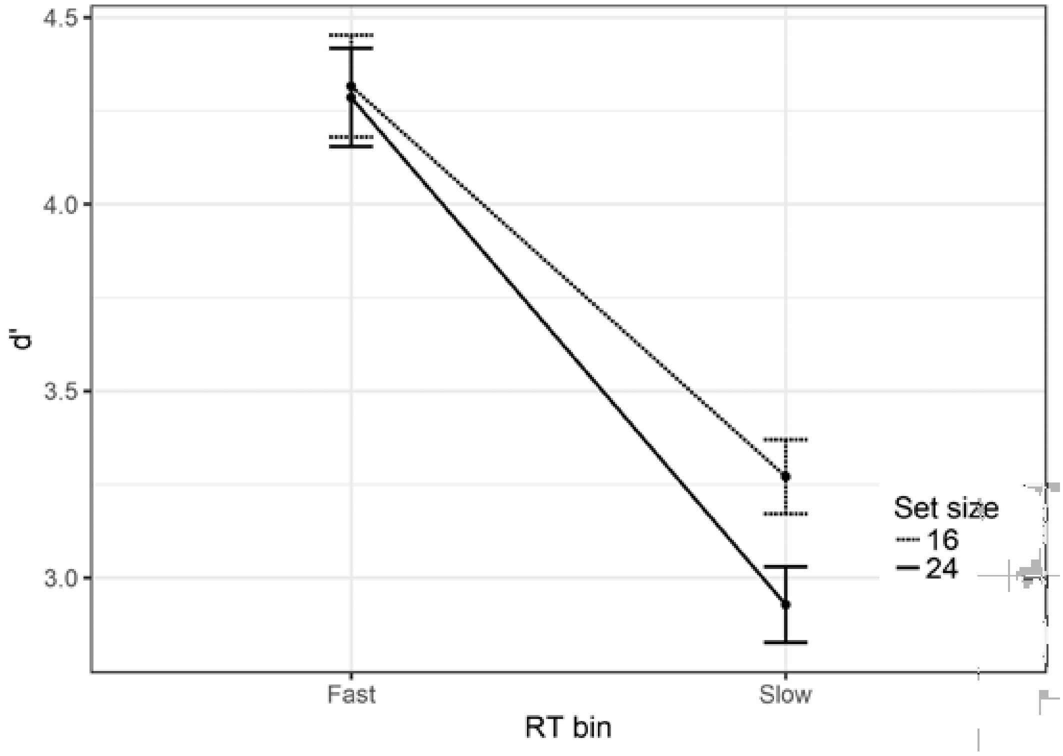

Figure 4.4: Means of the sensitivity index for set size 16 and 24 per reaction time bins. Error bars indicate the standard error of the mean.

difference between set sizes was found in the fast RT bin (t (16) = .239, p = 1.0, Δ M = 0.03, with 95% CI [-.239, .299]).

Criterion

A significant main effect of RT bin (F (1, 16) = 175.25, $p < .0001$, η^2_G =.87) was found, with fast RT bin characterised by lower criterion values. No significant main effect of set size was found (F (1, 16) =5.67), $p < .03$, η^2_G = .004). A significant interaction between set size and RT bin (F (1, 16) = 16.759, $p < .001$, η^2_G =.184) was also found (Figure 4.5). Follow-up pairwise comparisons (Bonferroni corrected) revealed significant differences in criterion between fast and slow RT bins in both, set size 16 (t (16) = -9.357, $p < .0001$, Δ M = -.612, with 95% CI

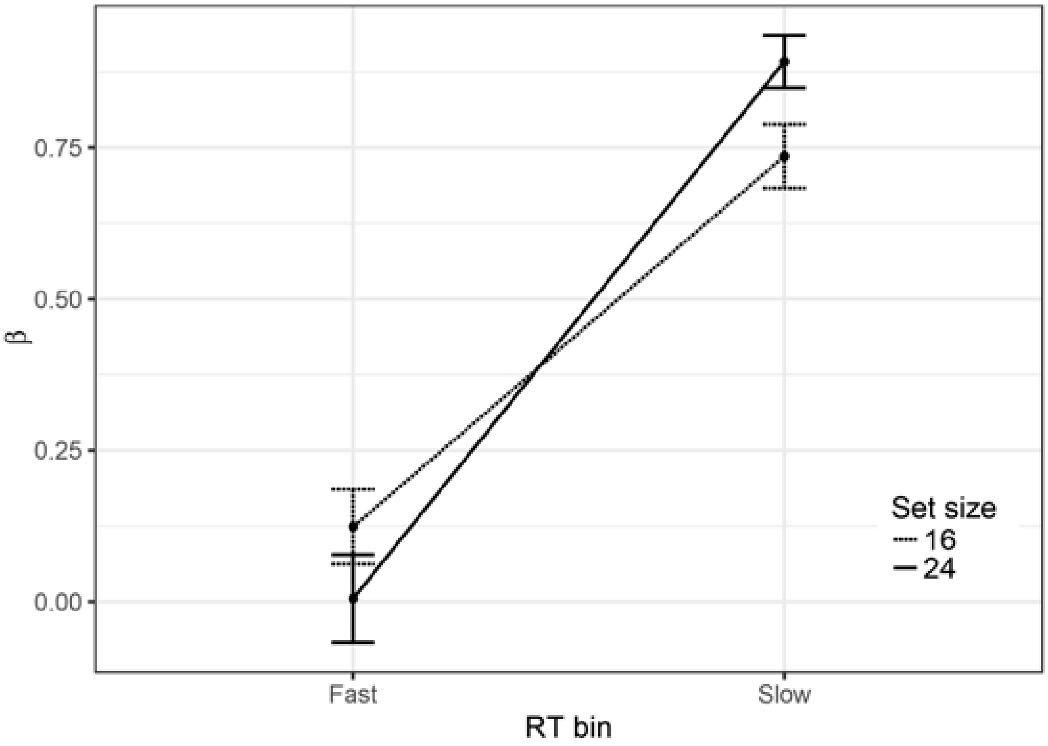

Figure 4.5: Criterion means for set size 16 and 24 as a function of reaction time bin. Error bars indicate the standard error of the mean.

[-.75, -.473]) and set size 24 (t (16) = -13.384 , p < .0001, ∆ M = -.887, with 95% CI [-1.027, -.746]). Whereby criterion values were significantly higher in the slow RT bin as compared to fast RT bin. Furthermore, a significant difference between set size 16 and 24 in the slow RT bin was reported (t (16) = 4.598, p = .001, ∆ M = -.156, with 95% CI [-.228, -.084]), with criterion value being significantly lower in the set size 16 as compared to the set size 24. No significant difference between set sizes was found in the fast RT bin (t (16) = 2.2, p = .17, ∆ M = 0.119, with 95% CI [.004, 0.233]).

Time-in-session behavioural analysis

To investigate the effect of time-in-session on RT, data was separated into a third of trials from the beginning of the session and third of the trials from the end of the session across set size conditions. Reaction times in both set size conditions were faster at the end of the session as compared to the beginning of the session (Figure 4.6).

Table 4.5: Mean reaction times [ms] for time-in-session bins per set size condition in Experiment 5.

Time in Session	Set Size 16		Set Size 24	
Beginning of the session	1908.07	(732.57)	2211.64	(888.07)
End of the session	1693.3	(723.03)	1967.74	(904.67)

Note: The standard deviations are reported in parenthesis.

A 2 x 2 repeated measures ANOVA was carried out to statistically assess the differences and interactions between the 2 set size and 2 time-in-session conditions. A significant main effect of visual search was found (F (1,16) = 68.636, p < .0001, η^2_G = 0.121), as well as a significant effect of time-in-session (F (1,16) = 47.25, p < .0001, η^2_G = .08), with RTs being significantly faster at the end of the session as compared to the beginning of the session (t (16) = 6.634, p

< .0001, Δ M = 219.845, with 95% CI [149.596, 290.093]). No significant interaction was found (F (1,16) = 0.383, p = .545, η_G^2 = .0005).

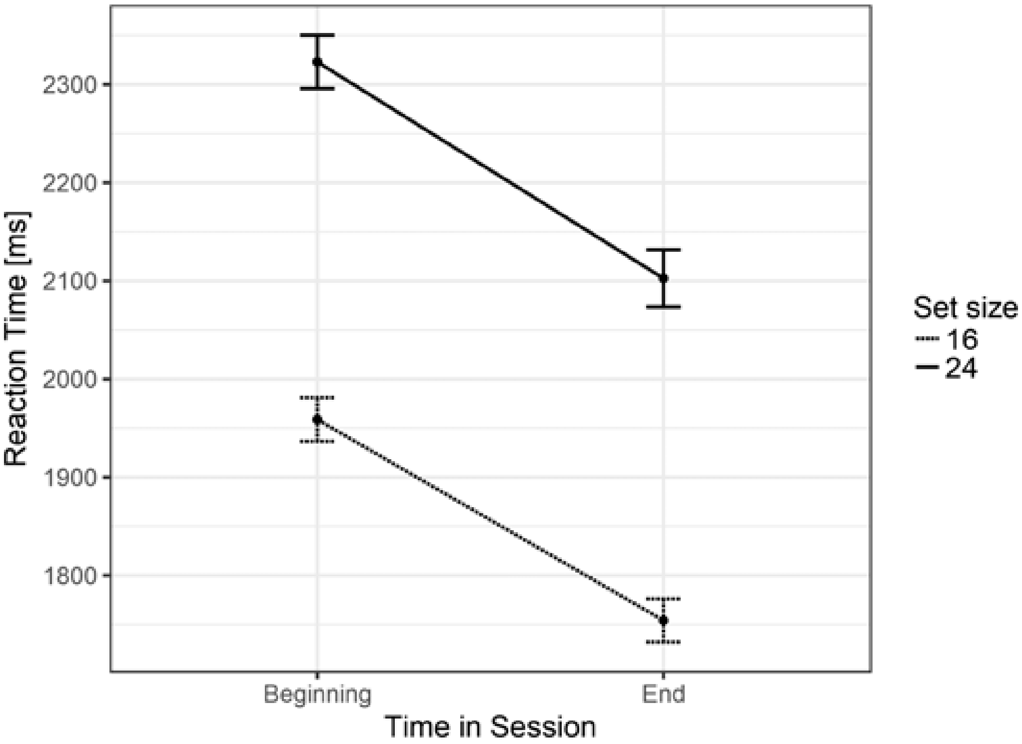

Figure 4.6: Mean reaction times for set size 16 and 24 as a function of time-in-session. Error bars indicate standard error of the mean.

4.2.2.2 EEG analysis

Comparison of IAF power between the set size conditions

The time-frequency decomposition of IAF power (±1 Hz, Table 4.2), for each set size condition, was computed. Since no experimental modulation was present in the pre-stimulus period, a difference in pre-stimulus alpha power between set size conditions was not expected to be found. All participants showed a prominent alpha power pattern prior to stimulus onset. Topographies of grand-averaged (averaged across participants) IAF power can be seen in Figure 4.7. No difference between the two set size conditions was found following a two-tailed, dependent-samples, cluster permutation test (no clusters were found).

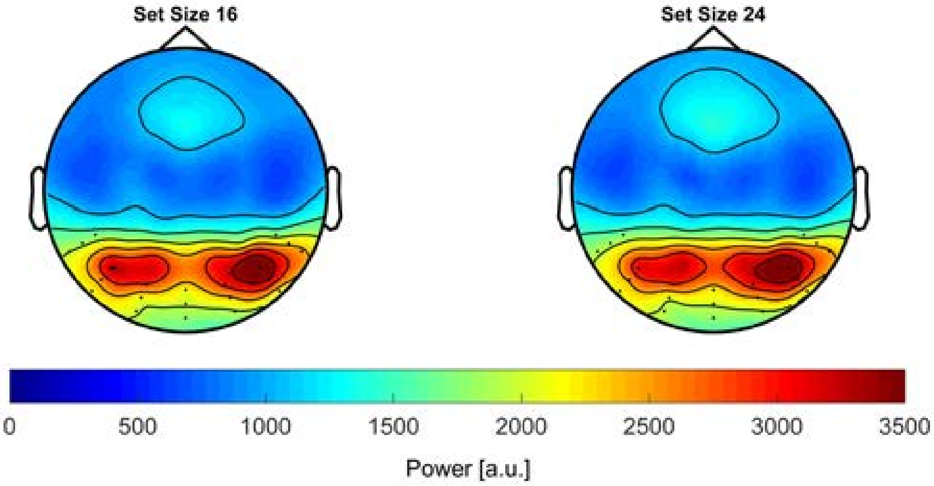

Figure 4.7: Grand averages of IAF power averaged across 300ms of pre-stimulus period, for sets size 16 and set size 24.

IAF power – RT correlation

The power of IAF was then correlated with RTs. A two-tailed, cluster permutation test was performed on the correlation coefficients (tested against zero). A significant negative cluster was found in set size 16, with T = -32.449, p = .02 at approximately 150ms - 30ms pre-stimulus onset (Figure 4.8). This result revealed a negative correlation between pre-stimulus alpha power and reaction times, with high pre-stimulus alpha power related to faster reaction times and vice versa. This is consistent with the hypothesis of alpha mediated distractor inhibition, proposing that alpha oscillations act as a filter for distracting information. Set size 24 showed no significant correlation clusters (no clusters were found). Furthermore, a correlation analysis was carried out in source-space, to estimate the sources of the correlation effect. No significant effects of reaction time – power correlation were found in source-space[3].

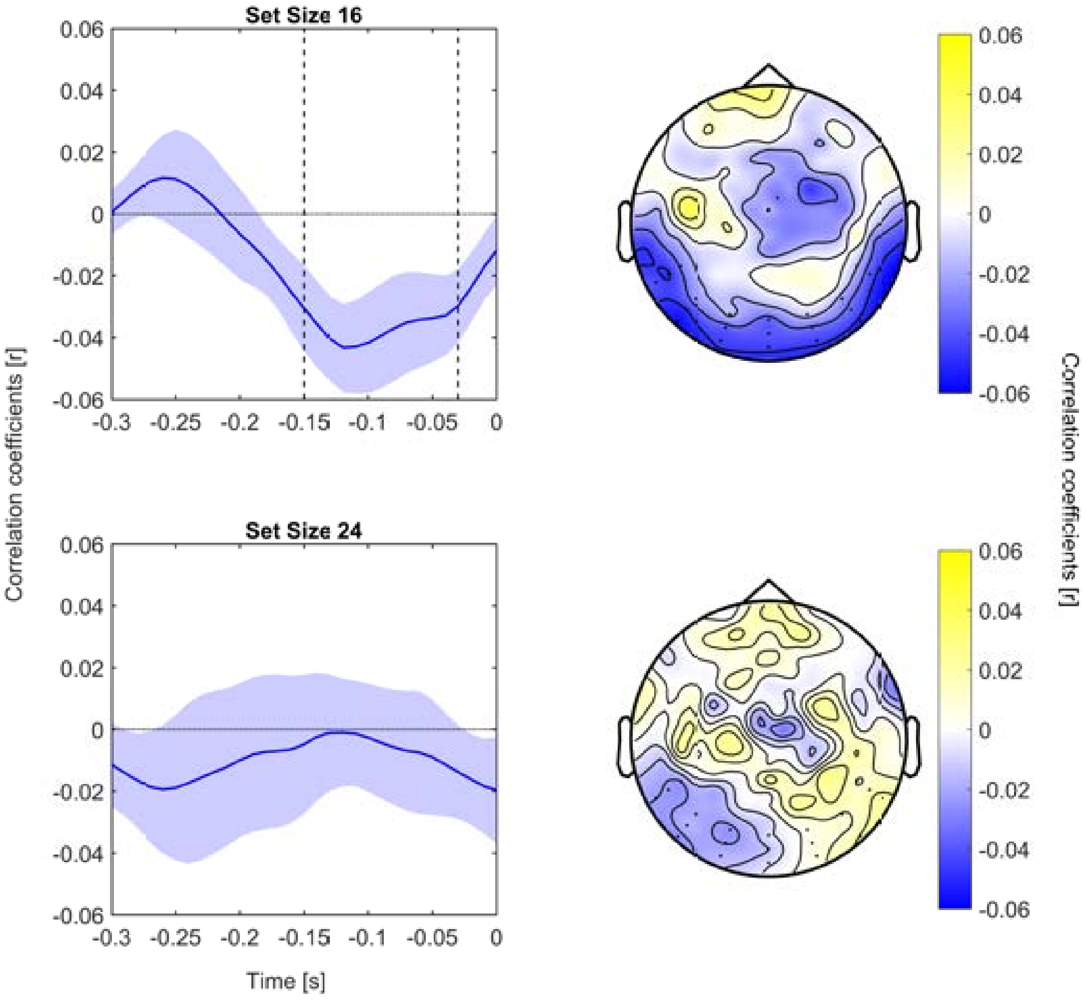

Figure 4.8: IAF power - reaction time correlation results. Left: Correlation coefficients (with standard deviation of the mean) as a function of time, with significant cluster indicated as area between the dashed lines. Right: Corresponding topographical plots of grand averaged correlation coefficients, averaged over the time window of significant cluster found in set size 16.

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[3] Figures are not presented.

Since the reaction times in set size 24 were significantly longer, the null effect in set size 24 condition may have been due to the time-dependent decay of potential pre-stimulus alpha influence. Consequently, the trials with fastest RTs in set size 24 should also display a negative relationship between pre-stimulus alpha power and reaction times. To this end, a follow-up analysis was carried out on the fastest subset of trials in set size 24 condition (a fastest third of trials; approximately 45 trials per participant) and the time window within which the significant effect was found for set size 16 (approximately -160ms to -30ms). Correlation results showed a negative trend (Figure 4.9). One-tailed cluster-based permutation test resulted in a non-significant negative cluster (p = .054, T = -11.39, at approximately -80ms to -30ms).

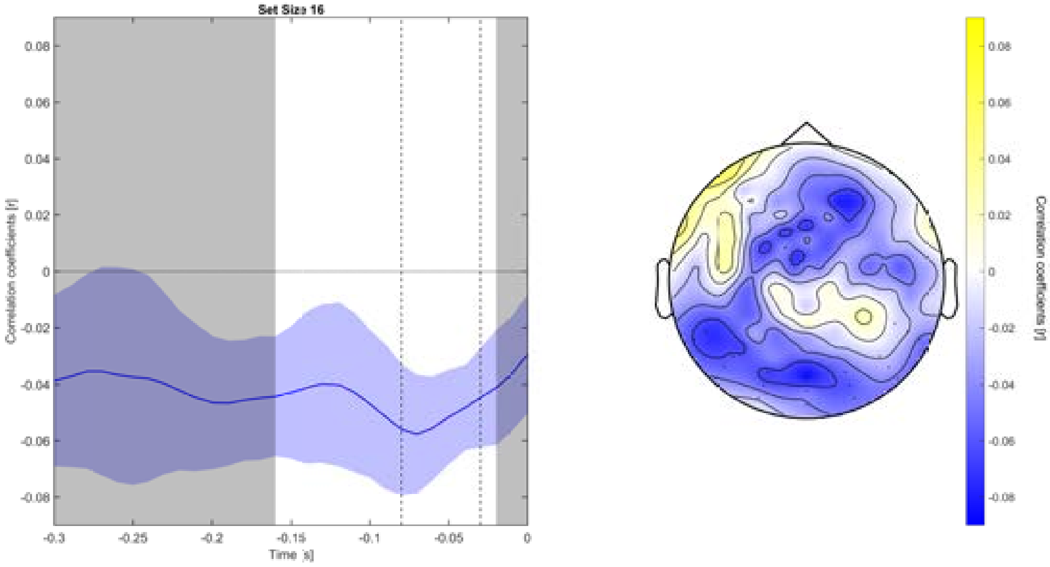

Figure 4.9: IAF power - reaction time correlation results for fast subset of RTs in set size 24. Left: Correlation coefficients (with standard deviation of the mean) as a function of time, with negative cluster indicated as area between the dashed lines. White area indicates the time window of interest used in the statistical analysis. Right: Corresponding topographical plot of grand averaged correlation coefficients, averaged over the time window of the negative cluster.

Power binned by reaction times

An analysis, comparing IAF between fast and slow RT bins, was performed using a one-tailed dependent samples cluster-based permutation test. Pre-stimulus alpha power was anticipated to be higher in fast reaction time bin as compared to the slow reaction time bin in set size, based on the correlation analysis results.

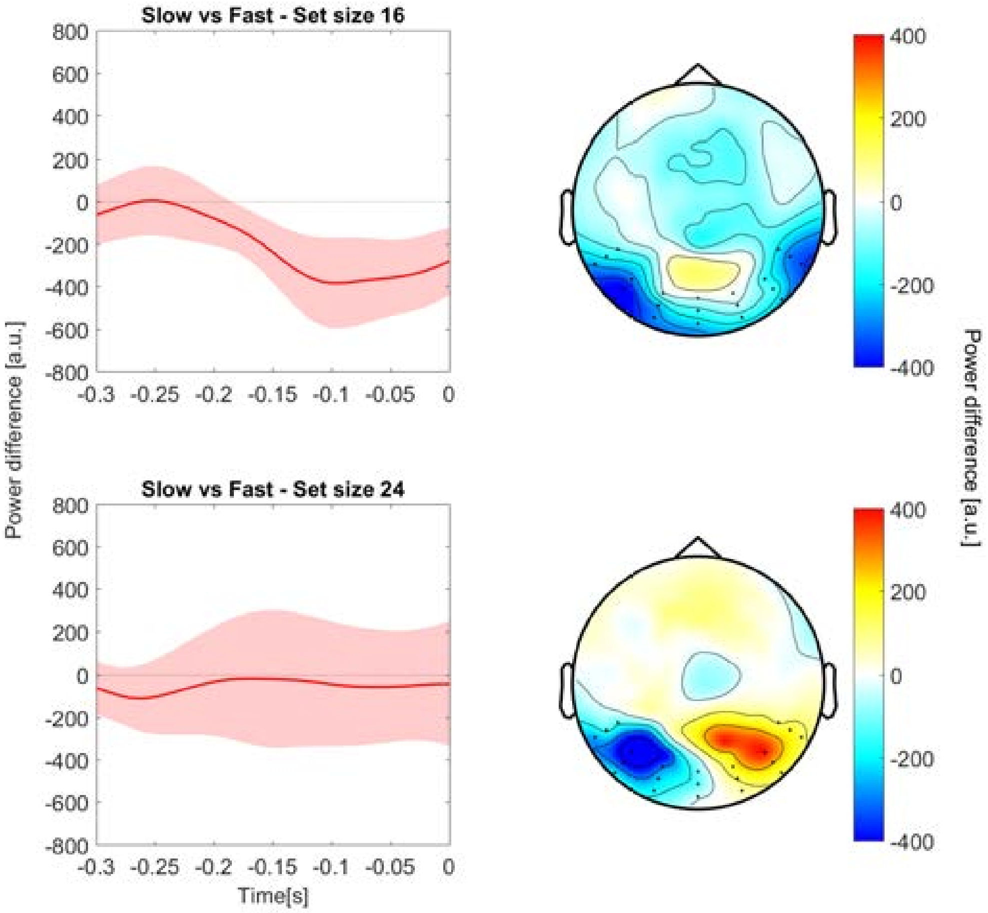

Figure 4.10: Power difference plots for slow vs fast RT bins. Left: Mean power (with the standard deviation of the mean) differences between fast and slow conditions as a function of time. Right: Topographical plots of power differences between conditions averaged over the 300ms pre-stimulus time window.

In both set size conditions pre-stimulus alpha power in the fast reaction time bin was higher than in the slow reaction time bin, however, only the difference in set size 16 was found to be significant, with T = 45.153, p = .007 (-160ms to 0ms). No clusters were found for set size 24. Power difference plots are presented in Figure 4.10.

Power binned by time-in-session

An EEG analysis investigating the differences in IAF power between the beginning and the end of the experimental session was then carried out for both set size conditions. Topographies and spectra of IAF power differences between time-in-session bins, across the pre-stimulus period are presented in Figure 4.11. Both set sizes show increased pre-stimulus alpha power at the end of the session as compared to the beginning. Significant clusters spanning the entire time window of interest (-300 to 0) were found in both set size conditions following a two-tailed, dependent samples, cluster permutation test, with T = 81.118, p < .001 in set size 16, and T = 82.24, p = .004 in set size 24.

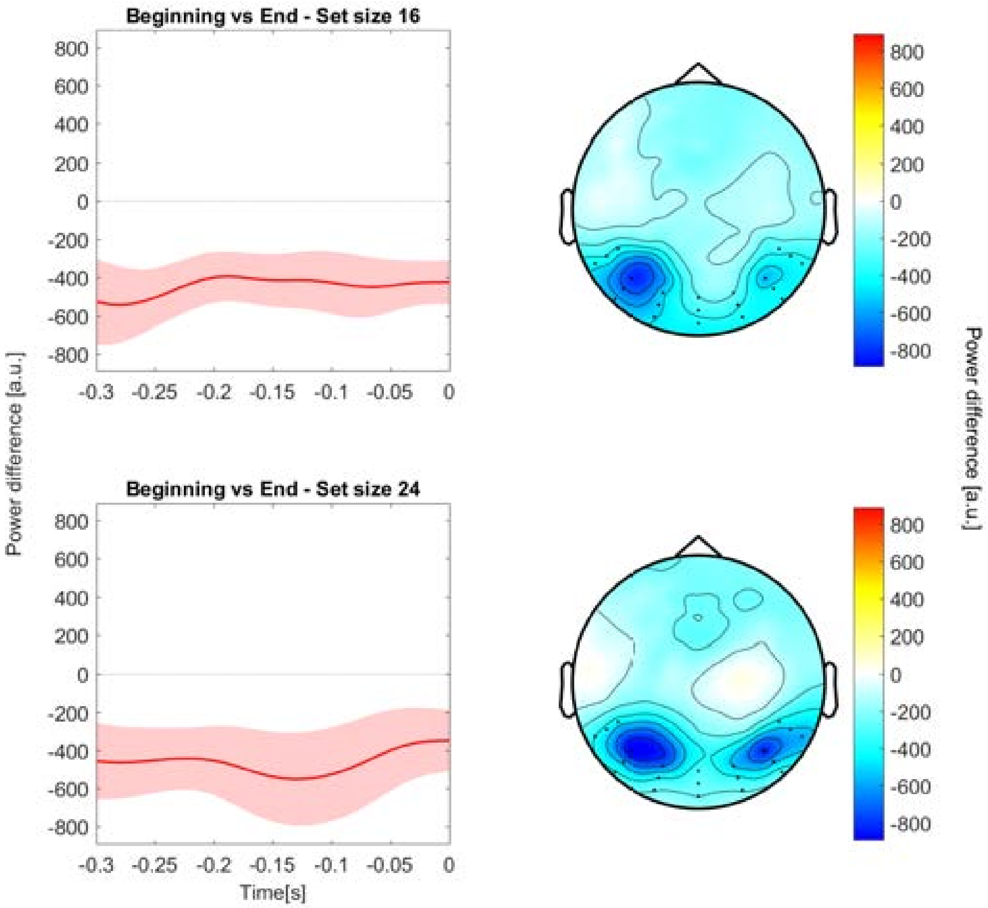

Figure 4.11: Power difference plots for slow vs fast RT bins. Left: Mean power (with the standard deviation of the mean) differences between beginning and end of session conditions as a function of time. Right: Corresponding topographical plots of power differences between conditions averaged over the 300ms pre-stimulus time window.

IAF phase - RT correlation

A circular-to-linear correlation of IAF phase and RTs was carried out. Significant correlations between reaction time and phase were found in set size 16 between -300ms and -190ms (permutation test; $p < 0.05$, Benjamini-Hochberg corrected). No effect was found in set size 24. Grand averaged correlation coefficients plotted against time in the pre-stimulus time window are presented in Figure 4.12.

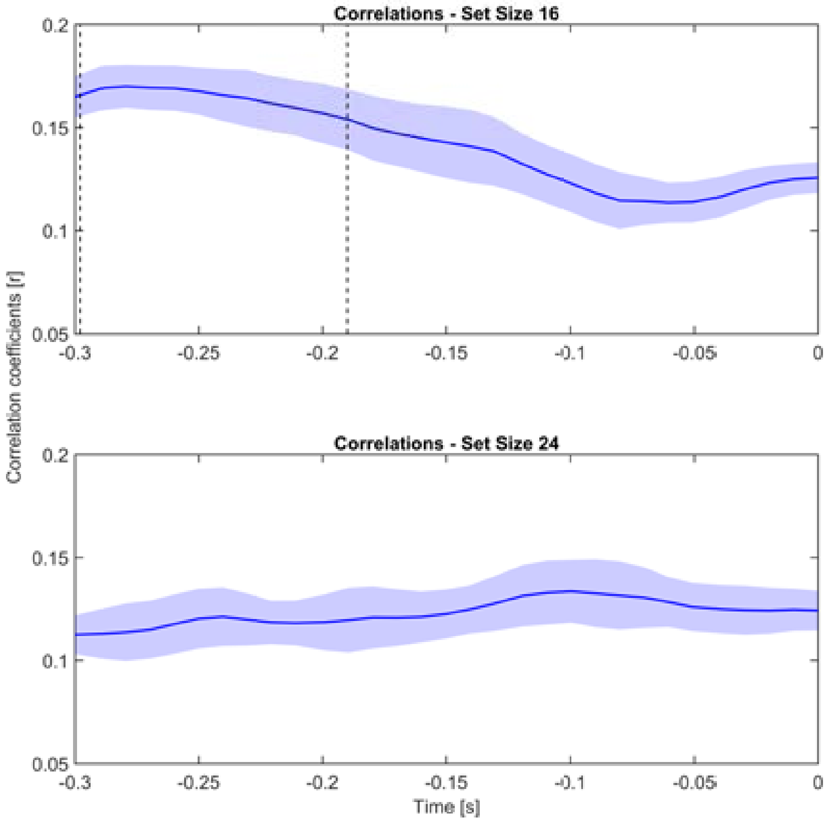

Figure 4.12: Phase - reaction time correlation results (with standard deviation of the mean) for set size 16 (top) and set size 24 (bottom) as a function of time. Significant effects are indicated by the area between the dashed lines.

Phase bifurcation index

Furthermore, to investigate whether trials with fast and with slow reaction times may be clustered in opposite phases of alpha oscillation, PBI was calculated for RT time bins and tested using a permutation test. No significant difference from zero was found suggesting no phase locking for either of the two RT bins. Grand averaged phase bifurcation values plotted as a function of time are presented in Figure 4.13

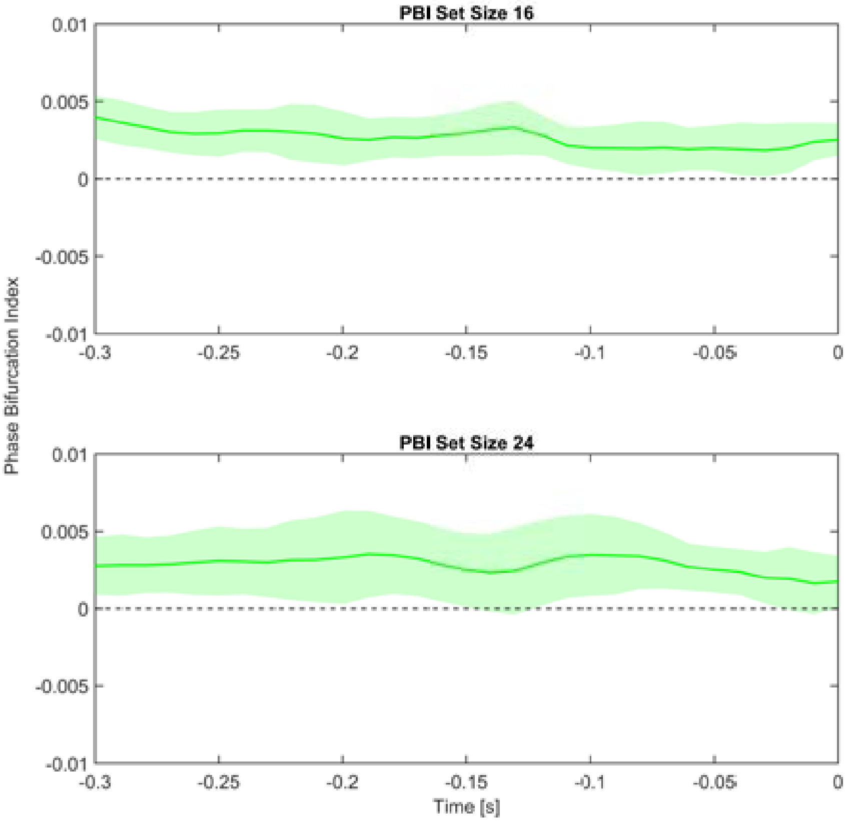

Figure 4.13: Phase bifurcation index results (with standard deviation of the mean) for set size 16 (top) and set size 24 (bottom) as a function of time.

4.2.3 Experiment summary

To summarise, the experiment presented in this chapter was an exploratory EEG study performed to investigate the relationship between alpha oscillations and performance on a visual search task. The results of the analyses performed for Experiment 5 indicated that pre-stimulus alpha oscillations were inversely related to RTs in a conjunction visual search task. Pre-stimulus IAF power correlated negatively with RTs in set size 16, with high alpha power related to fast RTs, and low alpha power to slow RTs. The correlations between IAF and RTs in the fast subset of reaction times for set size 24, while not statistically significant, followed the pattern found in set size 16, with a negative correlation coefficient. A comparison of pre-stimulus IAF power between fast and slow RT bins, showed higher alpha power in the fast RT subset, with a significant difference in set size 16. The behavioural analysis of signal detection measures performed on fast and slow RT bins indicated that fast reaction times are associated with both liberal criterion and increased sensitivity index. Furthermore, an effect of time-in-session was explored, and improvement in behavioural performance was reported for a subset of trials from the end of the experimental session, as compared to the trials from the beginning of the session. Pre-stimulus IAF power was found to significantly increase as a function of time-in-session for both set size conditions. Moreover, a significant phase correlation was observed in set size 16, in line with previous research showing a modulatory effect of alpha phase on perception (Hanslmayr et al., 2013; Mathewson et al., 2011). However, no effect was observed for set size 24. No evidence of opposite phase clustering of fast or slow RTs has been found.

4.3 Discussion

The exploratory study presented in this chapter aimed to investigate the relationship between pre-stimulus alpha oscillations and performance on a conjunction visual search task. It is widely accepted that high alpha power is associated with inhibition of visual stimuli, while low alpha power facilitates target detection (Feng et al., 2017; Jensen and Tesche, 2002; Kizuk and Mathewson, 2017; Klimesch et al., 2007; Thut et al., 2006). Furthermore, modulations of performance have also been related to the phase of the underlying alpha oscillations (Bonnefond and Jensen, 2012; Hanslmayr et al., 2007, 2013; VanRullen and Dubois, 2011). The majority of previous research focused on investigating these effects for single, near-threshold stimuli, often using cued paradigms. Hence, here spontaneous pre-stimulus alpha oscillations were investigated with relation to performance on a conjunction visual search task. This paradigm is characterised by simultaneous presentation of the target, and distractors which share several features with the target stimulus. Thus, for optimal performance on the task, both, facilitation of target detection and efficient distractor inhibition are necessary.

Based on previous research two potential outcomes could have been anticipated. Literature demonstrating impaired target detection as a consequence of high alpha power, indicated that a positive correlation could be observed, with increases in alpha power corresponding to longer reaction times. Alternatively, as pre-stimulus alpha power has been shown to play a role in distractor inhibition, a negative correlation could have been observed, with trials showing high pre-stimulus alpha power characterised by faster reaction times (Feng et al., 2017; Jensen and Tesche, 2002; Kizuk and Mathewson, 2017; Klimesch et al., 2007; Thut et al., 2006). The results presented in the current chapter support the latter hypothesis. Both correlation and analyses of alpha power revealed a negative relationship between the power of alpha oscillations and reaction times, with high alpha power associated with fast reaction times, and vice versa. The negative correlation effect, as well as the difference in power between fast and slow RTs is only evident in the lower set size condition (set size 16), but not in the higher set size condition (set size 24). This may be due to the long search termination times in the latter condition. Thus, a follow-up correlation analysis was performed on the fastest subset of trials in set size 24. Here a negative correlation trend was also observed, albeit not reaching statistical significance.

These effects may seemingly be at odds with the existing body of research, showing the opposite effect of alpha power on target detection. In particular, the previously mentioned work by Van Den Berg et al. (2016) demonstrated that trials showing low pre-stimulus alpha power were characterised by faster reaction times in visual search. Arguably, the paradigm they employ is comparable to previous studies, which require detection or discrimination of a single, often near visual threshold, stimulus. In their study, Van Den Berg et al. (2016) presented participants with a discrimination task, where one target and one distractor are present in all trials. Moreover, the target and distractor colours are consistent throughout the experiment. In this type of visual search task (feature search) target detection is typically driven by the bottom-up salience of the target stimulus (“pop-out”). Similarly, single target detection is typically driven by bottom-up processes. Conversely, the conjunction visual search task used in Experiment 5, is understood to reflect top-down biasing of attention. Here, the target stimulus shares several features with distractors, so that “pop out” effect doesn’t occur. Thus, a top-down established attentional template (Desimone and Duncan, 1995) representing the target helps to eliminate distractor stimuli, and to determine the presence of the target. This distinct ratio of noise (distracting information) with regards to signal (target) may cause the divergent results.

Results presented in this chapter are in line with the premise that alpha oscillations reflect a filtering mechanism and play an important role in inhibition of irrelevant information (Jensen and Mazaheri, 2010; Klimesch et al., 2007; Payne, 2014). Indeed, the effects of such a filter, mediated by alpha oscillations, would vary depending on task demands. Specifically, if the task requires detection of a single target at a specific location, with no concurrent distractors present, it follows that all information provided should be processed for successful performance. In such a situation none or a very low filter would be optimal. In contrast, if distracting information is presented simultaneously and in the same space as the task-relevant stimulus, a narrow bandwidth of the filter may be beneficial to successfully inhibit the task-irrelevant information and thus, facilitate target detection. Bonnefond and Jensen (2012) have provided evidence corroborating this hypothesis, showing the modulation of alpha power by the distractor salience during a working memory task. When a stronger distractor was anticipated, alpha power was higher as compared to when a weak distractor was expected. Similarly, the previously discussed study by Mazaheri et al. (2011) shows that successful inhibition of salient stimuli is associated with increases in parietal alpha. Given the importance of distractor inhibition in a visual search task (Luria et al., 2016; Luria and Vogel, 2011; Vogel et al., 2005) and provided that alpha oscillations serve a role of a filtering mechanism, optimal performance on a conjunction visual search task should be characterised by higher alpha power.

This is supported by the negative correlation between IAF power and performance found in Experiment 5. However, it has recently been suggested that alpha oscillations modulate the probability of reporting the target as present, regardless of trial type (target absent or present), in that an increase in hit rate is accompanied by an increase in false alarm rate on trials with low pre-stimulus alpha oscillation. Meanwhile, no difference in the sensitivity index, indicating an actual improvement of target detectability was reported (Iemi et al., 2017; Limbach and Corballis, 2016). Thus, the effect of alpha power on perception was proposed to be the result of general excitability modulation, with no effect on the sensitivity index. Under these circumstances, alpha-mediated filtering mechanism would affect all sensory information presented invariably.

Therefore, it should be considered that the correlation effect observed in Experiment 5, may not be limited to correct responses, but also extend to false alarms, which were not examined here, and thus, not reflect an actual improvement in target detection. Consequently, it would be expected that fast reaction times, related to high alpha power, should be associated with a conservative criterion, while slow reaction times with a more liberal criterion (Iemi et al., 2017; Limbach and Corballis, 2016). Sensitivity index, on the other hand, should not differ between fast and slow reaction times. Since EEG signal analyses in Experiment 5 were carried out using correct data only, the information regarding false alarms was discarded. Moreover, the design of the study precluded performing an EEG analysis on incorrect trials, as due to high accuracy rates, the numbers of incorrect trials were low and would not provide enough statistical power. Thus, only a behavioural analysis of the signal detection theory measures was performed. The results demonstrate that fast reaction times are associated with significantly higher sensitivity index, as well as with higher probability of both hits and false alarms (more liberal criterion). Whereas it is not possible to directly relate these behavioural results to power of alpha oscillation, they nonetheless suggest that the relationship between high alpha power and fast reaction times reflects an actual improvement in target detectability, and vice versa.

In line with previous research showing effects of alpha phase on behavioural performance in attentional tasks (Dugué et al., 2011; Hanslmayr et al., 2007, 2013; VanRullen and Dubois, 2011), IAF phase and RT correlation effects were demonstrated for set size 16. This result indicated that certain reaction times may be preferentially clustered in specific phases of the oscillation. Animal studies implicate both alpha power and phase in the modulation of neuronal spiking, with increases in alpha power associated with lower firing rates, as well as selective inhibition of neuronal activity at specific phases (Haegens et al., 2011). Concurrently, Mathewson et al. (2009) show a modulation of single target detection rate by both power and phase, where for high alpha power condition, characterised by lower detection rate, performance is further modulated by specific phase. The most optimal inhibition effect should result from an interplay between alpha power and phase. The correlation effect found in Experiment 5 was therefore, further explored by means of phase bifurcation index. This analysis, however, did not yield significant results. The null effect may be due to the specificity of the task. Typically the effects of phase on performance are observed for tasks with shorter response times than in Experiment 5. It may be possible that the effects of alpha phase dissipate with time. Hence, effect of phase on performance may be too weak to yield a significant result, when inspected by means of phase opposition measures. Moreover, this analysis required data to be separated into bins, which effectively decreased the power of the analysis by reducing the number of trials used per condition. The preliminary results of correlation analysis do, however, provide an interesting venue for future research.

Previous research shows an effect of the time-in session on the behavioural performance on a visual search task and relates it to pre-stimulus alpha power modulation across time (Van Den Berg et al., 2016). Behavioural results in Experiment 5 demonstrate a significant improvement in performance on the visual search task between the beginning and the end of the experimental session, with reaction times significantly lower towards the end of the experiment. Pre-stimulus alpha power, in turn, shows a significant increase towards the end of the experimental session as compared to the beginning. This pattern is consistent with the results found in the IAF power - RT correlation analysis. However, since the relationship between power and reaction times was not formally tested between the beginning and the end of the session due to an insufficient number of trials, this seemingly consistent result may be spurious. Furthermore, it could be argued that the negative correlation observed may derive from this time-related alpha increase and practice-based improvement in visual search performance. However, if that were so, the same correlation effect should have been observed across both set size conditions, rather than the reported significant effect in set size 16 only.

In conclusion, the effects observed may result from an interplay between alpha oscillations mediated filter, and a top-down imposed bias in favour of target stimulus. It has been demonstrated that both, alpha power and phase reflect increases and decreases in neuronal spiking (Haegens et al., 2011), which indicates that alpha-mediated filter may be a reflection of general neural excitability of the cortex. Furthermore, baseline neuronal activity has been shown to be modulated in areas corresponding to task-relevant locations or features via top-down anticipatory biasing of attention (Chawla et al., 1999; Li et al., 2004; Milnik et al., 2013; Sigman and Gilbert, 2000). Thus, it could be speculated that while the filter mediated by alpha oscillations reflects general baseline excitability modulation, the top down attentional influences (attentional templates) result in regulation of sensitivity index in a conjunction VS task.

4.3.1 Chapter conclusions

Experiment 5 presented in this chapter was an exploratory study investigating the relationship of pre-stimulus alpha oscillations with reaction times on a conjunction search task. These results indicate an inverse relationship between the pre-stimulus alpha oscillations and reaction times, with higher pre-stimulus alpha power being associated with improved performance and vice versa. This is in line with research implicating alpha oscillations in distractor inhibition (Jensen and Mazaheri, 2010; Payne et al., 2013). With no prior information as to when or where the target will occur it may be beneficial to keep the narrow width of the attentional filter, requiring higher alpha power, to prepare for optimal filtering of the upcoming distractors.

Chapter 5

The relationship between pre-stimulus alpha oscillations and task demand

5.1 Introduction

In Chapter 4 we demonstrated a negative correlation between the power of pre-stimulus alpha oscillations and performance on a conjunction visual search task (Experiment 5). Specifically, trials with fast reaction times were characterised by higher alpha power than trials with slow reaction times. This is in line with previous research emphasizing the importance of distractor inhibition in a visual search task (Hout and Goldinger, 2010, 2014; Luria and Vogel, 2011). The apparent discrepancy of these results with the existing literature, demonstrating the detrimental effect of high alpha power on target detection (Bompas et al., 2015; Kizuk and Mathewson, 2017; Mathewson et al., 2009; Schubert et al., 2008), can be resolved when they are considered in the context of the alpha inhibition hypothesis (Jensen and Mazaheri, 2010; Klimesch et al., 2007). This hypothesis proposes that alpha oscillations reflect a filtering mechanism subserving the successful suppression of irrelevant and distracting information. Previous literature provides substantial support for the role of alpha power in distractor inhibition. For instance, Händel et al. (2011) used a cueing paradigm with bilaterally presented moving stimuli. The presented exogenous cue (arrow) resulted in higher alpha power contralateral to the unattended hemifield. They show that this increased lateralisation was detrimental to performance when participants were asked to report on the stimuli presented in the unattended hemifield. Importantly, it is reasonable to expect the effects of a filtering mechanism mediated by alpha oscillation to vary depending on task demands. We propose that depending on the amount of distracting information, with respect to task relevant information, different levels of alpha filter will be advantageous.

The experiments presented in the current chapter aim to investigate the modulation of pre-stimulus alpha power by task demands, while replicating the negative correlation effect reported in Chapter 3. Experiments 6 and 7 were both conducted in a manner analogous to Experiment 5. Here, a conjunction visual search paradigm, with three set size conditions (2, 8 and 16) was used. In both experiments the participants were naïve as to which of the two possible targets would be presented during the subsequent trial, or where on the display it might appear. In Experiment 6 the set size conditions were randomly intermixed within the blocks, while in Experiment 7, a blocked design was used. For both experiments a correlation analysis between pre-stimulus alpha power and reaction times was conducted. Given the proposed alpha filter hypothesis, it was anticipated that the higher set sizes (8 and 16) will show a negative correlation between IAF power and reaction times. Meanwhile the lowest set size (2) was not expected to show a significant negative correlation. Furthermore, IAF power was compared between the set size conditions in both experiments. As mentioned, in Experiment 6 the set size conditions were randomised and thus the difficulty of the oncoming trial was not predictable. In Experiment 7 trial difficulty could be anticipated as, at the beginning of each block, participants were told which set size condition to expect. Hence, in Experiment 7, but not in Experiment 6, the pre-stimulus alpha power was expected to be modulated by anticipation of task difficulty. An increased alpha power was expected in high set size conditions, as compared to the low set size. Furthermore, we anticipated that the sources of both, the power differences between the set size conditions, as well as the correlation effects, will be localized in the posterior areas, particularly in the occipital and parietal areas (Linkenkaer-Hansen, 2004; Romei et al., 2010; Spaak et al., 2016; van Dijk et al., 2008).

5.1.1 The alpha filter hypothesis

The research presented in the previous chapter led us to put forward the “alpha filter hypothesis”. As previously indicated, the effects of the power of alpha oscillations could be anticipated to be task dependant. Here it is argued that different levels of alpha filter will be optimal depending on the amount of distracting information in relation to task relevant information. Accordingly, when the task requires a detection or discrimination of a singleton stimulus, a minimal amount of filtering, or even lack thereof, is advantageous. Since, in this case only task relevant information is presented, all of it should be processed. Hence, low alpha power would be beneficial for performance. High alpha power instead may 'filter out' the relevant information, thus resulting in impaired performance. On the other hand, if distracting stimuli are presented high alpha power would be beneficial in facilitating their inhibition. Likewise, if a target stimulus is presented simultaneously with salient distractors, without a spatial cue, keeping a narrow bandwidth of the filter would be the most appropriate strategy. Correspondingly, the results presented in Chapter 3 demonstrate that when the target is presented concurrently with multiple distractors, high alpha power is related to improved performance.

It was proposed that alpha oscillations reflect the general neural excitability (Haegens et al., 2011; Lange et al., 2013). Consequently, the alpha filter should affect all of the presented information in an identical fashion, regardless of its relevance. Indeed, the previous research demonstrates that, in a simple target detection task, alpha power modulation was associated with decreases and increases in hit rates and false alarm rates alike (Iemi et al., 2017; Limbach and Corballis, 2016). However, top-down biasing in favour of the target stimulus, via attentional templates, is understood to play a crucial role in visual search tasks (Desimone and Duncan, 1995; Hout and Goldinger, 2014). Moreover, top-down modulation has been demonstrated to affect neuronal excitability in areas corresponding to task-relevant locations and features (Beck and Kastner, 2009; Chawla et al., 1999; Li et al., 2004; Milnik et al., 2013; Sigman and Gilbert, 2000; Stokes et al., 2009). This top-down bias in favour of target stimulus is likely to result in the target representation being stronger than that of the distractors.

Thus, we propose that alpha filter effects are a result of an interplay between the modulation of the general neural excitability (affecting all stimuli equally) and the target template (resulting in a stronger representation of the target as compared to distractors). Moreover, we hypothesize that the proposed alpha filter can be modulated in anticipation of task difficulty. A conceptual representation of the effect of the proposed alpha filter on performance in a conjunction visual search task is presented in Figure 5.1.

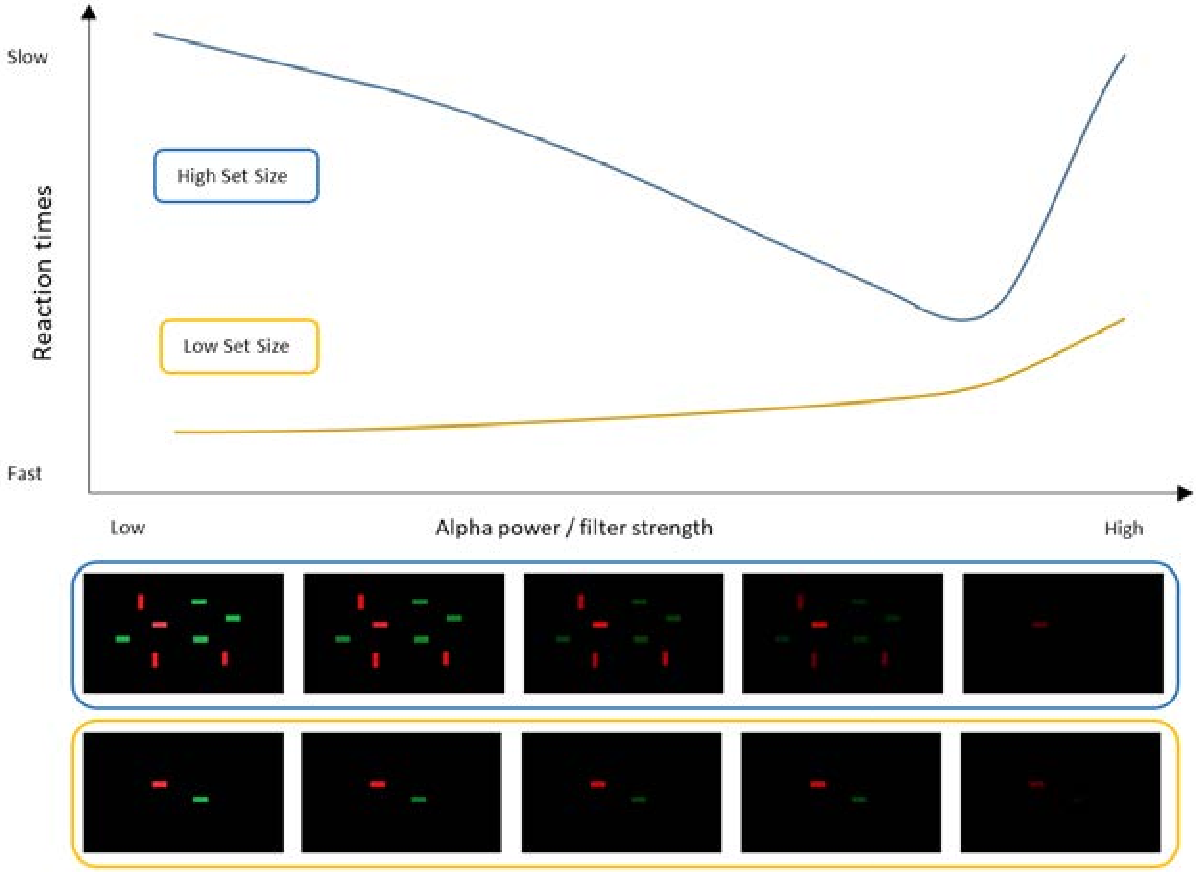

Figure 5.1: A conceptual representation of reaction times on a visual search (top), and task difficulty (bottom), as a function of alpha power mediated filter for high (blue) and low (yellow) set size conditions. It is likely that the top-down bias in favour of target stimulus results in the target representation being stronger than that of the distractors. Considering this assumption, the target detection should improve when the filter increases. Furthermore, previous literature indicates that a very high filter strength may result in impaired detection of both the distractors and the target (Hanslmayr et al., 2007; Linkenkaer-Hansen, 2004; Romei et al., 2010).

5.2 Experiment 6

Experiment 6 was conducted in a manner analogous to Experiment 5. Here likewise, EEG was recorded during a conjunction visual search task. In Experiment 6, as in Experiment 5 set size conditions were mixed within the blocks and unpredictable. Here, however, three set size conditions were used. Spontaneous alpha oscillations prior to visual search onset were analysed with respect to reaction times. High set sizes, but not the lowest set size, were expected to show a negative correlation between RT and IAF power.

5.2.1 Method

5.2.1.1 Participants

27 University of Birmingham students were recruited for the study according to the sampling procedure described in Chapter 2. Due technical problems with EEG recording data from six participants were excluded, while two participants were excluded due to not conforming with the study criteria, one participant withdrew during the recording sessions. Data from 18 participants (3 males) with mean age of 21 (19-26) was used in the analysis.

5.2.1.2 Materials

Visual search task The visual search task was identical to Experiment 5 (Chapter 4), with the exception of the number and type of set size conditions used (three set size conditions: 2, 8 and 16).

5.2.1.3 Design

A within-subjects design was used, with the independent variable of set size (2, 8 and 16), and dependent variable of RT in target present condition for correct trials. The trial sequence is presented in Figure 5.2. The experimental design summary is presented in Table 5.1.

Table 5.1: Summary of the experimental design used in Experiment 6.

Conditions	Design	Levels
Visual Search		Conjunction
Set Size	Mixed	2
		8
		16
Target	Mixed	Present
		Absent

Note: Level in grey was excluded from the final analysis.

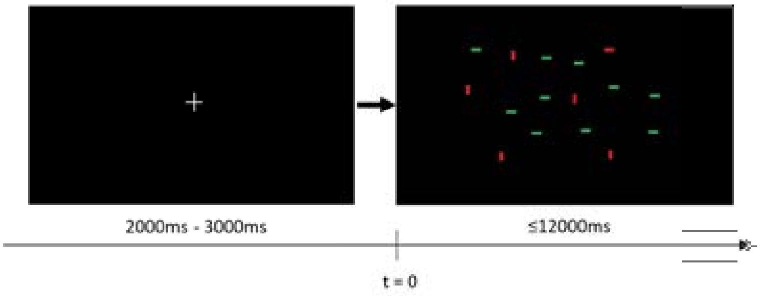

Figure 5.2: Example of a trial sequence in Experiment 6.

5.2.1.4 Procedure

The procedure was identical to Experiment 5 (Chapter 4), apart from the following: the head position of participant was stabilised using a chinrest; Response keys (‘z’ and ‘m’ on a standard qwerty keyboard) were counterbalanced across participants; All participants completed 2 practice blocks and 12 experimental blocks (a total of 960 trials).

5.2.1.5 EEG recording and analysis

The pre-processing was performed as described in Chapter 2. The time-frequency decompositions (TFR; -500ms to 100ms, locked to the onset of visual search) and statistical analyses were conducted as described in Chapter 2. Individual alpha frequencies per participant are shown in Table 5.2.

Table 5.2: Individual alpha frequency per participant in Experiment 6.

Subject Number	IAF [Hz]
1	11.4
2	10.6
3	11.2
4	9.8
5	7.6
6	11
7	10
8	10
9	9.4
10	8.6
11	11.4
12	10.6
13	10.6
14	11.2
15	8.8
16	9.8
17	10.2
18	9.6

Comparison of IAF power between the set size conditions An analysis comparing IAF power between set size conditions was carried out, using a 300ms pre-stimulus time window. A difference between set size conditions was not anticipated as there was no modulation in the pre-stimulus period.

IAF power – RT correlation A correlation analysis was performed as described in Chapter 2. The power output for each time point (61, -500ms to 100ms, in steps of approximately 9.8ms), frequency bin (9, in steps of 0.25 Hz) and channel (128) was correlated with RTs for each participant. Based on the effects found in Experiment 5, a time window between 190ms and 20ms pre-stimulus was chosen for statistical analysis.

To formally test the evidence for the null hypothesis, Bayes factor (BF) analysis was used (Rouder et al., 2009). BF is a statistical index which can be used to test the evidence for null hypothesis as compared to the alternative hypothesis, given the assumed prior. The value of BF indicates how much more likely data are to be observed under alternative hypothesis (typically if $BF > 3$), than under the null hypothesis (typically if $BF < .3$). A BF between .3 and 3 indicates that the evidence is inconclusive[1]. Here, Jeffreys-Zellner-Siow Bayes Factor was estimated using a Cauchy distribution of .707 (Rouder et al., 2009). BF was calculated for all t-statistics (18) obtained from the cluster permutation test of correlation values (tested against zero) for all set size conditions.

Furthermore, the IAF power – RT correlations for significant effects found in sensor-space were also carried out in source-space in an analogous manner. To estimate the sources of the correlation effects, an LCMV beamforming method was used (see Chapter 2). Template volume conduction and source models as provided in the FieldTrip toolbox (Oostenveld et al., 2011), with individual electrode positions, digitized as detailed in Chapter 2 were used[2].

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[1] $BF > 1$ is also customarily assumed to suggest ‘anecdotal’ evidence for the alternative hypothesis, while $BF < 1$, ‘anecdotal’ evidence for the null hypothesis (Schönbrodt and Wagenmakers, 2017).

[2] For 3 participants in Experiment 6 electrode positions were either lost or corrupted. In this instance a template BioSemi 128 electrode coordinates as provided by Brainstorm software were used in source localisation analysis.

5.2.2 Results

5.2.2.1 Behavioural analysis

Mean accuracy was 93% (with 24% standard deviation). Boxplot presenting raw data across experimental conditions is presented in Figure 5.3. Data were trimmed as determined in Chapter 2. No speed accuracy trade-off was found (r = -.14, p = .58). The means and SDs of recorded reaction times calculated for correct, target present trials for three experimental conditions (set size 2, 8 and 16) in both experiments are presented in Table 5.3. Reaction times as a function of set size are presented in Figure 5.4.

Table 5.3: Mean reaction times [ms] per set size condition in Experiment 6.

	Set Size 2		Set Size 8		Set Size 16	
Experiment 6 (Mixed Design)	996.37	(343.64)	1536.79	(574.18)	1883.59	(816.21)

Note: The standard deviations are reported in parenthesis

Differences between conditions were evaluated by means of one-way repeated measures analysis of variance (ANOVA), with independent variable of set size (3) and a dependent variable of RT. Significant main effect of set size (F (2, 34) = 202.12, $p < .0001$, η^2_G = 0.667) was found[3].

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[3] Post hoc tests using Bonferroni correction show significantly faster reaction times in set size 2 as compared to set size 8 , with t(17) = -14.434 , $p < .0001$ (M = -545.63, with 95%CI [-625.38, -465.88]) and set size 16, with t(17) = -14.53 , $p < .0001$ (M = 888.67, with 95%CI [-1017.67, -759.66]), as well as significantly faster reaction times for set size 8 as compared to set size 16, with t(17) = -12.168 , $p < .0001$ (M =-343.03, with 95%CI [-402.51, -283.55]).

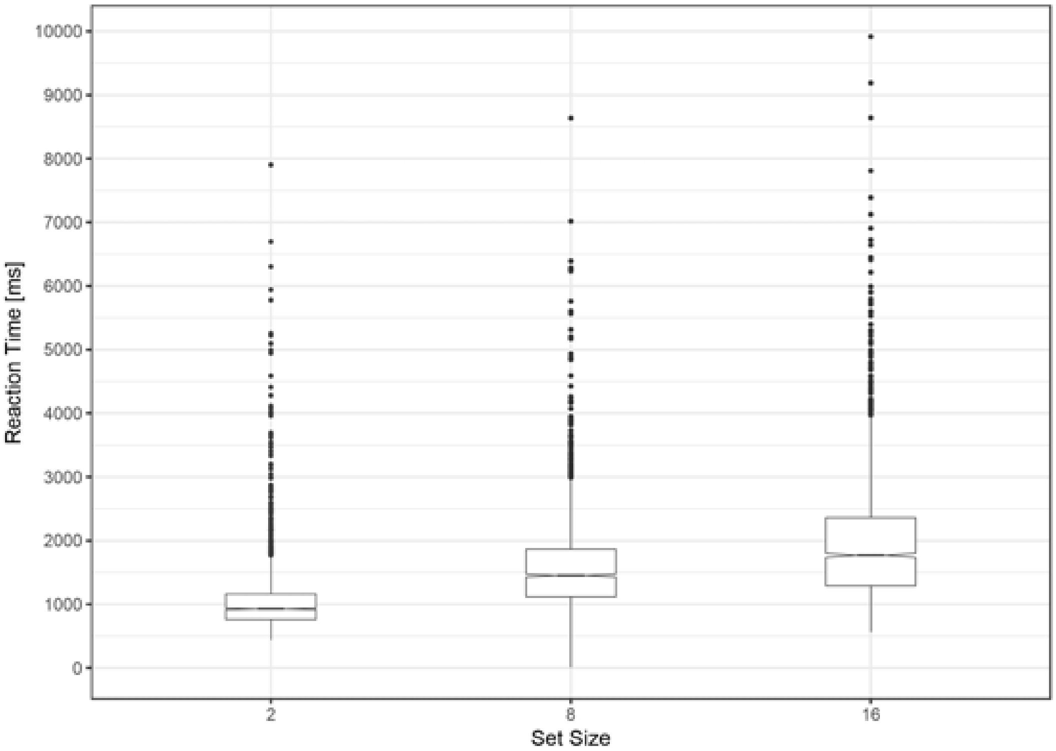

Figure 5.3: Raw reaction times for correct responses per set size in Experiment 7.

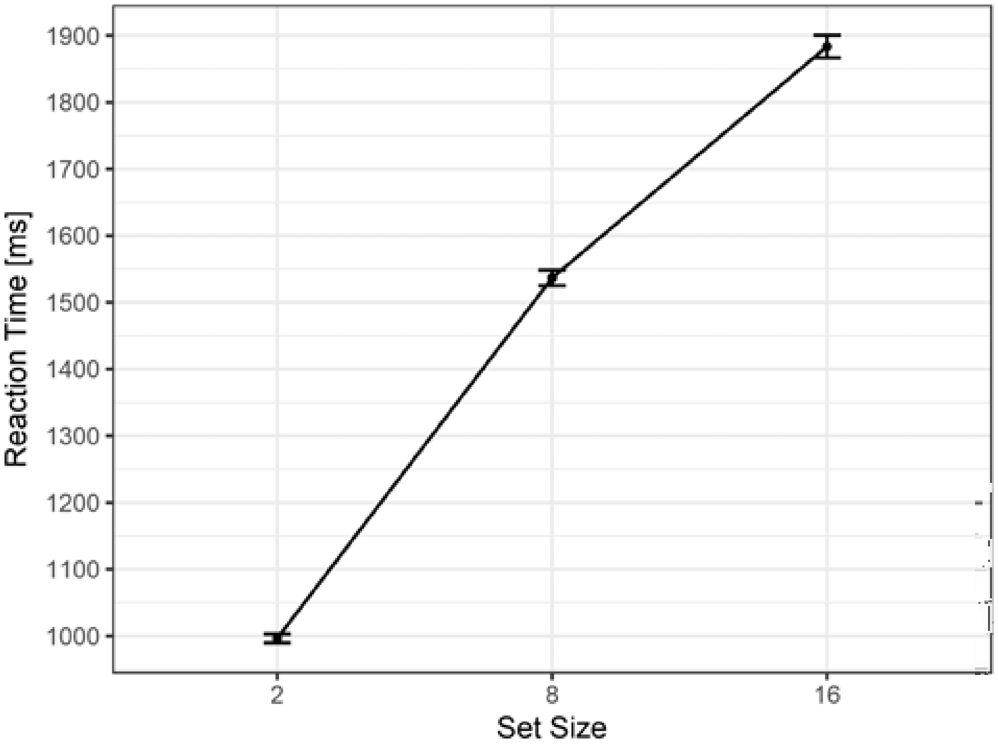

Figure 5.4: Mean reaction times as a function of set size in Experiment 6.Error bars indicate the standard error of the mean.

5.2.2.2 EEG analysis

Comparison of IAF power between the set size conditions

Since no experimental modulation was present in the pre-stimulus period, no difference was expected to be found in pre-stimulus alpha power between the set size conditions. Topographies of grand-averaged (averaged across participants) IAF power can be seen in Figure 5.5. No differences between the three set size conditions were found following a two-tailed, dependent-samples, cluster permutation test. Plots of differences between conditions are presented in Figure 5.6.

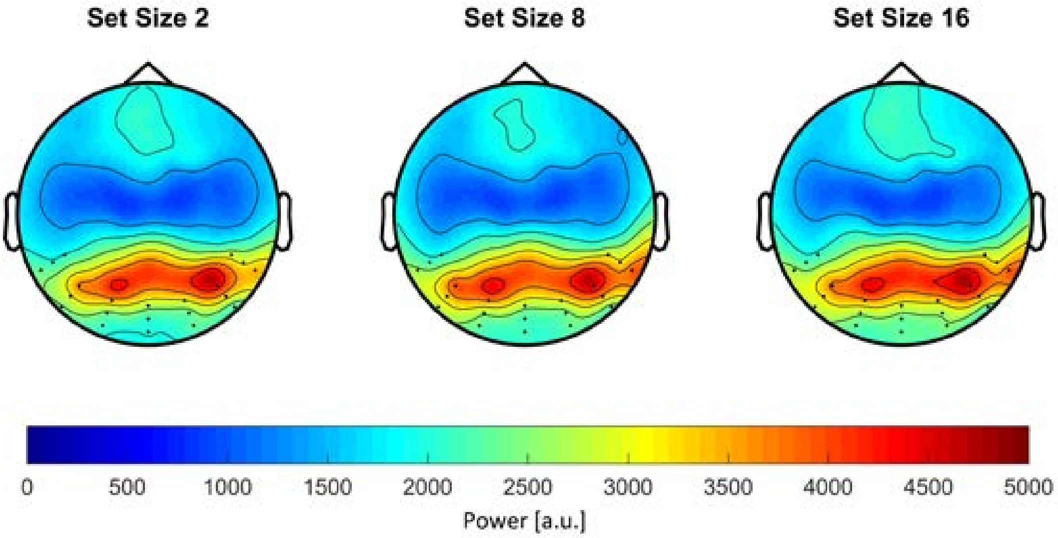

Figure 5.5: The topographies of grand-averaged individual alpha power per set size condition, averaged over a 300ms pre-pre-stimulus time window, in Experiment 6.

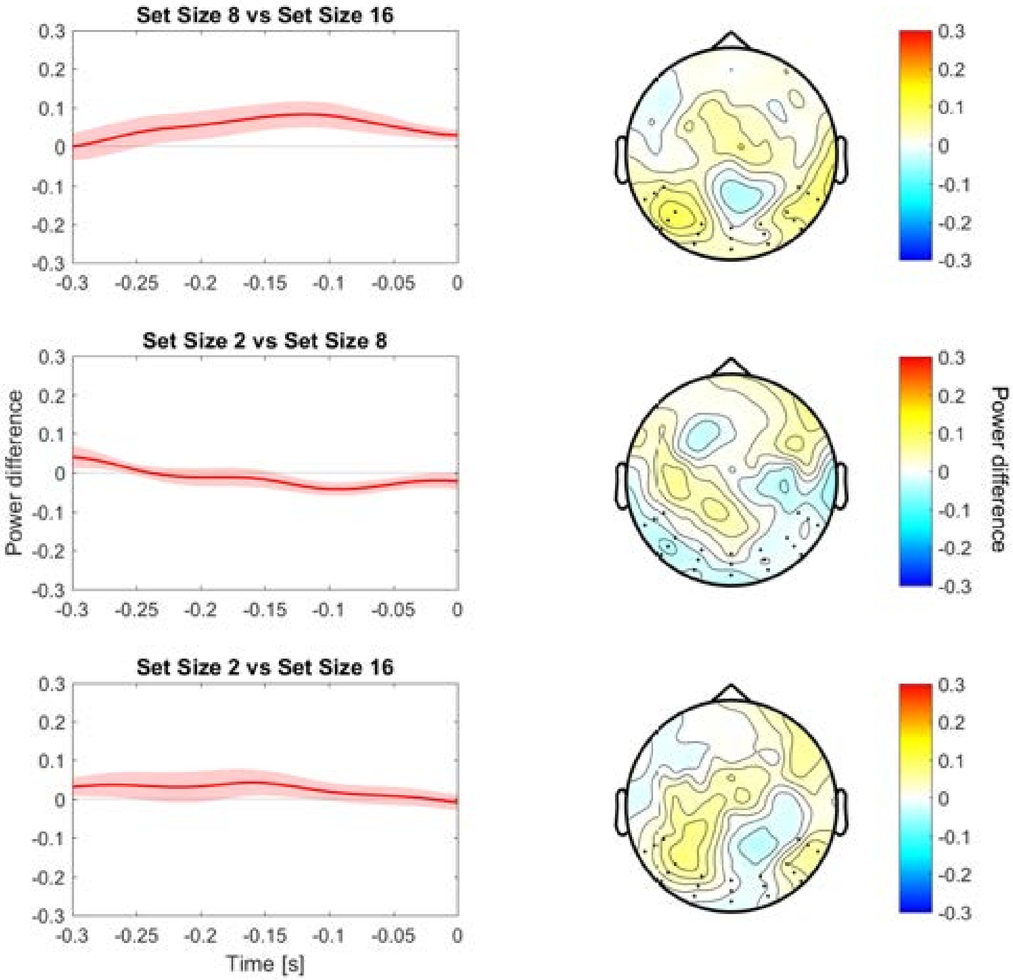

Figure 5.6: Power differences between set size conditions as a function of time (left) with corresponding topographies (right), averaged over 300ms of pre-stimulus window in Experiment 6. For comparison purposes the the y-axis and colour bar ranges throughout this chapter are kept constant for both presented experiments. For plotting purposes power difference values are normalised as follows: (Condition A-Condition B)/Condition B.

IAF power – RT correlation

The IAF power was correlated with RTs for each participant. A one-tailed, cluster permutation test was performed on the correlation coefficients (tested against zero). Two negative clusters were found in set size 16, with one reaching the significance threshold (T = -13.05, p = .048), approximately between -190ms to -140ms pre-stimulus onset[4]. This result in set size 16, indicating a negative correlation between pre-stimulus alpha power and RTs, replicates the effect found in Experiment 5. Mean correlation values for set size 8 were consistently negative, however no clusters were found. As hypothesized, no correlation was found in set size 2. Figure 5.7 shows the results of the correlation analysis.

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[4] The second negative cluster in set size 16 did not reach significance, with T = -3.63, p = .122, at approximately -40ms to -30ms.

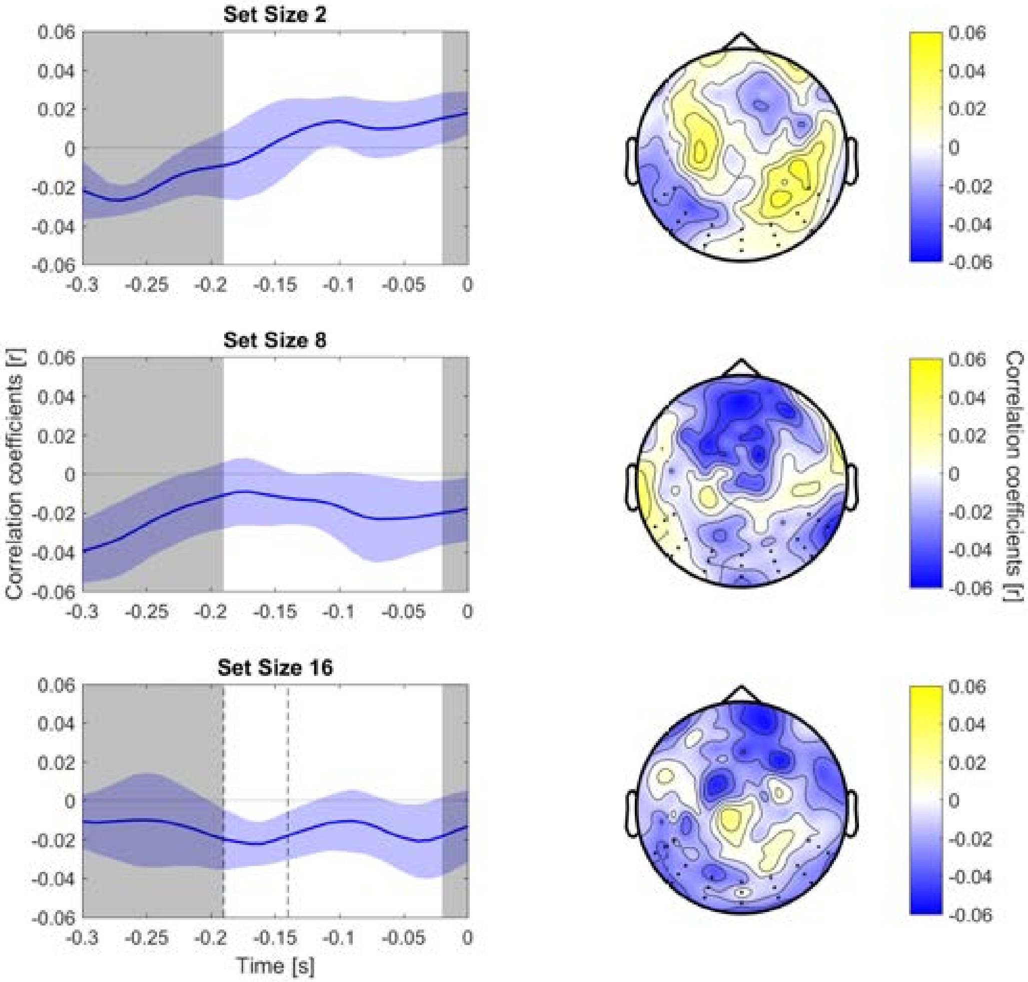

Figure 5.7: IAF power - reaction time correlation results in Experiment 6. Left: Correlation coefficients (with standard deviation of the mean) as a function of time, with significant cluster indicated as area between the dashed lines. Right: Corresponding topographical plots of grand averaged correlation coefficients, averaged over the time window of significant cluster found in set size 16. Time window of interest, used for statistical analysis is indicated by the white are of the graphs.

Furthermore, the null effect found in set size 2 was formally tested. Bayes factor was calculated, for all timepoints included in the statistical analysis. This allowed us to investigate whether the data provided more evidence towards the null hypothesis (no correlation) as opposed to the alternative hypothesis (negative correlation). For consistency, data from all set size conditions were investigated and results are presented in Figure 5.8. The majority of BF values in set size 2 were at or below .03, indicating support for the null hypothesis (a mean of .325 across the time window of interest). Likewise, for set size 8 condition (a mean of .334 across the time window of interest). For set size 16 BF values in the observed correlation cluster time period were all above 1, indicating more support for the alternative hypothesis. However, they did not reach the customary threshold of 3, suggesting that the evidence is inconclusive. None of the values in the entire time window of interest were below 0.3.

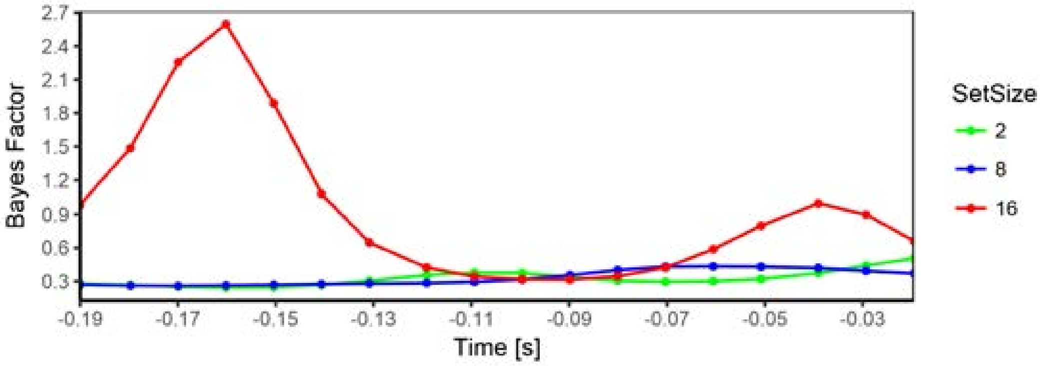

Figure 5.8: Bayes factor values as a function of time, for each set size condition, in Experiment 6.

The significant effect observed on sensor-level for set size 16, between -190ms and -140ms pre-stimulus, was then investigated on the source-level. The negative correlation cluster found (T = -1970.7, *p* = .007) spanned frontal and prefrontal areas, with a peak in the right caudate [MNI, x = 13, y= 0.5, z= 20]. Figure 5.9 shows the strongest effect within the found cluster (T < -3).

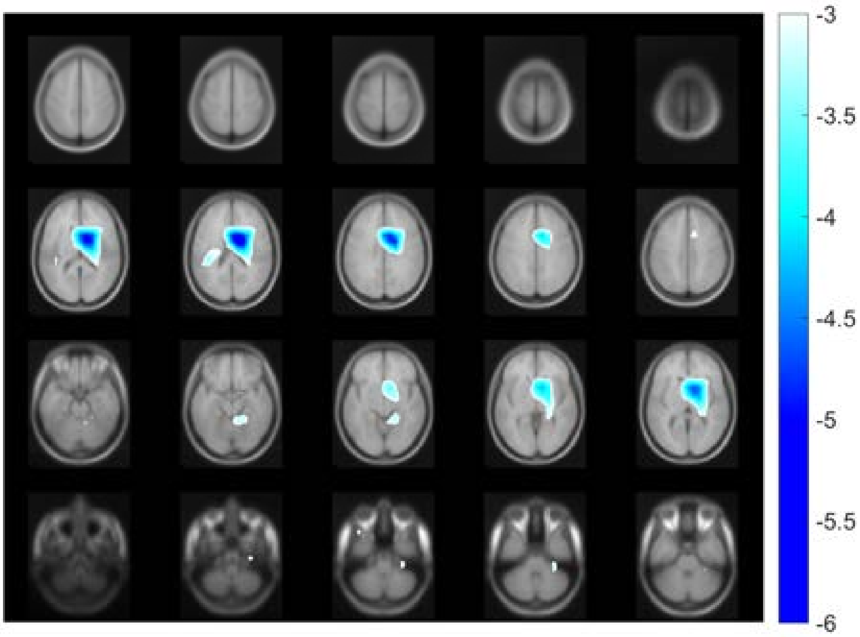

Figure 5.9: Source localisation results of correlation analysis in Experiment 6 (threshold set at T = -3 for plotting purposes).

5.3 Experiment 7

Experiment 7, was conducted in a manner analogous to Experiment 6. Here, the main difference from the previous experiment was the manipulation of the set size condition by block. High set sizes were expected to show a negative correlation between RT and IAF power. This effect was not expected to occur in set size 2. Furthermore, task difficulty was hypothesized to modulate the pre-stimulus alpha oscillation, with the highest pre-stimulus alpha power found in set size 16 condition, and the lowest in set size 2 condition. Moreover, the differences between set size conditions were compared between Experiments 6 and 7.

5.3.1 Method

5.3.1.1 Participants

31 University of Birmingham students were recruited for the study according to the sampling procedure described in Chapter 2. Due technical problems with EEG recording data from seven participants was excluded, one participant was excluded due to responding at chance level, one participant withdrew during the recording sessions[5]. Data from 24 subjects (3 males) with mean age of 20 (18-29) was used in the analysis.

5.3.1.2 Materials

Visual search task A visual search paradigm identical to Experiment 6 was used in Experiment 7.

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[5] Furthermore, for one participant, data from 3 experimental blocks from the middle of the session were lost.

5.3.1.3 Design

Behavioural differences between set size conditions A within-subjects design with independent variable of the set size (2, 8 and 16) and the reaction times for correct target-present trials, as the prime dependent variable, was used. The experimental design summary is presented in Table 5.4

Table 5.4: Summary of the experimental design used in Experiment 7.

Conditions	Design	Levels
Visual Search		Conjunction
Set Size	Blocked	2 8 16
Target	Mixed	Present *Absent*

Note: Level in grey was excluded from the final analysis.

Behavioural interaction analysis between Experiments 6 and 7 A 2 x (3) mixed design analysis, comparing Experiment 6 and Experiment 7, was conducted. The between-subjects variable was experimental design (blocked, with set size cue, or mixed with no cue), while the within-subjects variable was set size condition (2, 8 and 16). Reaction times for correct, target-present trial were the dependent variable.

5.3.1.4 Procedure

Procedure was identical to Experiment 6, apart from the following: the set size condition was manipulated between blocks, while target type, and target present and absent conditions were manipulated randomly within each block; Block order effects were controlled for by using a Latin square design between participants; Prior to every block participants were informed, through an explicit onscreen instruction, which set size condition will be presented in the subsequent block of trials. All participants completed 3 practice blocks and 9 experimental blocks (9 blocks, 3 of each set size, total of 1008 trials). The trial sequence is presented in Figure 5.10.

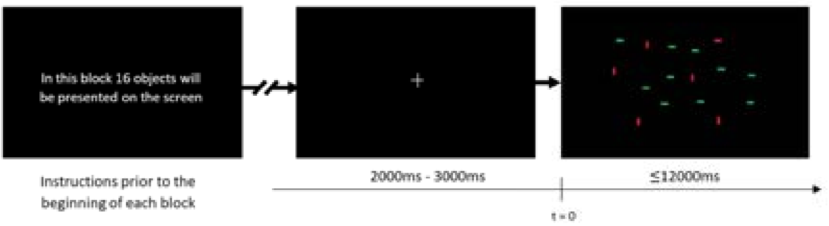

Figure 5.10: Example of a trial sequence in Experiment 7.

5.3.1.5 EEG recording and analysis

Pre-processing was performed as described in Chapter 2. The time-frequency decompositions (TFR; -500ms to 100ms, locked to the onset of visual search) and statistical analyses were conducted as described in Chapter 2. Individual alpha frequencies per participant are shown in Table 5.5.

Comparison of IAF power between the set size conditions An analysis comparing IAF power between set size conditions was carried out in an identical fashion, as in Experiment 6.

IAF power – RT correlation A correlation analysis was performed in an identical fashion as in Experiment 6, apart from the following: due to paradigm differences between Experiments 5 and 7, a 300ms time window pre-stimulus onset was used for statistical analysis[6]; BF was

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[6] For 2 participants in Experiment 7 electrode positions were either lost or corrupted. In this instance a template BioSemi 128 electrode coordinates as provided by Brainstorm software were used as in source localisation analysis.

calculated for all t-statistics (31) obtained from the cluster permutation test of correlation values (tested against zero) for all set size conditions.

Table 5.5: Individual alpha frequency per participant in Experiment 7.

Subject Number	IAF [Hz]
1	8.6
2	9.8
3	8.8
4	9.8
5	10
6	9.2
7	10.4
8	11.6
9	11.6
10	11.4
11	8
12	11.4
13	10.6
14	7
15	11.2
16	9.4
17	10.2
18	10.6
19	8
20	7.6
21	9.4
22	8.4
23	9.8
24	11

IAF power differences comparison between Experiments 6 and 7 An analysis contrasting the IAF power differences between set sizes in Experiments 6 and 7 was performed. To this end, normalised IAF power differences between set size 2 and 8, as well as set size 2 and 16, were calculated for both experiments [7]. These differences were then statistically tested using a two-tailed, independent samples, cluster permutation test.

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[7] Normalisation was conducted as follows: (Condition A – Condition B)/ (Condition B).

5.3.2 Results

5.3.2.1 Behavioural differences between set size conditions

Mean accuracy in Experiment 7 was 92% (with 26% standard deviation). Boxplots presenting raw data across experimental conditions is presented in Figure 5.11. Data were trimmed as determined in Chapter 2. Speed accuracy trade-off (Chapter 2) was found (r = .42, *p* = .04), driven by one participant. However, since they did not meet the exclusion criteria their data were included in the final analyses[8]. The means and SDs of recorded reaction times calculated for correct, target present trials for three experimental conditions (set size 2, 8 and 16) in both experiments were presented in Table 5.6. Reaction times as a function of set size are presented in Figure 5.12.

Table 5.6: Mean reaction times [ms] per set size condition in Experiment 7.

	Set Size 2		Set Size 8		Set Size 16	
Experiment 6 (Mixed Design)	989.66	(447.97)	1557.55	(654.1)	1906.74	(778.58)

Note: The standard deviations are reported in parenthesis

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[8] After excluding subject SJ017 from analysis speed accuracy trade-off was not reported (r = 0.34, p=.109). Results of subsequent analyses did not change after excluding participant 17.

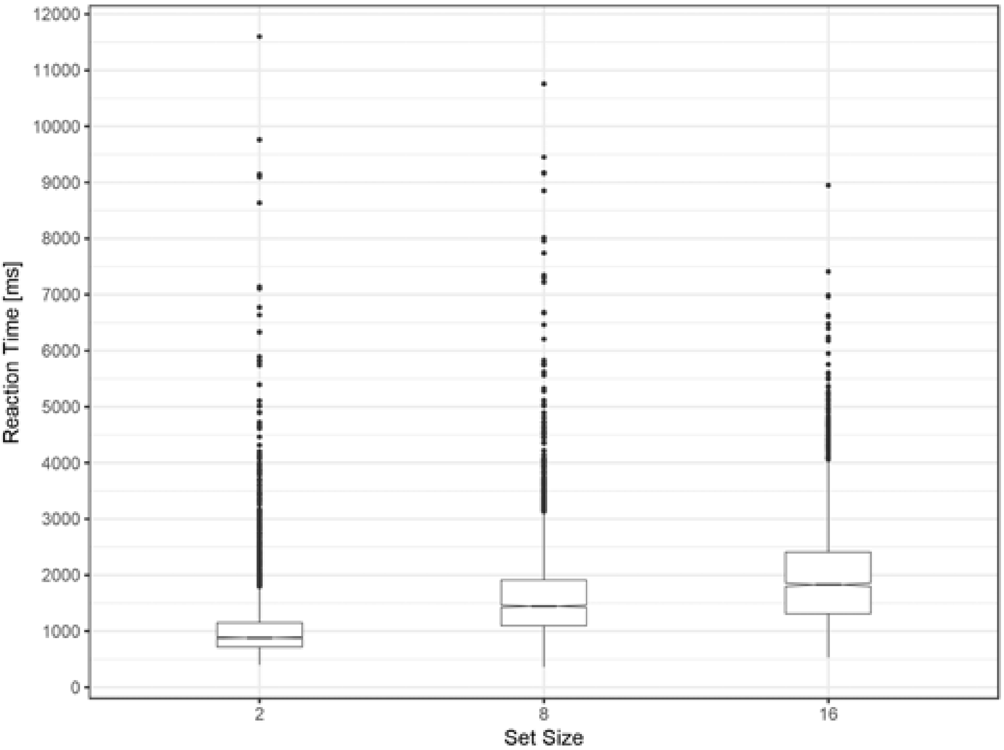

Figure 5.11: Raw reaction times for correct responses per set size in Experiment 7.

Differences between conditions were evaluated by means of one-way repeated measures ANOVA, with the independent variable of set size (3) and the dependent variable of RT. Significant main effect of set size (F (2, 46) =294.12, $p < .0001$, η^2_G =.626) was found[9].

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[9] Post hoc tests using Bonferroni correction show significantly faster reaction times in set size 2 as compared to set size 8 , with t(23) = -17.45 , $p < .0001$ (M = -567.27, with 95%CI [-634.54, -500]) and set size 16, with t(23) = -22.12 , $p < .0001$ (M = -907.78, with 95%CI [-992.66, -822.9]), as well as significantly faster reaction times for set size 8 as compared to set size 16, with t(23) = -8.65, $p < .0001$ (M =-340.51, with 95%CI [-421.93, -259.09]).

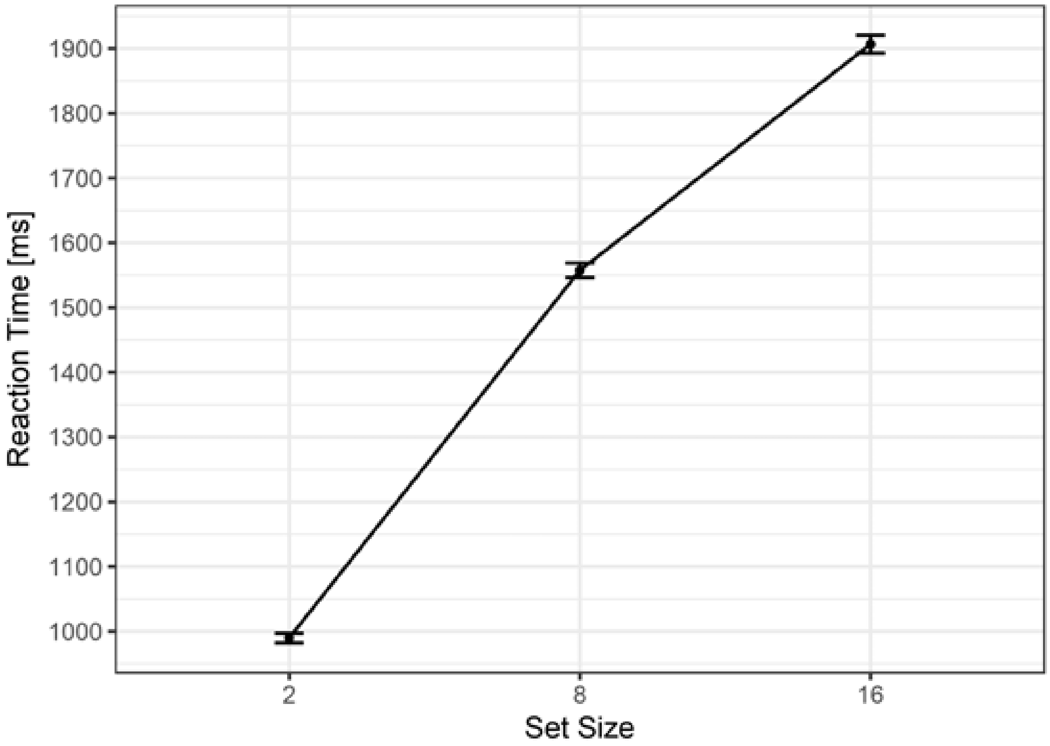

Figure 5.12: Mean reaction times as a function of set size in Experiment 7. Error bars indicate the standard error of the mean.

5.3.2.2 EEG analysis

Comparison of IAF power between the set size conditions

Unlike Experiment 6, in Experiment 7 set size conditions were blocked, and at the beginning of each block participants were told which condition to expect. This was expected to result in anticipatory modulation of pre-stimulus alpha power. Alpha power was expected to be highest in set size 16 and lowers in set size 2. Topographies of grand-averaged IAF power across set size conditions can be seen in Figure 5.13.

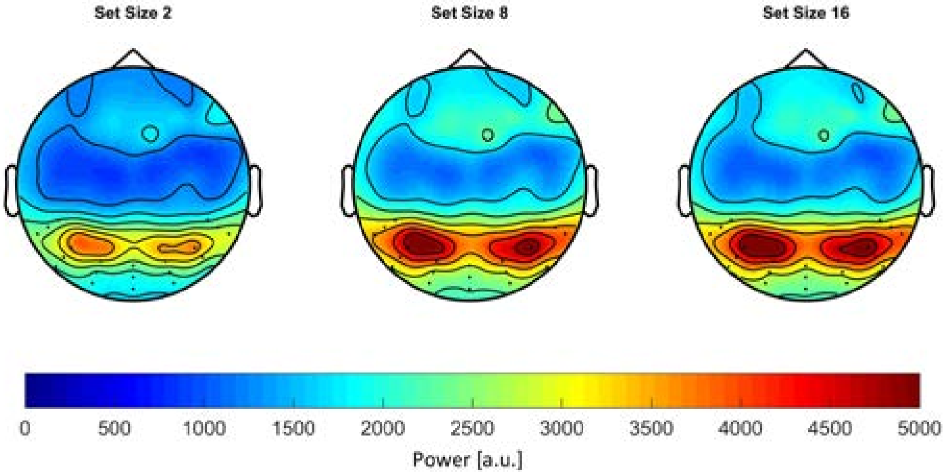

Figure 5.13: The topographies of grand-averaged individual alpha power per set size condition, averaged over a 300ms pre-pre-stimulus time window, in Experiment 7.

A one-tailed, dependent samples, cluster permutation test was employed as the directionality of the differences was predicted a priori. A significant difference was found, with set size 2 characterised by a significantly lower pre-stimulus IAF power compared to set size 8 (T = -129.33, $p < .001$) and set size 16 (T = -127.93, $p < .001$). Both significant clusters spanned the time window of interest (-300ms to 0ms). No significant difference was found for set size

8 and set size 16 comparison. Plots of differences between set size conditions are presented in Figure 5.14.

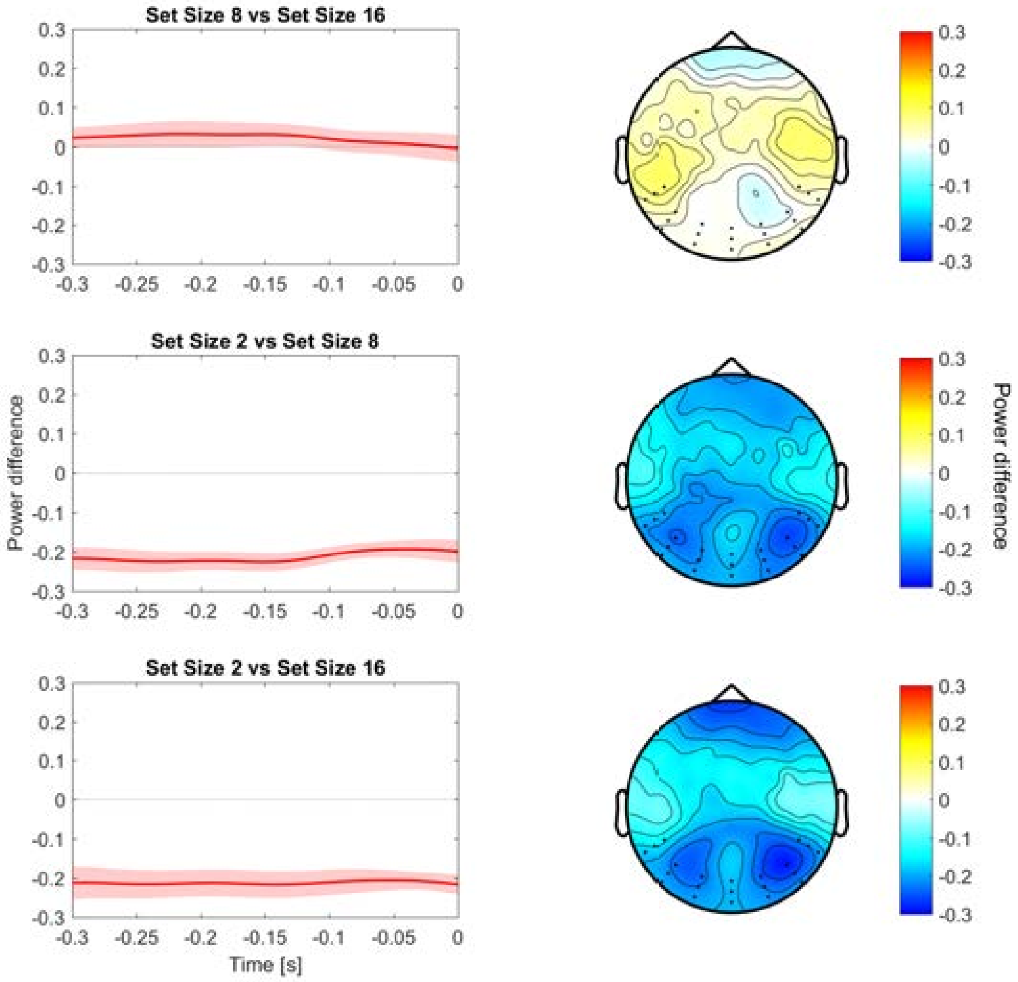

Figure 5.14: Power differences between set size conditions as a function of time (left) with corresponding topographies (right; averaged over 300ms of pre-stimulus window) in Experiment 7. For plotting purposes power difference values are normalised as follows: (Condition A-Condition B)/Condition B.

The significant effects found on sensor-level were localized in the source space. Significant differences between set size 2 and set size 8 (T = -6869.4, *p* = .0002), as well asset size 2 and set size 16 (T = 5974.5, *p* = 0.0002) were found occipital and parietal areas. In both comparisons the peak difference was found in the occipital cortex in the left visual association area (Brodmann area 18; set size 2 vs 8 [MNI, x = .5, y = -79.5, z = -.5]; set size 2 vs 16 [MNI, x = -10.5, y = -69.5, z = .5]). Source localisation results are presented in Figure 5.15.

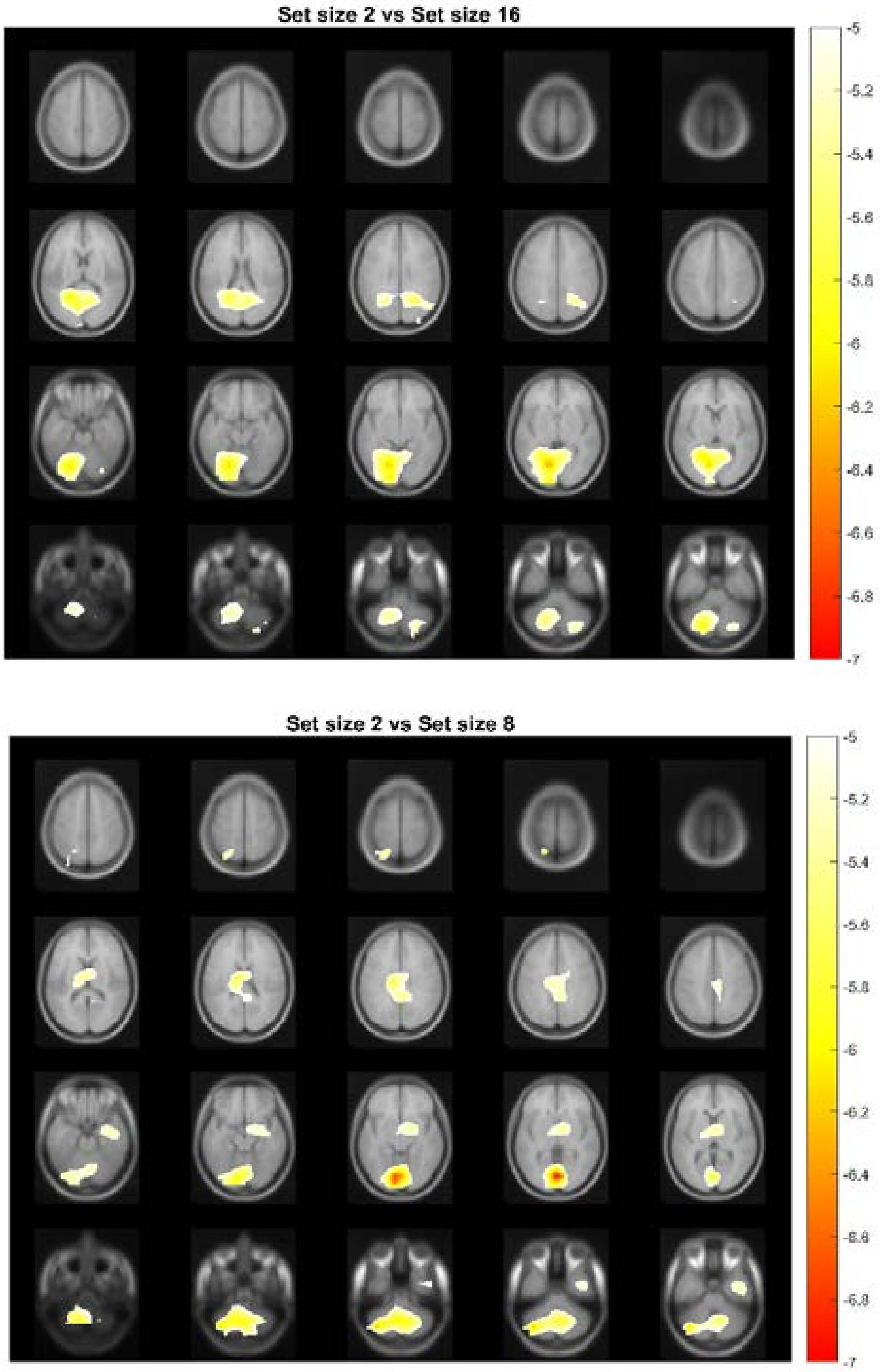

Figure 5.15: Source localisation results of power comparison analysis (threshold set at T = -5 for plotting purposes).

IAF power – RT correlation

The power of IAF was correlated with RTs (Figure 5.16). A one-tailed, cluster permutation test was performed on the correlation coefficients (tested against zero). One significant negative cluster was found in set size 16 condition, with T = -27.43, p = .038 approximately between -290ms to -160ms pre-stimulus onset . This result in set size 16, indicating a negative correlation between pre-stimulus alpha power and RTs, replicates the effects found in Experiment 5 and Experiment 6. Mean correlation values for set size 8 showed were consistently negative, however the cluster found in this condition did not survive the multiple comparison correction (T = -7.82, p = .12, at approximately -300ms to -270ms). As hypothesized, no correlation was found in set size 2.

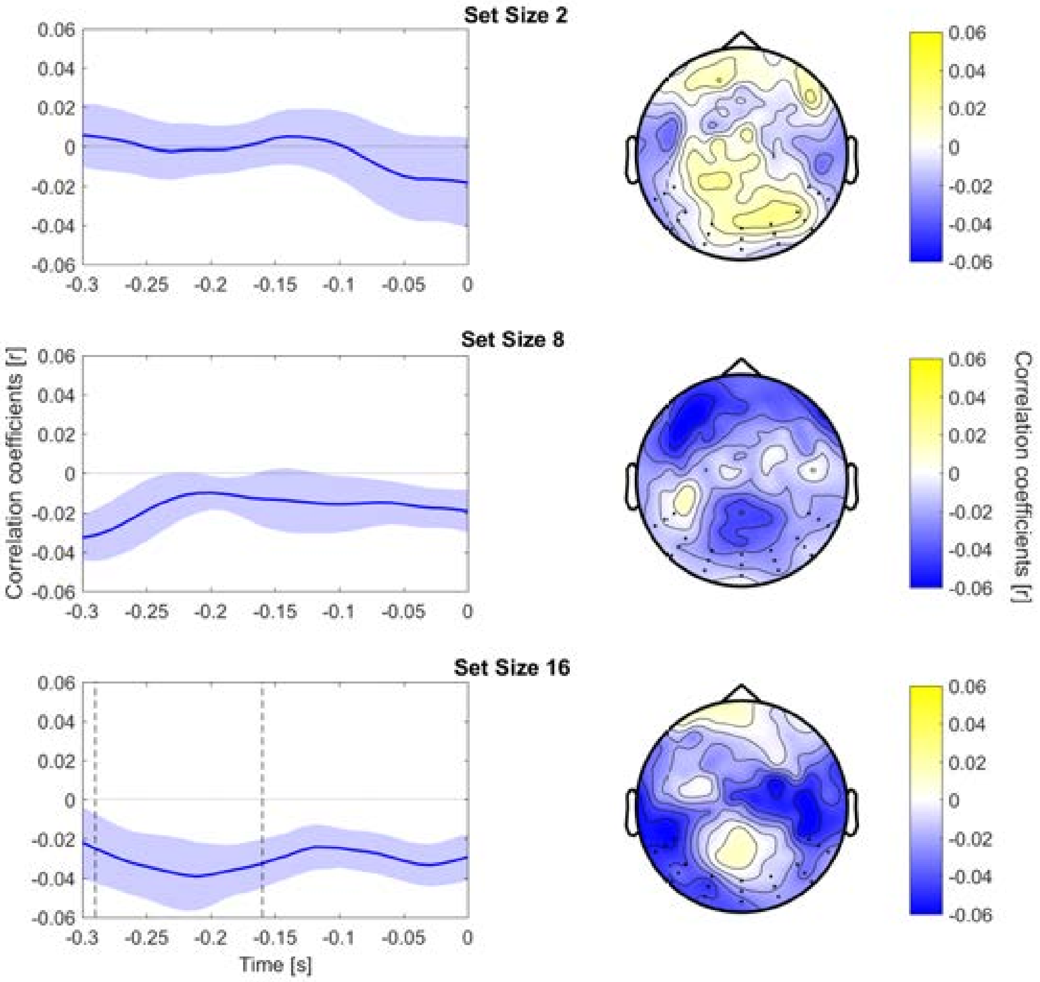

Figure 5.16: IAF power - reaction time correlation results. Left: Correlation coefficients (with standard deviation of the mean) as a function of time, with significant cluster indicated as area between the dashed lines. Right: Corresponding topographical plots of grand averaged correlation coefficients, averaged over the time window of significant cluster found in set size 16.

Furthermore, the null effect found in set size 2 was formally tested in an identical fashion to Experiment 6. Likewise, for consistency, data from all set size conditions were investigated and is presented in Figure 5.17. The majority of BF values in set size 2 were below .03, indicating support for the null hypothesis (a mean of .249 across the entire time window of interest). In set size 8 condition most values were above 0.3, with values between -300ms and -270ms above 1, suggesting that data is inconclusive (a mean of .429 across the whole time window of interest). For set size 16 BF values in the time period of the observed correlation effect, were all above 1, suggesting more support for the alternative hypothesis. However, they did not reach the criterion threshold of 3, indicating that the evidence is inconclusive. In set size 16, none of the values in the time window of interest were below 0.3.

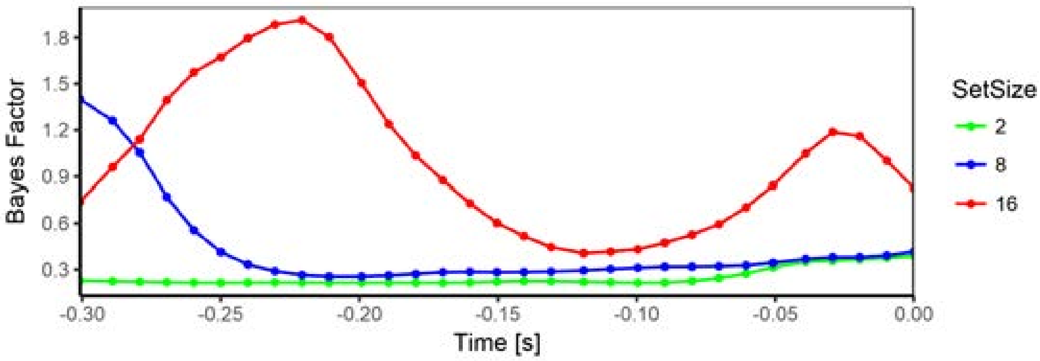

Figure 5.17: Bayes factor values as a function of time, for each set size condition, in Experiment 7.

The significant effect observed on sensor-level for set size 16, between -290ms and -160ms pre-stimulus, was investigated at the source-level. The negative correlation cluster found (T = -1900.6, *p* = .003) spanned frontal, parietal and occipital areas, with a peak in the right parietal cortex (Brodmann area 39) [MNI, x = 49.5, y= 69.5, z= 19.5]. This is in line with the involvement of fronto-parietal attentional networks in alpha mediated inhibition (Mathewson et al., 2014). Figure 5.18 shows the strongest effect within the found cluster (T < -3).

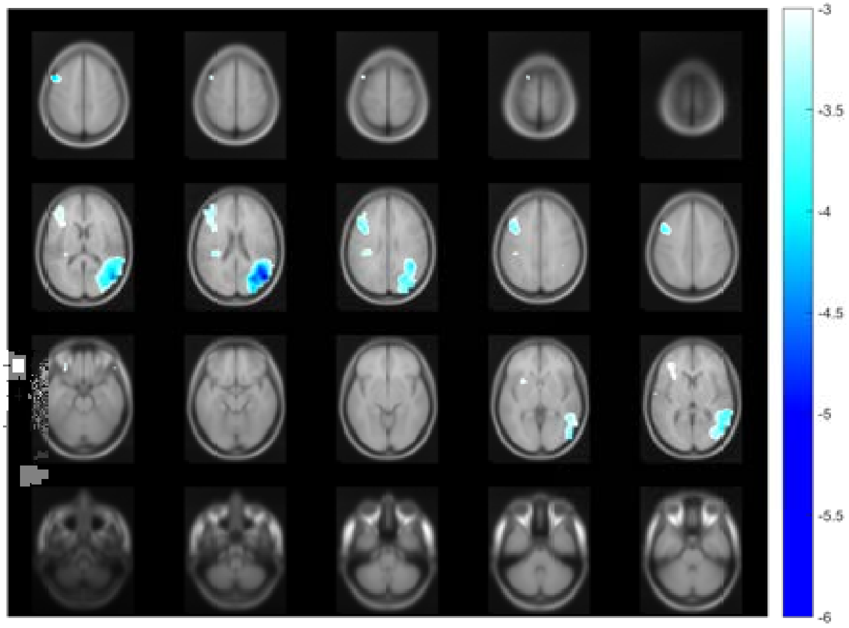

Figure 5.18: Source localisation results of correlation analysis in Experiment 7 (threshold set at T = -3 for plotting purposes).

5.3.2.3 Behavioural interaction analysis between Experiments 6 and 7

Boxplots presenting raw data across experimental conditions for both experiments are presented in Figure 5.19. The means and SDs of correct, target present trials for both experiments are presented in Table 5.7. Following a 2 x (3) mixed design ANOVA a significant main effect of set size (F (1, 80) = 495.79), p < .0001, η^2_G = .642) was found. The results show no significant main effect of experimental design type (F (2, 40) = .017, p = .896, η^2_G =.0003). No significant interaction between set size and experimental design (F (2, 80) =0.082, p = .92, η^2_G = .0002) was found[10] (Figure 5.20).

Table 5.7: Mean reaction times [ms] per set size condition in Experiments 6 and 7.

	Set Size 2		Set Size 8		Set Size 16	
Experiment 6	996.37	(343.64)	1536.79	(574.18)	1883.59	(816.21)
Experiment 7	989.66	(447.97)	1557.55	(654.1)	1906.74	(778.58)

Note: The standard deviations are reported in parenthesis

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[10] The significant main effect of set size is not followed up here, as individual behavioural analyses of Experiments 6 and 7, have already explored the set size condition effects.

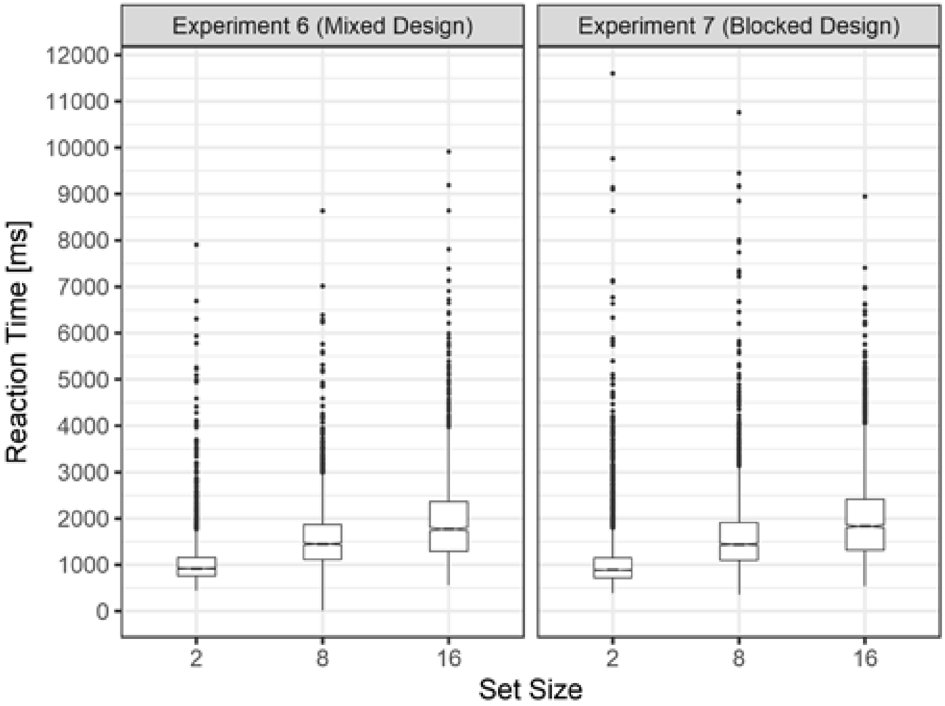

Figure 5.19: Raw reaction times for correct responses per set size in Experiment 6 (left) and Experiment 7 (right).

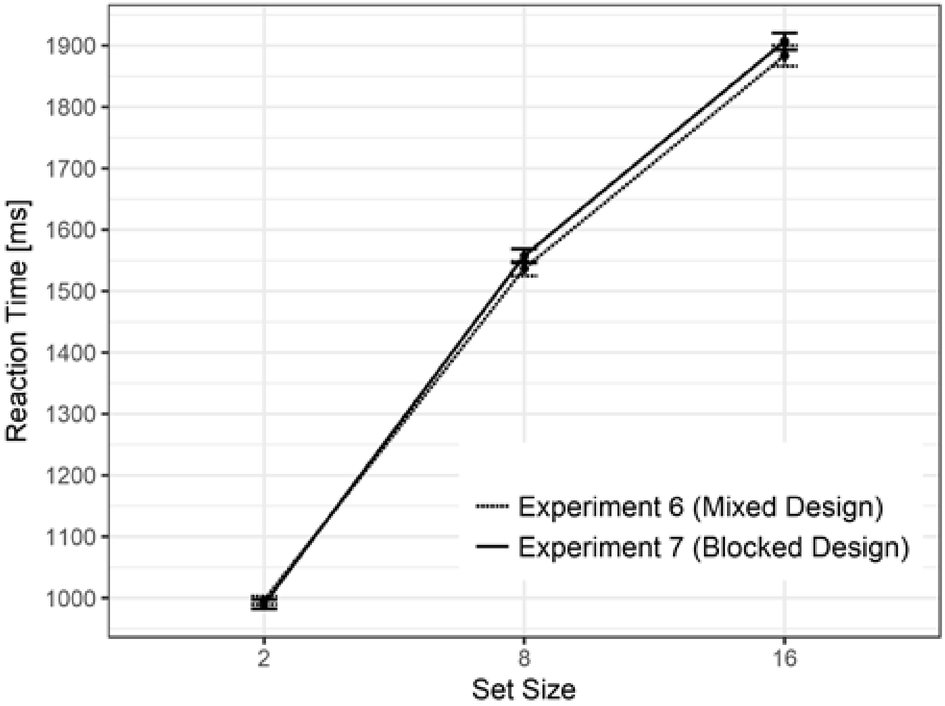

Figure 5.20: Mean reaction times [ms] as a function of set size in Experiments 6 and 7. Error bars indicate the standard error of the mean.

5.3.2.4 EEG analysis - Experiments 6 and 7 comparison

IAF power differences comparison between Experiments 6 and 7

Experiment 6 and Experiment 7 were found to differ with respect to IAF power differences between set size conditions. A significant cluster (T = -154.92, p = 0.002) spanning the 300ms pre-stimulus (the whole window of interest) was found when contrasting Experiments 6 and 7 with regards to the difference between set size 2 and 8 (Figure 5.21). Likewise, the differences between set size 2 and set size 16 (Figure 5.22) in the two experiments were found to differ significantly (T =-131.18, p = 0.002, -300ms to 0ms). IAF power differences found in Experiment 7 between set sizes 2 and 8, as well as 2 and 16, were significantly greater than differences between corresponding set size conditions in Experiment 6. No differences were found with regards to difference between set sizes 8 and 16. This result indicates an interaction between the set size conditions and the experimental design.

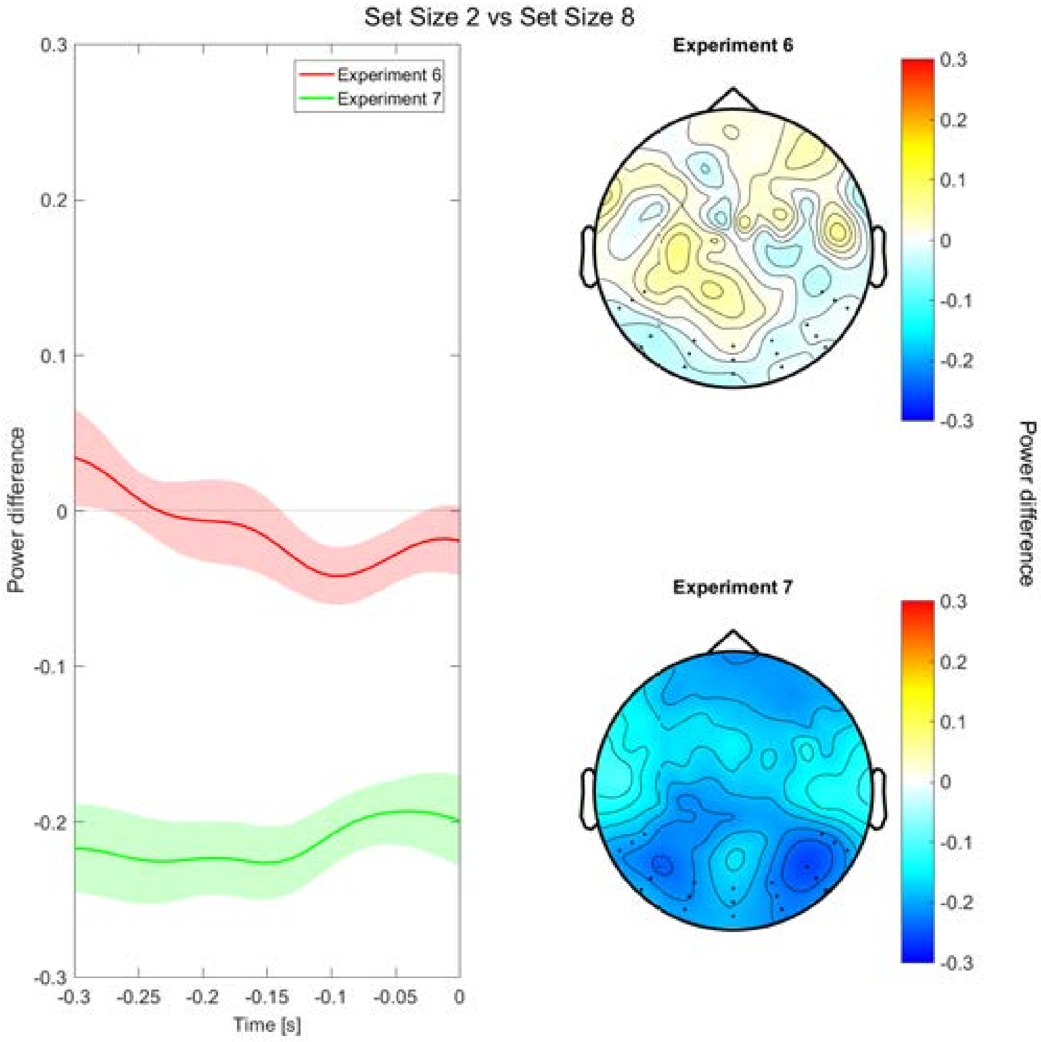

Figure 5.21: Power difference plots between set sizes 2 and 8 in Experiments 6 and 7, as a function of time (left) with corresponding topographies (right; averaged over 300ms of pre-stimulus window).

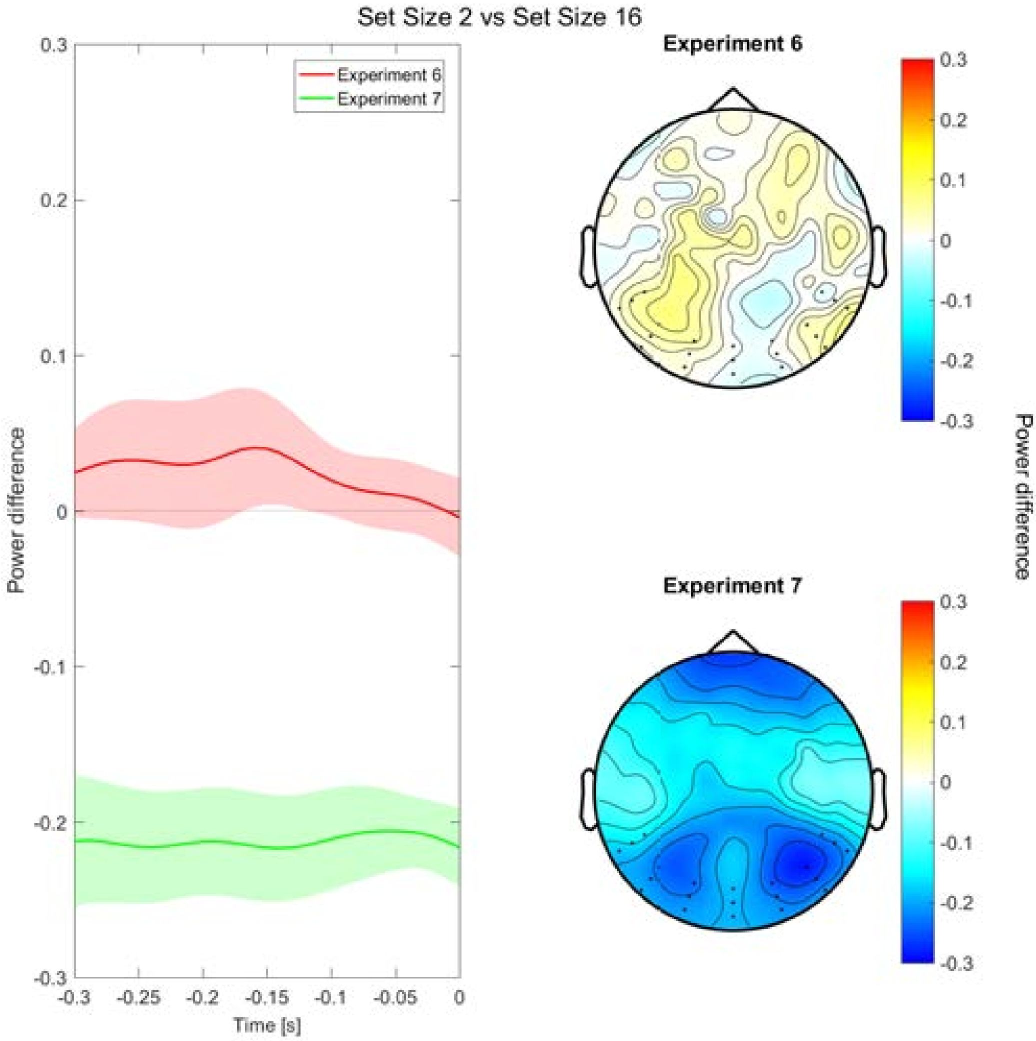

Figure 5.22: Power difference plots between set sizes 2 and 16 in Experiments 6 and 7, as a function of time (left) with corresponding topographies (right; averaged over 300ms of pre-stimulus window).

5.4 Discussion

We proposed that the effects of the alpha filter, reflecting an interplay between general excitability and top-down biasing towards target stimulus, would vary depending on task demands. Furthermore, we argued that anticipation of task difficulty will result in modulation of pre-stimulus alpha oscillations to match the demands of the task. The experiments presented in this chapter investigated the relationship between pre-stimulus IAF power and performance in the context of the alpha filter hypothesis. Since successful performance on a visual search task depends on the strength of the target representation as well as the successful inhibition of distracting information (Hout and Goldinger, 2010, 2014; Luria and Vogel, 2011), a conjunction search paradigm was used. Specifically, Experiment 6 aimed to provide evidence that the effect of pre-stimulus alpha power is related to task demands, while Experiment 7, aimed to demonstrate modulation of pre-stimulus alpha power by anticipation of task difficulty. Both experiments were expected to replicate the effects found in Experiment 5 (Chapter 4).

Task difficulty in the presented experiments was manipulated by varying the set sizes. Either 2, 8 or 16 objects, including the target (in the target present condition) were presented on the screen during the trial. The alpha filter hypothesis proposed that when little distracting information is presented concurrently with task relevant information, a low filter strength will be optimal for performance. This is supported by previous research indicating that when the target stimulus is presented on its own (Hanslmayr et al., 2007), or with one distractor of the same saliency (Van Den Berg et al., 2016) high alpha power is detrimental. Null results of the correlation analysis in set size 2 further corroborate this notion. Furthermore, it was argued that when the target is presented simultaneously with multiple distracting stimuli, a high alpha filter will facilitate their inhibition. While previous research supports the role of high anticipatory alpha power in inhibition of distracting information, the majority of literature presents this effect in lateralisation paradigms, whereby a spatial cue indicates task relevant areas (Händel et al., 2011), or when stimuli are presented consecutively (Bonnefond and Jensen, 2012). In Experiments 6 and 7 a negative correlation between IAF power and reaction times was found in set size 16. Set size 8 condition, likewise, was characterised by a consistent pattern of negative correlations, albeit not reaching the significance threshold. While the Bayes factor analysis indicated that the correlation effects may be inconclusive, their strength is supported by their consistency and replicability, across the three experiments presented in Chapters 4 and 5 (Experiments 5, 6 and 7). Thus, we provide evidence that high pre-stimulus alpha power is beneficial when the target and distractor stimuli are presented simultaneously, without a spatial cue indicating the location of the target. Source localisation analysis of correlation effects in Experiment 6 showed an involvement of frontal and pre-frontal areas. This was not altogether dissimilar from the correlation sources found in Experiment 7, which while showing peaks in occipital and parietal areas also spanned the frontal areas. It can be speculated that this pattern reflects the involvement of fronto-parietal attentional networks in alpha mediated inhibition (Mathewson et al., 2014).

It has previously been suggested that the power of alpha oscillation is modulated by the anticipation of the saliency of the oncoming distractor (Bonnefond and Jensen, 2012; van Diepen et al., 2016). Thus, it was hypothesized that the prior knowledge regarding the set size condition will result in modulation of pre-stimulus alpha power. To this end, in Experiment 7, set size conditions were manipulated by block, and participants were told which set size to expect prior to the beginning of every block. In line with the proposed alpha filter hypothesis, set size 2 was characterised by significantly lower pre-stimulus alpha power, as compared to set sizes 8 and 16. In contrast no differences between set size conditions were found in Experiment 6, in which the difficulty of the oncoming trial was not predictable. A comparison of Experiments 6 and 7 indicated that the pre-stimulus alpha power modulation found in Experiment 7, was indeed a result of the experimental manipulation. The sources of alpha power differences between the activation patterns in Experiment 7 were localised, as anticipated, mainly in occipital and parietal areas.

5.4.1 Chapter conclusions

Here, we proposed that the effects of alpha filter vary depending on task demands, in that when a target stimulus is presented with a singleton distractor, low alpha power is advantageous. Meanwhile when more distractors are presented simultaneously with the target, high alpha power is preferential for successful inhibition of distracting information. While previous research supports the role of alpha power mediated inhibition, the majority of literature presents the effects of the alpha mediated filter in lateralisation paradigms, or presenting the stimuli consecutively (Bonnefond and Jensen, 2012; Händel et al., 2011). Here, the target and distractors were presented simultaneously, without cueing to the location of the target stimulus. The results of Experiments 6 and 7 replicate the effect found in Experiment 5 (Chapter 4), in that high alpha oscillation power correlates to fast reaction times in the highest set size. In line with the proposed alpha filter hypothesis no correlation effects were found in set size 2. Moreover, it was demonstrated that anticipation of the task difficulty results in modulation of pre-stimulus alpha oscillation, whereby the lowest set size was characterised by significantly lower alpha oscillation power than the high set sizes. Thus, the results of Experiments 6 and 7 support the proposed alpha filter hypothesis.

Chapter 6

General discussion and conclusions

Being able to voluntarily attend to specific objects and locations in the surrounding environment and is one of the most fundamental abilities used in everyday life. Selective attention subserves goal-directed behaviour through facilitation of relevant, and suppression of irrelevant information. A substantial body of literature has associated neural oscillations in the alpha frequency range with the modulation of attention (Händel et al., 2011; Hanslmayr et al., 2007, 2005; van Dijk et al., 2008). Previous research investigated this relationship predominantly employing spatial paradigms, or target detection tasks in which the target was presented simultaneously with one distractor, or by itself. However, looking for relevant information in real life situations most often requires searching through a multitude of distracting and irrelevant objects. Visual search task, characterised by presenting a target with a varying number of distractors resembles such situations. Thus, in this thesis a visual search paradigm was employed to investigate the role of alpha oscillations in selective attention. Specifically, the relationship between the anticipatory (pre-stimulus) alpha oscillations and reaction times of target detection was investigated in a series of experiments. In this chapter the current thesis will be summarised and discussed in the context of existing literature, followed by the limitations and future directions.

6.1 Thesis summary

In Chapter 1, the theoretical background was presented, with focus on the theories of selective attention, and the role of alpha oscillations. In Chapter 2, research methods employed in the experiments presented in this thesis were detailed.

A body of literature demonstrated that entrainment of alpha oscillations via visual stimulation results in modulation of behavioural performance (Mathewson et al., 2009; Spaak et al., 2014). While there is some indication that entrainment can affect performance on a visual search task, the reported effects are inconsistent (Gonzalez-Rosa et al., 2015; Müller et al., 2015). Hence, the experiments presented in Chapter 3 aimed to resolve the conflicting evidence. In all experiments presented in Chapter 3 (Experiments 1-4) a visual flickering stimulus in 10 Hz frequency (alpha condition) was used aiming to increase alpha power, while a non-rhythmic stimulus, with a mean of 10 Hz (non-alpha condition), was expected to decrease alpha power. Importantly, this modulation of the underlying oscillation was anticipated to affect the behavioural performance on a visual search task used in Experiments 1, 2 and 3. A non-flickering stimulus was used as a control. Based on the previous research indicating the detrimental effects of high power of alpha oscillation on performance (Ergenoglu et al., 2004; Hanslmayr et al., 2007; Mathewson et al., 2009; Thut et al., 2006; van Dijk et al., 2008), it was anticipated that the reaction times of target detection will be longer following alpha stimulation condition, as compared to non-alpha stimulation. However, no effects of stimulation conditions were found in Experiment 1, in which the flickering stimulus was a filled in rectangle, covering the whole area of the visual search display. It was concluded that the intensity of the flickering stimulus may have resulted in substantial visual discomfort, as indicated by participant's accounts and supported by previous literature (Allefeld et al., 2011; Collins and Hopkinson, 1957; Mauro et al., 2015; Zhu et al., 2010). To address this limitation in Experiment 2 a less salient flickering stimulus was used - a frame encompassing the same area. This manipulation, while resulting in a performance benefit of non-alpha stimulation as compared to non-flickering condition, did not show alpha stimulation effects. In Experiment 3 the flickering stimulus was presented bilaterally, with simultaneous presentation of alpha and non-alpha stimuli. Here it was anticipated that when target is presented congruently to the alpha flickering stimulus, the reaction times will be longer as opposed to the target presented incongruently. This was not supported by the results. In Experiment 4, which employed electroencephalography (EEG) to assess the efficacy of the visual stimulation, it was demonstrated that the flickering stimulus used did not result in the expected entrainment of the underlying oscillation. This lack of entrainment was likely the result of the wide visual angle of the flickering stimulus. Previous research indicates that the effect of flickering stimulus is attenuated with the increasing eccentricity (Parks et al., 2013). Moreover, it has recently been shown that entrainment effects are more likely to be observed if stimulation frequency reflects the individual alpha frequency of the participant (Gulbinaite et al., 2017). Considering the results of Experiment 4, it can be speculated that the effect found in Experiment 2 may have been due to the variation in general vigilance, which resulted from a difference in the rhythmicity of the trial sequence between the stimulation conditions.

The Experiments 1, 2 and 3 were conducted under the premise that entrainment of alpha oscillations will affect the target detection on a visual search task. Although previous findings suggest that alpha power does play a role in performance on visual search task, most of the existing evidence considers the post stimulus period (Gonzalez-Rosa et al., 2015; Spaak et al., 2016; van Diepen et al., 2016). Moreover, there is still considerable ambiguity with regards to the effects of alpha power on reaction times (Gonzalez-Rosa et al., 2015; Müller et al., 2015). Thus, in Chapter 4, an exploratory study investigating the pre-stimulus alpha oscillations with respect to reaction times on a conjunction visual search task, with two set size conditions (16 and 24), was conducted.

Previous evidence demonstrates the role of both, the power and the phase of alpha oscillations in target detection and discrimination (Busch et al., 2009; Chaumon and Busch, 2014; Hanslmayr et al., 2005; van Dijk et al., 2008). Successful target detection is associated with different phases of the underlying oscillations, as compared to when the target is missed (Busch et al., 2009; Hanslmayr et al., 2013). Similarly, the reaction times have been related to the phase of the ongoing oscillations (cf. VanRullen and Dubois, 2011). In Experiment 5 a correlation analysis between the phase of the pre-stimulus alpha and the reaction times was performed. Furthermore, trials characterised by fast and slow reaction times were investigated using a phase opposition measure (the phase bifurcation index, PBI). While a modest correlation effect was observed in the lower of the two set sizes (16 and 24), the investigation of the PBI yielded a null result, indicating that fast and slow reaction times were not associated with specific phases of the underlying oscillation. It was concluded that phase did not have a strong effect on performance.

Furthermore, the power of pre-stimulus alpha oscillations was considered. There is a consensus in the existing literature that low alpha power is associated with an increased hit rate in the target detection tasks (Thut et al., 2006). It is also established that high alpha power reflects inhibition of distracting stimuli and task-irrelevant locations (Händel et al., 2011; Janssens et al., 2017). Successful performance on a visual search task requires an efficient inhibition of distractors as well as an effective identification of the target stimulus (Hout and Goldinger, 2010, 2014).

Here, unlike in the majority of previous research, multiple distractors and the target were presented simultaneously with no indication as to where the target stimulus may occur. Consequently, two potential outcomes were considered. A positive correlation between alpha power and reaction times would be in line with research demonstrating that low alpha power is associated with improved performance (Van Den Berg et al., 2016). On the other hand, considering the role of alpha oscillations in distractor inhibition (Spaak et al., 2016; van Dijk et al., 2008), a negative correlation could be anticipated. The latter hypothesis was supported by the results presented in Chapter 4. A significant negative correlation between alpha power and reaction times was was observed in set size 16. However, it was argued that the null effect found in the set size 24 may result from the significantly longer search termination times. It is reasonable to assume that the effects of pre-stimulus alpha power on performance decay over time. A follow up analysis examined the fastest third of trials in set size 24. The correlation, albeit not significant, exhibited the same negative pattern as was observed in set size 16.

These results, while to extent in line with the alpha inhibition hypothesis (Klimesch et al., 2007), provide a seemingly divergent account to a body of research demonstrating adverse effects of high alpha oscillation on target detection (Mathewson et al., 2009; Thut et al., 2006; van

Dijk et al., 2008). The differences between the paradigms used in previous research and the conjunction visual search task employed in Experiment 5, imply that depending on task demands the effects of pre-stimulus alpha power are likely to differ. Previous research in the working memory domain demonstrated analogous effects, with alpha oscillations increasing in power with an increased memory load. This suggested that the increases in task demand required a corresponding increase in inhibition of external intruding stimulation (Jensen and Tesche, 2002; Klimesch et al., 1999; Tuladhar et al., 2007). Similarly, tasks employing mental imagery have associated alpha power increases with internally directed attention and task demands (Cooper et al., 2003).

Therefore, in Chapter 5 an “alpha filter hypothesis” was proposed and investigated by means of two electroencephalographic experiments (Experiments 6 and 7). Based on previous research, and the results presented in Chapter 3, it was proposed that if the target is presented with just one distractor, none or little filtering will be needed for optimal performance. On the other hand if multiple distractors are simultaneously with the target more inhibition will be required and high alpha power will be beneficial. Hence, the task demands in Experiments 6 and 7 were modulated by means of set size (2, 8 and 16). It was anticipated that in the high set size conditions (8 and 16), but not in the low set size condition (2), high pre-stimulus alpha power will be beneficial for target detection. Indeed, a negative correlation between alpha power and reaction times was found in both experiments for set size 16, replicating the results of Experiment 5. Importantly, in line with the hypothesis, the lowest set size did not show a negative correlation in either of the experiments. Moreover, it was proposed that the anticipation of set size condition would result in the adjustment of the alpha filter. To this end, in Experiment 7, set size was manipulated by block, and participants were told which condition to expect. The predictability of the task demands resulted in a significant modulation of pre-stimulus alpha power, with high set size conditions showing higher alpha power as compared to the low set size condition.

Previous findings provide evidence for the inhibitory role of alpha oscillation in protecting the working memory against distractors by effectively blocking out the intrusive external stimuli, when the distractors and task-relevant stimuli are preesented consecutively (Bonnefond and Jensen, 2012). Consequently, the results of Experiment 6 and 7, presented in Chapter 5 are novel findings demonstrating that pre-stimulus alpha oscillations represent a filtering mechanism, effects of which vary with task demands, and are modulated in an anticipatory fashion in the context of a conjunction visual search task. The results presented in Chapters 4 and 5 show that these anticipatory effects of alpha oscillation are related to performance, when the target and distractors are presented concurrently.

6.1.1 The alpha filter hypothesis

The association of high alpha power with fast reaction times and vice versa, demonstrated in this thesis, is in line with the alpha inhibition hypothesis. The “alpha filter hypothesis”, proposed in Chapter 5, can serve to reconcile these results with the literature indicating that high alpha power is detrimental to target detection (Ergenoglu et al., 2004; Hanslmayr et al., 2007; Mathewson et al., 2009; Thut et al., 2006; van Dijk et al., 2008). In this hypothesis, the effects of the alpha mediated filter were proposed to be related to task demands. We argue that depending on the amount of distracting information, with relation to task relevant information, different amounts of alpha filter will be optimal for performance (Figure 5.1, Chapter 5).

If the task requires detection or discrimination of a single stimulus, unaccompanied by any distractors, no filtering may be necessary, it would in fact be likely to result in an impaired performance. For instance, Thut et al. (2006) show that increased hit rates are associated with low alpha power, and vice versa, when a near visual threshold target is briefly presented. Similarly, Hanslmayr et al. (2007), show that participants with lower alpha power perform better as opposed to participants with higher alpha power in a target discrimination task, where a singleton stimulus is briefly presented. On the other hand, in lateralisation paradigms the area of interest is determined by a spatial cue, while all other locations are to be ignored. Here, the filter can be applied spatially, due to the retinotopic properties of the alpha oscillations (Ikkai et al., 2016; Kelly et al., 2006). It is crucial, however, that all information presented within the area of interest is processed. Thus, none, or a minimal filter should be applied to the task relevant region. In these examples the requirement is to process all the information presented within the area of interest and in the limited amount of time. Likewise, in the low set size condition of a visual search task, when the target is presented together with one distractor, increasing the filter would result in impaired performance, as shown by Van Den Berg et al. (2016). This is further supported by the null effect of the correlation between alpha power and reaction times in set size 2, in Experiments 6 and 7.

In contrast, in a high set size condition of a conjunction visual search, the target is presented simultaneously with multiple distractors. Moreover, in the experiments presented in this thesis, the location of the target was not predictable. While the performance on a conjunction visual search task relies on the successful identification of the target stimulus, it is also dependent on efficient inhibition of distracting information. This is evidenced by research demonstrating the dependency of search performance on the working memory capacity (Luria and Vogel, 2011), which in turn has been related to the ability to successfully suppress the distracting information (Vogel et al., 2005). Hence, applying a filtering mechanism to facilitate inhibition of distractors would be appropriate, as evidenced by the negative correlations demonstrated for set size 16 in Experiments 5, 6 and 7.

As it has been discussed in the previous chapters (Chapter 1 and Chapter 4), alpha oscillations were proposed to reflect the general neural excitability of the cortex (Haegens et al., 2011). Limbach and Corballis (2016) demonstrated that high alpha oscillations are related to a more conservative criterion, resulting in an increase of missed targets and correct rejections alike. Iemi et al. (2017) also show that low alpha power is associated with an increase of both the hit rates and false alarm rates, and thus, reflects a more liberal criterion. Furthermore, they demonstrate that alpha oscillations have no effect on the sensitivity index, which indicates that the actual detectability of the target is not affected by alpha power. In short, this suggests that low pre-stimulus alpha power affects the likelihood of reporting the target and does not represent an actual improvement in detecting it. In the experiments presented in this thesis, it was not possible to directly relate the sensitivity and criterion measures to pre-stimulus alpha power. However, the behavioural results presented in Chapter 4, indicate that fast reaction times show a higher sensitivity index than slow reaction times. This suggests that the reported negative correlation between pre-stimulus alpha power and reaction times represents an actual improvement in task performance.

However, following the premise of alpha power reflecting general excitability, the alpha filter should affect both task relevant and task irrelevant information in an identical fashion. Both, Limbach and Corballis (2016) and Iemi et al. (2017) have used a singleton target detection task in their studies. Thus, the target detection is driven by bottom-up processes. Conversely, target detection on a conjunction search task is understood to be guided by top-down imposed attentional templates (Desimone and Duncan, 1995; Hout and Goldinger, 2014). Moreover, cueing a target activates areas of the visual cortex selective to the target specific features (Giesbrecht et al., 2006). Effectively, the representation of the target is likely to be stronger than that of the distractors, which might result in distractors being more readily affected by the alpha filter than the target. With this in mind, we argue that the alpha filter effects reflect the interplay between the top-down biases in favour of the target and the modulation of general excitability.

Importantly, the notion of task demands in the proposed alpha filter hypothesis, does not necessarily imply task difficulty. To exemplify this, the target-distractor similarity can be considered. Early attentional selection theories (Duncan and Humphreys, 1989) point out the importance of the feature-based distinction between distractors and targets. It has been demonstrated that visual search slopes are sensitive to this parameter, with increased reaction times when targets and distractors are more alike, as compared to when they are distinct (Wolfe and Horowitz, 2017). In line with the proposed alpha filter hypothesis, increasing homogeneity between the target and the distractor, despite the effective increase in task difficulty, should result in a decrease of alpha filter. The more similar the distractors are to the target, the more likely it is that high alpha power would result in “filtering out” the target. Indeed, research concerning post-stimulus alpha power effects, provides supporting evidence. Van Diepen et al. (2016) demonstrated that following a spatially non-informative cue, post stimulus alpha showed increased lateralisation when a low similarity distractor was presented simultaneously with the target, but no lateralisation effect when high similarity distractor was presented. Similarly, Roberts et al. (2014) demonstrate higher post-stimulus alpha power if the target and the distractor are more similar in orientation. Moreover Feldmann-Wüstefeld et al. (2017) present decreases in post-stimulus alpha with increased in heterogeneity of the surrounding distractors.

To conclude, the results presented in this thesis demonstrate that high pre-stimulus alpha power is related to performance improvement in a visual search when the task demands are high, while no benefit is observed in the low task demand condition. It has been argued that these results, although seemingly divergent from the majority of previous research, are in fact consistent with the findings to date if the differences in paradigms employed are scrutinized. The demonstrated effects provide novel evidence with regard to the inhibitory role of pre-stimulus alpha oscillation in selective attention.

6.2 Limitations and future directions

The research presented in the current thesis has its limitations, which will be now addressed. Firstly, the entrainment experiments will be considered. The failure to effectively entrain the underlying oscillation may have been due to a number of reasons. It was considered, that the flickering stimulus used in Experiment 1 was too salient and may have resulted in both discomfort as well as illusory precepts (Allefeld et al., 2011; Mauro et al., 2015; Zhu et al., 2010), which would have confounded the effect of stimulation. In Experiment 2 we aimed to address this limitation by introducing a less salient flickering stimulus, however this manipulation also proved to be ineffective, as the results of Experiment 4 indicated that the underlying alpha oscillations were unlikely to have been affected. It is plausible that the visual angle of the flickering stimuli was too wide to result in strong enough entrainment. In their study Parks et al. (2013) present the evoked responses to visual flicker at various visual angles, and the effect of stimulation is shown to subside with the increasing visual angle. Notably, none of the stimuli used by Parks et al. (2013) are as wide as used in Experiments 2-4. Our aim in using a wide stimulus was to ensure that the whole space within which the target and distractors could appear was affected. Thus, in future investigations it may be advisable to design the visual search display in a manner which would allow the use of a smaller flickering stimulus. Furthermore, it has recently been demonstrated that for the most effective entrainment using visual stimulation, the frequency of the flickering stimulus should be as close as possible to the individual alpha frequency of the participant (Gulbinaite et al., 2017). It may be that the 10 Hz frequency used in alpha condition did not correspond with the individual alpha frequencies of participants. Hence, in future research it may be beneficial to customize the flickering stimulus frequency to the individual alpha frequency of the participant.

Furthermore, the paradigm in the Experiments 5, 6 and 7 should also be considered in the context of the alpha filter hypothesis. It was proposed that the effects of alpha filter are related to the strength of the target representation with regards to the distracting information. It could be argued that using two potential targets, both sharing a different combination of features with the distractors, results in an increased target-distractor similarity and may weaken the strength of said representation. Hence, potentially a more pronounced effect could have been observed if only one target type was used. Moreover, using two potential targets results in substantially longer reaction times. While no formal comparison is presented in this thesis, this dependency is suggested by the descriptive statistics, with the reaction times in Experiments 1 and 2 being shorter as compared to the corresponding set sizes in Experiments 5 - 7. In Chapter 4 we proposed that the effects of pre-stimulus alpha oscillation on performance are likely to dissipate with time. This further indicates that more prominent effects of pre-stimulus alpha could potentially be observed if the task involved only one target type.

Due to the high accuracy rates, it was not possible to directly investigate the signal detection measures with respect to the power of alpha oscillations. Future research could address this limitation, by increasing the difficulty of the task (i.e. through time-limited exposition of the visual search display), and thus directly relate these behavioural measures to pre-stimulus alpha power. If high alpha power in the higher set size condition resulted in increased sensitivity, this would further support the proposed alpha filter hypothesis. Importantly, it would allow a more direct comparison to the recent studies employing signal detection measures (Iemi et al., 2017; Limbach and Corballis, 2016).

6.3 Thesis conclusions

In a series of 7 experiments this thesis aimed to elucidate the relationship between pre-stimulus alpha oscillations and target detection in a visual search task. Initially, the visual entrainment was employed, aiming to modulate the underlying alpha oscillations, and thus affect the reaction times of target detection (Experiments 1-3). This manipulation, however, proved unsuccessful, as demonstrated by the results of the Experiment 4. Since the existing evidence of the role of alpha oscillations in performance on a visual search task was contradictory, an exploratory EEG study was conducted (Experiment 5). The results demonstrated an inverse relationship between the power of alpha oscillations, whereby high pre-stimulus alpha power was related to fast reaction times, and vice versa. While, these results were in line with the alpha inhibition hypothesis to a certain extent, they were seemingly contrary to the previous research, demonstrating detrimental effects of high alpha power on target detection. Consequently, an “alpha filter hypothesis” was proposed to reconcile the existing literature and the results reported in Experiment 5. It was proposed that the power of alpha oscillations reflects a filtering mechanism, effects of which are dependent on task demands. This hypothesis was investigated in two further EEG experiments (Experiments 6 and 7). It was shown that high pre-stimulus alpha power is related to fast reaction times only in the highest set size, while no such relationship was observed in the low set size. Thus, the proposed hypothesis was supported. Moreover, evidence demonstrating the anticipatory modulation of alpha filter by task demands was presented, indicating that alpha power reflects an active filtering mechanism. This thesis substantially added to the existing body of literature by demonstrating effects of pre-stimulus alpha power on target detection, when a target is presented simultaneously with multiple distractors in a spatially unpredictable manner.

Appendix A

Visual search pilot study

A.1 Pilot Experiment - Visual Search

Methods

Paticipants

14 participants were recruited from among students from the University of Birmingham (12 female, mean age of 24.3 years with 19 to 31 years of age range). All subjects had normal or corrected to normal vision and were not colour-blind.

Visual search

A modified classical Visual Search (VS) paradigm (Triesman et al., 1980) was used in order to assess its validity as a measure of attention.

Design

A within subjects design with independent variables of target present/absent condition (2), visual search type (2) and set size (3) and the primary dependent variable of reaction times were used.

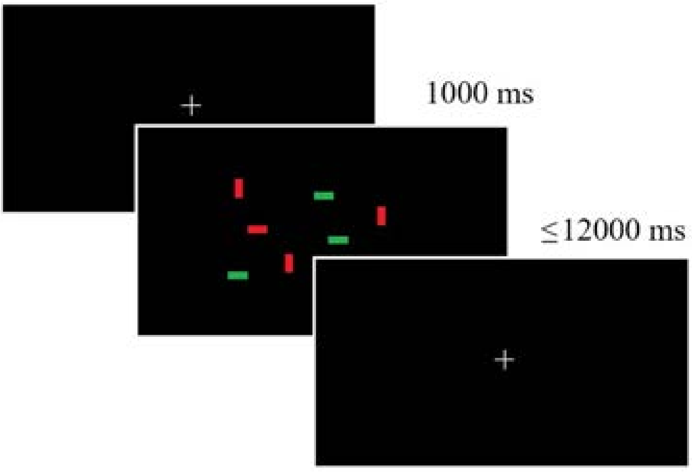

Figure A.1: Pilot Experiment: Example of a trial sequence.

Procedure

Participants were seated approximately 55 cm from the display, which gave 22°x13° visual angle in relation to the fixation cross in the centre of the screen. Each trial began with a fixation cross (1000 ms), which participants were instructed to focus on and followed by an onset of a Visual Search display. The Visual Search display remained on screen a maximum of 12000 ms or until a response was given by the participant. Participants were instructed to swiftly and accurately respond with an appropriate key in order to indicate presence or absence of a target – red horizontal rectangle (80x29 pixels) - among distractors: green horizontal rectangles and red vertical rectangles. Participants were asked to complete a practice run consisting of 18 trials and four blocks of 150 (50% absent, 50% present) trials of the experimental run – two blocks of each Visual Search type, with Set Size randomized across each block (50 trials of each set size). Participants were given breaks between each block.

Results

Reaction time means and standard deviations were calculated for all conditions. Data used in the analysis was trimmed using low (250 ms) and high (average + 3 SD) cut off values. Overall average accuracy on this task was 93.8% (SD =3.33%).

A within-subjects factorial design with factors of Set Size, VS type and Target Present/Absent condition was used. The slopes of target absent versus target present conditions were investigated in order to assess whether our paradigm achieved the expected ratio of reaction times in

Table A.1: Pilot Experiment: Mean reaction times per experimental condition.

	Set size 8		Set size 16		Set size 24	
Feature search						
Target absent	490.34	(25.82)	477.63	(27.99)	483.26	(38.05)
Target present	493.51	(48.48)	478.82	(41.03)	482.82	(45.06)
Conjunction search						
Target absent	778.58	(102.42)	983.01	(170.3)	1185.73	(245.87)
Target present	713.1	(74.85)	809.35	(90.36)	931.66	(133.75)

Note: The standard deviations are reported in parenthesis.

target present vs target absent conditions (Triesman et al., 1980; Wolfe, 1994). A ratio of 2:1 was found between target absent and target present slope in the conjunction condition and 1:1 in feature condition as anticipated.

A repeated measures ANOVA on reaction times (RTs) in target present condition was conducted in order to assess whether the differences between conditions and set sizes, as well as the interaction between factors were significant.

The results show main effect of visual search type (F (1, 13) =236.853), $p<.0001$) and set size (F (2, 26) =33.845, $p<.0001$) were found, as well as a significant interaction between Visual Search type and Set Size (F (2, 26) = 52,671, $p<.0001$).

Appendix B

Speed accuracy correlation analysis

B.1 Experiment 1

1. Feature condition with alpha condition: r (22) =.435, p=.033
2. Feature condition with non-alpha condition: r (22) =.251, p=.236
3. Feature condition with non-flickering condition: r (22) =.321, p=.126
4. Conjunction condition with alpha condition: r (22) =.435, p=.033
5. Conjunction condition with non-alpha condition: r (22) =.401, p=.052
6. Conjunction condition with non-flickering condition: r (22) = .467, p=.021

B.2 Experiment 2

1. Feature condition with alpha condition: r (22) =.347, p = .105
2. Feature condition with non-alpha condition: r (22) = .381, p = .073
3. Feature condition with non-flickering condition: r (22) =.107, p =.627
4. Conjunction condition with alpha condition: r (22) = .228, p = .296
5. Conjunction condition with non-alpha condition: r (22) = .25, p = .251
6. Conjunction condition with non-flickering condition: r (22) = .073, p = .742

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