

Investigating the function of alpha frequency oscillatory activity.

A thesis submitted for the degree of Doctor of
Philosophy
by

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Declaration

I hereby declare that this thesis has not been, and will not be submitted, in whole or in part to another University for the award of any other degree.

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Undertaking this PhD degree has been a truly life-changing experience for me, and it would not have been possible to do without the help and support of some people who have played a significant role in my success.

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Abstract

A fundamental challenge in modern neuroscience is to understand the role of synchronous oscillatory activity of groups of neurons in information processing. This thesis addressed the problem of how alpha frequency oscillatory activity might help control the flow of information from both the external world and from higher cognitive areas (responsible for inhibitory control, top-down and bottom-up information flow).

A series of experiments investigated how alpha neuronal dynamics might aid/control cognition. In order to study the functional significance of alpha frequency oscillatory activity, the effects on performance in cognitive tasks of alpha activity directly elicited using photic stimulation were examined.

Initially, we were interested in the role of alpha oscillations in information transfer across cortical areas, which was probed using a numerical Stroop task with every trial preceded by a flicker prime. The incongruent trials of the Stroop task introduce a conflict between competing responses which results in people being slower in responses to the task compared with congruent trials. That slower response has been related to increased communication between conflict processing fronto-parietal and early somatosensory regions. If alpha oscillations improve communication efficiency across the cortex it was predicted that inducing stronger alpha oscillations would affect the performance, (i.e. the Stroop cost would diminish). That hypothesis was tested in a series of three experiments. None of the manipulations (different frequencies, amplitudes induced and alpha phases where the Stroop task was initiated) showed that alpha oscillatory activity reduces the Stroop effect. However, the last task showed that people were faster when the task was preceded by an alpha frequency flicker prime, especially around 10Hz.

The fourth experiment built on the well-established phenomena that when alpha activity is elicited in a particular hemisphere it attenuates processing of sensory information in that hemisphere, while the opposite hemisphere, is characterised by increased efficiency of information processing/flow. The study tested whether that could occur within a hemisphere by localised entrainment of part of the visual field. This hypothesis was tested by examining whether it could resolve differences in results previously published by Mathewson et al., (2012) and Spaak et al., (2014). In this study, a target circle was presented

at time points after the offset of an alpha flicker prime, such that it was either in or out of phase with the prime. The target was displayed briefly, and then a masking ring appeared around the target location. There were two experimental conditions. First priming occurred at the central target location, and this was expected to inhibit perception at that location, (i.e. the target would be best detected at out of alpha phase time points). In contrast, in the second condition, the target surround area (e.g. the mask location) was stimulated, and this was expected to inhibit perception at that location, (i.e. the mask would be most effective in phase time points and so the target more easily detected). However, in both instances, target detection was best at in-phase time points and attenuated at out of phase time points, in line with Mathewson et al., (2012) results. This gives us some insight into the role of the alpha phase in allowing the external stimuli to be perceived/detected.

The fifth experiment tested whether the level of spatial uncertainty of briefly presented target determines the alpha phase position for its best detection. This task used a similar masked circle paradigm as the fourth experiment, but the target could appear at one of two locations either side of fixation, which were both preceded by a flicker prime (either alpha frequency or randomly jittered) and followed by masking rings. The hypothesis was that the optimal alpha phase for target detection depends on whether people are pre-guided (by an arrow cue) to the target location or uncued (a higher level of spatial uncertainty). This hypothesis was again tested by examining whether it could resolve differences in results previously published by Mathewson et al., (2012) and Spaak et al., (2014). This experiment showed that the level of spatial uncertainty of briefly presented target determines the optimal alpha phase for its detection. Targets whose location was not pre-guided were the most likely to be detected when presented at time points out of phase with the entrained alpha prime; targets whose location was pre-guided by a brief arrow were the most likely to be detected when presented at time points in phase with the entrained alpha prime.

The sixth experiment used EEG to investigate the neural dynamics underlying the behaviourally tested phenomenon in the previous experiment. Results showed that for targets with a high level of spatial uncertainty, the average alpha power peak was detected earlier in anterior electrodes compared with posterior electrodes, which is consistent with a greater reliance on alpha top-down dynamics. In contrast,

for targets at a spatially cued location, the average alpha power peak was detected earlier at posterior electrodes, which suggests a greater reliance on bottom-up alpha neuronal dynamics.

In summary, this thesis confirmed that mid-alpha phase determines the probability of detection of a briefly presented target. Also, it showed that optimal alpha phase for detecting briefly presented target would differ depending on the level of spatial uncertainty of that target. Targets at non-predictable locations are more likely to be detected at a trough in the phase of alpha activity whilst those at cued locations are most likely to be detected in-phase. Hence, perception depends not only on the internal neuronal alpha dynamics but also on the type of the visual percept. This difference may highlight the role of two different neuronal alpha sources which dominate in the different scenarios. When the target location is uncertain, top-down alpha dynamics dominate. However, when the target location is pre-guided, bottom-up alpha dynamics dominate.

Keywords: Alpha oscillations, photic driving, perception, attention, behavioural experiments, EEG, inhibitory control

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1 Introduction

1.1 The brain as an oscillatory system.

1.1.1 Fundamental concepts in Neuronal communication.

Cognitive functions result from the coordinated interaction of many networks of neurons distributed across the brain, which has been termed population coding (Bressler & Menon, 2010). Importantly, individual neurons can participate in many different networks (termed neuronal assemblies) whose function depends on with which other neurons they group. A significant area of research within the neurosciences is to understand how the activity of individual neurons can lead to their being rapidly grouped into functional assemblies, representing perceptual and cognitive processes (Uhlhaas & Singer, 2006).

A pioneering account of neuronal network formation was proposed by Donald Hebb (1949). Hebb proposed that any two cells that are repeatedly activated at the same time will become associated together and so tend to facilitate each other's activity. This strengthening comes from either developing a new synapse (or physical connection between the cells) or by lowering the activation threshold of a neuron's action potential. Thus, for example, a visual stimulus that evokes a particular pattern of neuronal activity will more easily elicit that activity the more frequently it is presented (Goldberg, 2000). This proposal has formed the basis of most subsequent theories of neural plasticity, network formation and learning (D'Angelo et al., 2011).

Traditionally, most models of neuronal assembly formation were based on rate coding accounts of neuronal activity, (e.g. as the intensity of a stimulus increases then the firing rate of neurons responding to it increases). For example, neurons in the primary visual cortex of cats viewing a centrally fixated grating have been shown to increase their firing rate in response to a change in the orientation of the surround, which increases the perceived contrast of the grating (Bartels & Zeki, 2006). However, a fundamental challenge for any model of neuronal assembly formation is to identify how neurons can contribute to more than one assembly that is activated concurrently. Von der Malsburg (1981) argued that the only solution to this problem is by *segregating these networks in time*, which he proposed could in

principle be done in two ways. The first possibility is that neuronal assemblies form for very brief periods of time and then break-up and then form into new assemblies. Both, old and new assemblies contain the different configuration of neurons with some neurons common to both assemblies and others contributing to only one of them. Some models of rate coding network formation have been proposed using this short duration approach, e.g., spike-count rate, time-dependent firing rate (Forrest, 2014).

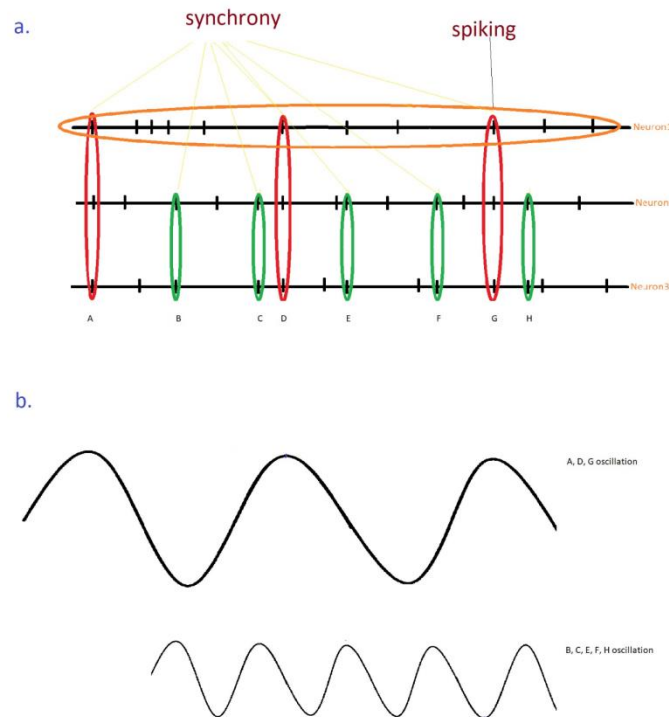


Figure 1.1 illustrates spiking trains for three typical neurons (a) and how individual spikes may be synchronised across neurons. Oscillations occur when synchronous spikes of different neurons fire at regular specific intervals (b) and their frequency, amplitude (depending on the number of neurons engaged) and phase (relative to other oscillations) may encode information.

However, von der Malsburg (1981) focussed on the second proposal that neuronal activity provides an additional mechanism for encoding when they form a part of an assembly. Building on earlier models proposed by Milner & colleagues (1974) and Grossberg (1976), he suggested that neurons synchronise parts of their activity in time and that this synchronisation indicates the neurons are part of a common functional network. Figure 1.1a illustrates an example of the proposed grouping of neuronal interactions in time, where individual neurons contribute simultaneously to more than one functional structure. Each

neuron fires a spike train of action potentials across time. When spikes in a train of two, or more, neurons occur at corresponding points in time (e.g. Figure 1.1a) it creates synchronous spiking, and when this synchronisation occurs at regular repeated intervals, it is termed oscillatory activity. The same neuronal cell can thus be involved in more than one assembly (e.g. Figure 1.1a –A+D+G or B+C+E+F+H) by synchronising activity at different time intervals. Importantly, synchronisation of neurons can occur in two specific ways. First, neurons can group briefly (form functional ensembles) by firing virtually simultaneously in rhythmic repetitions (synchronous spiking activity can be time locked). Second, neurons can group briefly when they fire rhythmically at the same rate but where spikes in different neurons occur at a fixed, regular delay (phase shift). This is particularly critical as there are inherent latencies in the propagation of activity across the cortex.

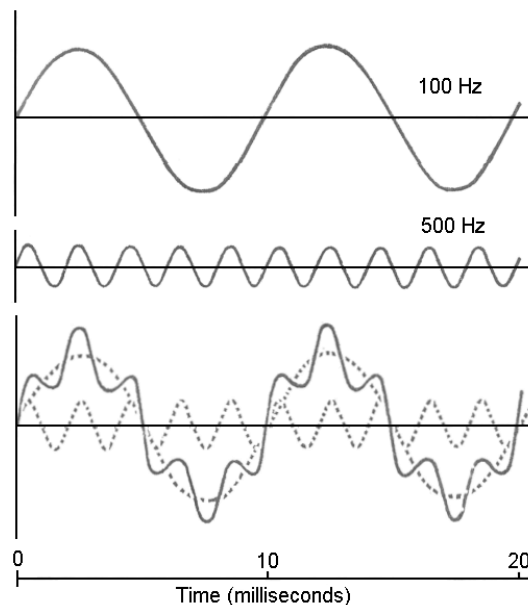


Figure1.2 Complex waveform can be decomposed into simple sinewaves
<http://clas.mq.edu.au/speech/acoustics/waveforms/waveadd01.gif>.

This view is best conceptualised by considering neuronal spike trains as complex waveforms (see 1.2). All such waveforms can be divided into a series of component sin-waves, which characterise activity at different frequencies (or temporal intervals). Thus, the synchronisation of activity across the spike trains can be characterised as a sin wave with its consequent associated properties. First, the frequency is the

number of repetitions within a fixed period. Typically, frequency is measured in Hertz (Hz), the number of repetitions within one second (Stevenson, 2010). It is determined by the rate (fast or slow rates) at which neurons synchronise their activity. Second, the amplitude is a distance between the maxima and minima of the oscillation (Stevenson, 2010). The amplitude of an oscillatory wave will be determined by the number of neurons contributing to it, a larger group of neuronal spikes in synchrony – larger amplitude. Third, the phase is the proportion of a wave cycle that has elapsed relative to its origin (measured in degrees from 0° - 360°). When combining activity across spike trains (each described by a different sin wave), the critical concept is a phase shift which is the relative distance between matched points. An example of synchrony with virtually zero phase shift is when people clap simultaneously during the concert, which is usually achieved after some time of clapping. In this example, each person is a single oscillator and is initially in random relation (phase) to others. However in time all oscillators become locked in phase with each other by clapping simultaneously, and the phase shift between individual oscillators virtually disappears (Stevenson, 2010; Buzsáki, 2009).

Importantly, von der Malsburg, (1981) proposed that neurons form functional groupings (neuronal assemblies) by synchronising oscillatory activity at different frequencies and that this could occur independently of the firing rate (spiking). This proposal has the advantage of indicating how cells that are not directly physically connected can form part of the same functional assembly. In contrast, Hebbian models of neuronal connectivity emphasise the strengthening of physical connections between neurons rather than purely functional connectivity. Critically, in synchrony, the precise timing of spikes plays a crucial role in encoding the relationship between neurons while Hebb emphasises the overall simultaneous activity of the cells, (i.e. the precise timing of individual spikes does not play a significant role). However, these models are not mutually exclusive and, von der Malsburg, (1981) argues that synchrony provides an additional mechanism for encoding information rather than an alternative. The relationship between neuronal spikes (action potentials) forming cell assemblies, and electrical activity recorded remotely from the scalp (EEG) will now be considered in more detail.

Any synaptic activity generates a subtle electrical impulse referred to as a postsynaptic potential. The firing of a single neuron is difficult to detect. However, whenever thousands of neurons fire in synchrony,

they generate an electrical field which is strong enough to spread through tissue, bone, and skull. It has to be emphasised that EEG does not measure neuronal spikes directly, it measures electric potential difference fluctuations resulting from ionic current within the neurons of the brain - post-synaptic potentials (Niedermeyer & Lopes da Silva, 2005).

Rhythmic neural activity was initially observed in the 1920s in pioneering electroencephalogram (EEG) studies by Berger (Adrian & Matthews, 1934), who published the first reports of the alpha wave rhythm. However, the theoretical concept of a synchronous grouping of neural activity was not proposed until the 1970s by Grossberg, (1976) (Milner, 1974) and then formalised by von der Malsburg, (1981). Nonetheless, it was not until the late 1980s that Singer and colleagues (Gray, König, Engel, & Singer, 1989; Singer, 1990) conducted empirical investigations into this proposal by investigating the role of synchronous activity, particularly gamma frequency (~40Hz) EEG waves, in encoding visual binding (The brain processes the visual attributes of objects such as colour, motion, shape, in different pathways or regions, and it is generally believed that there must be neural mechanisms that 'bind' this information to generate coherent perception (Bartels & Zeki, 2006). This work ultimately stimulated a more generalised interest in the notion of synchrony, as one of the mechanisms orchestrating and regulating neuronal activity (Palva & Palva, 2007; Sadaghiani et al., 2012; Singer, 2010; Uhlhaas, 2013). Contemporary theories have proposed that synchronisation at different frequencies sub-serve distinct functions and that low and high frequencies may operate over different spatial scales, (i.e. facilitate intra or inter-area groupings; Stein & Sarnthein, 2000). The dominant frequencies typically distinguished in research in the human and their hypothesised functions are as follows:

1. Delta band activity (0.5-4Hz) is a high-amplitude and low-frequency wave, which is associated with deep sleep. Delta is also found during some continuous attention tasks (Millett, 2001, 2002).
2. Theta activity (4-7Hz) is associated with idling states and with inhibition of elicited responses (Millett, 2001, 2002).
3. Alpha (8-15Hz) is associated with inhibition control, gating information (inhibiting reigns not involved in the specific task) and long-range communication across brain areas. Alpha will be discussed in detail later in the thesis (Busch, Dubois, & VanRullen, 2009a; Klimesch, 2012)

4. Beta (16–31Hz) is pronounced during active thinking, focus and high alert states (Millet, 2002; Millett, 2001).
5. Gamma (> 32Hz) is strongly associated with memory and attentional processes (Bauer, Cheadle, Parton, Muller, & Usher, 2009; Fries, 2009) and in general higher cognitive functions (Fries, 2009).

From this perspective, it is now essential to consider the way in which we can measure the properties of neuronal oscillations embedded in various frequency bands. In animal studies, direct recordings can be made of individual neurons spike trains, but in general, this is not possible in humans. For many years human waves of neural activity have been commonly measured using electroencephalogram (EEG) and more recently Magnetoencephalography (MEG) due to their high temporal resolution, but due to their poor spatial resolution, recordings are based on aggregate activity across large groups of neurons. EEG, among other neuroimaging techniques measuring neuronal oscillatory activity, will be discussed in more detail in section 1.1.3.

However, an important point to consider in all studies measuring synchrony is that in the natural world it is virtually impossible to observe perfect synchrony as there is a degree of noise in any signal. Therefore, in the thesis, when neural synchronisation is discussed, it is not assumed that phase locking is perfect in a mathematical sense, but there is a high degree of correspondence alongside a certain amount of noise (Singer, 2010; Singer, 2013). The lower the variance in the time difference between corresponding spikes, the higher the degree of synchronisation and a higher signal to noise ratio.

In summary, the brain is a complex system where different operations takes place simultaneously without a central single controlling hub. This creates specific questions as to how a oscillating neuronal structure processes the information from the sensory input towards decision centres and vice versa and how that processing is coordinated between spatially segregated processing clusters – assemblies. This introduction has presented the basic concepts of neuronal communication and network formation (e.g. Hebbian learning, rate coding, oscillations, spiking, synchrony). In this thesis, the focus will be on a synchronised oscillatory activity which is characterised using the fundamental properties of sinewaves. In particular, this thesis will examine the functional significance of alpha oscillatory activity.

1.1.2 Initial investigations of neuronal synchrony

The role of synchronous neural activity in perception and cognition was initially considered on the theoretical level in the 1970s and early 1980s (see section 1.1.1). However, that role was first empirically tested in the late 1980s by Charles Gray and Wolfgang Singer using an animal model to measure activity in the visual cortex (Gray & Singer 1989). In a series of experiments on cats, the researchers discovered that specific neurons which are distant from each other create simultaneous, synchronised oscillatory responses (correlated local field potentials) in the gamma range (40-60Hz) in response to a bar stimulus crossing their receptive fields simultaneously at the same angle (areas 17 and 18) (Gray & Singer, 1989). They argued that this mechanism could create connections between features in various parts of the visual field. They also presented evidence showing the effect of that synchrony during movement. When researchers moved one stimulus simultaneously across the receptive fields, specific cells became strongly synchronised at the time of crossing. Importantly, however, when two separate stimuli moved in the same direction and crossed the receptive fields of the selected cells at the same time the degree of synchrony was greatly reduced. Furthermore, when the two stimuli moved in opposite directions but still crossed the cells receptive fields at the same time, there was no synchronisation inactivity. Critically, the mean levels of activity (firing rate) did not vary across these conditions. Therefore, they concluded that synchronisation of activity connected related features across the visual field (Gray & Singer, 1989).

In addition, the authors concluded that “the responses for the large fraction of cortical neurons are oscillatory” (Gray & Singer, 1989, p.335), which suggests that this activity is potentially widespread and that oscillations as a neuronal communication mechanism might be not only limited to visual binding but can be utilised in other perceptual and cognitive processes taking place in the cortex.

This research supported the theoretical suggestions by von der Malsburg (1981). This author argued that visual system segments the scene into individual objects, which combine properties processed in spatially distinct brain areas that are interconnected by synchronisation of related neural activity. This proposal resolves the visual segregation and binding problem. Namely, how the component features of the objects in an image are processed in specialised centres but then bound back together into a coherent gestalt,

which we can consciously see/perceive (Bartels & Zeki, 2006; Herzog, 2009; C. Von Der Malsburg, 1999).

In summary, pioneering research into visual binding suggested that synchronised activity could link activity associated with different processes simultaneously across brain areas. It opened a new avenue for understanding the neural code in general in the whole brain, and how it might operate. However, numerous questions are not answered, which are crucial to our understanding of this phenomenon (Singer et al., 2009).

1.1.3 Measuring synchrony

Neuronal communication mechanisms based on neuronal oscillations have become increasingly researched beyond simple mechanisms of visual binding (Bonfond, Kastner, & Jensen, 2017; Lobier, Palva, & Palva, 2018; Singer, 2009).

A fundamental problem in understanding the function of neuronal oscillations involves altering and measuring their activity, as only by successfully influencing the oscillation under specific experimental condition/s and subsequently reliably quantifying and interpreting the changes we are able to infer about their function. Since the neuronal assemblies are considered to form, process information and dissipate rapidly, only a limited number of neuroimaging techniques have the temporal resolution to measure them. Single cell recordings are an obvious choice for this type of research as they directly measure the spike trains of individual neurons. These recordings provide high temporal resolution and also excellent spatial localisation (limiting distortions from other networks active simultaneously). However, the method is invasive, as the electrodes are implanted directly in the brain tissue and while common in animal models, it is not usual for studies of humans (where they only tend to occur as a by-product of neurosurgery). Also, they do not show neuronal dynamics on a larger scale, as identifying neurons that form part of a common network across disparate brain areas is difficult and the area over which electrodes are implanted is frequently limited, especially in human subjects. Moreover, a larger scale view is crucial, as cooperating neuronal networks are frequently distributed across the whole brain structure (Beck, Wagemans, & Vogels, 2001).

A second choice and the most prevalent neuroimaging methods for measuring synchrony and neuronal oscillatory activity in humans are electroencephalography (EEG) and magnetoencephalography (MEG). These methods are described together as they have many similarities from the point of view of measuring synchrony. The essential difference between both methods is the signal that each method detects: EEG measures differences in electric potentials on the surface of the scalp and MEG measures a weak magnetic field that is generated by the varying electric potentials of oscillating neurons (as only changing potential in semiconductor emits magnetic field - Maxwell's equations). Nonetheless, both electromagnetic and electric energy originates from the electric activity of neural structures, especially those the surface of the cortex (though subcortical sources do make some contribution to the signals recorded from the scalp), (van Straaten & Stam, 2013).

Activity in both techniques is generated by averaging across the activity generated by large populations of neurons. Therefore, only large groups of neurons which oscillate simultaneously create an observable electric or magnetic pattern, as smaller or non-phase locked in a large numbers oscillations either cancel each other out or are lost in the averaging process (Buzsáki, 2009; Beeck et al., 2001; Pockett, Bold, & Freeman, 2009). Also, it is thought that some neuronal structures are more pronounced on EEG/MEG recordings than others. Specifically, pyramidal cells of the neocortex for their close location to the surface, parallel alignment and high density are believed to disproportionately influence measurements on the surface of the scalp (Nunez & Srinivasan, 2010).

A variety of analytical techniques have been developed for quantifying oscillatory activity using EEG/MEG data. Typically, in EEG and MEG, the same trial type (i.e. a specific condition) is repeated several times and the recordings from all the epochs are superimposed (averaged) on each other to eliminate the influence of the noise and non-related factors. There are two techniques for doing this: measuring evoked or induced activity. Evoked activity is phase locked to the onset of the stimulus (i.e. peak amplitudes occur at broadly the same latency on each trial); while induced activity is stimulus-related change – each epoch is locked to the peak point of the sinewave (amplitude driven). In other words, induced activity is also elicited by the stimulus, but its peak amplitude occurs at variable latencies across trials and is not phase locked to the stimulus onset. Figure 1.3 illustrates the differences between

evoked and induced activity. In the left panel (evoked) peak activity is tightly time locked to the stimulus onset so relatively closely aligned across epochs, and so a simple averaging produces a relatively high amplitude of evoked activity. On the other hand, in the right panel (induced) the peak activity is jittered across trials and so it has a greater temporal variation, which means a simple averaging would result in this activity being lost. However, if the peaks of the activity in each trial are aligned then a high average will be produced (i.e. induced activity) (Tallon-Baudry, 2002, Yin, Zhang, & Wang, 2004).

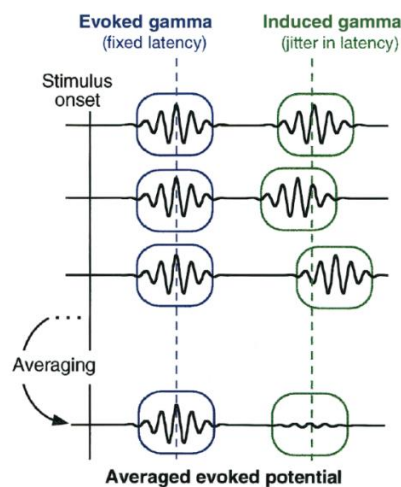


Figure 1.3 Evoked and induced activity (Tallon-Baudry, 2002).

What also has to be acknowledged, is that the synchrony is typically estimated from spectral power rather than direct measures of synchronisation, as it is the case in single cell recordings. Namely, before epochs for each condition are averaged, the bandpass filter is applied, so only a specific frequency window (for example 9.5-10.5Hz) is taken for further analysis (Cohen, 2014). Therefore, in many EEG/MEG brain studies, researchers assume that these larger more readily measured oscillations play a more critical role in cognition compared to smaller less synchronous oscillations. However this assumption might not be correct (Beck et al., 2001).

There are no techniques which are optimal to observe the behaviour of oscillating neurons, as there is a dilemma in selecting the optimal scope-spatial resolution. This can be considered by the analogy of observing a large group of ants, where by focusing on an individual or small group it is difficult to spot any overall patterns of movement/behaviour (e.g. a single cell recording technique). In contrast, by observing the whole ant mound only large patterns of the movement become visible and presumably smaller also substantial patterns of behaviour could be easily lost. This is the case with EEG/MEG where only larger oscillations are perceivable and smaller, oscillations disappear or are cancelled out by averaging with nearby occurring oscillations with different phases. Someone might suggest that the outlined ‘observing scope’ problem might distort the objective observation of the behaviour of neuronal oscillations in the mammalian brain. Therefore researchers should keep in mind that dilemma while choosing investigatory methods in this area of research (Buzsáki, 2009; Wilson, 1975).

Another problem which researchers of neuronal oscillations are facing is that a large number of experiments investigating oscillatory neuronal mechanisms are correlational studies. Only a limited number of experiments in the field of cognitive neuroscience are casual studies which directly manipulate and measure neuronal activity (Buzsáki, 2009). Thus, it is vital to take into account causational design while planning own experiment or at least consider this type of study when establishing one’s own hypothesis.

In conclusion, measuring synchrony is limited by assumptions about its temporal and spatial characteristics; also, as it is not known how exactly synchrony facilitates information encoding, it does not allow researchers to find the aspect of synchrony on which they should be focused and how to interpret the signals emerging from the seemingly random noise (an apparently random EEG is in fact meaningful). Also, as measuring synchrony requires high temporal resolution techniques, which has its consequence that the researchers focus on the time domain and frequently omits the spatial domain in this type of studies. However, merging spatially and temporarily sensitive tools together, or alternatively comparing similar but independent experiments allow researchers to have an insight into convoluted meanders of neuronal synchrony

1.1.4 Cross-frequency coupling

Thus, so far the thesis has discussed the measurement and functional significance of synchronous oscillatory activity at specific frequencies. Although there are distinct hypothesised roles for activity at various frequency bands it is important to note that activity at different frequencies is not entirely discrete, i.e. Fries (2009) suggests that properties of oscillatory activity at high frequencies can be modulated by the amplitude or phase of lower frequencies (Fries, 2009). Many researchers have also examined interactions across these frequencies, termed cross-frequency coupling (Canolty & Knight, 2010; Händel & Haarmeier, 2009; Jensen & Colgin, 2007).

Fries (2009) in his review paper on gamma role in cortical computations suggest that gamma strength (amplitude) is controlled by low frequencies such as theta and alpha rhythms. As evidence for the theta-gamma interlocking Pascal Fries (2009) refers to, the work of Chelazzi and colleagues (Leonardo Chelazzi Earl Miller, John Duncn, 1993). They recorded activity in neurons in the inferotemporal cortex (IT) of macaques the response to a preferred stimulus (triangle or square). Importantly, however, when competing stimuli were introduced 600ms later, then there was a cyclical reduction of gamma activity in line with slower frequency envelope. In other words, when a slow frequency phase is reduced, the gamma amplitude reduces as well, and when the phase goes up, the gamma amplitude becomes larger. The cycle of reducing gamma amplitude was repeated about every 200ms which is with 5Hz frequency (within theta range), therefore slower frequency phase appeared to be controlling gamma amplitude. Further, high gamma amplitude in IT indicates selection of preferred stimulus; thus, it is possible that theta (as theta controls the gamma – information conduction vehicle) modulated the likelihood of processing the chosen stimulus and facilitate snapshotting of competing stimuli. It is in line with the concepts which indicate that phase of slow frequency controls information flow (more on the phase in section 1.3.2) (Fries, 2009; Leonardo Chelazzi Earl Miller, John Duncn, 1993).

Similarly, Lakatos, Karmos, Mehta, Ulbert, & Schroeder, (2008) reported data that delta frequencies could also encapsulate and control higher frequencies. They found that in every delta frequency cycle, gamma power increases and subsequently drops down in line with the delta phase. Thus yet again, low-frequency phase determines momentary power in high-frequency activity (Lakatos et al., 2008).

Also, research on humans confirms earlier findings of frequency coupling. Canolty et al., (2006) conducted a study where they investigated how the theta phase rhythm modulated power in the high gamma in humans. They recorded and analysed subdural electroencephalogram (ECoG) from the five patients undergoing brain surgery. The authors concluded that theta – gamma oscillatory coupling allows coordinating activity in distributed regions, and provides a mechanism for communication which subsequently makes cognitive processing more effective (Canolty et al., 2007).

Research on animals (Lakatos, 2005) and also humans (Canolty et al., 2006) indicates that neuronal oscillations couple hierarchically with the phase of lower frequencies by modulating the amplitudes of higher frequencies (Lakatos et al., 2008). There is, also, growing evidence that the neuronal excitability of higher frequencies is coupled to the phase of lower frequencies (Buzsáki & Draguhn, 2004; Fries, 2005; Lakatos, 2005; Lakatos et al., 2008). Therefore, it seems that there is a complex system of communication between groups of neurons oscillating at various frequencies.

However, this raises the question about the reason behind low – fast frequency cooperation. One possible proposal relates to a difference in physical properties between low and high-frequency oscillations, i.e. low-frequency electromagnetic waves are less susceptible to attenuation (absorption) and random noise than higher frequency waves (Berry, 1964; Waagan, 2014). For this reason, synchrony based on lower frequencies may underlie long-range communication across brain regions (Hipp, Engel, & Siegel, 2011; Gross et al., 2004) (Stam & van Straaten, 2012). For example, it is argued that alpha frequency synchronisation tend to operate across the whole cortex (Lobier et al., 2018) and serve controlling mechanisms (by amplitude and phase) such as gating by inhibition, (Jensen & Mazaheri, 2010; Ole Jensen, Gips, Bergmann, & Bonnefond, 2014) and inhibition-timing hypothesis (Klimesch, Sauseng, & Hanslmayr, 2007).

In contrast, although high frequencies are more subject to signal distortion than lower frequencies they can encode and transmit more information in a unit of time because they have more periods (cycles) in that time. Therefore, high frequencies such as gamma have been linked to cognitive processes which encompass a large volume of information flow within a more localised area. Hence, faster oscillations are

capable of conducting larger volumes of information within a unit of time, but they do not have the capacity to propagate on longer distances. (Lisman & Jensen, 2013; Nakasaki et al., 1989).

Several different mechanisms for cross-frequency coupling have been observed by Canolty and colleagues (2006) and Jensen and Colgin, (2007). Figure 1.4 illustrates the examples of possible cross-frequency interactions between underlying slow theta and fast gamma frequency waves: power to power (a & b power of slow frequency – red line controls the power of higher oscillation – black line) phase to phase, (phase of slower frequency (a) controls phase of higher frequency (c)), phase to frequency (phase of slower frequency (black line in a) controls frequency changes in d) and phase to power (phase of slower frequency (black line from a) controls power of higher frequency – e).

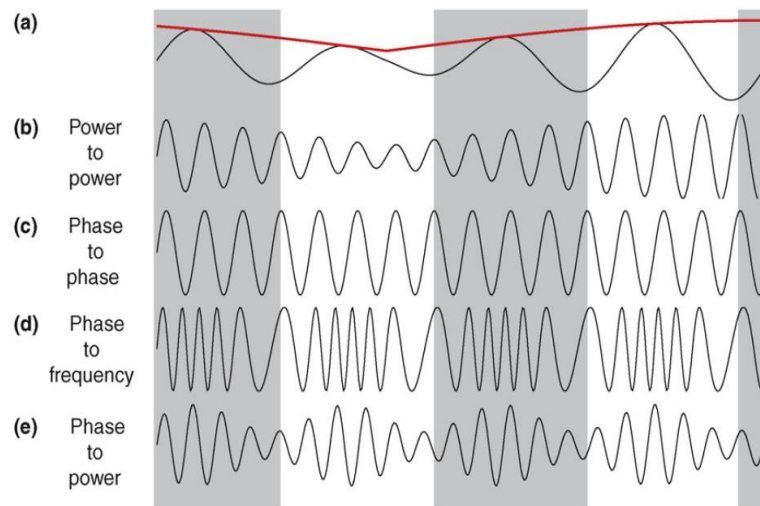


Figure 1.4 depicts the cross-frequency coupling mechanism where (a) is the underlying theta frequency (red line indicates the power shift of theta), and b, c, d, e are the examples of gamma oscillations coupled by its power, phase and frequency to the theta power or phase (Jensen & Colgin, 2007).

The variety of possible inter-frequency communication possibilities shows the complexity of possible neuronal information processing mechanisms and at the same time its large capacity, as in principle each coupling mechanism may be utilised to encode different information simultaneously (Jensen & Colgin, 2007). More recently, Canolty et al., (2006), conducted an experiment using subdural electrocorticogram during neurosurgery. During an auditory language related target detection task, the authors recorded in the left middle frontal gyrus of humans a strong coupling between the theta phase and gamma power for

normalised time-frequency observation, which provides additional evidence about the role of cross-frequency coupling shows that the mechanism is not limited to the visual domain (Canolty et al., 2006).

In addition to the above evidence of cross-frequency coupling between theta and gamma frequencies, it was proposed that other low-frequency bands such as alpha engage in cross-frequency coupling. Several studies have reported that the phase of alpha oscillatory activity may control the amplitude of higher frequency (e.g. gamma) oscillations (Cohen & Ridderinkhof, 2013; Händel & Haarmeier, 2009; Wacker et al., 2011). Cohen and Ridderinkhof suggested that alpha and frontoparietal gamma networks utilise cross-frequency coupling. Also, the evidence from near threshold detection experiments suggests that amplitude-phase coupling between high and even lower than alpha frequencies might serve the detection of weak sensory signals (Händel & Haarmeier, 2009). The authors recorded MEG responses during a near-threshold motion discrimination task. Results showed that the delta band oscillations were phase locking the amplitude of occipital gamma frequency oscillations. The strength of gamma amplitude modulation correlated with visual discrimination accuracy (Händel & Haarmeier, 2009). So, there is no single low-frequency band which cross frequency locks with higher frequencies, but various bands may play different functional roles.

In summary, there is growing evidence that some, (usually slower) oscillating patterns of neuronal activity interlock with other (usually faster) patterns of neuronal activity to convey information between them. This cross-frequency coupling probably plays a critical role in creating a functional hierarchy, which allows neurons interlocked by fast oscillations in one assembly to be in synchrony with another similar but distant assembly thanks to cooperation with low-frequency oscillator, which bridges both oscillating systems (Başar, Başar-Eroglu, Karakaş, & Schürmann, 2000; Buzsáki & Draguhn, 2004; Jensen, Kaiser, & Lachaux, 2007).

1.1.5 Concepts explaining neuronal communication

Most of the recent models attempting to explain how neuronal communication take place are based on neuronal synchrony (e.g. binding by synchrony, assembly coding, neuronal communication through neuronal coherence). However, the first models were non-synchrony based (e.g. rate coding – spike count

rate, time-dependent firing rate). In this section, they will be presented in more detail in order to outline the scope of the contemporary understanding of neuronal communication models.

1.1.5.1 Overview of neuronal communication coding schemes

1.1.5.1.1 Rate Coding

Rate coding was the first proposed model of neuronal communication which was initially described by Adrian & Zotterman (1926). Rate coding model attempts to explain how neuronal communication takes place based on the rate of action potentials fired by the neuron. Namely, when the intensity of the stimulus increases, also the spike firing intensity increases. This model assumes that most of the information about the stimulus is encoded in rate in which neuron fires. However, what might cause difficulty in translating stimulus intensity to the firing rate is that in sensory systems in general, firing rate increases non-linearly with the amplified intensity of the stimulus. This model also disregards spike temporal structure. In consequence, this model is understood by Singer, (1999) and Van Rullen & Thorpe, (2001) to be insufficient in conveying the information. On the other side, it tends to be robust and resilient to noise comparing to synchrony based models (Singer, 2010).

Also, Singer (1999) suggests that rate coding is more dependent on the high level of neuronal plasticity which dominates during development. On the other hand, synchrony-based communication models could be advantageous when a fast change in neuronal structure is more difficult (e.g. in adulthood); thus, the more hard-wired brain must adopt other mechanisms which in a fast manner integrate new patterns of information (Singer, 2010).

There are two main ways of calculating the rate of spikes that constitute the rate coding model. First, the spike-count rate (also called temporal average) is calculated by counting a number of spikes during one trial and dividing by the length of that trial. Second – the time-dependent firing rate is the average number of spikes appearing during a short interval divided by the interval length, i.e. the number of spikes between times t and $t+\Delta t$ divided by Δt (van Rullen & Thorpe, 2001).

As most of the elements in the natural world also rate coding model does not exist in separation. It is suggested that rate coding and other coding models such as coding based on synchrony (deliberated below) coexist together (Singer, 2010). Grouping responses by synchronisation can enhance discharge rates of selected target cells in areas receiving synchronised input. Singer (1999) suggests that fast synchrony-based codes and more sustained rate codes could co-occur and probably optimally complement one another.

Others criticise this model of neuronal communication; van Rullen and Thorpe, (2001) argue that rate coding does not have sufficient capacity to process visual information quickly enough compared to temporal coding mechanisms; as visual processing relies on very short transmission times, in the order of 10 to 20ms between two consecutive visual processing stages and less than 50ms between the retina and the visual cortex (van Rullen & Thorpe, 2001). However, some argue that in order to achieve such a profound transmission efficiency in vision, it is likely that both rate coding and temporal mechanisms are involved in information processing (Hemmen & Sejnowski, 2005).

1.1.5.1.2 Temporal coding

Whereas the rate coding model ignores time delays, in the temporal coding model, they constitute one of the means of communication. As neurons spike, the time delays between individual spikes vary. This creates the illusion that neurons spike randomly especially if we only observe one neuron or small group of neurons. However, if we observe larger groups of connected neurons, it is becoming apparent that some seemingly random spikes are firing at the same time points with other neurons (they are time-locked). Therefore, that irregularity in spiking is proposed to be a way to encode and transfer information between neurons. It is suggested by Singer (2013) that temporal coding model is more sufficient as in this model neuron can quickly switch its synchrony to various other neurons, or the assemblies are syncing with them. Arguably, evolutionary mechanisms of natural selection would eliminate irregularities in spiking if it were not functionally needed. To illustrate how the irregularities in spiking could encode information the following clear example is presented by Singer, (2013):

Let's assume that 1 encodes a spike and 0 the absence of a spike. Therefore, the example: 001011 and 011001 in the rate coding model convey the same information (3 spikes within the period), whereas in

the assembly coding model (more about this model in section 1.1.5.1.5), they can potentially encode two distinct pieces of information (Singer, 2013). This achieved by grouping neurons based on the synchronisation of neuronal discharge. Moreover, it groups neurons briefly into neuronal assemblies and it groups assemblies into functional neuronal networks. Figure 1.5 illustrates the basis of that mechanism of communication (Gray & Singer, 1989; von Der Malsburg, 1994).

1.1.5.1.3 Population Coding

Population coding is another proposed way of coding information by neurons. It is a method of representing stimuli by using the shared activities by groups of neurons. In population coding, every neuron has a distribution of responses over some established inputs, and the responses of many neurons are combined to calculate/determine the value of the inputs (De Tré & Zadrozny, 2015).

1.1.5.1.4 Sparse coding

The sparse code is when each item is encoded by the robust activation of a relatively small set of neurons, such that a unique set of neurons encodes each element. The specific code derived from that small number of neurons (compared to the whole population) is activated to encode a particular item. In this model, information is widely distributed across neurons (Perkel & Bullock, 1968).

1.1.5.1.5 Assembly coding

Assembly coding derives from the concept of neural assembly (or ensemble), which is a population of neurons involved in the neuronal computation. Such neuronal computation of functionally connected neurons is served by assembly coding. Donald Hebb (Hela, 1986) had suggested that individual neurons could participate in various cell assemblies and be involved in multiple computations. Thus, the term “neuronal assembly” and its functional role – coding, was initially developed before the concept of synchrony. Donald Hebb proposed that well-connected groups of cells are those where neuronal activity reverberated between them in an organised fashion and that these connected groups of cells represented information. Thus he named them cortical representations (Hebb, 1949). It has been suggested that cell assemblies which connect distributed functional areas are linked together using synchronised firing of cells (Gray et al., 1989; Weiss & Freeman, 2007). One of the suggestions for a response binding strategy is based on the dynamic selection and grouping of responses. In figure 1.5 binding of shape and colour

can be achieved by increasing their saliency comparing to other not bound sets. Therefore, neuronal discharge synchronisation may play a crucial role in integrating distributed neurons into functional ensembles that code an object's shape and colour. Such a dynamic functional neuronal connection would let neurons engage at different times in different functional assemblies.

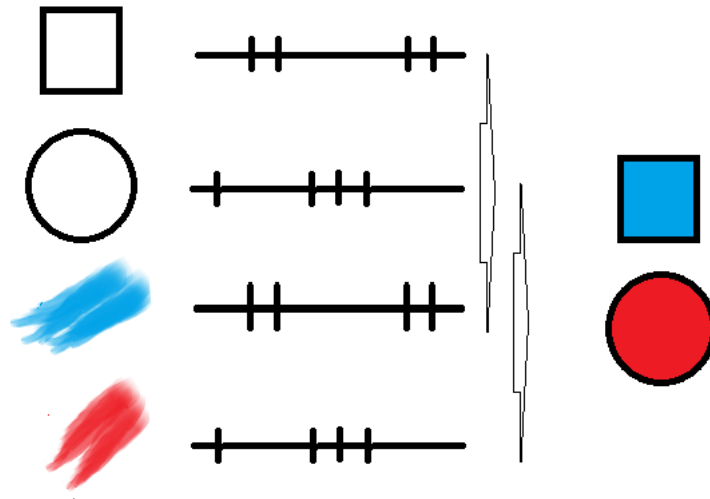


Figure 1.5 Assembly coding. When two cells fire in synchrony they encode different properties of the same object. The same cell can encode information about different objects by synchronising with various cells at various time points (Haenschel, Linden, Bittner, Singer, & Hanslmayr, 2010).

Further, the described mechanism (figure 1.5) illustrates that neurons could utilise temporal resolution (how fine temporal distinction you can make) to segregate signal from noise and dynamically connect with distant neurons and its groups. At the same time, coarse temporal resolution coding models (e.g. rate coding) are widely accepted, and both types may exist alongside as an assembly coding model (Gray & Singer, 1989; Siegel et al., 2012; Singer, 2010; Singer, 1999).

1.1.5.2 Binding by synchrony

The visual system is known to simultaneously process various perceived visual features (such as shape, colour and motion) simultaneously in different parts of the brain, and so needs to associate (or bind) the features to perceive them in a coherent, cohesive way. Therefore, the problem occurs how distinct features of the object such as its colour and motion, which are processed in different locations, are linked

back together. As introduced above, it was proposed that these features are bound together by neuronal connectivity (Bartels & Zeki, 2006; Herzog, 2009; Singer, 2010). Neurons in visual cortical areas tend to be selective for specific subsets of visual features such as colour-V4, motion-V5 (Goldberg, Kandel, Schwartz, & Jessell, 2000). Therefore, the different properties of the object are spatially segregated; to be more exact: the neuronal representations of the object are spatially distributed. The binding problem relates to how these properties are bounded back together to one cohesive, representing realistic external world image, which we perceive; and also, to what neuronal mechanisms underpin that process (Chalupa, 2003; Feldman 2013).

For example, two differently painted cars which are moving in opposite directions should be perceived with the colours as they are, and not mixed up. Therefore, the question occurs how these distributed groups of neurons functionally connect to avoid ambiguity in perception. It must be noted that the problem of reconnecting distributed features was initially experimentally investigated in the late 1980s (the visual binding problem discussed earlier) (Feldman, 2013; Singer, 2010).

1.1.5.3 Neuronal communication through neuronal coherence hypothesis

Pascal Fries (2005) has proposed an important concept that adopts a different perspective on the role of synchronisation in neuronal communication, termed ‘the neuronal communication through coherence hypothesis’ (NCTNC). In this view, by synchronising the phase of their activity, sending and receiving neurons create a series of consistent time windows for communicating between themselves. Thus, in contrast to the standard synchrony view, oscillations do not encode relationships between neurons per se but facilitate communication between them.

Fries (2005) proposed that the level of facilitated communication between neurons, or neuronal groups, depends on the degree of coherence between them. Neuronal communication is based on the distribution and reception of neuronal signals within the specific functional structure. That functional structure is based on anatomical connections, which are a necessary but not sufficient condition for effective communication. The author argues that mental processes require more flexibility in routing the signals that are provided just by neuronal fixed, hardwired (in short timescale) structure. A pattern of coherent

interactions provides that additional facilitation of communication between neurons on the top of the structure. Namely, a sending and receiving neuron with intrinsic oscillating properties must go into a coherent state, where both are, in a predictable (for both neurons) temporal interval, open for sending and receiving information. These repetitive time intervals are modulated by neurons' firing frequency, amplitude and phase shift. The fixed reoccurring intervals create temporal windows for communication (Fries, 2005).

In summary, NCTNC is similar in its role to the syntax of the language. It does not contain information which needs to be conducted. However, it creates a means and rules for effective information transfer across the brain (Akam & Kullmann, 2012; Fries, 2005).

1.1.5.4 Neuronal communication - summary

The early understanding of neuronal communication was based on Hebbian learning theory. Namely, if one neuron firing frequently directly activates another neuron then the connectivity between them is strengthened, and the efficiency of communication between them increases and becomes more stable. That notion was understood for several decades as explaining the mechanism of neuronal communication (Hebb, 1949). However more recently, the mechanism was expanded by adding an extra dimension – synchrony. That accelerated development of neuronal communication theories (Corballis, Miller, & Morgan, 1971). The synchrony concept was further theoretically developed by von der Malsburg (1981) who developed the concept of dynamic link architecture, which is a system of rapidly switching fragments of the neuronal network. Namely, the same neuron can be involved in coding different functions/properties/information within different neuronal ensembles. Specifically, the neuronal ensemble in which the neuron is engaged depends on the time relative to other neurons when it fires. Moreover, Fries (2005) with his communication through coherence theory created a link between neuronal oscillations and a flexible communication structure which better matches flexible cognitive processes; also, he suggested that frequency, amplitude and phase of neuronal oscillations form the basis for encoding information (Freunberger et al., 2008; Fries, 2005; Jensen & Colgin, 2007; von der Malsburg, 1981). However, our understanding of how neurons select, encode and transmit information is still provisional, and science lacks a holistic understanding of this process.

1.2 From neuronal networks towards perception and cognition

Until now, relatively theoretical concepts attempting to explain neuronal communication have been presented. However, this section will introduce the reader into the relations between communication served by neuronal networks and perception/cognition.

The primary focus of the thesis is the role of low-frequency oscillatory activity in organising cognition and perception. The mammalian brain is not capable of processing the vast amount of information bombarding our senses. Thus, in the world of vision, only certain stimuli are selected for preferential processing, based on the probability of their utility (saliency from the point of view of survival for example) (Buzsáki, 2009; Feldman, 2013). Therefore, organisms have developed perceptual and attentional mechanisms which allow non-salient/less important information for survival to be ignored and salient information to be processed further (Buzsaki, 2009; Feldman, 2013). Perceptual and attentional selection involves a competitive interaction between bottom-up mechanisms that bias processing towards perceptually salient stimuli and top-down mechanisms that allocate processing resources based on internal goals (Buschman & Miller, 2007; Leij, Sligte, Lamme, & Scholte, 2016; von Stein, Chiang, & Konig, 2000). The current thesis investigates how this battle for processing is in part facilitated by oscillations. The aim here is also to further the understanding of neural mechanisms underlying these processes (Benedek, Schickel, Jauk, Fink, & Neubauer, 2014; Foxe & Snyder, 2011; Hanslmayr, Volberg, Wimber, Dalal, & Greenlee, 2013; Jensen et al., 2014; van Dijk, Schoffelen, Oostenveld, & Jensen, 2008).

Also, it is interesting to unravel how neuronal low-frequency oscillations, especially alpha frequency control the deployment of neuronal resources in a visual scene (across space) and how they gate the availability of attention across time (Buzsáki, 2009; Neuling, Rach, Wagner, Wolters, & Herrmann, 2012; Sato, 2013; VanRullen & Koch, 2003).

Nevertheless, there are significant limitations regarding the efficiency of temporal coding. The brain is a noisy environment where the appearance of the single spike can be easily lost on longer distances. Therefore, the information can be easily distorted. Also, the brain does not act like a computing machine, where a precise single clock controls the overall timing of the system. It instead, works as a set of

competing, only semi-dependent, self-organising functional structures, (Hutchison et al., 2013; Tartar, 2013). VanRullen, (2016) suggests that the self-organising functional structure of the brain is built from several semi-dependent oscillating generators, which operate on individual frequencies and serve various functions of cognition. For example, he proposes that 7Hz oscillations participate in controlling discrete attention and 10Hz oscillations – in discrete perception (VanRullen, 2016). As our knowledge of self-organisation of the brain is in its infancy, there are some studies on self-organisation of artificial neural networks (Di Marzo Serugendo et al., 2004; Flanagan, 1996; Girolami, 1999). However, that is not a focus of this thesis.

1.2.1 External modulation of neuronal activity

Measurement of neuronal activity without its manipulation limits the scientific scope of exploration. Thus, neuroimaging studies which more, or less directly manipulate neuronal activity and behavioural correlates/ cognitive performance of that activity are becoming popular. One of the first attempted neuronal activity modulating methods was done in the visual domain. In 1934, Adrian and Matthews presented an experiment where the alpha rhythm was "driven" above and below its natural frequency with a simple flicker (Adrian & Matthews, 1934). That research was followed by several other EEG flicker inducing studies (Bartley, 1937; Durup & Fessard, 1935; Jasper, 1936; Toman, 1941).

In time, the EEG equipment improved and as a consequence this, the interest in the brain's electrical response to photic driving also increased (Barlow, 1960; van der Tweel & Verduyn Lunel, 1965). Several exciting studies involving photic hypnotic induction were conducted (Freedman, 1963; Kroger & Schneider, 1959). Some research was also conducted on the influence of photic driving on relaxing patients suffering from trauma and post-traumatic stress disorder (Siever, 2006).

The recent technological advances increased the interest in manipulating and measuring human brain oscillations. One of these technological advances is the development of the mathematical methods of measuring and making oscillations statistically interpretable. Also, currently computer software makes spectral analysis less technical, and modern computers have sufficient speed and memory capacity to apply these techniques to large datasets. Further, development of computational neuroscience has pushed

life science disciplines such as neurophysiology to work in the paradigm of the neuronal network, rather than focusing on small-scale methods such as single recording (Ekstrom et al., 2005; Raghavachari, 2006). What is more, it was suggested that evoked potentials observed in some cognitive and perceptual tasks might actually reflect the reset of phase shifting of oscillations. This is supported by research on stimulus-induced phase resetting of EEG by Makeig et al., (2002) and Rizzuto et al., (2003).

There is a wide range of ways how we can influence that internal neuronal dynamics by a single pulse, or repetitive outbursts of energy. Some of them will be discussed below:

1. Rhythmic sensory stimulation - steady-state visually evoked potentials – SSVEPs (Norcia, Appelbaum, Ales, Cottureau, & Rossion, 2015)
2. Transcranial magnetic stimulation – rTMS (Thut & Miniussi, 2009)
3. Transcranial alternating current stimulation - tACS (Herrmann, Strüber, Helfrich, & Engel, 2016).

As oscillating neuronal networks are fed stimuli from the outer world via the senses, it is feasible to interact with them in the same way by applying energy which they are receptive to (e.g. Herrmann, 2001; Kawaguchi, Jijiwa, & Watanabe, 1993; Mathewson, Prudhomme, et al., 2012; Spaak, de Lange, & Jensen, 2014). A second gateway to influencing neuronal oscillations could be by exploiting the electromagnetic properties of neurons. Namely, a changing magnetic field creates a flow of electric charge in the neuron. This can be done by single short bursts, repetitive bursts or sinusoidal magnetic waves (Herring, Thut, Jensen, & Bergmann, 2015; Taylor, Nobre, & Rushworth, 2007; Thut & Miniussi, 2009; Thut, Veniero, et al., 2011). A third way of influencing neuronal dynamics externally is via electrical modulation – transcranial alternating current stimulation. Similarly to alternating magnetic waves, alternating electric current applied to the surface of the scalp modifies neuronal dynamics (Helfrich et al., 2014; Jaušovec & Jaušovec, 2014; Neuling et al., 2012; Toralf Neuling, Rach, & Herrmann, 2013; Ruhnau et al., 2016; Wach et al., 2013).

The notion that the brain is actively responding and synching to external energy entity gives scientists the window of opportunity to influence more directly that internal neuronal equilibrium and further, to

observe its cognitive and perceptual effects. After this brief introduction, examples of experiments applying these methods in the EEG alpha band will be presented.

1.2.2 Steady-state visually evoked potentials (SSVEPs).

As outlined earlier, their first reported attempts to use repetitive external visual modulation of the brain were recorded in the third decade of the twentieth century, when participants were exposed to the flickering light while their electrical brain activity was recorded. SSVEPs were initially reported by Adrian and Matthews (1934) in article which also demonstrated suppression of the alpha rhythm by attention. There are three main interpretations of what may constitute SSVEPs stimulation. First - the additive effect of changes taking place in all trials; second – transient resetting of the phase in ongoing activity (Klimesch, Sauseng, Hanslmayr, Gruber, & Freunberger, 2007); third – baseline shift of ongoing activity (Nikulin et al., 2007). However, the exact mechanisms are still the matter of scientific debate (Vialatte, Maurice, Dauwels, & Cichocki, 2010).

In addition to the experiment outlined above on visual neuronal pathways, it also has to be noted that a small shift in phase between external light and measured neuronal activity is acceptable (due to the synaptic delays and complex neuronal processing) which does not jeopardise phase locking (Vialatte et al., 2010). However, Herrmann (2001) indicated that sometimes there is a lack of phase-locking phenomena, and external light flicker induces intrinsic oscillatory activity but without a clear time relation (locking) to the external source of flicker (induced activity) which was typical for some frequencies which the author tested (Herrmann, 2001). Therefore, the views on the mechanisms of SSVEPs are still subject to scientific debate and are not clearly defined (Buzsáki, 2009; Vialatte et al., 2010; Wu, 2014).

Crucially, Herrmann's (2001) study provides valuable insight into the relationship between external light and neuronal dynamics. Namely, the author attempted to entrain a wide range (1-100Hz) of frequencies visually and observed that some frequency bands differently influenced neurons: only light flicker with specific frequencies induced strong resonance - harmonic neuronal responses, which are observed as phase locked to external stimuli. Other frequencies also induce neuronal response; however, it was not as robust. Namely: 10, 20, 40 and 80 Hz light flicker produced a strong neuronal resonant responses at the

same frequencies in occipital regions projecting towards the anterior locations. In detail, the most active/strongest SSVEP signal was picked from posterior electrodes suggesting their source from primary visual event-related potential (ERP) components. Thus, generators of those SSVEPs are mainly in the posterior region of the cortex.

What is more, Herrmann also observed SSVEP projections towards the anterior locations (Herrmann, 2001) which may suggest that the harmonic flicker also induces neuronal activity propagation towards the frontal areas, as also observed by Dugue, Marque, & VanRullen, (2011). The phenomenon of a strong neuronal response to specific flicker frequencies is called resonance. These processes occurring in the brain are parallel to the resonance phenomena in physics. Explicitly, resonance in physics is “a phenomenon in which a vibrating system or external force drives another system to oscillate with greater amplitude at specific frequencies” (Billah & Scanlan, 1991). Herrmann’s (2001) research showed that the brain, as much as most of the elements of the natural world, is a harmonic oscillator. Thus, the brain (that is, the neuronal networks of the brain), as for every harmonic oscillator, if exposed to external energy with specific oscillating properties will resonate. Exposure to some frequencies produces stronger, and to other – weaker responses; as was shown in Herrmann, (2001) study.

There is a growing evidence that SSVEPs influence perception, attention and other cognitive functions (Bauer et al., 2009; Busch & VanRullen, 2010; Busch et al., 2009; Fuchs, Andersen, Gruber, & Müller, 2008; Gulbinaite, van Viegen, Wieling, Cohen, & VanRullen, 2017; Kashiwase, Matsumiya, Kuriki, & Shioiri, 2013; Keitel, Andersen, & Müller, 2010; Mathewson, Basak, et al., 2012; Mathewson, Prudhomme, et al., 2012; Mora-Cortes, Ridderinkhof, & Cohen, 2017; Wan et al., 2016; Wong et al., 2011; Wu, 2014; Xie et al., 2016). The alpha frequency band is in the spotlight of interest of this thesis, and part three of the introduction is dedicated to alpha. Hence, research on SSVPS and alpha is discussed in more detail in section 1.3 on alpha frequency.

Research on SSVEPS employs a broad frequency range from very low frequencies such as 3.5 Hz to 75 Hz (Beverina, Palmas, Silvoni, Piccione, & Giove, 2003).

As an example of non-alpha SSVEP research, gamma frequency visual entrainment is well investigated in the literature. As one of the fascinating examples of research Bauer, Cheadle, Parton, Muller, & Usher, (2009) demonstrated the effect of SSVEPs in the gamma range on attention. In this study, SSVEPs in the mid-gamma frequency (50Hz) applied at the target location prior to the target onset enhanced target detection and shortened RTs. The authors conducted an experiment where three Gabor patches were presented on a CRT monitor and the task was to detect a target—a small change in spatial frequency in one of the three patches. Gabor patches were flickering at 50 (Gamma), 100/120 or 30Hz. The authors concluded that a 50-Hz flicker at a target location, before target appearance, enhances target detection and RT. This research, alongside that of Hermann (2001), shows that external photic stimulation does affect neuronal dynamics and consequently perception.

In summary, SSVEPS constitute a relatively simple in application, robust and non-invasive way of influencing neuronal dynamics in posterior and, as some suggest, also anterior regions.

1.2.3 Inducing Oscillatory Activity by Transcranial Magnetic Stimulation (TMS)

Transcranial Magnetic Stimulation (TMS) is a non-invasive technique in which magnetic pulses are applied to a localised area of the brain via a coil. These pulses induce an electrical current in the stimulated area of the brain. In repetitive TMS several pulses in a row are applied, and initially, this was frequently used to disrupt processing in areas of the brain (see for example Kosslyn et al., (1999). More recently, rTMS has been used to induce oscillatory activity at various frequency bands (Dugué, Marque, & Vanrullen, 2011; Herring, Thut, Jensen, & Bergmann, 2015; Hung, Driver, & Walsh, 2011; Kanai, Chaieb, Antal, Walsh, & Paulus, 2008; Thut & Miniussi, 2009; Thut, Veniero, et al., 2011).

Several critical studies concerning external rTMS stimulation of alpha frequency were conducted and have added to the discussion on the role of the low-frequency band in human perception and cognition. Romei et al., (2010) applied 5Hz, 10Hz or 20Hz magnetic pulses over occipito-parietal regions and concurrently with the last pulse a near threshold dot like stimulus appeared either in the field contra - or ipsilateral to the stimulated hemisphere. Both occipital and parietal rTMS pulses at 10 Hz reduced target perception in the visual field contralateral to the stimulated hemisphere (e.g. the field represented by the

stimulated area) and increased detection in the ipsilateral field in comparison to the control stimulation at 5 and 20 Hz. The authors concluded that lateralized r-TMS applied to the posterior region at the alpha frequency is biasing perception away from contralateral and toward ipsilateral to stimulation, space. Also, they acknowledged that, when a particular perceptual/attentional area of the visual field is susceptible for information pickup, the low alpha amplitude is present in the neuronal representation of that location. This is in line with other research on alpha power/amplitude (Hanslmayr et al., 2007; Thut, 2006; van Dijk et al., 2008).

Also, the Romei et al., (2010) study adds to the evidence that increased amplitudes of alpha oscillatory activity are linked to stimulus inhibition, which is in line with the inhibition-timing hypothesis of Klimesch, Sauseng, & Hanslmayr (2007). To reiterate, low alpha, in particular, might create functional channels in a neuronal structure which facilitates information processing. On the other hand, high alpha in the specific region may limit the information flow (this hypothesis will be discussed in 1.3 section of this chapter in greater detail), (Klimesch, Sauseng, & Hanslmayr, 2007).

The above research by Romei et al., (2010) confirms the previous findings about the relation between the amplitude of alpha oscillatory activity and perception. Also, a study by Herring, Thut, Jensen, & Bergmann, (2015) confirms the findings of Romei et al., (2010) and adds the essential notion that alpha TMS amplitude modulation has cross-hemispheric effects. Namely, the authors, by inducing alpha power in the left occipital lobe, were observing amplitude effects in the right hemisphere (suppression or high amplitude). Also, they confirmed that TMS-locked alpha relies on the same neuronal processes as the spontaneous pre stimulated activity. In addition, they also outlined (similarly to Mathewson et al., 2009) that top-down attentional modulation influences occipital alpha power but not the phase (Herring et al., 2015; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009).

As the term top-down is introduced, one crucial differentiation has to be outlined. Across the thesis, the author uses both groups of terms: 1. Internally vs externally directed attention. 2. top-down vs bottom-up neuronal communication; The terms are similar and are not always clearly distinct, frequently used interchangeably. However, in this thesis the first group will be understood after Benedek et al., (2016) who suggests that internally vs externally directed attention is based on the fact where the percept occurs:

in the mind's eye (self-directed) thought, or in external world. Internally directed attention is associated with high activity in right inferior parietal lobule lingual gyrus and the cuneus and suppressed activity in superior parietal and occipital regions representing parts of the dorsal attention network. The second group (top-down, bottom-up) emphasises not the source of the stimuli (in the mind's eye, or in the external world) but the dominant direction of the neuronal processes either originating in the retina, LGN, V1 etc. and projecting towards prefrontal regions, or vice versa (Benedek et al., 2016; Buschman & Miller, 2007; Cooper, Croft, Dominey, Burgess, & Gruzeliier, 2003).

Another interesting TMS study was conducted by Thut and colleagues (2011). The authors measured the relationship between alpha rTMS and subsequent neuronal activity directly. The authors found that alpha rTMS boosted alpha power in the simulated alpha band at the location of stimulation. They also found increased activity in other frequency bands (from theta to beta) in response to the initial stimulation. However, the activity became more distinct and clear alpha oscillations were present. The effect disappeared shortly after the last entrainer offset: 100ms to 150ms (Thut, Veniero, et al., 2011).

As the above research elaborates on alpha amplitude/power and confirms inhibition timing hypothesis (ITH) by Klimesch et al., (2007), the alpha phase as a perception periodicity controlling mechanisms (perception is a discrete phenomenon) in TMS studies will be discussed below.

In the Romei et al., (2010) study, the stimulus was always presented in-phase with the TMS stimulation. It opens the question as to how modulating the alpha phase to the task might affect perception in the light of the perception periodicity hypothesis (for example called by Jensen – gating by inhibition-GBIH) (Jensen & Mazaheri, 2010; Romei et al., 2010).

The causal relationship between the alpha phase and visual perception was subsequently investigated by Jaegle & Ro, (2014). In this study, either 10Hz rTMS or sham TMS was applied to the posterior parietal or occipital cortex while recording EEG activity. Three 10Hz rTMS alpha pulses were applied followed by various SOAs and a near threshold (10ms) masked target. The minimal discrimination accuracy was observed in one phase of the alpha oscillatory waveform, and the maximum was observed in the opposite phase. Namely, when 10 Hz r-TMS was applied 50ms prior the target, detection accuracy was lowest, as

the alpha phase in time point when the target was presented was in the trough – or low energetic state. However, when 10 Hz r-TMS was applied 100ms prior to the target onset (target presented in phase with the alpha peak phase) target detection was at its highest. They provided direct casual evidence for the involvement of alpha phase modulation in the posterior parietal cortex in stimulus detection, which suggests it may relate to attentional processing linked to this area (Lewis & Bates, 2013).

Enhanced detection of targets presented in phase with alpha oscillations compared to the targets presented out of alpha phase has been reported by several authors (see for example Mathewson et al., (2012), Bush, van Rullen (2010), Bush et al., (2009), Romei, Gross, Thut (2012), and Dreves, van Rullen (2011). On the other hand, opposite results (low detection threshold out of alpha phase) have also been reported (see: Neuling et al., (2012), Herring et al., (2015), Jensen, Mazaheri (2010), Eelke et al., (2014), Haegens et al., (2011). The discrepancy is considered in detail later in this chapter (see section 1.3.2) and will form the theoretical basis for studies later in this thesis.

Exciting research investigating the notion that ongoing oscillations create periodic windows of excitability and enhanced perception was conducted by Dugue, Marque, & VanRullen, (2011). Namely, the authors observed the phase of ongoing 10 Hz alpha oscillations at various time points prior to a single TMS pulse to the right occipital lobe. Participants' task was to detect and report the presence of the near threshold TMS-induced phosphene. Interestingly ongoing alpha phase recorded 400ms prior to the TMS pulse significantly covaried with the perceptual outcome. The observation was conducted in two regions: occipital and frontal. In occipital recordings, the best phosphene perception was at the minimum alpha amplitude at the phosphene onset. However in the frontal region, the best phosphene perception was at the maximum alpha amplitude (Figure 2 a, b, Dugue et al., 2011). The opposite alpha phase on the fronto-occipital axis was also observed by Kawaguchi, Jijiwa, & Watanabe, (1993). Hence, this research confirms Kawaguchi et al., (1993) findings and shows that modulation of occipital alpha oscillations propagates across the cortex to anterior regions.

Another study exploring the alpha phase and perception using TMS induced phosphenes was conducted by Romei, Gross, & Thut, (2012). Interestingly they used sound to reset ongoing alpha activity and observed occipital lobe induced probability of phosphene detection. Crucially the highest detection rate

was in phase with the sound reset. Namely, the phosphenes induced 100ms after the sound reset were the most likely to be detected. This study provided additional evidence that perception periodicity is controlled by alpha phase. They suggested that the best perception is achieved in phase with the prime. In addition, this study shows that controlling properties of alpha oscillations are cross-modal and auditory reset influences also visual perception (Romei et al., 2012).

In summary, magnetic stimulation adds an extra dimension into neuronal dynamics research. Especially it allows the gathering of causal evidence for the role of neuronal oscillations both for alpha amplitude/power as well as its phase.

1.2.4 Inducing Oscillatory Activity by Electrical modulation

In addition to photic and magnetic stimulation, there have been recent attempts to investigate oscillatory brain activity by applying directly to the scalp a small electric current. There are two main types of transcranial electric stimulation: transcranial direct current stimulation (tDCS) and transcranial alternative current stimulation (tACS). The tDCS applies a direct current which does not fluctuate in an electric potential – does not alternate; and tACS current is characterised by sinusoidal electric potential variations which generate alternating electric fields in the cerebral cortex (Neuling et al., 2012). Therefore the oscillating characteristics of the weak electric current can be matched with spontaneous oscillations of neuronal networks, (alternating electric current might entrain - become harmonically related to oscillations with specific properties), which makes it an ideal tool for engaging neuronal activity (Neuling et al., 2012). tACS, similarly to alternative magnetic modulation can be adjusted to the individual endogenous alpha rhythm and also can be applied over somatosensory areas. However, to achieve harmonic cooperation of neuronal oscillations with tACS, detailed criteria must be fulfilled. They are outlined by Thut, Schyns, & Gross, (2011). A second advantage of this method is the precision in which the desired frequency, amplitude and phase can be adjusted, which is crucial for example, in cross-frequency studies. A third advantage of this method over alternated magnetic stimulation is that applied energy can be better controlled, as magnetic waves are easily dispersed (Wolters, & Herrmann, 2012).

There is a growing body of research applying tACS and measuring its effect upon cognition. Neuling, Rach, Wagner, Wolters, & Herrmann, (2012) mimicked the sine wave of alpha neuronal oscillatory activity and interlocked that frequency oscillations with ongoing tACS (Neuling et al., 2012). In the experiment, detection thresholds were modulated by the phase position of tACS induced alpha oscillations (peak - high detection threshold, trough - low detection threshold – which goes in line with Jensen’s and Spaak’s conclusions), (Jensen & Mazaheri, 2010; Spaak et al., 2014). The results indicate that stimuli presented at the peak of induced alpha phase were significantly harder to detect, compared to the stimuli presented in the trough - out phase position of the oscillatory alpha activity, where high detectability was observed. The results go in line with research by Herring, Thut, Jensen, & Bergmann, (2015); Jensen & Mazaheri, (2010); Spaak, de Lange, & Jensen, (2014) and in contrary with Mathewson et al., (2012), (Busch & VanRullen, 2010) which suggest that the peak alpha phase position enhances momentary information flow from the environment.

A second thought-provoking research study applied alternating current stimulation and investigated cross-frequency coupling(Boyle & Frohlich, 2013). It was the first study which applied EEG-based feedback brain stimulation with tACS to controlling cortical dynamics. The authors managed to control cortical state dynamics by combined EEG feedback and controlled tACS. They directly manipulated cross-frequency coupling activity between alpha and gamma oscillations, and in consequence, they managed to control cortical state dynamics. Namely, the authors observed endogenous alpha frequency activity and accordingly stimulated, using tACS in a biofeedback procedure, the occipitoparietal gamma frequency band (40 Hz). They found that the alpha amplitude dictated the gamma stimulation intensity. In consequence, they were able to control biological state of the neuronal network with biofeedback (Boyle & Frohlich, 2013).

In summary, tACS augments another prospect to manipulate neuronal oscillations, especially those close to the surface of the scalp where the electric current applied has the most substantial impact. The studies such as Boyle & Frohlich, (2013) and Neuling et., al. (2012) present an excellent example for casual manipulations of neuronal oscillations. The study by Neuling et., al. (2012) presents the causal relationship between neuronal oscillations controlled by tACS, where the neuronal phase timing was

strictly controlled and detection threshold, which varied in line with induced alpha phase. This study adds crucial evidence of the role of the alpha phase in controlling access to information from the environment.

1.3 Alpha oscillatory activity - the role of cognition

The primary focus of this thesis is alpha oscillatory activity and its role in neuronal dynamics - i.e. mechanisms underlying patterns of neuronal activity and its potential meaning for information processing in the context of perception and cognition (Singer, 2013; Uhlhaas, 2013). This section will deliberate on historical and current concepts on the role of alpha activity in human perception and cognition and the potential sources of alpha neural activity in coordinating coherent neuronal communication.

Alpha range frequency waves were discovered by Hans Berger, in the early twentieth century. Alpha was the first natural wave which was documented, and in those early stages of research, it was already suggested that the alpha rhythm reflects idling behaviour when a participant is conscious but relaxed (Adrian & Matthews, 1934). Already in 1949 Jasper and Penfield found alpha activity over nearly the entire cortex (Jasper & Penfield, 1949).

A new wave of research on alpha emerged in the 1960s and 1970s of the twentieth century, when biofeedback was popularised (Kraft, 2006). For several decades it was understood that alpha frequency plays an idling role and dominates the cortex while the participant is relaxed but awake. More recently it has been suggested that alpha activity might play a more active role in cognition. Namely, that the amplitude of alpha oscillatory activity may play a part in channelling resources towards neuronal representations processing relevant stimuli and inhibiting activity in non-relevant spatial representations. What is more, it has also been suggested that alpha activity may play an even more sophisticated role by exploiting its phase position to regulate discrete perception and attention (Bonfond & Jensen, 2013; Jensen, 2002; Jensen, Bonfond, & VanRullen, 2012; Klimesch, Freunberger, & Sauseng, 2010; Palva & Palva, 2007; Sauseng, 2012; Zumer, Scheeringa, Schoffelen, Norris, & Jensen, 2014).

Hence, the variation of ongoing alpha neuronal activity appears to be crucial in the deployment of attention over time (Hanslmayr, Gross, Klimesch, & Shapiro, 2011). As the amplitude changes typically occur on the scale of seconds, the faster fluctuation of the neuronal dynamics is reflected by modification in the individual phase (Milton & Pleydell-Pearce, 2016). Hence, both phase and amplitude of alpha could be engaged in controlling attentional mechanisms in space and time (where and when the stimulus is anticipated) but at different time-scales. When the near threshold target occurrence is temporally unpredictable, its detection rate varies in line with the phase of the alpha oscillation (Busch, Dubois, & VanRullen, 2009; Mathewson et al., 2009).

On the other hand, the amplitude may facilitate the coordination of distant cortical network homeostasis/dynamics (Buschman & Miller, 2007). Alternatively both: amplitude and alpha phase mechanisms may be vital for coherent neuronal dynamics (Nakasaki et al., 1989).

There is also a debate in the literature about top-down and bottom-up control. Some indicate that alpha power controls the dorsal attentional network during visuospatial tasks, which may imply that alpha power in occipital areas could be associated with top-down control (Zumer et al., 2014). Similar arguments are advanced in a review by Fink & Benedek, (2014). The authors argue that occipital alpha increases during creative ideation which might suggest more internally oriented attention. What is more, some suggest that high occipital alpha power indicates limiting of the influx of visual sensory information and simultaneously low alpha power in anterior regions indicates a dominance of top-down activity, which reflects internally directed attention (Cooper et al., 2003).

Alpha power dynamics might also be interpreted as a functional correlate of inhibition or top-down control of the region where it occurs. Frequently anterior locations by employing alpha synchronisation exert control over posterior regions which are mediated by functional coupling between both locations (Klimesch, Sauseng, & Hanslmayr, 2007; Sauseng, Klimesch, Schabus, & Doppelmayr, 2005).

In contrast, low posterior and high anterior alpha power might be switching high sensitivity towards external percepts - externally oriented attention (Benedek, Bergner, Könen, Fink, & Neubauer, 2011; Fink & Benedek, 2014; Sadaghiani et al., 2012; von Stein et al., 2000).

A similar relation to the alpha power dynamic on the anterior-posterior axis was observed for hemispheric differences in alpha power. Specifically, left hemisphere high alpha power and low alpha power in right hemisphere indicates processing sensory stimuli from left hemifield (contralaterally to the right hemisphere), and vice versa (Compton, Huber, Levinson, & Zheutlin, 2012; Doesburg, Green, McDonald, & Ward, 2009; Haegens, Nacher, Luna, Romo, & Jensen, 2011; Marshall, O’Shea, Jensen, & Bergmann, 2015; Toosy et al., 2001).

In summary, alpha oscillations can form a functionally coupled system which modifies its composition depending on the cognitive requirements. An alpha functional network, as probably the whole oscillatory neuronal network, seems to be a pattern generating system rather than only a stimulus-driven structure (i.e. external stimulation is only one of the factors influencing the outcome produced by the neuronal network). Therefore, it is suggested that alpha oscillatory networks may play an important role in channelling the information flow during a range of perceptual and cognitive processes (Gregoriou, Paneri, & Sapountzis, 2015; Singer, 2013).

Having introduced of the basic concepts of alpha frequency oscillatory activity (such as its historical role, amplitude and phase, alpha neuronal dynamics, as well as hemispheric differences), the following sections will deliberate on its putative role in perception and cognition in greater detail.

1.3.1 Alpha amplitude and cognition

A vast body of research suggests that increased alpha frequency activity results in a decrease in perceptual sensitivity at the related spatial location (Fu et al., 2001a; Sauseng et al., 2005; Thut, 2006; Wutz, Weisz, Braun, & Melcher, 2014). Alpha activity amplitude is high for the neuronal representations of spatial locations, where to-be-ignored distractors are present (Cooper et al., 2003; Fu et al., 2001a; Kelly, 2006; Rihs, Michel, & Thut, 2007). Both of these conclusions are consistent with the surround inhibition concept proposed by Suffczynski, Kalitzin, Pfurtscheller, & Lopes Da Silva, (2001.) They argue that at target locations there are low levels of alpha activity and this is surrounded (like a doughnut) by high alpha amplitude activity associated with adjacent spatial locations. The authors propose that this balance of high and low alpha activity underpins the mechanism of allocating attention to stimuli. The surround

inhibition proposal is similar to the inhibition timing hypothesis by Klimesch et al., (2007). Both elaborate on the alpha role in guiding neuronal resources to the active part of the network (Cooper et al., 2003). They are both consistent with the suggestions that alpha synchronization reflects active inhibitory processes and may infer that excitatory baseline shifts during orienting of attention go along with inhibitory mechanisms to increase the focus of visual spatial attention (Fu et al., 2001a; Kelly, 2006; Klimesch, Sauseng, & Hanslmayr, 2007; Rihs et al., 2007).

In support of these proposals several authors have demonstrated an inverse relationship between alpha amplitude and perceptual detection that can predict differences between subjects in performance (Babiloni et al., 2006; Del Percio et al., 2007; Hanslmayr et al., 2007; Linkenkaer-Hansen, 2004; Mazaheri, Nieuwenhuis, Van Dijk, & Jensen, 2009). Good perceptual performers tend to have lower pre-stimulus alpha power compared with bad perceptual performers. Klimesch et al., (2003) goes further and tests pre stimulus and during the task alpha power dynamics. The authors suggested that large alpha power in an interval preceding a task is related to large suppression of alpha power during the task and good performance. Hence, as it is widely accepted that alpha oscillations play a role in attentional and perceptual mechanisms the exact mechanisms are still debated (Hanslmayr et al., 2005).

However, it is important to state that although the focus of these studies on the active inhibition of sensory information might imply that alpha activity is associated with low level or bottom-up processes, there is an evidence indicating that alpha amplitude serves sensory and also higher internally oriented processes (Cooper et al., 2003). The relationship of bottom-up and top-down / internally versus externally oriented processes will be addressed further in section 1.3.4.

Many studies have investigated the sources of alpha oscillations in the brain with variations in findings. Buchsbaum et al. (1984) and Sadato et al. (1998) reported a dominant- negative correlation between alpha power and metabolism, or blood flow, in the occipital cortex. Lindgren et al. (1999) investigated alpha activity in the thalamus and found a similar negative correlation. Furthermore, some researchers have reported a robust pattern of negative correlation of alpha power between frontal and parietal cortices (Laufs et al., 2003), while others claim that this pattern is observed across both frontal and occipital regions (Goldman, Stern, Jr, & Cohen, 2002). Nonetheless, the most robust finding appears to be a

negative correlation between alpha band power and metabolic response in the occipital cortex where the alpha rhythmic activity is generally most prominent (Murta, Leite, Carmichael, Figueiredo, & Lemieux, 2015).

1.3.2 The Relationship between the phase of alpha activity and cognition

Let's consider the scenario that only the alpha amplitude (change in voltage across several alpha cycles) would be the central mechanism influencing neuronal dynamics and control of the information flow. The advantage of such a mechanism is that it is robust to small variations caused by noise in the signal, but the disadvantage is that the need for a temporal window loses information from fluctuations in the signal. However, it is now well established that the phase of ongoing alpha activity (plays a part in controlling information flow in the brain (Haenschel, Linden, Bittner, Singer, & Hanslmayr, 2010; Jensen et al., 2012; Mathewson et al., 2011; Nadasdy, 2010; Palva & Palva, 2011). If we add to that, that there could be several alpha generators, any of which might have top-down and bottom-up projections, and other mechanisms not discovered yet; the research on alpha becomes challenging.

The phase of a sinusoidal waveform is measured in degrees (or radians) such that one cycle represents 360 degrees or 2π radians. In practical EEG terms, phase is a point in time marked on the waveform of a specific frequency band oscillation such as a peak, a trough, or an upward or downward zero-crossing. The event occurs in phase with another event (such as the flash) when it occurs at the same point on the sinewave; and per analogy, something happens out of phase if it has 180 degrees delay about the external event (peak-trough distance). It has to be noted that it takes about 30-40ms for the signal to travel from the retina to V1 (Thorpe, Fize, & Marlot, 1996).

Recent studies investigated whether the phase position of neuronal oscillations influences the probability of perceiving stimuli briefly presented in various phases of alpha oscillations. For example, Shapiro and Hanslmayr (2014) suggest that EEG alpha phase imposes rhythmic firing onto neuronal assembly by providing precise time windows of inhibition and excitation.

However crucially, there is a substantial discrepancy in the literature as to which alpha phase position makes the external stimuli more accessible to awareness. Some of the studies which investigated the

matter lean towards the notion that the highest likelihood of perceiving an object is at the positive peak (in phase with external entrainment) of alpha oscillation when measured on posterior locations (Busch & VanRullen, 2010; Busch, Dubois, & VanRullen, 2009; Jaegle & Ro, 2014; Mathewson et al., 2011; Mathewson, et al., 2012; Romei et al., 2010; Romei et al., 2012). The second group of researchers agree with the previous notion that alpha oscillatory phase at stimulus onset indicates states that render the neuronal network more or less susceptible to external stimuli. However, they disagree when exactly it takes place. Namely, they argue that the best susceptibility to external stimuli is when they fall in the negative extrema (trough) of alpha oscillations - out of phase (Händel, Haarmeier, & Jensen, 2011; Jensen et al., 2012; Neuling et al., 2012; Spaak et al., 2014; Ter Huurne et al., 2013). The basis for this discrepancy is investigated in the studies in chapter three.

What is also interesting is that some argue that alpha phase switches the brain states between externally oriented perceptual modes and an internal focus (i.e. towards working memory and internal representations) (Smith, 2015). The author argues that alpha phase acts as an internal global clock, which in a fast manner, in one phase - captures information from sensory input (bottom-up processing) and in the opposite phase - diminishes perception and process top-down information flow (Smith, 2015). Thus, in this concept, by acting linearly (step by step instead of two processes simultaneously) the neuronal network can be more energy efficient. At the same time by adopting fast switching between leaning towards processing from the internal and external sources, minimal, or no vital information from the external world is neglected, for the reason that temporal resolution of snapshotting is about 100ms (Smith, 2015). Similarly, the gating by inhibition hypothesis (GBI) proposed by Jensen and colleagues (Bonfond et al., 2017; Jensen & Mazaheri, 2010) elaborates on the role of alpha peak and trough in perception. The GBI hypothesis is discussed in section 1.3.3.

In summary, understanding how both the phase of ongoing alpha activity and its mean amplitude across time contribute to the control of information flow from the external world and the processing of internal representations is crucial for acquiring greater insight into the mechanisms of human cognition and perception. Thus, this thesis focusses on exploiting outlined properties of oscillating neurons to attempt to increase understanding of the role of alpha in human cognition.

1.3.3 Alpha phase coherence between neuronal groups

As mentioned above, it is thought that alpha phase, alongside with the amplitude constitute essential elements of oscillatory activity. It has been suggested that phase coherence facilitates neuronal communication between cortical regions (Fries, 2009; Palva & Palva, 2011; Varela, Lachaux, Rodriguez, & Martinerie, 2001). In physics, two wave sources are entirely coherent if they have a constant phase difference and the same frequency (Angus Stevenson, 2010). In the neuroscience literature, phase coherence between two cortical regions is interpreted as evidence for communication between these two regions (Fries, 2005; Varela & Thompson, 2001). In particular, it has been argued that alpha oscillations and phase coherence play a significant role in communication between distant neuronal locations (Doesburg et al., 2009; Gross et al., 2004; von Stein & Sarnthein, 2000). Some suggest that that alpha phase coherence plays a vital role in top-down attentional control and working memory (von Stein, Chiang, & König, 2000). For example, Sauseng et al. (2005) and Palva et al. (2010) argue that fronto-parietal alpha phase coherence is higher during working memory (WM) tasks. As a high level of communication is needed during manipulation and maintenance of internal representations, it is argued that the high alpha phase coherence serves that purpose. Also, Hanslmayr and co-authors (2007) suggest that the level of alpha phase coherence correlates with perception performance. Specifically, increased alpha phase coherence shifts information processing towards internal representations and decreased alpha coherence guides processing towards external stimuli. Similar observations were reported by Todd & Fougine (2005) who observed that a high level of memory load causes inattentive blindness.

Importantly, the level of neuronal communication measured by alpha phase coherence has been examined between hemispheres. Nikouline et al., (2001) noted that among the lower frequencies, the phase lag between both hemispheres is about zero degrees, which is consistent with a phase locking mechanism between both hemispheres. Similar conclusions were made by Kawaguchi, Jijiwa, & Watanabe (1993), who established that interhemispheric phase differences are small when the peak power frequency was aligned with the bilateral photic stimulation frequency. In other words, when the neuronal oscillatory frequency is entrained by external photic driving, then the inter-hemispherical phase lag is minimal and close to zero, which equates to high synchrony between both regions. These results might suggest that

hemispheres may cooperate to form a single functional oscillatory source (or strictly synchronised sources). However, this is only speculation, and further research is needed to investigate it.

Another argument for the necessity of strong interhemispheric coherence, which could be served by EEG activity in low-frequency bands comes from the anatomy of the senses. Namely at a certain point of evolution, organisms developed two hemispheres and paired auditory and visual receptors. As dipodic perception needs to be organised into single coherent percept; coherent (and communication-wise efficient) communication between two sources of information and two hemispheres must be facilitated efficiently, as visual perception must be fast from the point of survival (Kawaguchi et al., 1993; Nikouline et al., 2001).

1.3.4 Inhibition timing and gating by inhibition concepts

In the current literature on the role of alpha in perception and cognition, there are two dominant concepts which deserve special attention:

1. inhibition-timing hypothesis (ITH) by Klimesch et al., (2007)
2. gating by inhibition (GBI), by Jensen & Mazaheri, (2010)

Fundamentally, ITH focuses on the amplitude of alpha activity (taken as a measurement of the magnitude of oscillations) averaged across a time window of several hundred milliseconds. In contrast, GBI focuses on role of the phase and so captures the full-time course of alpha activity. The alpha mechanisms managing perception and cognition including ITH and GBI were briefly introduced earlier, however here both concepts are elaborated in more depth.

ITH is a mechanism where high alpha amplitude suppresses neuronal processing of information flow in a specific part of the neuronal network (Klimesch et al., 2007). A number of studies has confirmed the predictions of ITH. For example, TMS induced phosphenes (conscious perception of light induced by a magnetic signal applied in visual areas of the brain) are less likely to be perceived when alpha amplitudes are high in corresponding neuronal representations (Romei et al., 2010).

On the other hand, GBI is a proposed mechanism where alpha phase controls temporal information flow (de Graaf et al., 2013; B. F. Händel et al., 2011; Jensen & Mazaheri, 2010; Mathewson et al., 2009; Nikulin & Brismar, 2006; Spaak et al., 2014) . The GBI hypothesis assumes that perception is blocked when the time-point phase of alpha is in a positive peak; however, when an alpha phase is descending towards the trough (low energetic state) the less salient information is allowed to be processed. (Jensen & Mazaheri, 2010).

All of the work considered above has been based on activity averaged across cortical areas using EEG to measure local field potentials from the surface of the scalp. However, Haegens et al., (2011) attempted to narrow down this gap in thinking between large-scale observations of local field potentials and single cell firing. They conducted an experiment on monkeys, where the local field potentials and neuronal spiking activity from the embedded sensorimotor region were recorded simultaneously while performing a vibrotactile discrimination task. As predicted, alpha power in the area involved in the cognitive task decreased and that reduction correlated with increases in performance. Importantly, the study showed that the neurons in the region of interest (ROI) fired with the highest intensity at the trough of the alpha cycle. These results are in line with both GBI (Jensen et al., 2012; Spaak et al.,2014) and Klimesch (2012). However, they contrast with those reported by Mathewson et al. (2012) and Hanslmayr et al., (2011) which found the highest perceptual sensitivity at points of peak phase. However, what must be noted is that Jensen et al. (2012) and Spaak et al. (2014) build their conclusions based on activity in perceptual areas, and Haegens et al. (2011) draws conclusions based on the sensorimotor cortex. Therefore, only the assumption that alpha oscillations are facilitated by the same mechanisms across the brain and are common across primates allows such a conclusion to be drawn. Haegens et al.'s (2011) result supports the notion that the alpha rhythm controls perception/cognition by modulating not only the amplitude of alpha oscillations but also by modulating the phase of alpha within the specific frequency period.

In summary, Haegens et al. (2011) results confirm Jensen and Spaak assumptions (however they are in apparent opposition to Mathewson et al. (2012) results), about alpha pulsed inhibition. Both authors suggest that within the alpha cycle - through phase position increases spiking and open neuronal

communication for perception. In contrast, alpha peak time locations decrease neuronal communication and limit perception (Haegens et al., 2011; Jensen & Mazaheri, 2010; Spaak et al., 2014).

Similarly to Haegens et al., (2011), Palva and co-authors (2011) noted that both ITH and GBI could be complementary and operate alongside each other. More specifically, Palva et al., (2011) propose that high amplitude alpha activity correlates with low, local cortical excitability and suppressed irrelevant neuronal processing, but the alpha phase dynamics may play a role in active task-relevant neuronal processing. The authors indicate that alpha phase synchrony between regions (which is the highest among all frequency bands) might contribute to effective long distance processing of information by influencing the local neuronal timing and interareal phase relations, which underpin attentional, executive and contextual functions (Palva & Palva, 2011).

Furthermore, Klimesch (2012) also attempted to bring together both theoretical perspectives (ITH and GBI) and to develop an understanding of the role of alpha in the light of amplitude and phase control over neural processes. To reiterate, the central notion of the inhibition-timing hypothesis is that when oscillatory alpha activity driven by interneurons is minimal (case one on figure 1.6) - the principal cells involved in information processing (red lines) are not affected by these alpha oscillations. However when alpha oscillations are in task-relevant networks (case 2), the action potentials of principal cells fire according to alpha phase orders (Figure 1.6, case b). However when the inhibitory power of alpha interneurons increases further, the principal cells with minimal excitation (cell1, case 2b), will stop producing action potentials, and as a consequence they will be disengaged from information processing. If the alpha inhibitory activity continues to increase then fewer major cells fire, and eventually the whole region becomes inhibited and virtually stop processing of the information involved in this task-relevant area. Klimesch (2012) concludes that increasing alpha amplitude which leads to increased alpha inhibitory power disengages activation of principal cells (cell 1 and 2) in the order from the minimally excited to the maximally excited (Klimesch, 2012).

Besides these outlined details, the author of this thesis has found no more research investigating both phenomena at the same time. Therefore it would be beneficial to explore further interactions between amplitude and phase (Palva & Palva, 2011; Shapiro & Hanslmayr, 2014). Thus, in chapter two of this

thesis the author attempted to manipulate the level of alpha amplitude by varying the level of luminance of an entraining stimulus and attempted to observe how varying this and other properties of the elicited alpha oscillations such as phase, influenced behaviour.

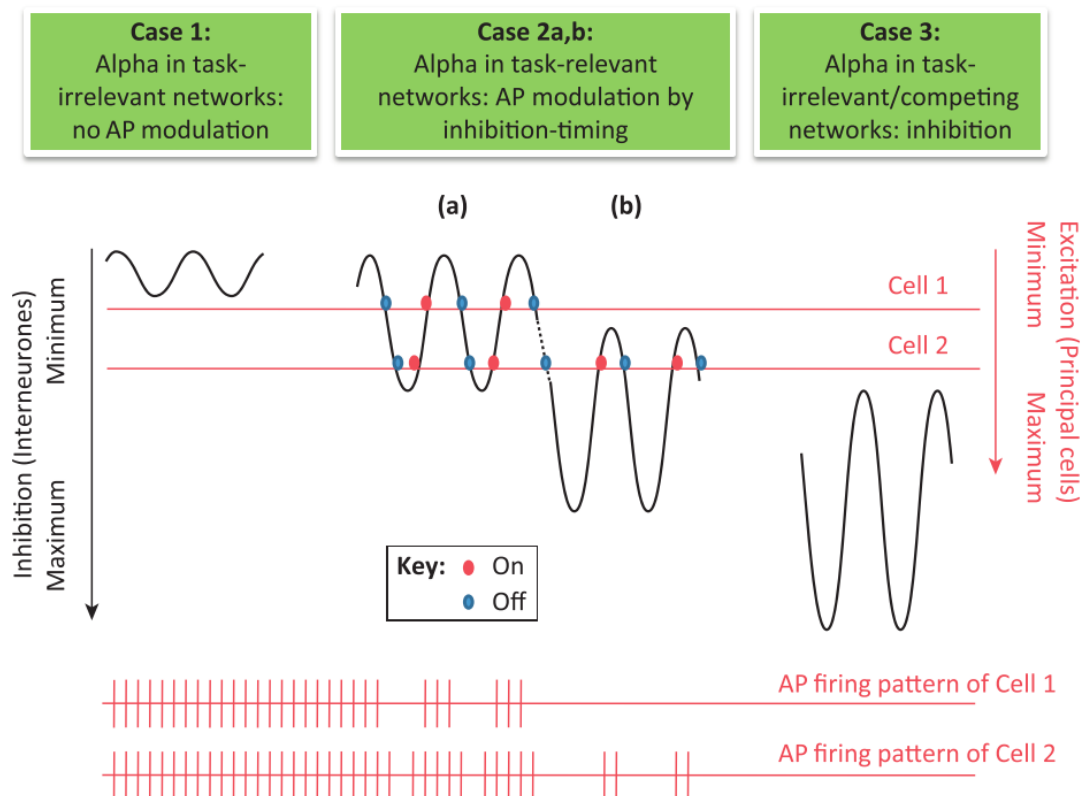


Figure 1.6 After Klimesch (2012) p. 608: “Three cases are distinguished. Example 1: In task-irrelevant networks, the amplitude of alpha oscillations is small and has no impact on cell firing rate, which is symbolised by short vertical lines representing action potentials (APs) in the lower panel. Case 2: In task-relevant networks, the amplitude of alpha oscillations increases and starts to inhibit the generation of APs in target cells during the inhibitory phase of the oscillation. Depending on the excitation level of target cells, the impact of the inhibitory oscillation is different (cf. Cell 1 and 2). With the increase in amplitudes, the inhibitory baseline increases, which means that inhibition increases not only during the phases with maximal inhibition (plotted here as troughs) but also during those with minimal inhibition (plotted here as peaks). Case 3: If inhibition increases further, all target cells are silenced. This case is assumed for neuronal

structures that are potentially competing relative to the processing of a task. A good example is the inhibition of potentially competing regions in the ipsilateral hemisphere.”

In summary, two outlined mechanisms could be simply illustrated by using an example of a philharmonic orchestra. The conductor controls which part of the team should be dominant at a specific time (High amplitude/power), and which should withdraw from activity (low amplitude, power) - ITH. At the same time, the conductor controls when the active players should e.g. blow the trumpets, and inhale together in synchrony (peak phase - blow trumpets; trough phase -inhale together) – GBI (Haegens, Nacher, Luna, Romo, & Jensen, 2011; Jensen & Mazaheri, 2010; Mathewson et al., 2009).

Both concepts which attempt to explain how properties of alpha oscillations could be employed in organising information flow in the brain. It is possible that both: alpha phase and alpha amplitude together participate in the perception and cognition.

1.3.5 Alpha-band activity and its bottom-up and top-down dynamics.

Rana and Vaina (2014) investigated the dynamics of alpha power and its internal synchronisation. The authors argue there are at least two separate functional sources of alpha in human cortex. One is located in the occipital, visual regions and the second found in prefrontal regions. Both sources work simultaneously and contribute with various intensities to different processing functions, such as top-down and bottom-up processing (Klimesch, 2012; Rana & Vaina, 2014).

Crucially, the authors show that the posterior and anterior alpha networks act independently during a simple visual task. While the alpha network of frontoparietal locations sustains a high level of synchrony, at about 10 Hz during the stimulus presentation period, there is a lack of such a strong sustained stable alpha synchrony between more distant anterior and posterior networks. The authors interpret this as indicating there is limited direct communication between anterior and posterior regions utilised by alpha (Rana & Vaina, 2014).

On the other hand, Kawaguchi et al., (1993) reported a posterior-anterior alpha phase difference of about half a cycle, and that this is stable, which might suggest a non-zero phase lagged alpha network synchrony between these regions. To add the level of complexity, alpha oscillations may also originate in subcortical regions, such as the thalamus (Omata, Hanakawa, Morimoto, & Honda, 2013; Valdes-Sosa et al., 2009). The outlined examples show that alpha networks are spread across cortex and subcortical regions, however, the debate about the level of synchrony (thus connectivity) between them and convoluted roles of alpha, will continue in the literature until considerably stronger empirical evidence is available.

In the light of what was outlined above, the critical question appears to be: whether external visual stimulation influences only the occipital alpha network or also the fronto-parietal (not to be mistaken with a larger anterior-posterior alpha network which interconnects occipital and prefrontal regions) alpha network? It can be postulated that the type of stimuli used in the task determines the level of engagement of alpha functional network. Thus, more purely visual detection tasks might drive the occipital alpha more strongly. However, in contrast, tasks that are more cognition-engaging, with conflicting responses (such as Stroop task, or working memory tasks) may engage both occipital and frontal alpha networks (Rana & Vaina, 2014).

As alpha activity is widely distributed across the brain it is crucial to attempt to identify potential locations where alpha activity is generated. Some studies suggest that alpha rhythms originate in the deep cortical layers (Lopes da Silva, 2013; Sun & Dan, 2009), with pyramidal cells in layer five, exhibiting rhythmic firing at about 10 Hz (Flint & Connors, 1996). However, other research on monkeys shows that alpha originates from all layers of visual cortex and the infragranular alpha current generator is the primary alpha pacemaker (Bollimunta, Chen, Schroeder, & Ding, 2008). A follow-up study by the same authors shown that in V1, layer 4 (the central thalamorecipient layer) together with infragranular layers constitutes primary pacemaker (Bollimunta, Mo, Schroeder, & Ding, 2011). They suggest that occipital alpha generators are closely interlinked with deeper thalamocortical alpha pacemakers. Also, Lorincz, and colleagues, (2009) suggest that the thalamus is a vital source of strong alpha oscillations which project via the thalamocortical network towards the cortex (Lorincz et al., 2009). Some suggest that long-range alpha synchronisation through the thalamus and cortex has been involved in the regulation of

synchronised activity at a variety of frequencies across large cortical networks (Schmid, Singer, & Fries, 2012). In more detail, the authors proposed that increased alpha synchrony between pulvinar and visual cortex during attentional tasks may influence gamma synchrony across cortical areas (cross-frequency coupling) (Schmid et al., 2012). Gregoriou et al., (2015) argued that a mechanism of increased alpha synchrony modulating gamma communication is inconsistent with the inhibitory role of alpha activity in information processing postulated by Klimesch (2012) and Jensen, (2002).

The property of alpha oscillations being widespread across cortical and subcortical regions led the suggestion that oscillations within this and lower frequencies could mediate long-range communication in the brain (Buschman & Miller, 2007). In particular, lower frequency oscillations tend to have a more extensive range of signal propagation as they are more robust and less susceptible to conduction delays with information more reliably transferred across long distances (Buschman & Miller, 2007; Kaufmann et al., 2005). Nonetheless, other authors have suggested that gamma frequency band oscillations subserve long range, communication during bottom-up attention (Buschman & Miller, 2007), and top-down attention (Sokal & Text, 2006)(Sokal & Text, 2006)(Sokal & Text, 2006)(Sokal & Text, 2006)(Sokal & Text, 2006)(Sokal & Text, 2006).

According to some authors, that widely distributed alpha network, reaches beyond thalamo-occipital connections. Goldman, and colleagues, (2002) discovered that increased alpha power (measured by EEG) is correlated with decreased oxygen metabolism (measured by fMRI) in occipital, superior temporal, inferior frontal, and cingulate cortex, and that increased alpha power is correlated with stronger neuronal dynamics in the thalamus and insula. Furthermore, Lobier, Palva, & Palva, (2018) argue that there is a strong alpha frequency synchrony across all cortical and sub-cortical regions. That synchrony serves the role of projecting visuospatial attention.

The picture presented above suggests that alpha oscillations are dominant, widely distributed and strongly interconnected across large neuronal networks. Therefore, they maybe an excellent candidate to play a vital role in managing cohesion between distributed ensembles, which are being part of large functional network. This idea is in line the famous old notion formulated by a founding father of neuropsychology

– Alexander Luria— that the brain is a system of distributed functional networks (Draper, 1974; Gray & Singer, 1989).

Chapter 2

2.1 Introduction

In this chapter the role of alpha oscillations in information transfer across cortical areas was investigated. Participants performed a numerical Stroop task, with every trial preceded by a flicker prime to elicit alpha activity. The incongruent trials of the Stroop task introduce a conflict between competing responses which results in people being slower in responses to the task compared with congruent trials. That slower response has been related to increased communication between conflict processing fronto-parietal and early sensory regions. If alpha oscillations improve communication efficiency across the cortex it was predicted that inducing stronger alpha oscillations would affect the performance, (i.e. the Stroop cost would diminish). That hypothesis was tested in three experiments.

Different types of visual tasks place different levels of demand upon internal neuronal processing. Visual information processing starts within the retina, and then the majority ascends through lateral geniculate nucleus (LGN), to posterior cortical sensory regions and onwards to decision making and conflict resolution locations in the frontal lobe. So, information travels in a bottom-up direction. However, anterior regions create feedback loops with the posterior locations, whereby a top-down path of neuronal communication between anterior and posterior regions is established. Hence, information flows in top-down and bottom-up loops.

Different levels of task complexity will place different processing requirements on visual stimuli, and so the level of engagement of the long-range neuronal communications in processing them might vary. More complex tasks require more cognitive control, and so engage anterior and posterior brain regions while less complex tasks engage less spatially distributed networks. One class of tasks which require efficient long-range neuronal communication are tasks that involve resolving a high level of conflict between stimulus characteristics. For example, looking into space with an ‘empty’ mind does not lead to conflict solving and making decisions. On the other hand, abstaining from eating during Christmas dinner, when everyone around is binge eating leads into conflict, where social norms and internal urges challenge top-

down control. So, the level of top-down neuronal communication between anterior - conflict processing regions and posterior - sensory regions must be increased to deal with higher cognitive demands. Crucially, processing conflict requires relatively well established long-range communication between remote dynamic functional networks (Fan, Flombaum, McCandliss, Thomas, & Posner, 2003; Lurii, 1973) such as prefrontal-parietal loops and sensory neuronal locations (Ganzetti & Mantini, 2013; Goffaux, Mouraux, Desmet, & Rossion, 2004; Klimesch et al., 2010; Womelsdorf & Fries, 2007).

Especially that conflicting tasks, engage large fronto-parietooccipital networks. On the other hand, more straightforward, perceptual tasks (as staring at space) employ relatively smaller low frequency networks (Hanslmayr et al., 2008; Kaufmann et al., 2005; Markela-Lerenc et al., 2009).

The reason behind increased neuronal engagement during incongruent Stroop tasks is the resources required to resolve the conflict, i.e. working memory (inhibiting, switching, monitoring), internally and externally driven attentional processes and response inhibition. All of these processes require cooperation between distant regions (Huang, Rossi, Hämäläinen, & Ahveninen, 2014; Oehrns et al., 2014; West, 2003). That distant communication requires some form of coherent connectivity between sensory, decision processing and motor response regions. Also here it has been proposed that low-frequency oscillations might sub-serve that role (Canolty & Knight, 2010; Gross et al., 2004; Lobier et al., 2018). Among these frequencies, alpha oscillations require special consideration. Firstly, because it is a dominant observable low-frequency phenomenon (Buzsáki, 2006; Millett, 2001). Secondly, alpha oscillatory activity can be relatively, straightforwardly induced externally by light (Herrmann, 2001; Vialatte et al., 2010). Also, alpha oscillations are good at phase alignment being induced at the visual stimulation frequency (Moratti, Clementz, Gao, Ortiz, & Keil, 2007; Thut, Schyns, et al., 2011).

Further, within the alpha frequency band lower alpha requires special consideration. What is crucial, the lower alpha is characterised by more widespread distribution across brain regions. Whilst the upper alpha bands have been proposed to reflect more visual processing and feature extraction, the lower alpha have been suggested to be more related to cognitive processing and attention which require cross-cortical neuronal communication (Pfurtscheller, Neuper, & Mohl, 1994). Hence, by strengthening the lower alpha

oscillations signal to noise ratio (by harmonically entraining them with external flicker), it might be feasible to increase effectiveness of long-range communication during conflicting tasks (Leij et al., 2016; MacDonald, Cohen, Stenger, & Carter, 2000; von Stein et al., 2000).

Traditionally, the alpha frequency was regarded as a functional mechanism for sustaining idling states of the brain during periods of wakeful relaxation (Adrian & Matthews, 1934). Alpha activity was conceptualised as a global neural mechanism occurring when a person is awake but relaxed. However more recently it is proposed that alpha may play a more active role – as a mechanism for controlling attention and perception, and as a local inhibitory mechanism - ITH (Herring et al., 2015; Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007; Mathewson, et al., 2012; Waldhauser, Johansson, & Hanslmayr, 2012).

For the current studies, it is proposed that alpha oscillations as a dominant frequency propagated across the cortex frequency are an ideal candidate to facilitate long-range neuronal communication required in processing response conflict tasks (Bench et al., 1993; Fries, 2005; Kopell, Kramer, Malerba, & Whittington, 2010; Palva & Palva, 2011; Siegel, Donner, & Engel, 2012; van Driel, Gunseli, Meeter, & Olivers, 2017). If this is correct, the alpha frequency band would be significantly more engaged in tasks with high levels of conflict (e.g. incongruent conditions in a Stroop task) compared to tasks with a low level of conflict (e.g. congruent conditions in a Stroop task). So, by externally entraining alpha oscillatory networks and increasing the signal to noise ratio in the alpha oscillatory network, it might be possible to improve the efficiency of long-distance communication driven by alpha. (Doesburg et al., 2009; Gruzelier, 2009). Long-range communication between perceptual and conflict resolving networks might be more engaged in incongruent Stroop conditions than in congruent conditions (Botvinick, Carter, Braver, Barch, & Cohen, 2001). Thus, alpha entrainment vs other frequencies and control conditions should significantly improve performance in incongruent as opposed to in congruent Stroop tasks. In other words, the alpha entrained neuronal network should significantly improve performance in the incongruent compared to the congruent Stroop tasks.

Consequently, a series of three experiments were designed. They aimed to investigate how visually induced alpha neuronal connectivity in various congruency levels influences behaviour as measured by error rates (ER) and reaction times (RT). We were interested whether alpha photic driving improves the effectiveness of long-range neuronal communication involved in solving cognitive conflict. Hence, we expected that an alpha prime preceding conflict incongruent tasks would improve performance – an alpha prime would reduce the Stroop effect. To induce the conflict a numerical Stroop test was used as a more culturally neutral test than the traditional colour word Stroop test (Ganzetti & Mantini, 2013; Goffaux et al., 2004; Klimesch et al., 2010; Womelsdorf & Fries, 2007).

The first study was designed which examined the influence of brief photic stimulation in lower alpha (8Hz), lower theta (4Hz) and beta (16Hz) frequencies on the RT and accuracy during numerical Stroop task. The purpose of the task was to investigate how photic driving of bands neighbouring the lower alpha frequency bands versus baseline influence behaviour during conflict processing (numerical Stroop) task. Specifically, the lower alpha frequency was chosen as it was reported by Nombela et al., (2014) that increased activity in that particular range was observed across the wider cortical area (including prefrontal and parietal regions) during the Stroop task, and an interaction was assumed between prefrontal and parietal areas. Hence 8Hz is a good candidate to be induced as it seems to spread across wider cortical locations.

We have chosen to examine specifically lower alpha as it seems to be characterised by more widespread distribution across brain regions. As the upper alpha bands have been proposed to reflect more visual processing and feature extraction the lower alpha is more related to cognitive processing and attention which require across cortex neuronal communication (Pfurtscheller et al., 1994).

The second study attempted to answer the question how the level of photic energy (amplitude) and the delay between the onset of the last entrainer and onset of the task (ISI – interstimulus interval) modified RTs (reaction times) and ERs (error rates) in the execution of a numerical Stroop task. This task aimed to manipulate the amplitude and phase of alpha oscillations. The ISI and amplitude manipulations were introduced because several studies suggested that alpha phase position and its amplitude level influence

probability of an object being perceived (Klimesch, Sauseng, & Hanslmayr, 2007; Sauseng & Klimesch, 2008; Voloh & Womelsdorf, 2016).

Finally, the third study focused on the question how more specifically (a narrow band of frequencies) than in the first experiment, frequency entrainment (6Hz, 8Hz, 10Hz) and three ISIs (50%, 75%, 100%), modify participants' RTs and ERs during execution of a numerical Stroop task.

Before stating our hypothesis, in the following few paragraphs, the current understanding of the neuronal basis for Stroop effect will be presented. It is suggested that the incongruent task in the Stroop test involves more top-down control to suppress the conflicting information and enhance processing of the salient information (Notebaert, Gevers, Verbruggen, & Liefoghe, 2006). To do that, stronger cortico-cortical connectivity needs to be achieved. As it was proposed above, alpha oscillations are long distance network facilitators. As discussed in section 1.22 a visual prime applied in alpha band frequency drives a strong neuronal resonant response (Herrmann, 2001). The author also observed SSVEP responses to alpha stimulation in anterior locations (Herrmann, 2001). Hence, alpha visual entrainment is a good candidate for driving substantial neuronal response across the cortex. That observation about the role of alpha harmonic entrainment in driving neuronal activity across the cortex towards the frontal regions, was also confirmed by Dugue, Marque, & VanRullen, (2011).

Hence, by strengthening the lower alpha oscillations signal to noise ratio (by harmonically entraining them with external flicker), it might be feasible to increase effectiveness of long-range communication during conflicting tasks (Leij et al., 2016; MacDonald, Cohen, Stenger, & Carter, 2000; von Stein et al., 2000). As Ermentrout et al (2008) suggests brain is a noisy environment, where each set of communicating elements try to send and receive information with minimal distortions. By increasing power of certain neuronal oscillators it the signal in relation to the noise strengthens, hence neuronal communication carried by these specific neuronal oscillators is more effective (Ermentrout, Galán, & Urban, 2008).

Conflicting tasks such as Stroop test involve a high level of activity across the cortex, for example, between dorsolateral prefrontal cortex, anterior cingulate cortex (ACC) and posterior regions (Kerns et

al., 2004; MacDonald et al., 2000). At the same time, to achieve effective conflict resolution, high neural communication is needed. This can be accomplished by synchronously closing and opening time windows for neuronal firing thereby information transfer (Fries, 2005; Hipp et al., 2011; Varela et al., 2001). At the same time, it has been reported that alpha and also some suggest theta (Sauseng et al., 2005) frequency bands facilitate long-range neuronal communication, which is crucial for effective connectivity between sensory locations, regions processing different features of the conflicting stimuli and prefrontal executive areas (Doesburg et al., 2009; Astrid Von Stein & Sarnthein, 2000).

Some suggest that the anterior cingulate cortex (ACC) plays an essential role (Hanslmayr et al., 2008; Liotti et al., 2000), other argue that dorsolateral prefrontal cortex (DLPFC) is also involved in conflict processing. However, as it was discussed in the general introduction, the brain is a dynamic system of functional networks, thus localising single loci for the specific function would not be appropriate. Hence, probably all mentioned above regions play a part in conflict processing up to some extent. Therefore, effective communication between them is crucial.

There is some evidence which supports this idea. Namely, it was found that there is a robust oscillatory coupling between DLPFC (dorsolateral) and DMPFC (dorsomedial prefrontal cortex) and parietal lobes during conflict processing (Oehr et al., 2014). Also, some suggest robust connectivity between ACC and prefrontal cortex (Hanslmayr et al., 2008). Also, Schack and colleagues (1999) point out that there is a strong frontoparietal oscillatory coherence within high alpha and lower beta bands during conflicting tasks (Schack, Chen, Mescha, & Witte, 1999).

In line with what has been emphasised, it is possible to argue that networks in fronto-parietal loops are involved in processing the conflict; as well as long distance communication between conflict processing and somatosensory regions requiring effective distant functional connectivity, which is proposed to be served by alpha oscillations. Hence, distributed network of neuronal locations which are involved in conflict processing and visual perception can work more efficiently thanks to alpha neuronal oscillations, which might be entrained external photic driving. Hence, it can be expected that behavioural performance

during a conflict-inducing incongruent Stroop task, with is preceded by alpha photic entrainment will be significantly better, compared to other conditions.

In summary, these studies aimed to investigate how various properties of external photic driving may influence cognitive processes driven by the Stroop task and in consequence their outcome – the behaviour was measured by RTs and ERs. The experiments, by modifying the level of conflict, modulated the engagement of distant neuronal networks. Consequently, it was tested whether a visual alpha prime reduces the stroop effect (i.e. whether the differences between congruent and incongruent conditions preceded by alpha prime would decrease compared to control conditions). Therefore, long-range communication between perceptual and conflict resolving networks might be more engaged in incongruent than in congruent tasks. Thus, alpha entrainment vs other frequencies entrainment/baseline condition might significantly differently affect performance in incongruent than congruent tasks. (Doesburg et al., 2009; Astrid Von Stein & Sarnthein, 2000).

2.2 Experiment 1

2.2.1 Aim of the study

The purpose of this study was to investigate how flickers at three sinusoidal frequencies in lower theta, lower alpha and beta bands (4Hz, 8Hz, 16Hz) influence neuronal dynamics and in consequence behaviour measured by RTs and accuracy compared to baseline. These frequencies were chosen as 4 and 16Hz as they constitute harmonics of 8Hz. As Herrmann (2001) noted, frequencies which were harmonically related to alpha oscillations produce stronger cortical resonant responses. The designed flicker stimuli had a sinusoidal character – light gradually appeared and gradually decayed with the rate of a given frequency. The advantage of using sinusoidal flicker is that it has a high ecological validity for this kind of stimuli; the disadvantage is the complexity of the code which executes timely controlled, gradual increases and decreases of screen brightness within the particular frequency (Townsend, Lubin, & Naitoh, 1975). This type of flicker is as close as technically possible, mimicking neuronal activity on early visual processing level. In consequence, it might have a profound influence on the resonant phase-locking

between external stimuli and neuronal processes (Cvetkovic, Simpson, & Cosic, 2006; Okamoto & Nakagawa, 2011; van der Tweel & Verduyn Lunel, 1965).

Most of the research on the Stroop effect is conducted on the colour-word variant. However despite this version being well established, it has a significant drawback – cultural and lexical interference. Namely, participants with various linguistic backgrounds whose first language is not the language in which the Stroop is conducted tend to have less of a conflict effect in the incongruent task. On the other hand, the numerical Stroop task has less linguistic influence (Tiesling-Rusch, Dimond, & College, 2012). Since the population of Brunel University is multilingual and linguistic segregation would further jeopardise the randomisation method of participant selection, the numerical Stroop test, as a more linguistically neutral task was chosen for all three experiments in this chapter. The conflict in numerical version is based on the difference between the arithmetic value of the printed number and its physical size (Kaufmann et al., 2005; Noël, 2016; Pansky & Algom, 2002; Tiesling-Rusch et al., 2012).

2.2.2 Participants

Twenty healthy right-handed participants (18 female, mean age 20.1 ± 2.7) with normal or corrected to normal vision were recruited using the Brunel University Psychology student participation pool. The Psychology Division Ethics Committee reviewed all procedures before the study being conducted, according to the current Brunel University Policy.

Participation was on an unpaid voluntary basis, but students received credit for the participation component of their research module, which requires them to either have a walkthrough of a psychology experiment or participate. Sixteen participants were native English speakers, and four were from other European countries (French, Polish, Italian and Greek). Volunteers with epilepsy, severe headaches, or a history of epilepsy in the family were excluded before participation. One subject was excluded, as they did not finish the task.

2.2.3 Materials and design

All testing was conducted using 17'' (CRT monitor) set to 85Hz situated in a dimmed room. A standard keyboard was adopted, and responses were assigned to two buttons (z, m) with yellow and green colours. The experiment was designed using E-prime 2.0 software. Each trial started with 1500ms horizontal black bar (10cm by 40cm) flickering at 4Hz, 8Hz, 16Hz or baseline control (a bar that flashed twice - at the beginning and the end of the 1500ms flicker period). It was followed by a presentation of the numerical Stroop stimulus for 2000ms. Large digit font size - No 16, small digit font size – No 11, (see fig. 2.1).



Figure 2.1 *Left:* Example of congruent stimuli - larger value and larger physical size. *Right:* Example of incongruent stimuli – larger value and smaller physical size.

Then a blank screen appeared for 1500ms, yielding an inter-trial-interval of 5000ms in total. The trials belonging to each condition were presented in random order. Each condition was repeated 96 times; hence 768 trials together were presented [(incongruent, congruent) X frequency (4, 8, 16, baseline) X 96].

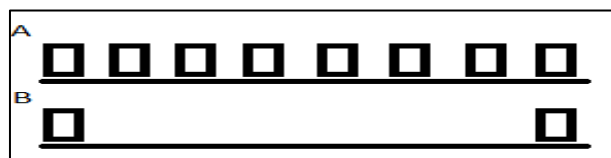


Figure 2.2 Example of A – entraining stimuli; B – control condition where each square represents one period of the sin wave. Some squares are equal to the number of entraining periods of the sinusoid.

The flicker stimuli in all three frequencies and control condition were produced by gradually (sinusoidal pattern – see fig. 2.3) increasing and decreasing the luminance level of the horizontal bar. The advantage

of using sinusoidal flicker is the high ecological validity of that kind of stimuli (Okamoto & Nakagawa, 2011). After the flicker entrainment, the numerical Stroop stimulus was presented.

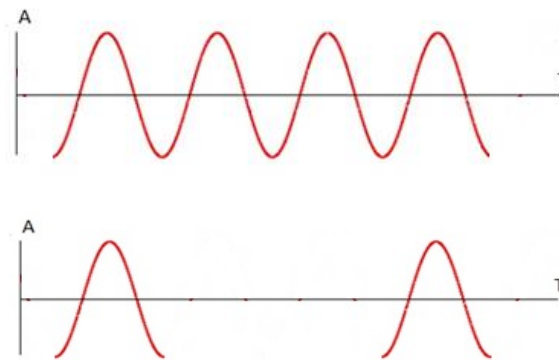


Figure 2.3 Graphical representation of sinusoidal flicker, used across all three experiments, where A represents amplitude (level of illumination) over time (T).

The following numeric pairs were presented: 2-3; 3-2; 2-9; 9-2; 8-9; 9-8. In fifty per cent of cases, the physical and numeric values were congruent. The screen was linearised with the luminance meter using look-up table and settings were applied across all the experiments in this thesis.

2.2.4 Procedure

Participants were welcomed into the dimmed room. They were asked to read and sign informed consent. Subsequently, they were given a brief explanation of the nature of the study and given the opportunity to ask questions. All subjects were informed that they could withdraw their consent and leave without any consequences. Participants sat 57cm away from the monitor where the task was explained, after which the practice trial was conducted. Each participant was asked to, as quickly and accurately as possible, judge the stimuli, and provide the answer to which digit in the pair is mathematically larger, by pressing one of the two buttons (z – value on the left side of the screen, m – value on the right side of the screen). Button z was representing yellow and m – green during the entire experiment.

If the task was not understood (the performance of the practice session was closely monitored), the practice session was repeated. After the procedure, which took approximately forty-five minutes,

everyone received a debriefing form and brief verbal explanation of the concept, hypothesis and methodology. The same procedure was applied in the following two experiments (sections 2.3 and 2.4)

After the experiment, the participants received a debrief form with brief information about the experiment and the contact details should they have any further questions, concerns or complaints.

2.2.5 Results

The data was analysed using Microsoft Excel and IBM SPSS statistics in this and other experiments in this thesis. Responses which were faster than 100ms or slower than 1600ms were discarded and not taken into further analysis. This rule was applied across all the experiments in this thesis. Means for each condition and for each participant's reaction times (RT) and error rates (ER) were calculated independently.

2.2.5.1 Reaction time analysis

A two (congruency: congruent, incongruent) by four (frequency: 4Hz, 8Hz, 16Hz, baseline) ANOVA was calculated on RTs. Participants were significantly faster in responding to congruent trials than non-congruent trials (main effect $F(1, 18) = 73.2, p < 0.05$), which confirms the Stroop effect that resolving non-congruent stimuli is more difficult than congruent tasks. Also, there was a significant difference across the different prime frequency conditions, $F(3, 54) = 8.56, p < 0.05$. The post-hoc tests showed significant differences in the '8Hz - baseline' pair ($t(18) = 5.74, p < 0.05$), and the '8Hz - 16Hz' pair ($t(18) = 2.17, p < 0.05$). There was no significant interaction between congruency and frequency, $F(3, 54) = 0.72, p > 0.05$. Hence, alpha prime did not appear to reduce the Stroop effect compared to other frequencies or control condition. The main purpose of this experiment was to find the optimal frequency for Stroop effect reduction. As none of the probed frequencies did reduce the effect, in the follow-up experiments other factors were tested to find such a reduction. Crucially, 8Hz significantly improved people's performance. Hence it was used as a benchmark frequency in the follow-up experiments.

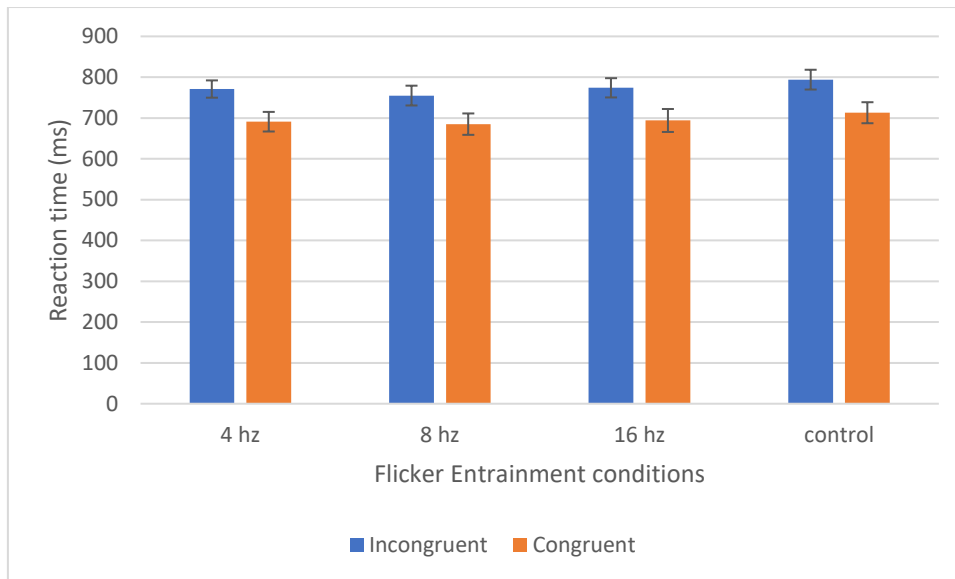


Figure 2.4 depicts the mean RT for each of the conditions; blue bars indicate incongruent trials and red - congruent (error bars show 1 SEM).

2.2.5.2 Error rate analysis

The same statistical analysis was conducted on ER as on RTs. Participants made significantly fewer errors in responding to congruent trials comparing to non-congruent $F(1, 18)=20.98, p<0.05$. There was no significant differences in the number of errors made in the four frequency conditions $F(1, 18) = 1.67, p>0.05$, nor any significant interaction between frequency and congruency $F(3, 54) = 1.06, p>0.05$). The error rate study also did not provide information about the optimal parameters for Stroop effect reduction. Also, as all (except Stroop effect) parameters were non-significant, ER seems to be less sensitive in detecting the effect of visual prime on performance. One of the reasons that ER results are not a sensitive measure and RTs appears to be better in detecting differences between conditions might be that participants focused on solving the task as quickly as possible; hence they made more errors, which were made not only because of the conflict but also because of the speed in responses. Alternatively RT can be just more sensitive measure and in fact most previous studies of the numeric Stroop task have focused upon RTs (see Henik & Tzelgov, 1982).

2.3 Experiment 2:

2.3.1 Aim of the study

In the previous experiment, it was established that 8Hz flicker compared to 16Hz and non-flicker baseline made people respond faster while solving the Stroop task. Three main properties characterise the oscillation: frequency, amplitude and the phase, hence it would be interesting to investigate how amplitude (luminance) together with the phase modulation (ISI shift) might influence behaviour. Hence, the study was designed to investigate how various luminance levels of sinusoidal photic stimulation and different ISIs between the last entrainer and the onset of the task, influence Stroop task performance.

Someone might ask why the brightness level of the prime and the ISI can play a role in influencing alpha neuronal dynamics? The inhibition-timing hypothesis (ITH) emphasised the role of phase and level of excitation (amplitude) of neurons (within the alpha band) in controlling connectivity in large networks (Klimesch, Sauseng, & Hanslmayr, 2007). In more detail, Klimesch et al. (2007) suggested that alpha amplitude influences the excitatory and inhibitory neuronal processes. When the alpha amplitude increases the cells with a high excitation level will fire rhythmically, and in consequence, increased rhythmic activity will lead to the more precise timing of neural activity. Also, ITH suggests that very high alpha amplitude limits information processing and low alpha amplitudes in given neuronal representation gate the information flow. Additionally, some suggest that the phase of alpha modifies the probability of the stimuli being processed (Bonfond, Kastner, & Jensen, 2017; Jensen & Mazaheri, 2010; Jensen, Gips, Bergmann, & Bonfond, 2014; Mathewson et al., 2012; Spaak, de Lange, & Jensen, 2014). Hence it is interesting to test which prime light intensity and phase of alpha in which task is instigated, are optimal for gating the information flow (Klimesch, Sauseng, & Hanslmayr, 2007). Therefore, it is hypothesised that neurons could be influenced by the stimulus intensity (amplitude) which alters their firing power. Also it is hypothesised manipulating the onset of the Stroop task relative to the phase of alpha flicker prime will modify the task performance.

In summary, the level of entrained alpha amplitude and phase might influence the effectiveness of long-range neuronal communication. It is not clear which level of alpha amplitude is optimal for conducting

information across the cortex. Also, it would be interesting to see whether the phase of alpha plays an additional role in modifying the effectiveness of that communication. Therefore, the experiment tested three different stimuli intensities and three ISIs. Three levels of flickering bar brightness were as follows: 52, 104 or 208 cdm^2 (all measured in the dimmed experimental lab). Correspondingly a manipulation of phase was introduced in order to investigate how this might co-influence neuronal communication. Hence, the task was presented out of phase (50%, in the midpoint - 75% and in phase – 100% of entrained 8Hz alpha), with the peak of the last sinusoidal entrainer (Bonnefond & Jensen, 2015; de Graaf et al., 2013; Jensen & Mazaheri, 2010; Mathewson, et al., 2012; Spaak et al., 2014).

2.3.2 Participants

Thirteen participants (5 men, mean age 21.7) were recruited from the Brunel University psychology participation pool. Initially more participants were recruited (nineteen), however 6 participants declined/did not show up for the experiment, hence only thirteen took part in the actual experiment. The Psychology Division Ethics Committee reviewed all procedures before the study was being conducted. The criteria for participation, exclusion of data, reward and procedure, were identical to the previous study (see 2.2.2).

2.3.3 Materials, design

The current experiment was like the previous study from the participant's point of view. The only difference was the applied 8Hz prime with three luminance levels and three ISIs, as introduced and justified in section 2.3.1. So, each trial was always preceded by 8Hz prime characterised by one out of three luminance levels (52, 104 or 208 cdm^2). Subsequently, it was followed by ISI50 - 59ms, ISI100 - 125ms or ISI75 - 184ms and finally, the Stroop task was displayed. The screen was linearised with the support of manual luminance meter, look-up table (<https://www.scantips.com/lights/gamma3.html>) and Palamedes software (Kingdom & Prins, 2010). The look up table is used to convert the 0-256 intensity value to a linear response so that the intensity change between successive values is the same. So we used luminance meter to measure 255 screen RGB values and then adjusted them in the Palamedes environment in order to adjust original screen brightness steps to the human eye brightness discrimination

sensitivity. Also, the same room and screen luminance conditions, as well as software and hardware, were used in the first experiment. Also, here RTs and ERs were measured. Each condition [(incongruent, congruent) X luminance (52, 104, 208) X ISI(50% 75% 100%)] were allocated 45 trials each, resulting in 1080 trials together, (24 X 45).

2.3.4 Procedure

The same procedure as in the first experiment was applied in this experiment.

2.3.5 Results

2.3.5.1 Reaction time

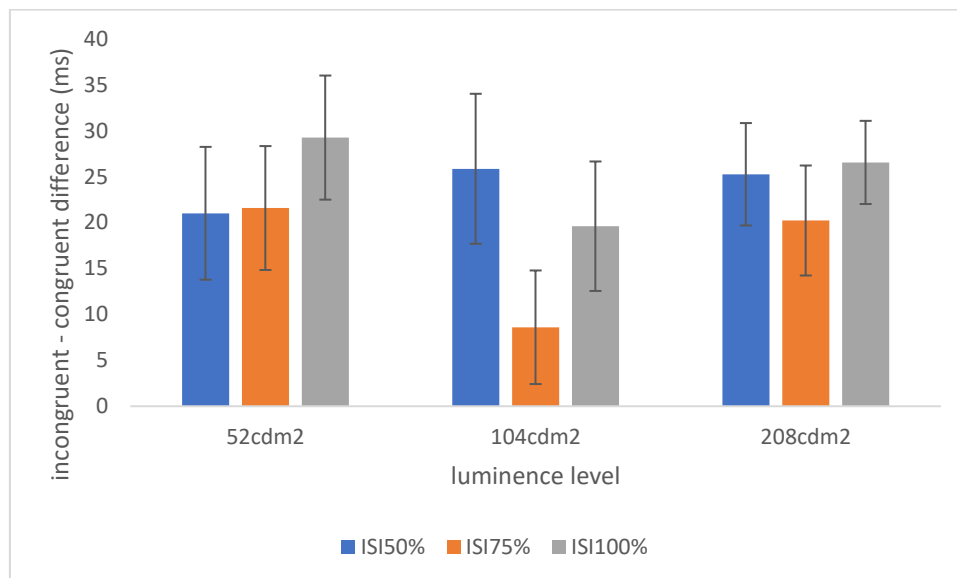


Figure 2.5 RTs difference between congruent and incongruent trials, sinusoidal flash (8Hz) 3 levels of luminance (52, 104, 208 cdm²) and three interstimulus intervals, equal to 50%, 75%, 100% of the length of frequency period (error bars show 1 SEM).

A three (ISI 50%, 75%, 100%) by three (luminance level: 52, 104, 208cdm²) by two (congruency) repeated measures ANOVA was conducted on the reaction times (see fig. 2.5). Mauchly's test indicated that the assumption of sphericity had been violated for both the interaction effect of ISI and luminance ($\chi^2=44.68$, $p<0.05$ $p=0.02$) and for the interaction of congruency, luminance and ISI ($\chi^2 = 65.46$, $p<0$). In both instances, the Greenhouse-Geiser correction was applied to the degrees of freedom. In other cases, the assumption of sphericity was not violated.

The main effects of congruency ($F(1, 12)=5.33, p<0.05$), luminance ($F(2,24)=11.17 p<0.05$) and ISI ($F(2, 24)=7.59 p<0.05$) were all significant. However, the interaction of congruency and luminance ($F(2, 24)=0.353 p>0.05$), as well as the interaction of congruency and ISI ($F(2,24)=1.19 p>0.05$), were not significant. Neither the interaction effect for ISI and luminance ($F(2.53, 30.4) = 0.935, p>0.05$) nor the interaction of congruency, luminance and ISI ($F(1.74, 20.96)=0.222, p>0.05$) was significant .

For the significant effects, post hoc tests were calculated, and significant results were reported. Namely, for main effect of luminance, people were significantly faster when the flicker luminance level was 104 cdm^2 than 52 cdm^2 (104I and 52I: $t(12)=-4.305 p<0.05$) and the flicker luminance level was 208 cdm^2 than 52 cdm^2 (208I and 52I: $t(12)=-3.937 p<0.05$). For the main effect of ISI people were significantly faster when the target was presented in phase (ISI 100) than out of phase (ISI 50) - $t(12)=3.535 p<0.05$ and in the midpoint between in and out of phase (ISI75% - ISI100%: $t(12)=3.277 p<0.05$).

Hence, medium and stronger flicker luminance levels were making participants significantly faster compared to the weakest brightness. Also, participants were slower to react in 50%ISI and 75%ISI comparing to 100% ISI. However, crucially none of the interaction effects were significant. Thus, none of the phase and amplitude manipulations applied with an 8Hz frequency significantly reduced the Stroop effect.

2.3.5.2 Error rate study:

The same analysis as for RTs above was conducted on ERs. The main effect of congruency was significant ($F(1,12)=3.23, p<0.05$). However, the main effect of amplitude was not significant ($F(2, 24)=2.69, p>0.05$). Also, there was no significant main effect of ISI $F(2, 24)=0.08, p>0.05$. Moreover, there were no significant interactions either between congruency and amplitude ($F(2, 24)=1.97, p>0.05$), congruency and ISI ($F(2, 24)=0.391, p>0.05$), .amplitude and ISI ($F(2, 24)=0.402 p>0.05$), nor for congruency, amplitude and ISI ($F(4, 48)=1.83, p>0.05$). In summary, only the main effect of congruency, (which shows only the Stroop effect) was significant. None of the other measures were significant. Also here as in the first experiment, ERs measures seem to be less sensitive to detecting differences than RTs.

2.4 Experiment 3 - Three frequencies and interstimulus interval.

2.4.1 Aim of the study

The third study attempted to find optimal parameters of the prime which would facilitate long-range neuronal communication and so reduce the Stroop effect. The first study failed to show that 8Hz flicker would reduce the Stroop effect. However, it has shown that people are significantly faster in all conditions when the task is preceded by 8Hz flicker compared to 16Hz and the baseline. Thus, 8Hz was chosen as a benchmark in this experiment accompanied by a closer range of reference frequencies compared to the first experiment, to test frequencies closer to 8Hz in their influence on performance in the Stroop Task. What is more, as discussed in chapter one there is an ongoing discussion in the literature about which phase within the alpha cycle is optimal for facilitating perception (Mathewson et al., 2012, Spaak et al., 2014). It is likely that not only a specific frequency within an alpha band but also other properties of alpha oscillation such as a phase, might take part in facilitating long distance information processing. Hence, the study examined whether the Stroop effect is be reduced when a 6Hz, 8Hz and 10Hz prime is applied and the onset of the task is presented 50%, 75% or 100% of the frequency period applied (e.g. for 10Hz it will be 50, 75, 100ms respectively).

2.4.2 Participants

Ten healthy, right-handed, (nine females, mean age 20.4 ± 2.2) with normal or corrected to normal vision were recruited using the Brunel University Psychology student participation pool. The Psychology Division Ethics Committee reviewed all procedures before the study was being conducted. The criteria for participation, exclusion of data, reward and procedure, were identical to the first study.

2.4.3 Materials and design

The same materials, hardware and settings as in two previous experiments were used. The only difference was the current experiment manipulated the frequency (6Hz, 8Hz, 10Hz) and interstimulus interval (ISI: 50, 75, 100 per cent of the period of preceded frequency)).

2.4.4 Procedure

The procedure was the same as in the first experiment except that three frequencies (6Hz, 8Hz, 10Hz) and three ISIs (50%, 75% and 100% of a cycle) were used.

2.4.5 Results

Results section is divided into reaction times and error rates analysis

2.4.5.1 Reaction time study

A three (frequency) by three (ISI) by two (congruence) repeated-measures ANOVA was conducted on the reaction times (see fig. 2.6). There were significant differences for the main effect of congruency ($F(1, 9)=8.85, p<0.05$) and the main effect of frequency ($F(2, 18)=14.92, p<0.05$) – see fig. 2.6. Post hoc tests for the frequency main effect indicated difference between 10Hz and both 8Hz ($t(9)=3.80, p<0.05$) and 6Hz ($t(9)=4.46, p<0.05$) conditions but not between 6Hz and 8Hz ($t(9)=2.09, p>0.05$), showing that 10Hz alpha entrainment compared to 8Hz and 6Hz significantly improves performance in Stroop task. There was no significant differences for the main effect of ISI ($F(2, 18)=3.22, p>0.05$).

There was a significant interaction between frequency and ISI ($F(4, 36)=2.96, p<0.05$), post hoc tests were conducted and the following pairs presented in table 2.1 were significant.

Table 2.1 shows significant differences for post hoc frequency and ISI effect. We did run t tests for all possible conditions' combinations. When the t test value is reported in the table, the indicated pair is significantly different.

	6 50	6 75	6 100	8 50	8 75	8 100	10 50	10 75	10 100
6 50									
6 75									
6 100									
8 50									
8 75									

8 100									
10 50	t(9)=3.8 8 p<0.05	t(9)=4.4 4 p<0.05	t(9)=3.2 8 p<0.05	t(9)=3.2 4 p<0.05	t(9)=2.5 1 p<0.05	t(9)=4.6 1 p<0.05			
10 75		t(9)=2.3 6 p<0.05				t(9)=2.3 0 p<0.05			
10 100	t(9)=3.5 3 p<0.05	t(9)=8.4 7 p<0.05	t(9)=3.9 6 p<0.05			t(9)=6.9, 6 p<0.05.			

Post hoc tests for the main effect of frequency indicated that 10Hz significantly improves RT of solving Stroop task compared to both lower frequencies. Post hoc tests for the **frequency-ISI** interaction indicated that 10Hz out of phase (10Hz⁵⁰) entrainment made people significantly faster compared to 6Hz and 8Hz (for all three ISIs). Also, people were significantly faster when exposed to 10Hz in-phase (10Hz¹⁰⁰) condition compared to all phases for 6Hz and in phase entrainment of 8Hz. That complex picture can be broadly summarised that 10Hz in and out of phase conditions tend to make people faster compared to 6Hz and 8Hz. Especially 10Hz out of phase presentation outperform all lower frequencies with all ISI options. Also, 10Hz in-phase condition outperforms all 6Hz conditions.

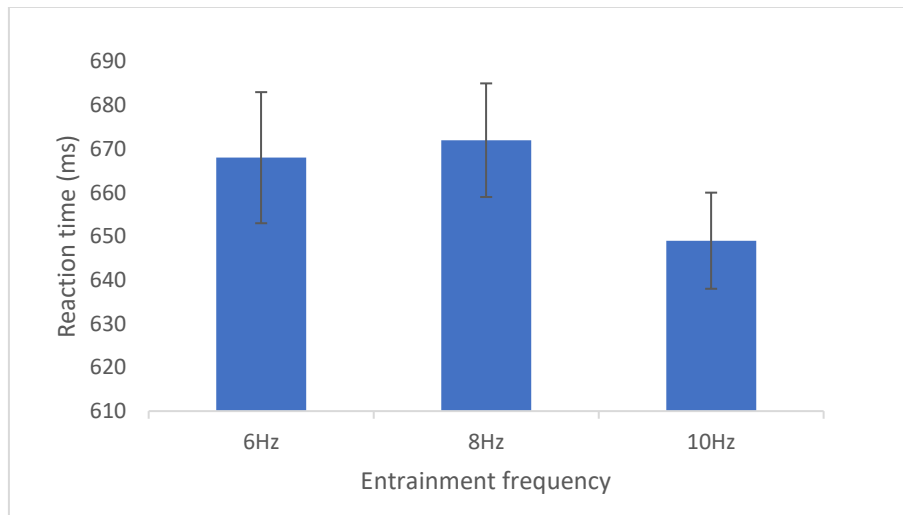


Figure 2.6 Depicts the main effect of frequency. The mean reaction times for three frequencies indicate that people were faster when the Stroop task was preceded by 10Hz prime.

None of the other interactions were significant congruency and frequency ($F(2, 18)=1.67, p>0.05$), congruency and ISI ($F(2, 18)=0.61, p>0.05$) and congruency, frequency and ISI ($F(4, 36)=1.39, p>0.05$).

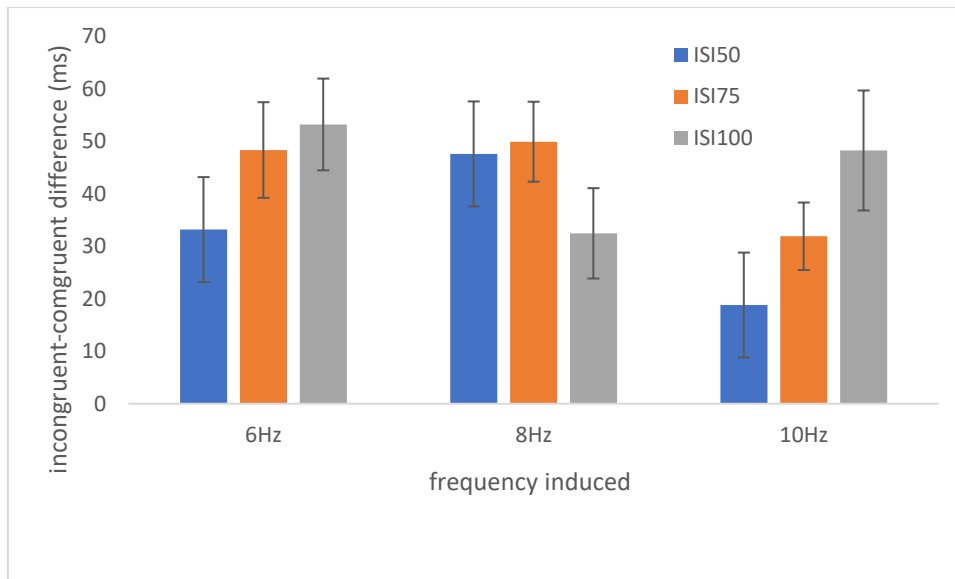


Figure 2.7 Differences between congruent and incongruent trails for each frequency and ISI (error bars show +/-1 SEM).

2.4.5.2 Error rate study:

The same analysis used for RTs was conducted for error rates. There was no significant differences main effects of congruency ($F(1, 9)=1.24, p>0.05$), frequency $F(2,18)=0.566, p>0.05$ or ISI ($F(2,18)=0.625, p>0.05$). There were also no significant interactions: congruency and frequency ($F(2, 18)=2.581, p>0.05$), congruency and ISI ($F(2, 18)=1.19, p>0.05$), frequency and ISI ($F(4,36)=1.125, p>0.05$) and congruency, ISI and frequency $F(4,36)=0.679, p>0.05$. Thus none of the main effects and interactions were significant for the error rates in this experiment. Also, in this experiment, ERs seemed to be less sensitive not only in diminishing the Stroop effect but also in other factors which achieved significance in RTs. These ER results are in line with the ER results in both previous experiments. In summary, it might suggest that people were focused on the responding speed and not on the accuracy.

2.5 Discussion

A series of three conducted studies systematically investigated how sinusoidal photic entrainment in alpha (compared to other frequency bands), and various levels of ISIs and luminance could influence neuronal dynamics underpinning long-range neuronal communication (LRNC) in the Stroop task. We were interested whether an alpha prime might influence neuronal dynamics in a way that the neuronal

communication would be more efficient and the Stroop effect would diminish thanks to enhanced communication between areas associated with cognitive processing and early visual areas. To assess this, we used the Stroop test preceded by alpha or other frequency photic stimulation, and we measured RTs and ERs as a behavioural signature of changes in neuronal processes. However, in none of the experiments was there any evidence for the manipulations diminishing the Stroop effect, as none of the manipulated variables interacted with the congruency effect. Hence, none of the manipulations seemed to affect the Stroop effect.

Nonetheless, the experiments gave some insights into the relationships between alpha neuronal oscillations and behaviour. The first experiment showed that people are faster in responding to the Stroop task when preceded by 8Hz compared to the no flicker conditions and 16Hz prime. It can suggest that 8Hz, in general, might improve peoples' performance during cognitive tasks compared to baseline and 16Hz prime. Interestingly, there was no increase in error rates in the 8Hz conditions which suggests it was not simply a speed-accuracy trade-off.

When the 8Hz prime was applied in the second experiment, with various flicker intensity and ISIs people were significantly faster in responding to the tasks with the medium (104 cdm^2) and high (208 cdm^2) level of luminance. That phenomenon might be explained by the signal to noise ratio phenomenon. Neuronal network (including senses) as a biological system is characterised by a particular spectrum of sensitivity to the external stimuli. Hence, probably two out of three tested brightness conditions had a stronger influence on neuronal dynamics.

What is more, people are significantly faster in providing a correct answer when 100% ISI precedes the task compared to 50% ISI and 75% ISI. The latter result goes in line with the findings of Mathewson et al., (2012).

Finally, the third experiment was conducted to investigate whether other, close to 8Hz frequencies might produce contraction of the Stroop effect when comparing it to the 8Hz prime. It did not confirm that expectation. However, this study showed that people are performing better when 10Hz prime precedes the Stroop task, compared to 8Hz and 6Hz. Thus, 10Hz emerges as an exciting frequency, especially that

a number of studies investigating this specific frequency band in the context of cognition and perception, already emphasised its importance (Gulbinaite et al., 2017; Herrmann, 2001; Landau & Fries, 2012; Rana & Vaina, 2014; van Dijk et al., 2008; van Driel et al., 2017; Wach et al., 2013). It emerges that 10Hz might be a good candidate for externally perturbing/arousing internal neuronal dynamics, which leads to better performance compared to the other two frequency primes. Thus, based on outlined literature and the current results, the 10Hz frequency will play a central role in the following paradigms of this thesis, testing the role of alpha oscillations in human perception and cognition. It came to the attention of the author of this thesis, most of the studies which apply photic stimulation, applying on-off visual prime and sinusoidal entrainment is less popular. The author did not find any evidence which would demonstrate that one type of entrainment is better than the other. Although as the on-off paradigm is widely used in current research and is relatively simple to be designed and applied, hence the subsequent experiments were designed with on-off photic prime.

In summary, as there was a lack of evidence for alpha prime diminishing Stroop effect, the study did not find significant evidence that sinusoidal alpha prime improves long-range neuronal communication engaged in solving conflicting visual tasks. However, the study allowed the experimenter to establish closer to optimal visual prime conditions, which induce changes in behaviour. Subsequently, the outlined parameters (luminance and frequency) can be used as a benchmark in the following experiments of this thesis.

Chapter 3

3.1 Introduction

In chapter two, the role of alpha oscillations in facilitating long-range communication across cortical areas was examined using an inhibitory control task. The experiments in the current chapter address the functional significance of alpha oscillations in human visual perception, which has been the basis of a number of theoretical proposals and empirical studies (Bressler & Menon, 2010; Ergenoglu et al., 2004; Lange, Keil, Schnitzler, van Dijk, & Weisz, 2014; Smith, 2015; Verstraeten & Cluydts, 2002; Ward, 2003).

From William James onwards there has been a debate as to whether visual perception comprises a continuous flow of information or a series of periodic events (Goodman, 2012). Gibson (1955,1968,1979) proposed a theory of vision centred on the importance of the constant dynamic flow of information across the retina, which continues to exert a major influence on the field. More recently, however, the interest in the neural dynamics of **visual awareness** has led researchers to argue that vision might be processed as a series of **discrete events** (Neuling, Rach, Wagner, Wolters, & Herrmann, 2012; Valera, Toro, Roy John, & Schwartz, 1981; Van Rullen & Koch, 2003). Some researchers have proposed that this is reflected in periodic fluctuations in visual sensitivity over time (Busch & VanRullen, 2010). More specifically, it has been suggested that such peaks and troughs are aligned with the phase of on-going alpha activity in the brain, which reflects a specific role for alpha activity in the control of perceptual and attentional processes (de Graaf et al., 2013; Milton & Pleydell-Pearce, 2016; VanRullen, 2016). This potential role is reviewed more fully in chapter one (see section 1.3).

However, there is conflicting evidence as to whether maximum sensitivity occurs at the **peak** or **trough** of alpha activity. For instance, many (Busch & VanRullen, 2010; Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Jaegle & Ro, 2014; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Mathewson et al., 2011; Mathewson, et al., 2012; Romei, Gross, & Thut, 2010; Vincenzo Romei, Gross, & Thut, 2012; Smith, 2015) argue that high perceptibility occurs on the positive peak of low-frequency oscillations. On

the other hand, (Haegens, Nacher, Luna, Romo, & Jensen, 2011; Herring, Thut, Jensen, & Bergmann, 2015; Jensen, Gips, Bergmann, & Bonnefond, 2014; Jensen & Mazaheri, 2010; Neuling et al., 2012; Spaak, de Lange, & Jensen, 2014) suggest that high perceptibility occurs at the minima (trough phase) of low-frequency oscillatory activity.

The experiments in the current chapter attempt to resolve this debate by considering these differences in the context of recent studies by Spaak et al., (2014) and Mathewson et al., (2012). Both researchers induced alpha frequency neuronal activity using SSVEPs (steady-state visually evoked potentials) and measured sensitivity to visual targets at a series of time points relative to the onset of the entrainer. Mathewson et al., (2012) reported that the most sensitive perception occurred at time points that were **in-phase** with entrained alpha (i.e. at times when an entrainer would have appeared). In contrast, Spaak et al., (2014) found people were the most likely to detect the near threshold target when they were presented at time points **out of phase** with entrained alpha (i.e. at time points that would be mid-way between entrainers). Critically, explaining the reasons for the difference in their findings may generate essential insights into the role of alpha activity in visual processing. More specifically, the current studies are based on the assumption that the functional significance of alpha oscillations may, in part, be identified by determining the specific difference between these studies that lead to the reversal of the relation between stimulus detection and phase. In order to isolate this difference, a single paradigm was developed where a simple manipulation in a single factor will result in a reversal of this relationship replicating both results and explaining the differences between them. However, initially, the crucial points of both paradigms are outlined below.

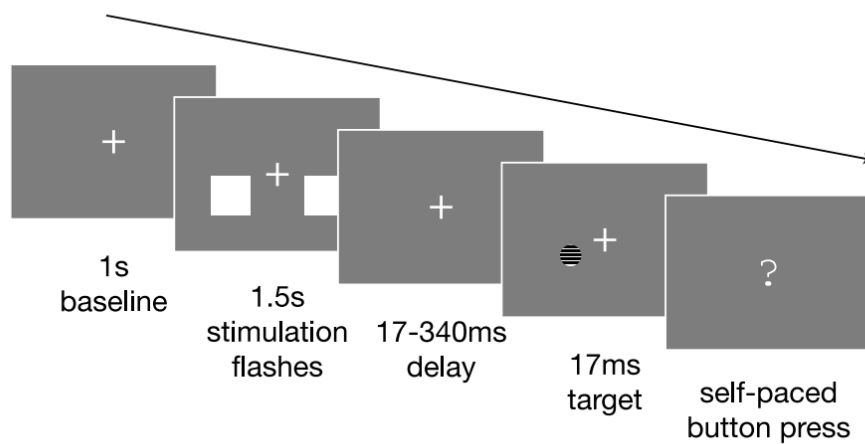


Figure 3. 1 Spaak paradigm: Inhibiting target location make target challenging to detect, however even during the high alpha there are momentary low alpha phases – alpha troughs. When the target is presented in that narrow time window, it is more likely to be detected (Spaak et al., 2014)

The Mathewson et al., (2012) task is illustrated in figure 3.2. In brief, each trial started with participants viewing a 2-degree ring (with a one-degree hole in its centre) that flickered at 12Hz for ~700ms (and so evoking SSVEPS). This was followed by a simple visual detection task in which participants indicated (yes/no) whether or not a small (1 degree) circular target was briefly presented (32ms) in the centre of the screen, i.e. in the location of the central gap in the entraining ring. The dot was presented at different ISIs after the entrainer that were either in-phase or out of phase with the presentation of the entrainer. Critically, as the target disappeared it was masked by the appearance of a ring (two degrees) at the same location as the entraining ring. For the purposes of the current studies, there are two critical characteristics of this task: i) entrainment took place at the mask location and ii) there was a single centrally presented target;

The Spaak et al., (2014) paradigm is illustrated figure 3.1. In brief, each trial started with participants viewing two six-degree flickering squares on either side of the screen for 1500ms, but only one square was flickering regularly at (10Hz) (and so evoking SSVEPS) whilst the other contained a randomly

jittered flicker. This was followed by a simple visual detection task in which participants indicated whether a small (1 degree) circular near-threshold Gabor patch was briefly presented (individually adjusted) in the left or right hemifield. For the purposes of the current studies, there are two essential characteristics of this task: i) entrainment took place at the target location and its surround and ii) the location of the target was uncertain.

In both experiments, alpha entrainment preceded near threshold target presentation. However, in the Spaak et al., (2014) experiment the entrainment, occurred at the location at which *a target subsequently appeared*, whilst in the Mathewson et al. (2012) experiments, entrainment occurred at *the location of the mask* adjacent to the target. In other words, the entrainer in the Mathewson experiment covered the mask but not that of the target location (the prime and mask were spatially superimposed, see figure 3.2). Hence, the increased sensitivity for targets presented in-phase may represent inhibition of the effectiveness of the mask rather than the enhancement of the target during alpha peaks. On the other hand, in Spaak et al., (2014) experiment the alpha prime may induce high alpha amplitudes in neuronal representations in the target location and inhibit target detection. A number of theoretical models (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007) suggest that alpha is used to suppress processing of external stimuli, and if that is the case the results of the two studies might be explained by spatially localised oscillations in alpha activity within a visual field.

So what evidence exists for spatial localisation of the effects of alpha entrainment? There is indeed evidence that alpha stimulation can be localised to one hemisphere. For example, Romei et al., (2010) observed that high alpha amplitudes induced by rTMS in one hemisphere inhibits the perception of visual stimuli in the contralateral hemifield. Also, Volberg, Kliegl, Hanslmayr, & Greenlee, (2009) argued that Fast RTs to local features of Navon figure are associated with high alpha amplitudes in the right centro-parietal cortex; on the other hand, fast responses to global forms might be associated with high alpha amplitudes in the left centro-parietal cortex. Hence interhemispheric alpha dynamics are also emphasised here. However, the current proposal is that it may be possible to stimulate alpha activity within a hemisphere selectively.

To assess this possibility, a novel variant of Mathewson's task was developed that allows manipulation of whether the target or mask location was entrained. The hypothesis is that entrainment leads to a suppression of perception *at the entrained spatial locations* in-phase with peaks in alpha activity and a facilitation out-of-phase with alpha stimulation. Thus, by entraining the area adjacent to the target the perception of the mask is reduced and results like Mathewson et al., (2012) would be expected. On the other hand, by entraining the area spatially superimposed on the target, the target perception is suppressed and results like Spaak et al., (2014) would be expected. If this is correct, it would indicate that alpha activity can lead to spatially localised inhibition in perception within the representation of the visual field in a single hemisphere.

In this experiment and all the subsequent studies, a 10Hz prime was chosen as the alpha band stimulation frequency. It is partially because Herrmann (2010) showed that for SSVEP stimulation 10Hz is a resonant frequency, i.e. the neural response to stimulation at this frequency is disproportionately higher than at neighbouring frequencies (9 or 11Hz). Additionally, other resonant frequencies (20Hz and 40Hz) are harmonics of this frequency which suggests that 10Hz may have a particular role in facilitating cross-frequency coupling. Also, results in the third experiment (chapter two) has shown that 10Hz visual prime plays a special role in improving cognitive tasks performance. Prior to the main experiment, a pilot study was conducted to identify the optimal parameters of the screen luminance (not specified in the original Matheson papers) and to ensure the paradigm could be replicated using a 10Hz entrainer.

3.2 Replication of Mathewson's experiment

3.2.1 Motivation and experimental design and hypothesis

The purpose was to try to replicate Mathewson's results in pilot study, including determining background luminance and the lighting of the room, as none of these variables were reported by Mathewson et al. (2012). Additionally, in the current study black targets, primes and masks were presented against a mid-grey background. The colour of the targets in Mathewson study (2012) was unspecified although their figure shows black targets/masks, but an earlier related study (Matheson et al., 2009) employed dark grey

stimuli. Finally, this pilot study aimed to ensure that the effects could be reproduced for a 10Hz entrainer, as the study in chapter two determined that as a well performing frequency.

3.2.2 Methods

3.2.2.1 Participants, stimuli, experimental design

Ten participants completed a brief 40 trial training session, in order to become familiar with the task. It was followed by the experimental session (4 blocks, each containing 250 trials divided by breaks). Participant had 1500ms from the onset of the target to respond by pressing one of two buttons – left (target not present) or right (target present). Flicker was set at 10Hz. On 20% of the trials, the target was absent to measure false alarms. In this study, only three ISIs, (between the onset of last entrainer and the onset of the target) were used (50ms, 100ms, and 150ms) and they matched the phase points at which Mathewson achieved the most robust differences in the error rates.

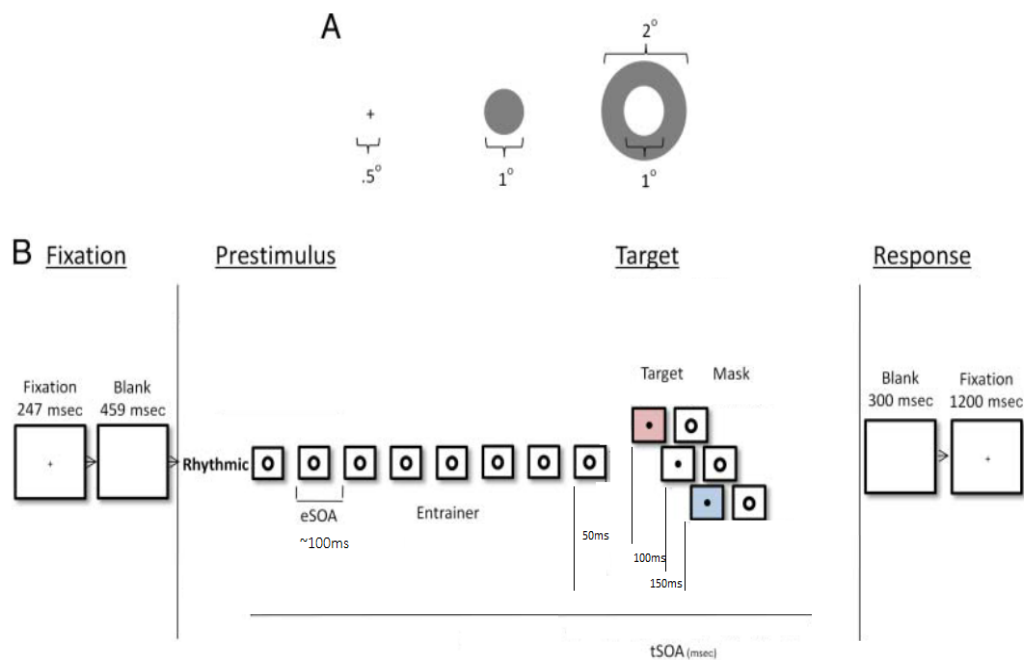


Figure 3.2 depicts replicated rhythmic condition from Mathewson study (2012) with modification from 12Hz to 10Hz - describes stimulus dimensions (A) and experimental design (B)

Participants sat at ~57 cm in front of an Electron Blue 22” monitor and set to 60Hz refresh rate CRT screen. The contrast response of the monitor was measured and linearised using a look-up table. The experiment was replicated from the original Mathewson et al., (2012) rhythmic condition as illustrated in figure 3.2, with 10Hz prime.

The luminance parameters used were measured. Initially, the luminance meter was calibrated in a dark laboratory with the monitor off. Subsequently, the monitor was switched on and allowed to run for 15 minutes to warm up. The luminance level of target, cross and mask was 1.8cd/m² and the grey background 23.1cd/m². The above parameters were applied across the following experiments in chapter three and four.

3.2.2.2 Procedure

Each trial began with the centrally presented cross as a fixation point (~250 ms) – see fig. 3.2. After ~450ms of the blank screen first entrainer was presented (black annulus – ring-like shape) for ~16.7ms followed by ~83ms (SOA 100ms). It was repeated eight times. In this point in time, various, depending on the condition, ISIs in equal proportions, appeared (~50ms; ~100ms; ~150ms). Subsequently, it was followed by the 16.7ms (one screen refresh) near threshold black target, followed by ~50ms ISI and black annulus mask (~33ms). Participants had 1500ms from the onset of the target to provide the answer by pressing one of the two buttons: left - target not present, right - target present – for illustration see fig. 3.2. The experimental phase was divided into four equal blocks consisting of 250 trials each. Between the blocks, participant had a rest break and the participant controlled its length. The participant was suggested to rest until he/she feels ready to conduct the next part.

After the session, the participant was informed about the purpose of the study and was briefed about the theoretical concept behind the experiment. Also, he/she was given debriefing forms with the literature and contact details, should they have any further questions.

3.2.2.3 Results

Mathewson et al., (2012) did not examine non-target data therefore to follow the author's pattern of analysis only the target data was taken into consideration. The prediction was that participants achieve significantly different error rates in detecting the near threshold target in (100ms) - and out of phase (50ms, 150ms) conditions. Results are presented in table 3.1 and figure 3.3.

Table 3. 1 Means of error rates, standard errors 50%-50ms. 100%-100ms, 150%-150ms

ISI/Trial type	Mean±SEM
50% target	31% ±7%
100% target	12% ±1%
150% target	16% ±2%
50% catch	11% ±2%
100% catch	22% ±8%
150% catch	23% ±7%

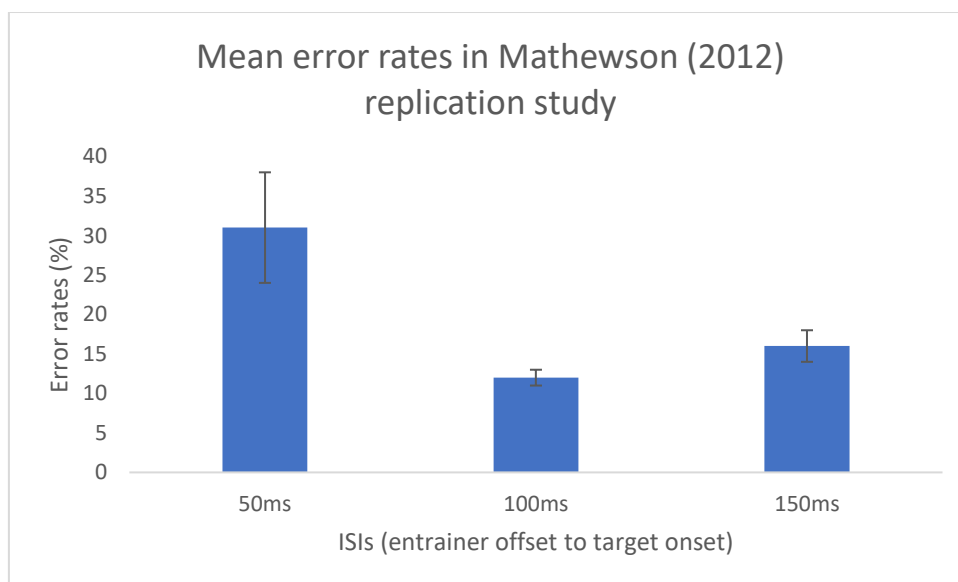


Figure 3.3 Mean error rates in the in-phase (100ms) and out of phase conditions (50ms, 150ms). Error bars represent 1 SE.

A repeated-measures ANOVA was conducted on the error rates. Mauchly's test indicated that the assumption of sphericity had been violated for the main effect of ISI, $\chi^{(2)} = 11.7$, $p < 0.05$. Therefore, degrees of freedom were corrected using Greenhouse-Geisser estimates of Sphericity ($\epsilon = 0.56$). The main effect of ISI was significant, $F(1, 9) = 5.57$, $p < 0.05$. In order to establish whether either out of phase (ISI50, ISI150) condition significantly differs from in-phase (ISI100) condition paired sample t-test was conducted on the two pairs: ISI50 vs ISI100 and ISI150 vs ISI100. The difference between ISI50 and ISI100 was significant ($t(9)=2.48$, $p<0.05$) but not that between ISI150 and ISI100 ($t(9)=-1.87$, $p>0.05$). Furthermore, mean D primes were calculated for all three ISI conditions: ISI50: 2.43, ISI100:2.45, ISI150:2.48 and were found to be higher than those reported by Mathewson et al., (2009), which ranged from ~0.9 to 1.8 (see: figure 2, p. 2727). This indicates that the current conditions provide a better signal-to-noise ratio than in the original study.

In conclusion, Mathewson's paradigm was replicated for ISI50 and ISI100 pair. People tend to be better in perceiving near threshold object if it is presented in phase (100ms) compared to out of phase (150ms). Furthermore, the version of the paradigm employed here achieved higher levels of sensitivity than in the original.

3.3 Experiment testing the influence of the spatial location of prime on target detectability

3.3.1 Aim and hypothesis

As proposed in the introduction to the chapter increased amplitude of alpha neural activity may limit information processing in the retinotopic locations associated with that processing (Herring et al., 2015; Klimesch, Sauseng, & Hanslmayr, 2007). That proposal has been tested at the interhemispheric scale, and it is accepted that externally entrained alpha in a given hemisphere limits perception in the contralateral hemifield and enhances perception in the ipsilateral hemifield (Marshall et al., 2015; Rihs et al., 2007; Romei et al., 2010; Thut & Miniussi, 2009). These results are in line with the alpha-inhibition hypothesis (Klimesch et al., 2007, 2012), which proposes that the high alpha amplitude induces an inhibitory effect

via interneurons that periodically limit information flow (see fig 1.4 case 2a,b, or fig 1 in (Klimesch, 2010)). This effect has been proposed to originate in retinotopically organised areas (Silver and Kastner, 2009) and so the current study assesses if inducing alpha in a spatially localised scale can create a localised inhibitory effect within the visual field of a single hemisphere. Thus, in this experiment, we selectively entrain parts of the visual field with alpha oscillations and measure how that intervention affects perception. To achieve this, a new paradigm was developed based upon that of Mathewson et al. (2012) and Spaak et al. (2014). In this new task flicker entrainment occurs in one of two conditions in which either a flickering white ring or circle stimuli (see fig. 3.4) entrains neurons representing a specific area of visual space (corresponding to either the target or mask locations). In this experiment a white entrainer, rather than the black entrainer used by Mathewson, was introduced because the target is black (and in 50% of cases in the same location as entrainer) and so using a black entrainer would make the target too difficult to distinguish from the priming sequence. This novel design allows us to directly compare the effects of stimulating target and mask locations and to examine the prediction that visual alpha rhythmic stimulation at a specific spatial location will selectively inhibit perception at that location and/or enhance perception in the neighbouring regions.

The current experiment hypothesises that perception will be reduced at time points in-phase with the presentation of the flicker prime. Critically, this will lead to an opposite time-course of target detection between the two conditions as this in-phase reduction can occur at the target locations (reducing target detection) or mask locations (reducing mask salience and hence increasing target detection). Thus, a single mechanism can resolve previously conflicting results (Mathewson et al., 2012; Spaak et al., 2014).

3.3.2 Method

3.3.2.1 Participants

Eleven participants (3 men) aged between 19 and 33 (mean=24, SD=5.15) were paid five pounds to take part for 40 minutes. All participants were right-handed, with correct or corrected vision and without a history of epilepsy and severe headaches. Participants received an appropriate introduction and debriefing

after the experimental procedure. The ethical approval was granted by the Brunel College of Health and Life Science Ethics Committee.

3.3.2.2 Stimuli, design, procedure

There were two conditions in the experiment defined by a difference in the entraining stimuli (see figure 3.4). The first condition comprised of white circle entrainer equal in dimensions to the mask, was followed by varying ISIs, target, ISI and mask. In the second condition only, the entrained area was different – the location of the target was entrained.

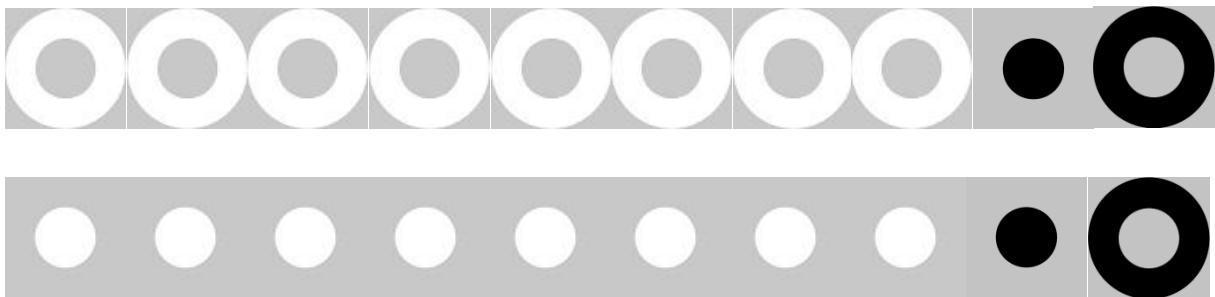


Figure 3.4 depicts the basic design of two conditions of the experiment, where entrainer (adjacent in upper image and superimposed in bottom image) with the target is followed (after variable ISI) by near threshold target and mask.

The first condition was analogous to Mathewson’s paradigm (Mathewson et al., 2012) in which a flicker entrainment ring had an external diameter of 2 degrees and a gap of 1 degree. The black target dot was 1 degree in diameter and was presented at the location of the entrainers gap. The stimuli differed from Mathewson’s in two ways. First, the entrainer ring was white (rather than black). Second, the target stimuli presented at one of two flanking locations (rather than centrally), which both had flickering entrainers (one at an alpha frequency and one jittered irregular flicker). The second condition was analogous to Spaak’s paradigm (Spaak et al., 2014) as entrainment was induced at the target location the target location using a 1-degree white dot (see fig. 3.4 lower panel).

A regular alpha flicker displaying one of the primes was at 10hz. It was followed by ISI, the target and the mask. The number of the trials was evenly balanced between both conditions. Other parameters were

as in the original experiment: four ISIs (ISI50, ISI100, ISI150, ISI200) and 40 preparation trials followed by four blocks (containing 250 trials each) (Mathewson et al., 2012).

After reading an information sheet and having the procedure was explained in detail individuals who agreed to participate signed a written consent form. Testing took place in a dimmed room. To acquaint the participant with the experimental task session, they were initially presented with 30 practice trials with easy to detect long duration targets (33 and 50ms). Next, the participant performed 40 trials with the experimental target detection displayed for the brief duration used in the main task (16.7ms). If the participant did not correctly detect 70% of the targets, the procedure was repeated. Feedback (auditory beep) was given after every incorrect trial during training but not during the main experiment.

The participant was seated ~57 cm in front of 22'' CRT screen (linearised) set to a 60Hz refresh. Each trial began with the centrally presented fixation cross (250ms). After 450ms of the fixation cross, a sequence of 8 entrainers was presented (white ring or white dot) for ~16.7ms followed by an interstimulus interval (ISI) of ~83ms. The final entrainer was followed in 80% of trials by a black target (16.7ms) after one of 5 ISIs (~50ms; ~100ms; ~150ms; 200ms) or by a blank screen (target absent condition). A further 50ms later the black masking ring appeared (~33ms). Participants had 1500ms from the onset of the target to respond by pressing a left button (target not present) or right button (target present). There were 50 catch (target absent) trials. Participants had a rest break for as long as they wanted between blocks. The participant was then debriefed and given an opportunity to ask questions.

3.3.3 Results

A two (entrainer type - mask area vs target area) by four (ISI) repeated-measures ANOVA was conducted on the error rates (table 3.2 and figure 3.5). Mauchly's test indicated that the assumption of sphericity had been violated for the main effect of ISI ($\chi^2(5)=11.46$, $p<0.05$) and for the interaction of entrainer type and ISI, ($\chi^2(5)=11.42$, $p<0.05$). So, degrees of freedom were corrected using the Greenhouse-Geiser. Error rates differed significantly across ISIs (main effect of ISI: $F(3, 30) =42.66$, $p<0.05$). Post-hoc t-tests indicated that all ISI pairs were significantly different: 50ISI-100ISI: $t(10)=10.5$, $p<0.05$); 100ISI-150ISI:

$t(10)=-3.5, p<0.05$; 50ISI-200ISI: $t(10)=11.9, p<0.05$; 150ISI-200ISI: $t(10)=4.9, p<0.05$, (see table 3.2).

There were no significant differences in the rate of errors for each type of entrainer, which indicates that the use of a white entrainer allowed people to clearly distinguish the target in both conditions (main effect of entrainer type: $F(1,10)=1.94, p>0.05$).

Table 3. 2 Describing the interstimulus interval (ISI), standard deviation (SD), standard error (SE) and error rate

Mask location entrainer:		Target location entrainer:	
ISI	Mean±SEM	ISI	Mean±SEM
50%	71% ±4.4	50%	51% ±3.6
100%	22% ±3.3	100%	27% ±4.2
150%	53% ±6.1	150%	35% ±7.7
200%	11% ±2.0	200%	28% ±3.0

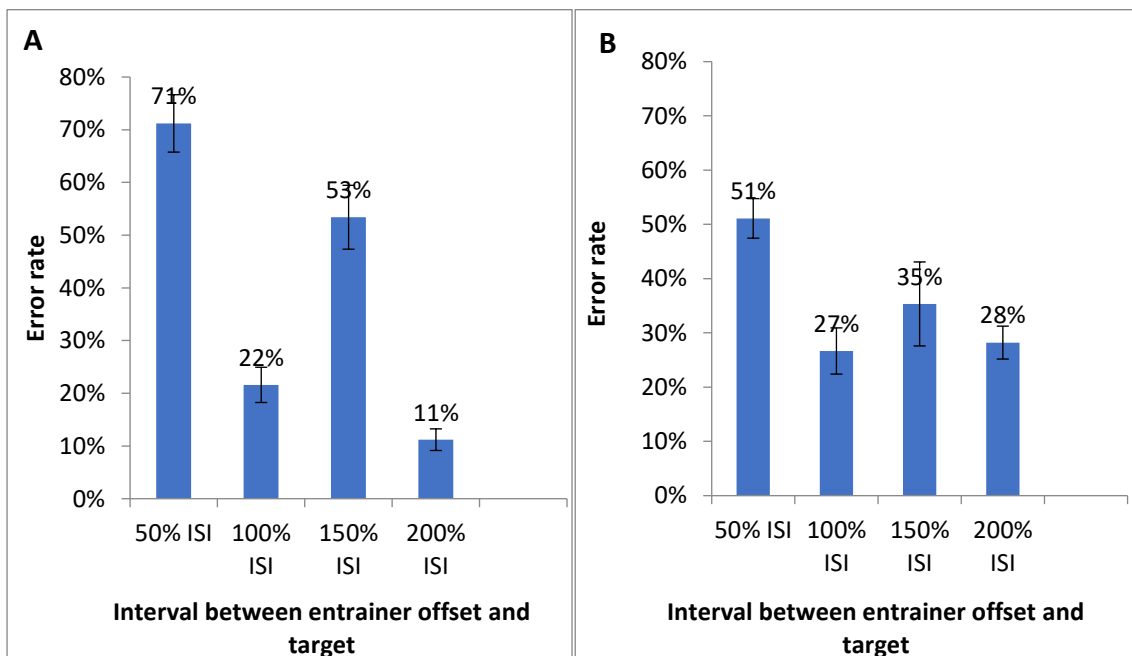


Figure 3.5 Percent of errors made in a) mask location entrainer condition (A) and target location entrainer condition (B).

As expected from the hypothesis, there was a significant interaction between the entrainer type and ISI, $F(2.07, 20.71)=9.40$, $p<0.05$, (see fig. 3.5). Post hoc tests indicated that the following pairs were significantly different for the above interaction: for ISI50 (mask/target): $t(10)=3.9$, $p<0.05$; for ISI100 (mask/target): $t(10)=-4.9$; for ISI150 (mask/target): $t(10)=1.9$; for ISI200 (mask/target): $t(10)=-4.5$. However, this effect appears to be due to differences in the magnitude of the effect in the target entrainment condition compared with the masked condition rather than the predicted reversal in the direction of the effect (expected in mask entrainer condition – less errors in phase than out of phase – achieved; expected in target condition – less errors out of phase than in phase – not achieved). This was supported by post hoc t-tests that revealed that for the target condition: average in-phase (ISI50 and ISI150) vs average out of phase (ISI100 and ISI200) ERs were significantly different, $t(10)=3.8$, $p<0.05$. Also, for the mask condition the average in-phase vs out-of-phase error rates were significantly different, $t(10)=7.1$, $p<0.05$. Thus, the same relationship between a target in- and out-of-phase ISIs existed in both entrainment conditions.

3.3.4 Discussion

Visual alpha rhythmic stimulation at a specific spatial location was hypothesised to inhibit perception in that location at time points out-of-phase with the stimulation. It was expected that varying the location of the entrainer would affect the performance depending on the phase where the target was placed. The reversal effect was expected between in and out of phase conditions for target and mask entrainer types. Varying entrainer location significantly affected the performance for in and out of phase conditions (interaction effect); however the expected reversal effect was not observed. It seems to be due to differences in the magnitude of the effect in the target entrainment condition compared with the masked condition rather than the predicted reversal in the direction of the effect.

Post hoc test shows that for both target and mask entrainer condition, people are significantly more accurate when the target is presented in phase than out of phase, which shows that the effect is

unidirectional for both entrainer types. Hence, the Mathewson et al., (2012) effect was replicated for both entrainer types, which was not expected for the target entrainer.

There might be several reasons for the absence of the reversal in the time course of the flicker entrainment effect. The problem might be caused by the target entrainer condition, which did not perform as expected. The differences in the Spaak paradigm (Spaak et al., 2014), which were not taken into consideration here, might be part of the problem. For instance, Spaak's original experiment presented targets laterally, and near-threshold targets were individually adjusted, so the mask was not necessary to be applied. Lateral target presentation in one of the two possible locations vs central presentation changes the level of spatial uncertainty of the target, which might result in neuronal dynamics changes, hence behaviour changes.

Also, alpha prime stimulated both target and surround location. On the other hand, a factor from Spaak et al. (2014) experiment - 10 Hz prime frequency, was applied in the current paradigm. That change seemingly did not modify the effect achieved by Mathewson who applied 12Hz prime, as we managed to replicate Mathewson paradigm with 10Hz prime.

In addition, people significantly varied in the level of accuracy depending on the phase, where in time the target was presented. It shows that the 10Hz prime is effective in modulating perception sensitivity in time (see fig. 3.5). Also it indicates that white, as much as black prime, drives alpha neuronal networks similarly facilitating perception, as a visual system is sensitive to change regardless of the colour of the stimuli (Tovee & Tovee, 1996).

In summary, although the error rates differed significantly across in and out of phase time points of the target presentation and despite that there was a significant interaction between the type of entrainer and interstimulus intervals, the expected reversal in results could not be confirmed. Hence, manipulation of the alpha prime spatial location and temporal location of the target does not produce reversal effect; hence Mathewson and Spaak results, can not be replicated by this paradigm.

A number of possible factors might influence the reversal effect between Mathewson's and Spaak's experiments. As it was incorporated in Spaak's, but not in Matheson's paradigm and it led into dramatically different levels of target's spatial uncertainty (SU), the possible effect of lateralisation

requires our spatial interest. Thus, the next section will focus on investigating SU phenomena and how visually induced alpha neuronal dynamics might influence perception of briefly presented targets.

3.4 Experiment testing spatial uncertainty

3.4.1 Introduction

The current experiment proposes to examine the role of alpha oscillations in coordinating the perception of targets when their spatial location is predictable (fixed) compared to when the location is uncertain. Participants performing the Mathewson et al., (2012) task maintained their attention on one central fixation point, where the prime, target and mask were presented. Thus, they could easily predict where the expected target might appear in space, i.e. the target has low spatial uncertainty (low SU), and their performance was best when the target was presented in phase with the alpha entrainer. In contrast in Spaak's et al., (2014) paradigm the target appeared randomly in one of two locations: on the left or the right of the screen, i.e. the target has high spatial uncertainty (high SU). Therefore, in that paradigm, the participants were not able to simply direct attentional resources to a single spatial location, but they had to divide their attention to monitor two possible locations. In contrary to Mathewson, in this paradigm, people had the best detection out of phase of entrained alpha oscillations.

Thus, in this experiment, we are proposing, that by manipulating the level of spatial uncertainty it is possible to replicate the different time course of Mathewson or Spaak' results. To achieve this, a new paradigm was designed based on the Mathewson task whilst presentation was based on the Spaak experiment. Initially, in one of the hemifields a 10Hz prime was presented, coupled with a scrambled prime in the second hemisphere. To manipulate the level of spatial uncertainty, in fifty per cent of cases a brief arrow cue was introduced towards the end of the prime to direct peoples' attention towards one hemifield. This was followed by a variable ISI, a target in one of the possible locations and the masks in both locations. Finally, participant had to record their answer by pressing one of two buttons whether the target was present, regardless of the site where it was detected (yes/no response).

The cueing idea was based on Posner's (1980) study, who suggested that a short lasting cue (about 100ms) reorients attention to its direction without the involvement of gazing (Landau & Fries, 2012; Mathewson, et al., 2012; Posner, 1980; Spaak et al., 2014). Participants have not been given any instructions regarding

the arrow appearance as the arrow influences the spatial attentional shift even without conscious awareness about its purpose (Posner, 1980).

This novel design allowed us to see whether different time delays between the entrainer and the target, as well as a manipulated level of spatial uncertainty (SU), significantly influence people's accuracy. It was hoped that this paradigm would allow us to replicate Spaak and Matheson results in one design by modifying a single variable – the spatial uncertainty.

The current experiment hypothesised that there is a mechanism which regulates human perception in two different ways depending on whether the salient object is spatially predicted, or not. Hence, whether that prediction allows attentional mechanisms to pre-allocate neuronal resources for the spatial location where a target is about to appear, or the target appears unexpectedly in one of two spatial locations without the same level resources allocated. We hypothesised that people would be better in detecting the target in high SU conditions, when it will arrive out of phase with alpha prime, and they would be better in detecting the target for low SU conditions when it will arrive in phase with alpha prime.

3.4.2 Methodology

3.4.2.1 Participants

Twenty-six participants (21 female) were recruited from the Brunel Psychology Participation Pool and other volunteering students from Brunel University (mean age 19.05, SD=1.05). The Brunel College of Health and Life Sciences Ethics Committee approved ethical procedures. Participants were informed of their rights to refuse participation and to withdraw from testing at any time without any consequences. They were also reassured that any information would be kept confidential. Consent from each participant was obtained before testing after any remaining questions were answered. All participants were also debriefed after testing and informed of the purpose of the study and were given the opportunity to ask clarifying questions. After the experiment, each participant was given the opportunity to ask questions and received debriefing form with the information about the background of the experiment and complaints procedure.

3.4.2.2 Stimuli

In the centre of the screen, the black fixation cross was presented throughout the entire experiment on a grey background (the same settings as in Mathewson preliminary experiment). Two sequences of entraining stimuli rings (2 degrees in diameter with a one-degree centre) were located horizontally and eccentrically (3 degrees either side of the fixation cross). The top edge of each entrainer was on a horizontal level with the top of the fixation cross, precisely how Spaak and colleagues (2014) located entrainers. The target (presented after the prime at variable ISIs) was a black 1-degree circle which aligned with a central gap of one of the primes (see fig. 3.8).

3.4.2.3 Design

The experiment had four independent variables

1. Interstimulus interval (ISI) between the onset of the last entrainer and the onset of the target on three levels.
2. Location of the entrainer: left or right side of the hemifield – 50% cases each.
3. Location of the target: the left or right side of the hemifield
4. Arrow pointing: left, right or no arrow (catch trials)

Though our primary interest here is the investigation of the differences between conditions with a high and low level of spatial uncertainty respectively: non-arrow conditions (high SU) and congruent arrow with target conditions (low SU). The non-congruent arrow condition was added to counterbalance the experimental design but does not play any significant role in the hypothesis. The experiment consists of 36 conditions, which are outlined in table 3.3 which are made of six conditions, which constitute the main building blocks of the experiment (figure 3.6). Three different ISIs precedes each of the six conditions and followed by the target (75%) or non-target conditions (25%) with all conditions presented to both hemifields (6x3x2x2).

Table 3. 3 Condition, entrainer, position, target type, arrow presence and ISI

Condition	Entrainer position: left, right	Target position left, right	Arrow presence	ISI
1	L. entrainer	L. target	No arrow	50ms
2	L. entrainer	R. target	No arrow	50ms
3	R. entrainer	R. target	No arrow	50ms
4	R. entrainer	L. Target	No arrow	50ms
5	L. entrainer	L. target	No arrow	100ms
6	L. entrainer	R. target	No arrow	100ms
7	R. entrainer	R. target	No arrow	100ms
8	R. entrainer	L. Target	No arrow	100ms
9	L. entrainer	L. target	No arrow	150ms
10	L. entrainer	R. target	No arrow	150ms
11	R. entrainer	R. target	No arrow	150ms
12	R. entrainer	L. Target	No arrow	150ms
13	L. entrainer	L. target	Left arrow	50ms
14	L. entrainer	R. target	Left arrow	50ms
15	R. entrainer	R. target	Left arrow	50ms
16	R. entrainer	L. Target	Left arrow	50ms
17	L. entrainer	L. target	Left arrow	100ms
18	L. entrainer	R. target	Left arrow	100ms
19	R. entrainer	R. target	Left arrow	100ms
20	R. entrainer	L. Target	Left arrow	100ms
21	L. entrainer	L. target	Left arrow	150ms
22	L. entrainer	R. target	Left arrow	150ms
23	R. entrainer	R. target	Left arrow	150ms
24	R. entrainer	L. Target	Left arrow	150ms
25	L. entrainer	L. target	Right arrow	50ms
26	L. entrainer	R. target	Right arrow	50ms
27	R. entrainer	R. target	Right arrow	50ms
28	R. entrainer	L. Target	Right arrow	50ms
29	L. entrainer	L. target	Right arrow	100ms
30	L. entrainer	R. target	Right arrow	100ms
31	R. entrainer	R. target	Right arrow	100ms
32	R. entrainer	L. Target	Right arrow	100ms
33	L. entrainer	L. target	Right arrow	150ms
34	L. entrainer	R. target	Right arrow	150ms
35	R. entrainer	R. target	Right arrow	150ms
36	R. entrainer	L. Target	Right arrow	150ms

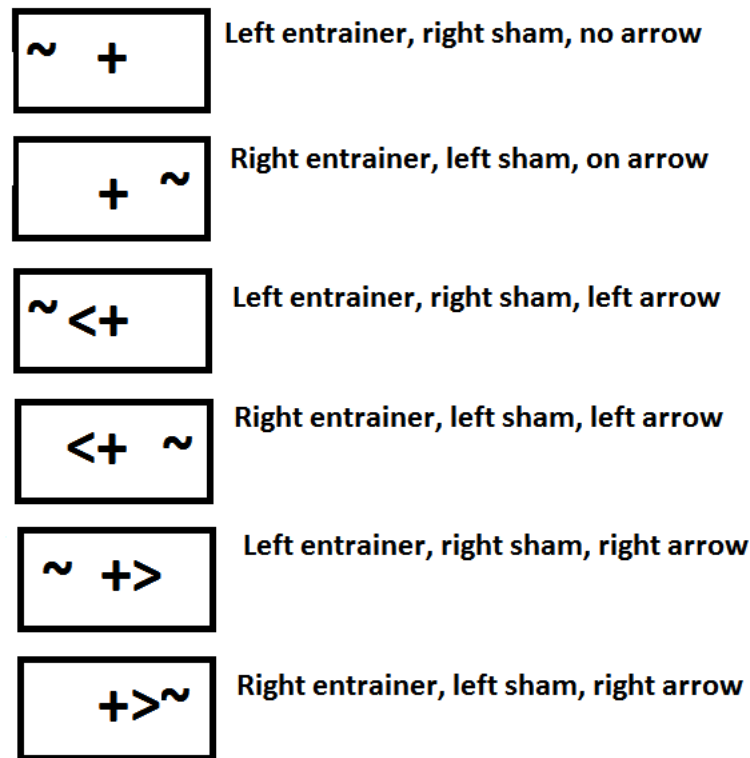


Figure 3.6 Illustration of the basic building blocks of the experiment. One of the three ISIs accompanies each of the conditions and followed by target present or absent condition. ‘~’ regular entrainer present side; ‘+’ fixation cross; ‘<’ ‘>’ arrows.

3.4.2.4 Procedure

All testing was performed in a dimmed room. The program was implemented in DMDX Display Software. The same hardware as in the previous experiment was used. Initially, each person was asked to read the study information sheet, the experimenter explained in detail of the task, the participant asked any clarifying questions and gave written consent for participation.

The participant sat 57 from the screen and pressed spacebar to instigate the training session. After the training, the experimental session was instigated. The testing session took about 45 minutes with breaks incorporated into the procedure, therefore after the break to continue the participant had to press the spacebar when rested and was ready for another part of the session. Participants kept their eyes on the fixation cross thought the whole experiment, also they were asked to spread their attention on both

possible target locations. Subsequently after eight regular in one hemifield, and eight irregulars in the opposite hemifield flashes of the black annuli, the target appeared randomly either on the left or right side, which adjoins the internal diameter of the entrainer.

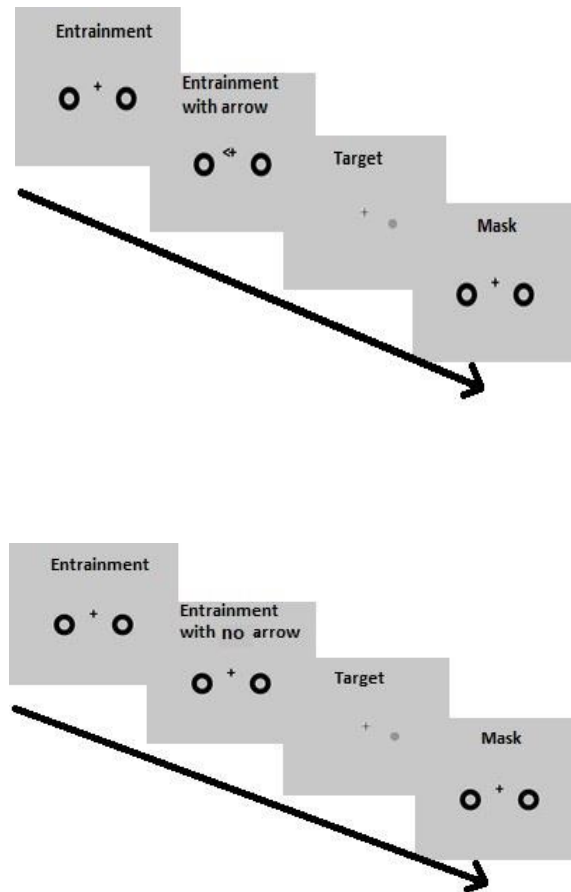


Figure 3.7 Experimental design. In entrainment phase one annulus flickers randomly, second with regular intervals (10Hz); 150ms prior the last entrainer left, right or no arrow appears in equal proportions; in the target, phase left or right near threshold (16.7ms) target appears which is subsequently masked by two annuli. Left figure low SU, right figure high SU condition.

The experimental timeline is presented in figure 3.7. Each trial began with ~250ms centrally presented fixation cross and ~450ms blank screen, followed by two flashing sequences of 10 entrainers either side of fixation. One entrainer sequence followed a regular 10hz rhythm, and the other was irregular such that timing of all but the first and last entrainers were jittered (see figure 3.8). In 50% of trials 100ms before the offset of the entrainer an arrow appeared point left or right (low SU condition), and in the other 50%

trial, no arrow was presented (Posner, 1980). The arrow was removed with the offset of the priming sequence. Each participant had been informed that sometimes the arrow would appear next to the cross, but its direction is entirely random, and it does not provide any information regarding the location of the target, which was also random.

The subject's task was to indicate whether a circular target had been presented irrespective of whether it was on the left or right of fixation. In target present conditions (80% of trials) it was presented randomly on the left or the right (with 50% probability each) for ~16.7ms. Targets were presented at three ISIs (50, 100 and 150ms). Masking stimuli were presented ~50ms after the target offset (or at the equivalent time point in the target absent conditions) on both sides of the screen.

Participant had ~1500ms from the onset of the target to indicate whether the target was present regardless of its location by pressing one of the two colour coded buttons – left arrow blue - present, right arrow yellow - absent. The buttons were not counterbalanced and they were not counterbalanced across all the experiments in this thesis.

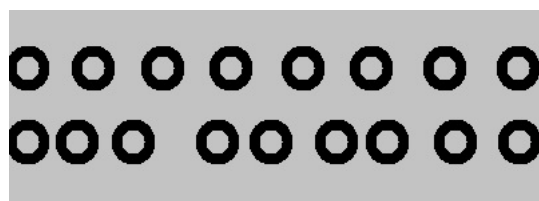


Figure 3. 8 Regular (top) and irregular flicker (bottom). Intervals between regular are constant, intervals between irregular vary, however, the mean of the intervals is equal to the regular interval timing. The same number of primes in both conditions controlled.

Each of the 36 conditions was repeated 30 times (1080 trials) for target present and 10 times with the target absent (360 trials). The experiment it was divided into six equal blocks and participants could rest between blocks until they pressed the continue 'button'. Participants were informed they could take a break as long as required.

3.4.2.5 Data analysis

All trials with RTs slower than 100ms and faster than 1500ms were excluded, as that rule was applied across all experiments in this chapter and chapter four. The percentage of correctly detected targets was calculated for each participant in each condition. Previous research (Spaak et al., 2014) did not report lateralisation effects, however initially results were calculated with lateralisation as an IV. As we did not find any lateralisation effect, the non-lateralised results were reported. Therefore, the experiment analysis involved 18 conditions collated from 36. Thirty-six conditions – (see table 3.3), were presented in the experiment. Each condition presented to the left hemifield has its mirror pair presented to the right hemifield. In order to simplify the analysis and respect lack of lateralisation effect in our and in the original Spaak et al (2014) experiment, the left and right mirror conditions were combined together, hence 18 final conditions taken to the further analysis. The lateralised trials were collated into congruent and incongruent trials as presented in the table below (table 3.4).

Table 3. 4 Collated conditions where lateralisation is disregarded.

1	No arrow	50ms	Entrainer at the target location
2	No arrow	100ms	Entrainer at the target location
3	No arrow	150ms	Entrainer at the target location
4	No arrow	50ms	Entrainer at opposite to target location
5	No arrow	100ms	Entrainer at opposite to target location
6	No arrow	150ms	Entrainer at opposite to target location
7	Arrow - target congruent	50ms	Entrainer at target location
8	Arrow - target congruent	100ms	Entrainer at target location
9	Arrow - target congruent	150ms	Entrainer at target location
10	Arrow - target congruent	50ms	Entrainer at opposite to target location
11	Arrow - target congruent	100ms	Entrainer at opposite to target location
12	Arrow - target congruent	150ms	Entrainer at opposite to target location
13	Arrow - target incongruent	50ms	Entrainer at target location
14	Arrow - target incongruent	100ms	Entrainer at target location
15	Arrow - target incongruent	150ms	Entrainer at target location
16	Arrow - target incongruent	50ms	Entrainer at opposite to target location
17	Arrow - target incongruent	100ms	Entrainer at opposite to target location
18	Arrow - target incongruent	150ms	Entrainer at opposite to target location

The purpose of the experiment was to primarily explore mechanisms underlying different alpha phase roles between Mathewson and Spaak paradigms (Mathewson et al., 2012; Spaak et al., 2014). In more detail, the level of spatial uncertainty was investigated. Thus, the conditions which varied in the level of spatial uncertainty were taken into further analysis. Firstly, the three ISI conditions without arrow cueing and with the target congruent with the prime followed the logic of Spaak's paradigm (high level of spatial uncertainty). Secondly, the three ISI conditions with arrow direction congruent with the target and the entrainer followed the logic of Mathewson's study (low level of spatial uncertainty). The brief appearance of the arrow pointing at target location prior that target onset shifts the attentional resources towards that location, increasing the likelihood of observing mostly that particular location (Posner, 1980). Moreover, they were taken into further analysis. ISIs (~50ms, ~100ms, ~150ms) represented 50%, 100% and 150% of the phase delay after onset of the last entrainment.

3.4.3 Results

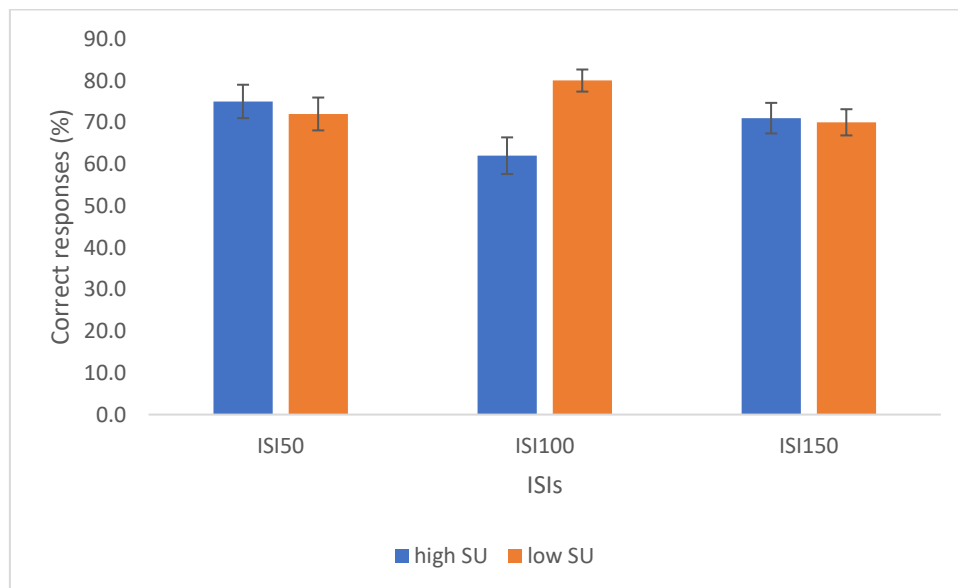


Figure 3.9 Mean percentage of correct responses for high and low SU in ISI50, ISI100 and ISI150 timepoints from the last entrainer onset

A two (high, low uncertainty) by three (ISIs) repeated-measures analysis of variance (ANOVA) was conducted on accuracy, in order to compare the error rate effect directly, between three ISIs in the only target present, high uncertainty condition (see fig. 3.9).

The main effect of ISI was not significant $F(1, 28)=0.41$ $p>0.05$. So, while ignoring spatial uncertainty, there is lack of significant differences in the proportion of correct responses between three ISIs. Also, the main effect of spatial uncertainty was not significant $F(1, 28)=1.476$, $p>0.05$. So, while ignoring other variables there was lack of significant differences in hit rate between high and low spatial uncertainty conditions. However, crucially the interaction between both was significant. $F(2, 56)= 12.248$, $p<.05$. The targets presented in phase (ISI100) in high SU condition were more likely to be omitted compared to out of phase (ISI50 and ISI150 collated) presentation times in the high SU condition (see post-hoc statistics below)

On the other hand, in the congruent arrow condition (low SU), the targets presented in phase (ISI100) were more likely to be perceived comparing to out of phase low SU condition (Figure 3.10) (see post-hoc statistics below). As the interaction between ISI and SU is significant, it would be interesting to see whether differences for congruent and incongruent trials between both high SU and low SU are significant. Hence posthoc tests were conducted to test the differences for high and low SU between all out of phase and in phase conditions. Post-hoc test indicated that the differences are significant between in and out of phase (for out of phase: ISI50 and ISI150 collated) for high SU conditions $t(28)=3.89$ $p<0.05$ (mean difference=1.09) and also low SU conditions, $t(28)=4.09$ $p<0.05$, (mean difference= -1.04).

In conclusion, there was a lack of significant effect on the type of the attentional shifter used while ignoring ISI. Also, there was a lack of significant effect of the type of the ISI used while ignoring attentional shifter type. However, there was a significant interaction between these two variables. Hence, in and out of phase differences were significantly different between high and low spatial uncertainty conditions.

3.4.4 Discussion

As discussed in chapter one and the introduction to chapter four, there is a body of research which suggests that perception is a non-continuous phenomenon and that alpha phase might participate in organising perception in a discrete fashion (Milton & Pleydell-Pearce, 2016; VanRullen, 2016; VanRullen & Koch, 2003; Wutz et al., 2014). There is also a body of research that argues that a specific phase of alpha is optimal for processing that discrete perception (Busch et al., 2009a; Kawaguchi et al., 1993; Peter Lakatos et al., 2008; Mathewson, et al., 2012; Spaak et al., 2014). However, there is a discrepancy in the literature which phase of alpha oscillation is optimal for the perception. Perhaps, because of the differences in design between the studies, they might trigger the most optimal perceptual snapshotting in various stages of the alpha phase. This study attempted to resolve that discrepancy between Mathewson and Spaak paradigms and managed to find a factor (spatial uncertainty) that by modifying replicates one or the other study.

Results of this study have shown that modifying the level of SU influences differently the detection rate of targets presented in and out of phase of entrained alpha oscillations. Explicitly, in a low uncertainty condition, where an arrow guided attention towards the location of the target, the optimal perception of the target was in phase with entrained mid- alpha oscillations. On the other hand, in a high uncertainty condition, (no arrow), the optimal perception of the target was found to be out of phase with entrained mid alpha oscillations. The interaction between both independent variables (ISI – three levels, level of SU– two levels) was significant which suggests that both: ISIs and level of SU (driven by the introduction of the arrow, also called the attentional shifter (Posner, 1980), significantly influence performance. Thus, it seems that both independent variables together significantly influenced the accuracy of detecting a briefly presented target.

The behavioural results achieved in this study raise questions about the neuronal dynamics causing these differences and subsequently underpinning neuronal mechanisms regulating perception and attention. Someone might speculate that alpha-led neuronal mechanisms employ both low and high energy phase (peak and trough) for snapshotting information from the external environment; with the difference that,

high energy alpha phase (peak) may snapshot stimuli from the spatial location where our attentional resources are pre-directed and allocated.

Also, it is possible that targets whose place in space are highly predicted, might employ more local perception. On the other hand, targets which can be scattered in more extensive visual space might drive global perception, which crucially has consequences in neuronal dynamics (Martens & Hübner, 2013; Navon, 1977). However, this study does not focus on global/local perception problem. The above results only open a new avenue for possible research which would investigate the role of alpha neuronal dynamics in perceiving local and global features in high vs low spatial uncertainty conditions.

Top-down and bottom-up alpha phase neuronal dynamics might also possibly explain the above results; as Kawaguchi et al., (1993) suggested, alpha oscillations which are detected by EEG originate from more than one source. The authors proposed that there are two sets of two dominant cortical alpha networks which propagate in opposite directions: anterior-posterior, top-down and posterior-anterior, bottom-up. It can be argued that low SU tasks drive mainly bottom-up alpha networks as they are more purely perceptual. On the other hand, high SU tasks might drive stronger top-down alpha neuronal communication as they involve more active visual space search (Hwang, Higgins, & Pomplun, 2009). Both top-down and bottom-up alpha networks are characterised by a phase shift between them (Kawaguchi et al., 1993). Hence, low and the phase shift might also characterise high SU tasks. This idea will be examined by observing neuronal fingerprints of behavioural effects in chapter five.

After phase, alpha amplitude is also a candidate that might be involved in the perceptual and attentional mechanisms employed in the current study. It is widely accepted that low alpha amplitude is observed in the neuronal representation of spatial locations where the subject predicts the stimuli to arrive, where the information is expected to be processed (Ming & Fu et al., 2001; Keitel, Quigley, & Ruhnau, 2014; Milton & Pleydell-Pearce, 2016) This is in line with ITH by Klimesch et al., (2007) and also with the research by Romei et al., (2010) They reported that actively stimulating alpha power in the occipital lobe in one hemisphere using TMS, improved detection rates for stimuli reaching the opposing hemisphere. It adds to the argument that amplitude dynamics play a crucial role in gating, shifting and concentrating cognitive

resources, and consequently, in narrowing and enhancing attention to a specific visual/spatial and also temporal location of the target.

Thus, someone could suggest that when information is snapshotted from predictable spatial location, which is most robust in the alpha peak phase, the alpha amplitude in that neuronal representation is low.

By analogy, if the subject does not predict that a target might appear in a particular spatial location, the level of alpha amplitude in their corresponding neuronal representation might be higher compared to the previous scenario. Subsequently, if the participant is not pre-guided to the left or right possible target locations, neuronal networks must evenly gate (share neuronal resources for) both possible locations, hence theoretically low alpha amplitude should occur in both hemispheres, which might be difficult, as the purpose of gating is to allocate scarce neuronal resources in as focused as possible visual space. Hence, allocating resources in several locations simultaneously might be challenging. Therefore, when monitoring more extensive visual space, gating alpha mechanisms might be not as effective as in the low SU scenario (where low alpha amplitude gates perception in a specific single visual location). So, perception in the high SU scenario could be processed by networks flooded by higher alpha amplitude compared to low SU situation. In high SU scenario mechanisms described in the GBI (gating by inhibition) hypothesis (Jensen & Mazaheri, 2010) might take place – high perceptual sensitivity occurs in the low energetic phase of alpha – the trough.

Hence, when we bring amplitude and phase concepts together, they both might behave differently, depending on the level of SU. For low SU conditions the target optimal time window may be in phase and low alpha amplitude; on the other hand, for high SU conditions, the target optimal time window may be out of phase and higher than the previous cases alpha amplitude. It is likely that both mechanisms: phase-controlled information snapshotting and alpha amplitude could be interlinked. However, the author of this thesis has not found relevant research which investigated both mechanisms simultaneously in this context. Hence this argument is based only on theoretical divagations (Hanslmayr et al., 2011; Jensen & Mazaheri, 2010; Klimesch et al., 2007; Mathewson et al., 2012; Spaak et al., 2014; Zumer, Scheeringa, Schoffelen, Norris, & Jensen, 2014).

Also, it is clear that an alpha prime entrains (probably increases) alpha amplitude in the neuronal representations where it is applied. Hence, in the current study, it might distort information gating, by interfering with low alpha amplitude in neuronal representations where the prime is applied. However, the results in this study are significant, thus it is likely that neuronal gating mechanisms are overpowering amplitude modifications introduced by external flicker.

In summary, this study showed that the level of SU influences phase is optimal for the discrete perception of the target. Hence, alpha oscillations might regulate the information flow differently for the object where attention was pre-allocated and for the object which appears unexpectedly somewhere in the visual field, or at least in two possible locations. Different concepts such as ITH and GBI were presented here as possible mechanisms co-facilitating neuronal dynamics in both high and low SU conditions. Also, possible dominance of top-down alpha networks in high SU and bottom-up in low SU conditions was proposed. This idea will be tested in the next chapter.

Chapter 4

4.1 Introduction

In the previous chapter, a behavioural investigation examined how the level of spatial uncertainty during mid-alpha (10 Hz) visual entrainment modified the probability of NTT (near threshold target) detection at two-time points: in phase or out of phase with the visual entrainment. In the high uncertainty condition, where the participant is not pre-guided to the single location, people are more likely to spot the NTT when it occurs at a time point that is out of phase with visual entrainment. However, in the low uncertainty condition, where a brief arrow guides attention towards one location, people are most likely to detect the NTT when it is presented at a time point that is in phase with visual entrainment. The experiment in the current chapter attempts to identify significant modifications in neuronal dynamics between these conditions.

In other words, it is plausible that if the NTT detection rate varies depending on whether it is presented in or out of phase of the alpha prime, and whether the subject's attention is directed towards the location of that target or is not indicated in any way, that a perceptual sampling mechanism served by alpha oscillations might be different for both conditions; this will be tested in the following EEG experiment.

It is increasingly accepted that perception may be considered a discrete phenomenon (Milton & Pleydell-Pearce, 2016; 2017; Neuling, Rach, Wagner, Wolters, & Herrmann, 2012; VanRullen, 2016; Wutz, Weisz, Braun, & Melcher, 2014), but there is a lack of consistency in the literature which phase position within alpha band frequency is optimal for visual detection and what neuronal mechanisms lie behind it (Busch et al., 2009b; Mathewson et al., 2012; Spaak et al., 2014). It is possible that the relationship between perceptual sampling and EEG alpha is more complicated than currently understood. The differences in the level of spatial uncertainty between the Mathewson et al., (2012) and Spaak et al., (2014) studies may trigger different neuronal mechanisms which produce the different behavioural outcomes. Thus, considering behavioural results from the previous chapter and the research which led to that investigation, it would be beneficial to examine the neuronal dynamics of that successful behavioural manipulation to clarify possible mechanisms behind this discrepancy.

The critical question is whether the alpha phase is in the minimum state when people are successful in detecting spatially uncertain targets. On the other hand, is the alpha phase in the maximum state when people are successful in detecting spatially specific (arrow indicated) targets (fig. 4.1). In the top part of the figure (low spatial uncertainty (LSU) as in Mathewson et al., (2012) experiment), the target was most likely to be perceived when in phase with alpha entrainer; and in this task the spatial uncertainty was low – the target always appeared in one location. In the second scenario - the bottom part of figure 4.1 (high spatial uncertainty-HSU, as in Spaak et al., (2014) experiment), the target was most likely to be spotted when out of phase with the ongoing alpha visual entrainment; and in this task the spatial uncertainty (SU) was high – the target randomly appeared in one of two separate locations.

These two scenarios vary in their reliance on top-down and bottom-up attentional processing mechanisms. Specifically, if the target is searched for in more than one expected location top-down mechanisms may be actively involved in guiding that search. In contrast, when an arrow directs attention to a specific hemifield, bottom-up perceptual mechanisms could dominate. Importantly, the balance between top-down and bottom-up mechanisms may be manifested in alpha phase dynamics on the anterior-posterior axis. Already, Inouye, Shinosaki, & Yagasaki, (1983) has proposed that alpha phase propagates simultaneously in top-down and bottom-up directions, although in their experiment top-down phase propagation dominated (probably determined by that non-perceptual task employed). More recently, Fries and Maris (2015), Fries, & van Ede, (2016) argued that simultaneous anterior-posterior and posterior-anterior alpha phase dynamics represents accordingly top-down and bottom-up controlled cognitive and perceptual processes.

Hence, in high SU tasks, top-down alpha dynamics might dominate. In contrary, in low SU tasks, bottom-up alpha dynamics might be prevalent. Therefore, it can be hypothesised that in the first case on average top-down alpha phase direction should be observed, and in the latter case on average the bottom-up alpha phase direction should dominate.

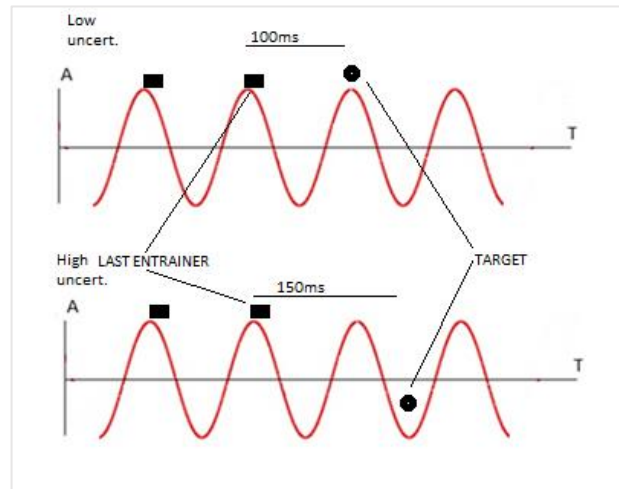


Figure 4.1 illustrates the possible alpha phase bucket for high detection rate in low uncertainty (as in Mathewson’s experiment) and high uncertainty (as in Spaak’s experiment).

The research supports the idea that alpha power peak might differ along the anterior-posterior axis by Kawaguchi et al., (1993) and Herrmann, (2001). Both studies were based on photic driving. The former study used 5-16Hz stimulation, the latter 1-100Hz photic driving. Kawaguchi et al., (1993) suggest that phase within alpha frequency band shifts by about 180 degrees (half a cycle) between occipito-frontal recordings and is also shifted between occipito-central recordings in each hemisphere. Although Kawaguchi et al., (1993) noted that their findings suggest a large variation in the phase relationships and that the photic driving response is not a fixed phenomenon.

What is not consistent in the literature is the direction in which the alpha phase travels. Kawaguchi et al. (1993), Herrmann (2001), Walter, Rhodes, Brown, & Adey, (1966), Nunez, (1974), suggest the posterior-anterior direction of the alpha signal propagation dominance. However, some authors suggest anterior-posterior direction: Shaw & McLachlan, (1968) Suzuki, (1974), or both directions: Cooper & Mundy-Castle, (1960), Pocock, (1980). Additionally, Inouye et al., (1983) suggested that alpha oscillations travel differently in the dominant and non-dominant hemisphere. Namely, in the dominant hemisphere:

anterior-posterior direction and in the non-dominant: posterior-anterior direction. In their results, they observed that in 60% of cases there is posterior-anterior alpha phase propagation when participants are resting.

In addition to the above discussion on the anterior-posterior axis alpha phase dynamics, Keitel, Thut, & Gross, (2017) emphasise that the level of stimulus locking to the EEG signal depends on the level of spatial attention allocation. Grand-average spectra showed greater cross-coherence (XCOH) when stimuli were attended vs unattended. It shows that allocating attention to a specific stimulus influences phase dynamics within the alpha band which processes that stimulus (Christian Keitel et al., 2017).

In the light what has been discussed above, it is interesting to investigate further alpha power dynamics (peak latency) after the target onset for:

1. Low spatial uncertainty (replicating Mathewson' results) and 100ISI-in phase
2. High spatial uncertainty (replicating Spaaks' results) and 150ISI-out of phase

Also, it might be expected to observe within the alpha spectrum, power phase shifts of peak latency of evoked alpha on the anterior-posterior axis. Namely a dominating, anterior-posterior phase direction would be expected in more top-down, high spatial uncertainty condition. On the other hand, dominating posterior-anterior phase direction would be expected in more bottom-up low spatial uncertainty.

In addition, despite the fact that Spaak et al., (2014) did not find any lateralised behavioural effects; as a good practice, it was decided to see if there were any lateralised behavioural effects (see section 4.4.2). Hence, the behavioural prediction in this experiment is as follows: manipulating inter-stimulus interval (on two levels: in phase - 100, and out of phase - 150) and presence or absence of the cue (an arrow pointing at the same direction as alpha entrainer and near-threshold target, or no arrow) would significantly modify accuracy level in perceiving near threshold target and that the effects of these variables on accuracy would be significantly different for stimuli originating from the **left** and the **right** hemifield.

4.2 Methods

4.2.1 Participants

Twenty-four subjects (7 male, age range, 18- 29 years, mean age:23.7+-3.8) with no history of epilepsy among them and their family members (based on self-report) participated in this experiment. All participants were recruited on voluntary bases and were paid only for their time dedicated seven pounds/h. All subjects gave written informed consent according to the Declaration of Helsinki. The study was approved by the Brunel University Ethics Committee (appendix no 4.1). Data for two subjects had to be excluded because of the recording error, and two subjects decided to terminate the participation in the experiment before the recording was initiated, so the analysis is based on the remaining 20 participants.

4.2.2 Materials and Design

The experiment was designed precisely in the same way as the behavioural experiment (chapter 3). However, it was implemented using different software - MATLAB 2015 with Psychtoolbox-3. The software was changed from DMDX 1.2 to MATLAB 2015 because only MATLAB could send initiation pulse and timestamps pulses reliably from the stimuli presentation computer to the EEG recording computer. That data was needed later to create epochs and identify the onset of the target as a point of reference for identifying two consecutive alpha power extrema latencies (peaks and troughs). The troughs represent times that the aggregate alpha waveform is close to zero and if the peak shifts, the trough should move too. The translation from power peak into a phase measurement is inherently ambiguous (see fig. 4.2).

All analysis is based on experimental trials (36 conditions x 45 trials). All testing was performed in a dimmed EEG laboratory, CRT set to 60Hz monitor Electron 22" Blue. The appropriately assigned keyboard was used for responding. The subject was sited in a magnetically shielded cage at the controlled distance 57 cm from the projection screen.

4.2.3 Procedure

The task was virtually identical to the previous study with the addition of EEG recording, and only two levels of ISI were applied (100% and 150% of the prime timing). Each participant was invited into the dimmed EEG lab at Brunel University. Participant received a full explanation, received information sheet, and subsequently, EEG cap (64 electrodes) was adjusted, electrodes were connected with the scalp using conductive gel (NeuroMedical Supplies, Quick Gel, Compumedics); the electric resistance of each electrode was tested and eventually adjusted before the experiment.

The participant was asked to sit in front of the monitor and the rest of the procedure except initiating EEG recording, was the same as in the previous – behavioural experiment. When the experiment was finished, the cap was removed, shampoo and towel was offered, and full debriefing was provided.

To acquaint the participant with the experimental task session, he/she was initially presented with 30 practice trials with easy to detect targets. Next, the participant had to do 40 trials with the experimental target detection threshold (16.7ms). If the participant did not detect correctly 70% of the targets, the procedure was repeated. Finally, the participant was asked to do the main experiment - the 1620 (36 conditions x 45 trials) conditions experimental trials. Each participant, when tired, could take breaks. The length and its frequency were controlled by the participant depending on his/her cognitive abilities. However, it was indicated that more prolonged and more frequent breaks would extend the experimental session. Participants were asked to keep eyes focused on centrally positioned fixation cross and spread attention to both possible locations, where the target might appear.

4.2.4 Neuroimaging - methods

In order to observe the neuronal dynamics, underlying the behavioural differences reported above electroencephalography was conducted with event-related time-frequency evoked band power analysis. EEG data was recorded with timestamps acquired from the experiment displaying computer. Raw EEG was recorded using a 64 channels system (Compumedics NeuroScan). Each participant was briefed about the procedure and signed consent after reading the information sheet. Subsequently, EEG cap was placed, and its position was adjusted in a way that electrode CZ was located $\frac{1}{2}$ of distance between the occipital

protuberance and nasal bridge. Each electrode was filled with conductive gel (Quick-Gel, Compumedics Neuromedical Suppliers), at the same time avoiding cross electrode shortcuts. Subsequently, the cap was attached to the amplifier and resistance of each electrode was tested and adjusted. Throughout the experiment, the EEG was recorded at a sampling rate of 250kHz using a Neuroscan 64 channel systems, Scan 4.4 and Curry 5 software.

4.2.4.1 Pre-processing

The preprocessing involved the following stages:

- 1) Acquisition of EEG time series at 1000Hz using 64 channel quick cap and Neuroscan Synamps2 recording system. Timestamps (event markers) generated by Matlab script on the separate machine and sent via parallel port to the Neuroscan Synaps2 computer.
- 2) DC correction of EEG time series
- 3) Filtering of EEG time series (probably 0.1 to 30 Hz bandpass, no phase shift).
- 4) Ocular artefact reduction using a PCA method
- 5) Generation of event files (.ev2)
- 6) Epoching (state onset and offset of epoch) to generate .eeg files for each experimental condition and each participant.
- 7) Baseline correction of '.eeg' files
- 8) Marking of bad channels
- 9) Artefact removal for amplitudes greater than 100 microvolts plus or minus
- 10) Generation of individual average data per participant - event-related bandpower (state settings). GFP reference, selecting trials with correct behavioural target detection, filtering event-related alpha band power 9.5 Hz – 10,5Hz
- 11) Measurement of peaks (peak detection latency) in two 100ms time windows form the target onset

The first level analysis produced cleaned EEG files for each condition for each participant. The second level procedure was conducted across subjects and involved analysis of group data in regions of interest. group analysis (mean and standard deviation for each condition of interest across all participants), conditions of interest – ANOVA.

The event-related spectral power (narrow band-power 9.5-10.5Hz) was calculated using the event-related band power transformation in Scan 3.4 (Compumedics Neuroscan). It provides a measurement of event-related (target onset) mid-alpha synchronisations and desynchronizations. The calculation is based on computing the power spectrum over a sliding latency window and subsequently calculating averages across correct trials within the single condition. From the point of reference – the onset of the target, two alpha band peaks and two troughs were identified by allocating their latencies. (Delorme & Makeig, 2004). Two (one peak and one trough) were marked in the time window 50 -150ms after target onset (Max1, Min1); and two 150-200ms after the target onset (Max2, Min2).

4.2.4.2. Design and analysis of group EEG data.

Afterwards, as a preliminary observation, the graphical representation of alpha power peak latencies was produced for all electrodes for max1 min1 (50ms-150ms latency window) max2 (see fig. 4.2), min2 (150-250 latency window) to identify possible patterns in neuronal activity. As expected, it can be seen that latencies for Max1 and Min1 cluster around 100ms and Max2 and Min2 cluster around 200ms. As there are potentially a considerable number of possible ways to analyse this dataset, the following comparisons were pre-selected which represented the main differences between the studies of Mathewson et al., (2012) and Spaak et al., (2014):

1. Entrainment left, target presented in phase with entrainer (100), target left; high spatial uncertainty
2. Entrainment right, target presented in phase with entrainer (100), target right; high spatial uncertainty
3. Entrainment left, target presented out of phase with entrainer (150), target left; high spatial uncertainty

4. Entrainer right, target presented out of phase with entrainer (150), target right; high spatial uncertainty
5. Entrainer left, arrow left, target presented in phase with the entrainer (100), target left; low spatial uncertainty
6. Entrainer right, arrow right, target presented in phase with the entrainer (100), target right; low spatial uncertainty
7. Entrainer left, arrow left, target presented out of phase with the entrainer (150), target left; low spatial uncertainty
8. Entrainer right, arrow right, target presented out of phase with the entrainer (150), target right; low spatial uncertainty

Initially, we planned to run maxima detection procedure on alpha (9.5-10.5) bandpass event-related potentials (see blue line in fig 4.2); however, the baseline was too unstable. Thus we decided to analyse latency of peak or trough (extrema) of alpha power (LofEAP).

The measurement of evoked alpha band power is the power of the mid alpha sub-band (9.5-10.5Hz) amplitude (μV^2) synchronised with the event marker. Thus, the peak detection procedure detects highest maxima as the most significant power peak within the range, and minima which are cross points (troughs of red sinusoid) between two power curves thereby the minima (troughs) and maxima (peaks) were identified within alpha (9.5-10.5Hz) bandpass filtered epochs. There would thus tend to be two power peaks and two power troughs per 10Hz cycle (Figure 4.2). Therefore detected troughs would be

shifted 1/4 of the cycle from the peak troughs.

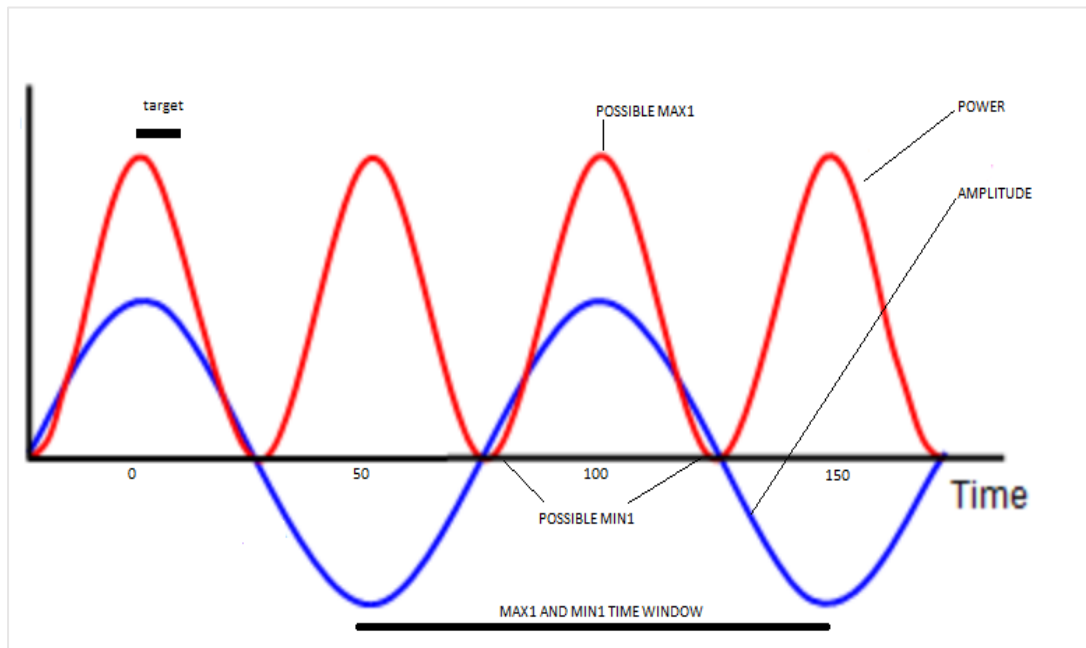


Figure 4.2 represents the relation between amplitude (blue line) and power (squared amplitude) – red line. The measurement of the power extrema are the peaks and troughs of the red sinusoid. The black horizontal line illustrates ma1, min1 time window where the extrema latencies were captured. Figure 4.3 The max2 and the min2 time window is 150-250ms.

The data from the following conditions were taken into the further neuroimaging analysis:

1. Left side prime, left pointing arrow, left target, 100ms ISI
2. Left side prime, left pointing arrow, left target, 150ms ISI
3. Left side prime, no arrow, left target, 100ms ISI
4. Left side prime, no arrow, left target, 150ms ISI
5. Right side prime, right-pointing arrow, right target, 100ms ISI
6. Right side prime, right-pointing arrow, right target, 150ms ISI
7. Right side prime, no arrow, right target, 100ms ISI
8. Right side prime, no arrow, right target, 150ms ISI

The chosen conditions thus follow the logic applied in the analysis of behavioural results. From the above list, numbers. 1 and 5 represent low spatial uncertainty for both hemifields for target presented in phase with visual prime. Numbers 2 and 6 represent low spatial uncertainty for both hemifields for target

presented out of phase of the visual prime. Numbers 3 and 7 represent high spatial uncertainty for both hemifields for target presented in phase with visual prime. The numbers 4 and 8 represent high spatial uncertainty for both hemifields for target presented out of phase with visual prime. Thus, the following independent variables were identified:

1. Visually stimulated hemifield: left, right (L, R)
2. Spatial uncertainty: high, low
3. ISI: in phase 100ms, out of phase 150ms
4. Hemisphere where the electric potentials were recorded: right (R) and left (L)
5. Anterior-posterior axis dynamics: Anterior and posterior electrodes

4.3 Behavioural results

The behavioural data were initially analysed regardless of whether the prime and congruent target (and in fifty per cent of cases congruent arrow) originated from the left or the right hemifield; as Spaak et al. (2014) did not report any lateralisation effect in behavioural data. Also, our spatial uncertainty behavioural experiment in chapter three did not achieve significant lateralised results. However, in this study, we found significant differences in lateralisation. Also, functional hemispherical differences influence the way perceptual and attentional mechanisms gather information from left and right visual fields. One example is research on the hemispheric specialisation in processing local and global features of the object (Navon, 1977). Several studies investigated the dominating tendency of the left hemisphere to process local features and the right hemisphere to process the global features of the image (Fink, Marshall, Halligan, & Dolan, 1998; Fink et al., 1997; Volberg & Hübner, 2004; Weissman & Woldorff, 2005). The current paradigm is composed of conditions which might require various levels of local and global perception for their efficient processing. It is likely that in the congruent condition, (where arrow guides attention towards the location of the target) local perception dominates hence left hemisphere also dominate. On the other hand, in the incongruent condition (where the lack of guiding arrow makes participants to observe the entire image) global perception dominate and the right hemisphere might lead the information processing. Taking together the evidence from the behavioural results (significant lateralised differences) and presented evidence on lateralised information processing of objects with

global and local perceptual features; it was decided that lateralised neuroimaging results will be presented below.

4.3.1 Behavioural results

A three-factor repeated-measures ANOVA was conducted on the response accuracy with independent variables: inter-stimulus interval (two levels: in phase – 100ms, and out of phase – 150ms), the spatial uncertainty (two levels: an arrow pointing to the subsequent target location or no arrow) and hemifield stimulated (left, right). Means and SDs for each of the conditions are reported in table 4.1 There was no main effect of the hemifield stimulated and target on the accuracy, $F(1, 19)=0.23$ $p > 0.05$. Thus, the presentation side of the stimuli does not differentiate how accurately people detect the target. Also, there was no main effect of spatial uncertainty. i.e. the presence of an arrow for congruent targets does not significantly increase accuracy compared with non-target conditions, $F(1,19) = 3.04$, $p>0,05$. There was also no main effect of ISI, $F(1, 19) = 0.21$, $p > 0.05$.

Table 4.1 Accuracy levels and standard deviations (%) for all four conditions when the stimuli are originating from the left and the right hemifield.

Condition	Spatial uncertainty	ISI	Accuracy (mean \pm SEM)
Left hemifield prime and target	High (no arrow)	100	61.9% \pm 4.4%
		150	66% \pm 4.4%
	Low (congruent arrow)	100	59.3 \pm 4.8%
		150	50% \pm 5.4%
Right hemifield prime and target	High (no arrow)	100	55% \pm 5.4%
		150	63% \pm 5.3%
	Low (congruent arrow)	100	64.9% \pm 5.3%
		150	67.4% \pm 5.4%

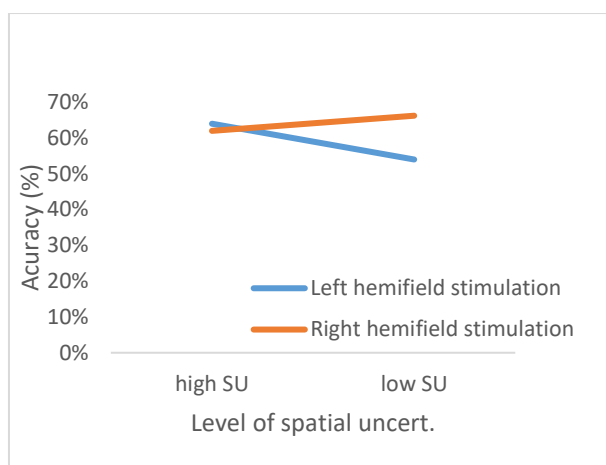


Figure 4.3 Stimulated hemifield and spatial uncertainty interaction - behavioural results

Importantly, there was a significant interaction between target/stimulated hemifield and the spatial uncertainty, $F(1, 19)=12.92$, $p < 0.05$. As presented in figure 4.3 when the target and stimulation were in the left hemifield then accuracy was higher for high ($M=64\%$, $SD=16\%$) rather than low ($M=54\%$, $SD=20$) spatial uncertainty conditions, $t(19)=3.38$, $p<0.05$. However, when the target and stimulation were in the right hemifield then the accuracy was higher for low ($M=66\%$, $SD=21$) rather than for high ($M=62\%$, $SD=23$) spatial uncertainty, $t(19)=-5.05$, $p<0.05$. Also, there was a significant difference in the scores for the level of uncertainty for the left versus right hemifield stimulation for low SU. High SU ($M=63\%$, $SD=16\%$) and Low SU ($M=55\%$, $SD=20$) conditions; $t(19)=3.38$, $p < 0.05$.

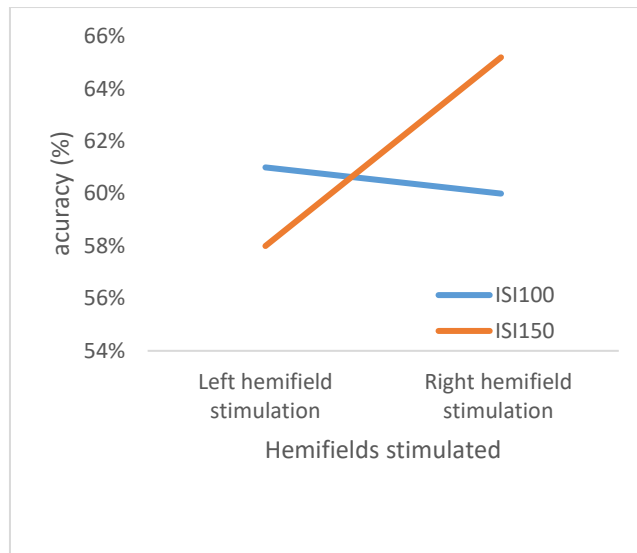


Figure 4.4 Interaction between hemifield stimulated and ISI

There was a significant interaction between hemifield stimulated and ISI, $F(1, 19) = 12.17, p < 0.05$ as presented in figure 4.4 the hemifield from which the stimuli originated significantly affected how the level of ISI applied influenced accuracy. As presented in figure 4.4 when the target was presented in phase with the visual prime (blue line), people were more accurate when the alpha prime and the target were presented in the left ($M=61\%, SD=21$) than the right ($M=60\%, SD=21$) hemifield, $t(19)=1.91, p > 0.05$. However, when the target was presented out of phase (orange line), people were more accurate when the alpha prime and the target were presented in the right ($M=65\%, SD=15$) than the left ($M=58\%, SD=18\%$) hemifield, $t(19)=-3.65, p < 0.05$.

4.4 Neuroimaging results.

EEG recordings for twenty individuals were included in the final analysis. Electrodes were clustered into four groups: right hemisphere (electrodes: FP2 F2 F4 F6 F8 FC2 FC4 FC6 FT8 FP2 AF4 AF8 C2 C4 C6 T8 CP2 CP4 CP6 TP8 P2 P4 P6 P8 PO4 PO8 O2) left hemisphere (electrodes: FP1 F1 F3 F5 F7 FC1 FC3 FC5 FT7 FP1 AF3 AF7 C1 C3 C5 T7 CP1 CP3 CP5 TP7 P1 P3 P5 P7 PO3 PO7 O1); anterior electrodes (FP1 FPZ FP2 AF7 AF3 AFZ AF4 AF8 F7 F5 F3 F1 FZ F2 F4 F6 F8); and posterior electrodes (TP7 CP5 CP3 CP1 CPZ CP2 CP4 CP6 TP8 P7 P5 P3 P1 PZ P2 P4 P6 P8 PO7 PO3 POZ PO4 PO8 O1 OZ O2). None of the independent variables was measured on more than two levels. Hence, Mauchly's

correction does not have to be applied (Field, 2012, p.475). The neuroimaging results are presented for four DVs:

1. Max1 – the latency of maximum alpha power (see figure 4.2 – red sin peak position) measured in the time window of 50-150ms from the target onset.
2. Min1 – the latency of minimum alpha power (see figure 4.2 – red sin trough position) measured in the time window of 50-150ms from the target onset.
3. Max2 – the latency of maximum alpha power measured in the time window of 150-250ms from the target onset.
4. Min2 – the latency of minimum alpha power measured in the time window of 150-250ms from the target onset.

4.4.1 Max1 analysis

A five-way repeated-measures ANOVA was conducted on the MAX1 alpha power latencies with spatial uncertainty (high or low), ISI (100 or 150ms), hemisphere recorded (left or right), stimulated hemifield (left stim. or right stim.) and electrode grouping (anterior or posterior loci) – see table 4.2. For max1 there was a significant 6ms latency difference between anterior (100ms) and posterior electrodes (94ms) (main effect of electrode grouping $F(1, 19)=6.00, p<0.05$). There were significant interactions between hemifield stimulated and SU ($F(1, 19) =6.28, p<0.05$), hemifield stimulated and ISI ($F(1, 19) =5.38, p<0.05$), hemifield stimulated, SU and hemisphere recorded ($F(1, 19)=7.45, p<0.05$) and; ISI, hemisphere recorded and electrode grouping ($F(1, 19)=5.48, p<0.05$). No other interactions were significant.

Table 4.2 presents mean alpha power peak latencies and standard deviations for each of the conditions for max1.

Spatial uncertainty	ISI	Hemisphere recorded	Anterior/Posterior electrodes	LH stimulation mean alpha power latency±SEM	RH stimulation, mean alpha power latency±SEM
High	100	Right	A	114±24	97±28
			P	97±29	87±20
		Left	A	105±23	96±23
			P	93±25	98±24
	150	Right	A	99±22	102±26
			P	111±23	98±20

		Left	A	102±26	96±25
			P	94±24	97±29
Low	100	Right	A	105±25	98±28
			P	97±30	84±27
		Left	A	108±26	97±27
			P	104±25	97±30
	150	Right	A	84±25	104±32
			P	83±19	96±28
		Left	A	90±28	104±29
			P	86±24	86±27

For the interaction between the hemifield stimulated and SU, the average LofEAP did not differ significantly between SU conditions when the stimuli originated from the right hemifield ($t(19)=0.03$, $p>0.05$), but there LofEAP was ~8ms slower for conditions of high SU compared with low SU originating in the left hemisphere, the difference was significant ($t(19)=2.71$, $p<0.05$). (see fig. 4.6).

For the interaction between hemifield stimulated and ISI, ($F(1, 19)=5.38$, $p<0.05$) when stimuli originated from the left side, the LofEAP was significantly higher (by ~8ms) for targets in phase with the prime compared with out of phase presented targets ($t(19)=2.71$, $p<0.05$). However, the reverse relationship occurred when the stimuli originated from the right side. The LofEAP was lower (by ~3ms)

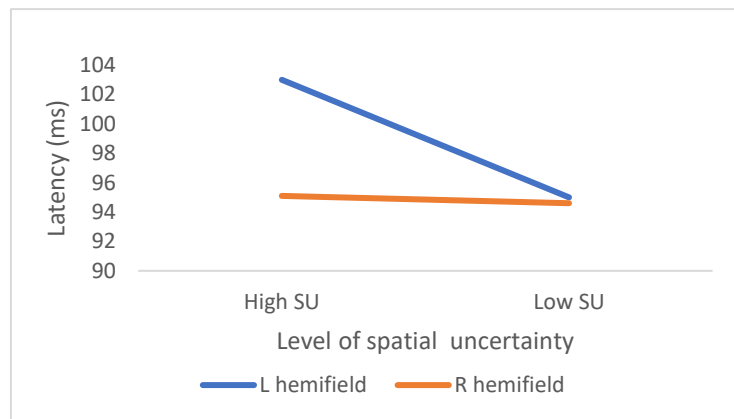


Figure 4.5 Latencies for spatial uncertainty, hemifield stimulated interaction.

for in-phase compared with out of phase presented targets ($t(19)=0.13$, $p>0.05$), (see fig. 4.7).

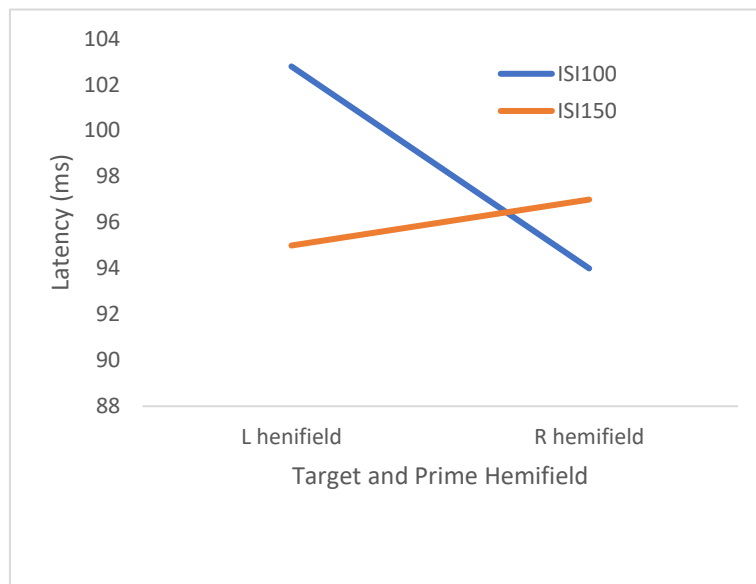


Figure 4.6 Latencies for hemifield stimulated, and phase in which target was presented

The three-way interaction between hemifield stimulated, hemisphere measured, and SU illustrated that when the stimuli arrived from the left hemifield (see fig 4.8 A): in high SU conditions, the latency of the alpha power peak was significantly longer by ~6ms in the right than the left hemisphere ($t(19)=2.48$, $p<0.05$). The opposite pattern was observed for the low SU tasks (with the arrow); however the difference between the hemispheres was non-significant ~5ms, ($t(19)=0.274$, $p>0.05$). Also, when the stimuli arrived from the right hemifield, the differences were not significant in high SU ($t(19)=1.07$, $p>0.05$) and low SU ($t(19)=0.068$, $p>0.05$) conditions (see fig. 4.8B).

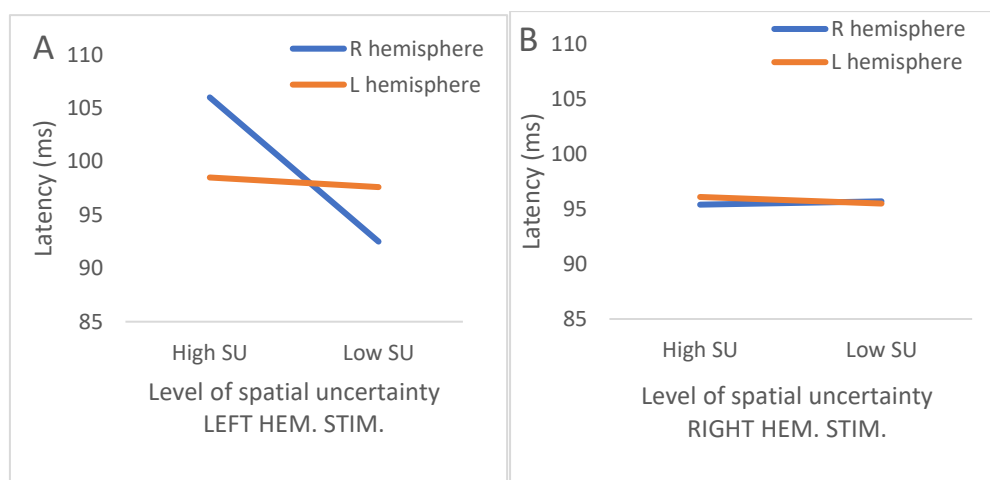


Figure 4.7 Latencies for the left (A) and right (B) hemifield both hemispheres SU interaction

The three-way interaction between ISI, hemisphere recorded and anterior-posterior electrodes, showed that for the tasks presented in phase with the alpha entrainment - ISI100 (see fig. 4.9A): the latency of alpha phase power on the A-P axis was significantly larger in the right hemisphere than the left hemisphere by ~8ms (right hemisphere AP difference – left hemisphere AP difference), $t(19)=3.12$, $p<0.05$ (fig. 4.9 A). The opposite tendency is observed when the target was presented out of phase to the entrainer - ISI150, where the latency of alpha phase power on the A-P axis was larger in the left hemisphere than the right hemisphere(right hemisphere AP difference – left hemisphere AP difference)by ~6ms, $t(19), =1.23$, $p>0.05$, but the difference here was not significant (fig. 4.9 B).

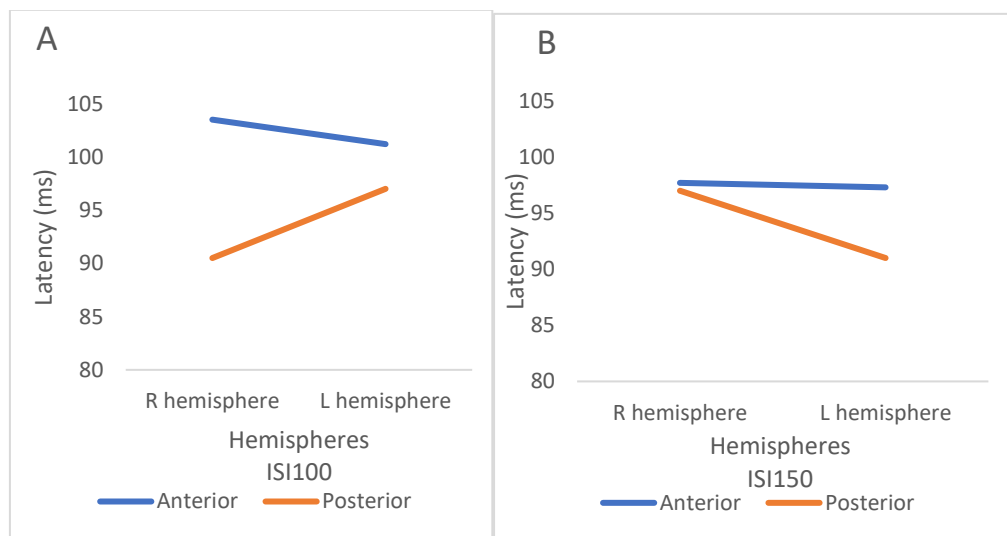


Figure 4.8 Latencies for ISI100 (A) and ISI150 (B) presented a target for ISI, A-P axis, hemisphere interaction

4.4.2 Min1 analysis

Detected minima, as illustrated in figure 4.2 are related to the induced alpha troughs (blue line), but they are shifted from them theoretically by 25ms in-plus and in-minus (see fig. 4.2). Therefore, statistical comparisons between maxima and minima would not be appropriate. However, in this thesis the comparisons within the max1, min1, max2, min2 time windows are conducted therefore the difference in troughs latency between alpha power peaks and alpha amplitude peaks should not have any critical effects on the overall results. Thus, the min1 analysis was conducted.

Table 4. 3 presents mean alpha power trough latencies and standard deviations for min1; (Lside/Rside - Hemifield stimulated; Math/Spaak–Low/High spatial uncertainty respectively; 100/150ISI – interstimulus interval; Lhem/Rhem

Level of spatial uncer.	ISI	Hemisphere recorded	Anterior/Posterior electrodes recorded	Left hemifield stimulation mean alpha power latency±SEM	Right hemifield stimulation, mean alpha power latency±SEM
High	100	Right	A	82±25	100±30
			P	102±26	116±24
		Left	A	97±23	94±23
			P	104±30	96±31
	150	Right	A	95±33	101±34
			P	89±23	103±27
		Left	A	90±28	96±33
			P	100±23	99±28
Low	100	Right	A	95±27	96±29
			P	100±20	109±19
		Left	A	91±28	109±30
			P	99±22	102±34
	150	Right	A	118±31	96±30
			P	107±27	103±28
		Left	A	108±31	100±32
			P	103±25	111±25

For the latency window from the onset of the target 50 -150ms, alpha power trough latencies were detected for each correctly target detected epoch, for each participant, tested condition and the qualifying electrodes. A five-way repeated measures ANOVA was conducted on spatial uncertainty (high low), ISI (ISI100, 150), hemisphere recorded, hemifield stimulated anterior/posterior loci. For min1 there was lack of significant main effects (see table4.6 for an overview). For min1 only two interactions were significant: hemifield, stimulated, spatial uncertainty, hemisphere observed, $F(1, 19)=11.68$, $p<0.05$; and ISI, hemisphere observed, anterior-posterior group, $F(1, 19) = 6.87$, $p<0.05$.

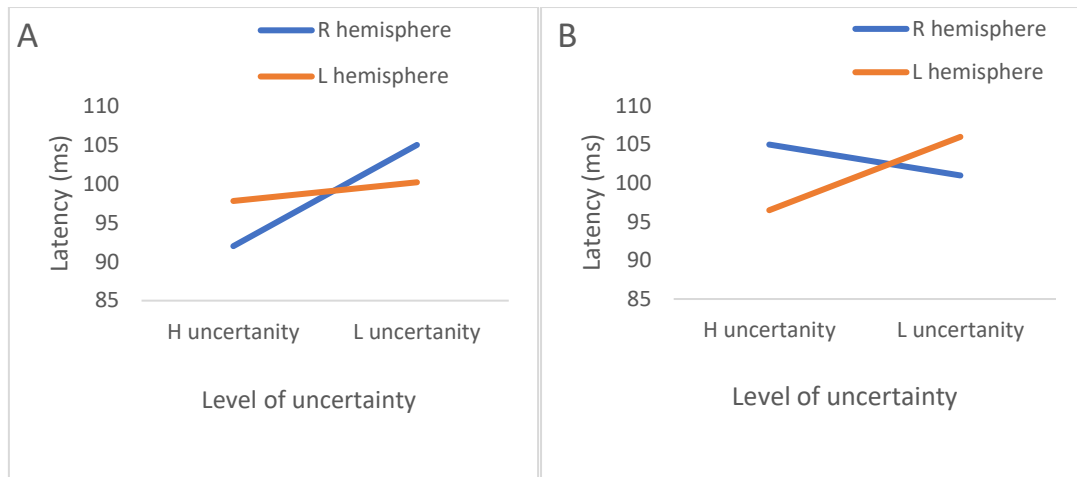


Figure 4.9 Latencies for the left (a) and right (b) hemifield in hemifield, hemisphere and uncertainty interaction

In min1 temporal window, for the interaction of hemifield stimulated, spatial uncertainty and hemisphere recorded, when the stimuli originated from the left hemifield (fig. 4.10 A): LofEAP occurred earlier for high uncertainty trials when measured in the contralateral hemisphere to stimulation but the difference was not significant, $t(19)=-1.44$, $p>0.05$. However, for low uncertainty trials (with arrow), LofEAP occurred later when measured in the contralateral hemisphere to the stimulation (left) comparing to the right hemisphere. Also, the difference between hemispheres was non-significant, $t(19)=1.74$, $p>0.05$.

In the min1 temporal window, when the stimuli originated from the right hemifield (fig. 4.10 B): for high uncertainty trials the alpha power peak latency occurred significantly earlier when measured in the contralateral hemisphere to stimulation, $t(19)=2.42$, $p<0.05$. However, for low uncertainty trials, the difference was not significant $t(19)=-1.56$, $p>0.05$. Hence, in this interaction, the significant differences between hemispheres were only detected for stimuli arriving from the right hemifield in high SU trails.

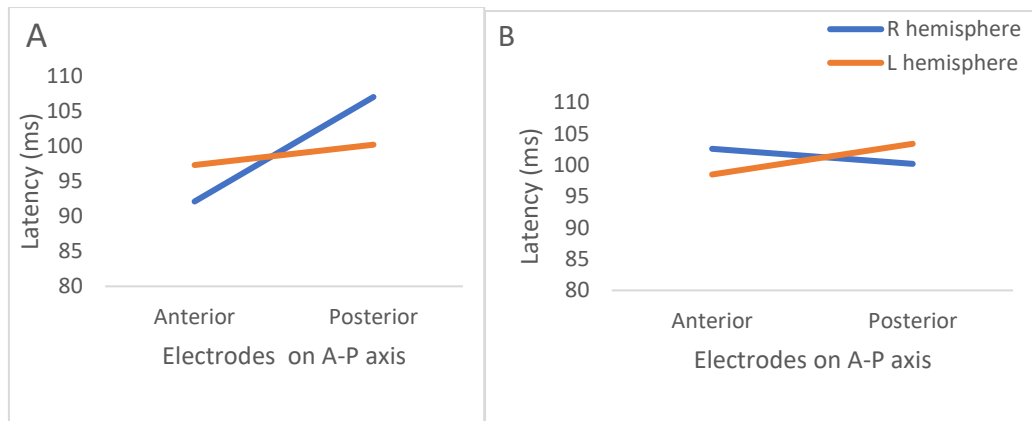


Figure 4.10 Latencies for ISI100 (A) and ISI150 (B) in the interaction of ISI, Anterior, posterior electrodes, hemispheres

For the interaction between ISI, hemisphere observed and anterior-posterior loci, alpha power peak latency – (fig. 4.11) there were significant differences in the scores for ISI100, right hemisphere electrodes between anterior (M93ms, SD=14ms) and posterior (M=105ms, SD=13ms); electrodes ($t(19)=-3.55$, $p<0.05$; fig.4.11 A). However, there were no significant differences in the scores for the left hemisphere electrodes between the anterior (M97ms, SD=11ms) and posterior electrodes (M=100ms, SD=18ms); (fig.4.11 A). Anterior and posterior $t(19)=0.03$, $p>0.05$. Also, there were no significant differences in the scores for ISI150, right hemisphere electrodes between anterior and posterior electrodes (fig.4.11 B). Anterior (M102ms, SD=11ms) and posterior (M=100ms, SD=18ms) conditions; $t(19)=0.54$, $p>0.05$. Finally, there was also lack of significant differences in the scores for ISI150, left hemisphere electrodes between anterior and posterior electrodes. Anterior (M99ms, SD=16ms) and posterior (M=103ms, SD=14ms) conditions; $t(19)=-0.95$, $p>0.05$.

4.4.3 Max2 analysis

For the latency window from the onset of the target 150 -250ms alpha power peak latencies were determined for each correctly detected target epoch (see table 4.4). A five-way repeated measures ANOVA was conducted on the max2 alpha power latencies with spatial uncertainty, ISI, hemisphere recorded, hemifield stimulated, anterior/posterior loci. For each participant and condition the following interactions were significant: hemifield stimulated and ISI, $F(1, 19)=6.24$, $p<0.05$; hemifield stimulated,

ISI and SU, $F(1, 19)=5.12$, $p<0.05$; hemifield stimulated, ISI and hemispheric electrodes, $F(1, 19) = 6.49$, $p<0.05$.

Table 4.4 Presents mean alpha peak power latencies and SEM for each of the conditions for max2.

Level of spatial uncertainty	ISI	Hemisphere recorded	Anterior/Posterior electrodes recorded loci	Left hemifield stimulation mean alpha power latency \pm SEM	Right hemifield stimulation mean alpha power latency \pm SEM
High	100	Right	A	193 \pm 30	196 \pm 29
			P	193 \pm 30	204 \pm 27
		Left	A	206 \pm 25	198 \pm 28
			P	196 \pm 29	196 \pm 29
	150	Right	A	207 \pm 28	202 \pm 33
			P	206 \pm 29	196 \pm 29
		Left	A	207 \pm 22	205 \pm 33
			P	194 \pm 29	197 \pm 31
Low	100	Right	A	194 \pm 29	206 \pm 30
			P	192 \pm 25	211 \pm 24
		Left	A	193 \pm 25	201 \pm 26
			P	193 \pm 30	196 \pm 29
	150	Right	A	193 \pm 30	204 \pm 27
			P	206 \pm 25	198 \pm 28
		Left	A	196 \pm 29	196 \pm 29
			P	207 \pm 28	202 \pm 33

In the hemifield stimulated and ISI interaction, for tasks presented in phase with the prime (ISI100), the LofEAP was significantly higher (by ~8ms) when target originates from right hemifield than from the left hemifield, $t(19)=-2.28$, $p<0.05$, (see fig. 4.12). However, the opposite pattern was observed when the target was presented out of phase with the prime as the LofEAP was higher (by ~4ms) for stimuli originating from the left hemifield than for stimuli originating from the right hemifield, however the difference was not significant ($t(19)=0.34$, $p>0.05$).

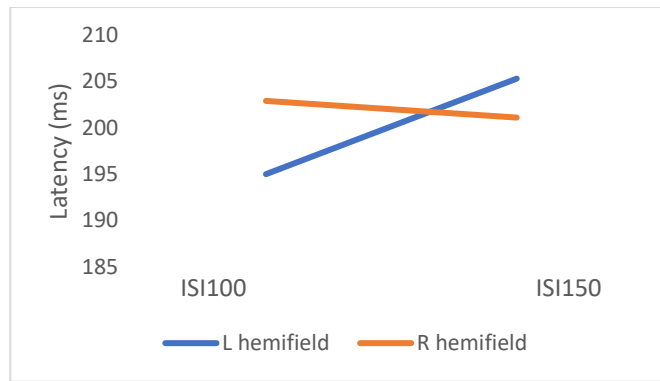


Figure 4.11 Latencies for A-P axis electrodes, hemifields interaction.

For the three-way interaction of hemifield stimulated, ISI and hemispheric electrodes, when the stimuli were presented in phase with the alpha prime - ISI 100, (fig. 4.13 A) and originated from the left hemifield the LofEAP for high uncertainty occurred ~5ms later than for low uncertainty tasks, $t(19)=1.19$, $p>0.05$. The opposite scenario occurred for the stimuli originating from the right hemifield, i.e. LofEAP for low uncertainty occurred later by ~10ms than for highly uncertain tasks, $t(19)=-1.74$, $p>0.05$., In both cases the differences were non-significant.

On the other hand, for stimuli which is presented out of phase - ISI150 (figure. 4.13 B) such reverse effect did not occur and for stimuli originating from both sides highly uncertain targets produced longer LofEAP compared to low SU targets. The differences between high and low SU for left ($t(19)=0.66$, $p>0.05$) and right hemifield ($t(19)=0.74$, $p>0.05$) were both non-significant.

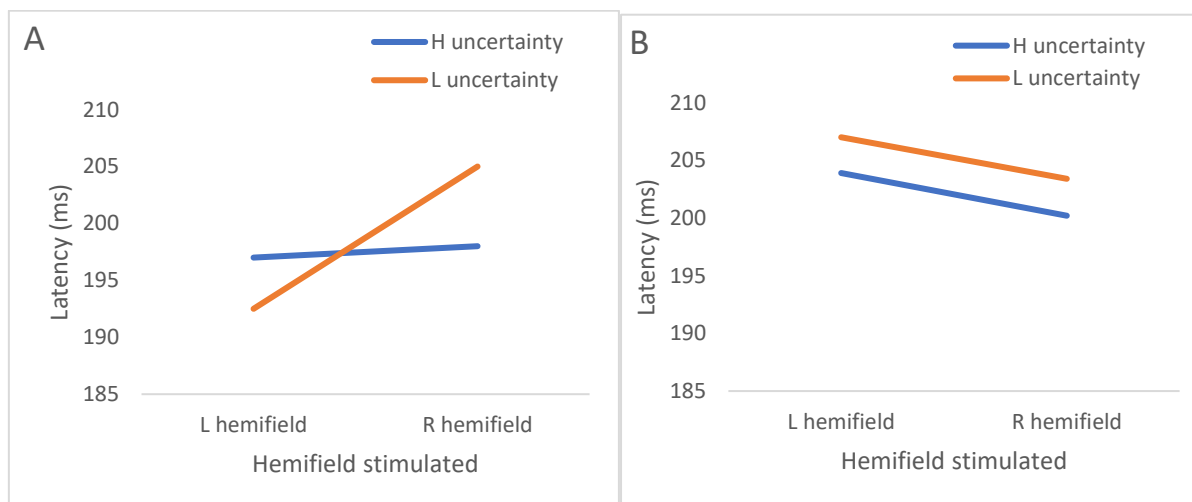


Figure 4.12 Latencies for ISI100 (A) and ISI150 (B) in ISI, uncertainty, hemifield interaction.

Finally for the three-way interaction between hemifield, ISI and the recorded hemisphere when the stimuli originated from the left hemifield (fig. 4.14 A), the LofEAP for stimuli presented in phase with an alpha prime (ISI100) occurred earlier in the right than the left hemisphere, ($t(19)=0.99$, $p>0.05$) difference was non-significant. However, for stimuli presented out of phase (ISI150) the effect reversed and was significant, $t(19)=2.0$, $p<0.05$. It is only significant post-hoc effect in this interaction. When the stimuli originated from the right hemifield (fig. 4.14.B), the LofEAP for stimuli presented in phase with an alpha prime (ISI100) occurred earlier in the left than right hemisphere, $t(19)=0.99$, $p>0.05$. However, for stimuli presented out of phase (ISI150) the effect reversed $t(19)=0.96$, $p>0.05$.

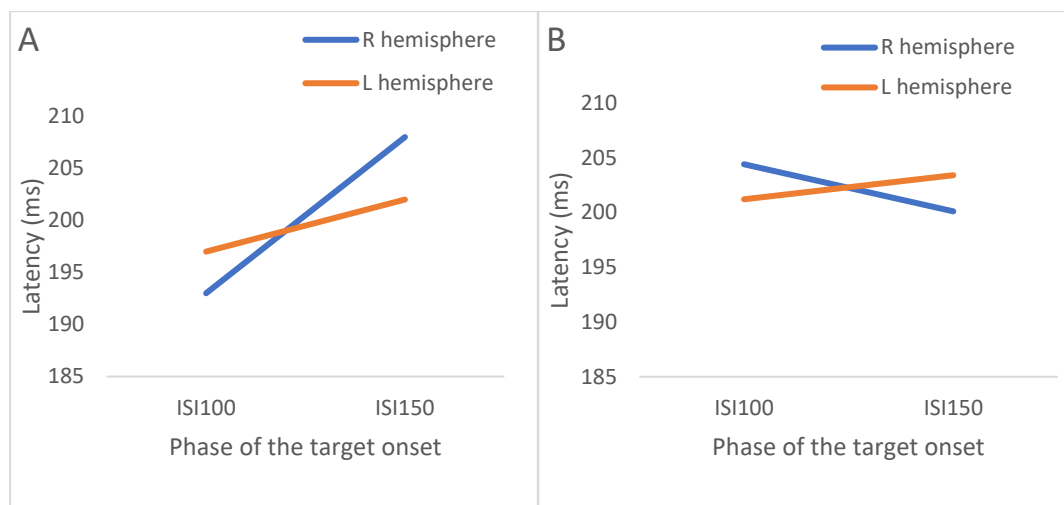


Figure 4.4 Latencies for left (A) and right (B) hemifield in hemifield, hemisphere and phase interaction

4.4.4 Min2 analysis

For the latency window of 150 to 250ms (target onset as a reference point) LofEAPs were analysed (see table 4.5). A five-way repeated-measures ANOVA was conducted on the Min2 LofEAPs with spatial uncertainty, ISI, hemisphere recorded, hemifield stimulated anterior/posterior loci. The following interactions were significant: hemifield stimulated and ISI, $F(1, 19)=9.42$, $p<0.05$; hemifield stimulated, ISI and hemispheric electrodes, $F(1, 19)=10.97$, $p<0.05$; SU and anterior-posterior electrodes $F(1, 19)=5.14$, $p<0.05$.

Table 4.5 presents mean alpha power trough latencies and standard deviations for each of the conditions for min2.

Spatial uncertainty	ISI	Hemisphere recorded	Anterior/Posterior electrodes recorded	Left hemifield stimulation mean alpha power latency±SEM	Right hemifield stimulation, mean alpha power latency±SEM
High	100	Right	A	205±33	195±28
			P	204±33	193±27
		Left	A	192±27	204±26
			P	209±27	212±22
	150	Right	A	194±24	201±26
			P	194±27	208±24
		Left	A	197±26	199±25
			P	202±31	208±29
Low	100	Right	A	205±24	194±26
			P	211±29	186±25
		Left	A	209±29	204±33
			P	205±33	195±28
	150	Right	A	204±33	193±27
			P	192±27	204±26
		Left	A	209±27	212±22
			P	194±24	201±26

For the hemifield stimulated and ISI interaction, in trials presented in phase with the alpha entrainer, the mean alpha power peak latency occurred significantly earlier (~8ms) when stimuli arrived from the right than from the left hemifield by, $t(19)=-2.3$, $p<0.05$. However, for trials presented out of phase with the entrained alpha (ISI150), the LofEAP was detected earlier (~8ms) when stimuli arrived from the left than from the right hemifield, $t(19)=1.9$, $p<0.05$ (see fig. 4.15). The difference was also significant.

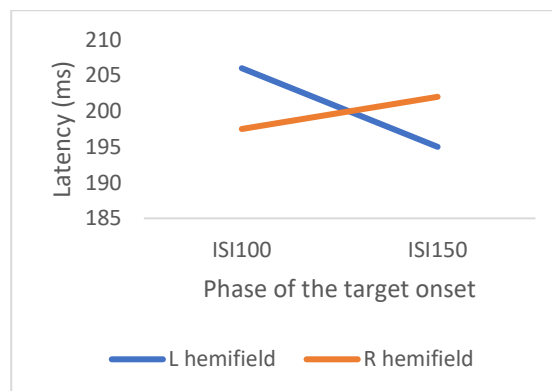


Figure 4.14 Latencies for hemifield and phase of the target onset.

For Anterior/Posterior and SU interaction, in high SU tasks where more top-down control is needed, alpha power peak latency was detected significantly earlier (~5ms) in anterior electrodes than in posterior electrodes, $t(19)=-2.28$, $p<0.05$. However, in low SU tasks (with arrow), the alpha power peak latency was detected earlier (~5ms) in posterior and subsequently in anterior loci, $t(19)=2.75$, $p<0.05$.

For the three-way hemifield stimulated, ISI and hemispheres interaction: when stimuli originated from the left hemifield in ISI100 condition the LofAPP was detected marginally (non-significantly) earlier for left than right hemisphere, $t(19)=0.29$, $p>0.05$. Also without significance, that peak was detected for ISI150 earlier in the right hemisphere, $t(19)=-1.2$, $p>0.05$. When the stimuli originated from the right hemifield (see fig. 4.16 B), in ISI 100 LofEAP was detected ~10 ms earlier in the right than the left hemisphere, $t(19)=-4.4$, $p<0.05$. The difference was significant. The opposite effect was observed for the ISI150 condition; however here the differences were small - ~1ms and non-significant, $t(19)=0.23$, $p>0.05$. For anterior/posterior loci and SU interaction, in high SU tasks (where more top-down control dominates), alpha power peak latency was detected significantly earlier by ~5ms in anterior electrodes than in posterior electrodes, $t(19)=-2.28$, $p<0.05$. However, in low SU tasks (with arrow), the alpha power peak latency was detected also significantly earlier by ~5ms in posterior than in anterior locus, $t(19)=2.75$, $p<0.05$.

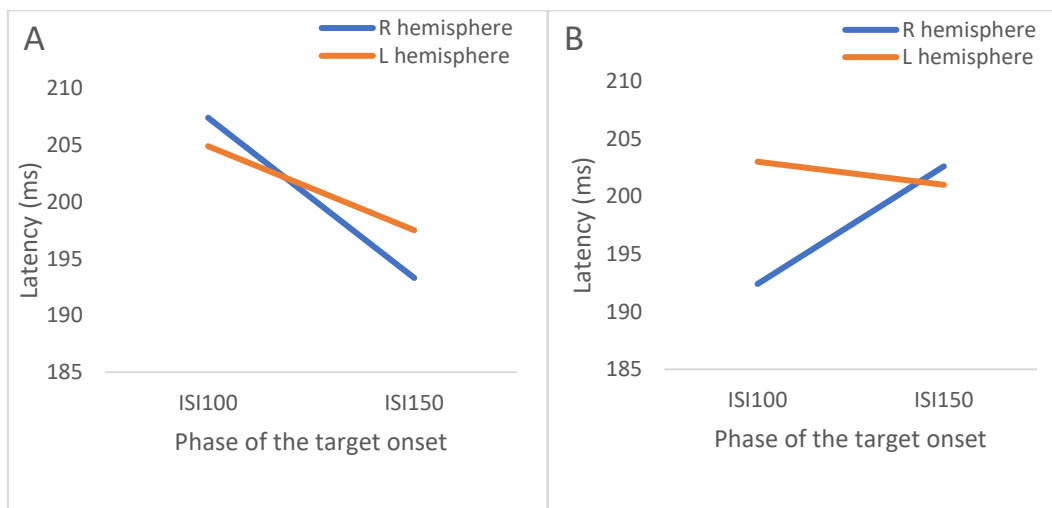


Figure 4.15 Latencies for the left (A) and right (b) hemifield in hemifield hemisphere and phase of the target onset.

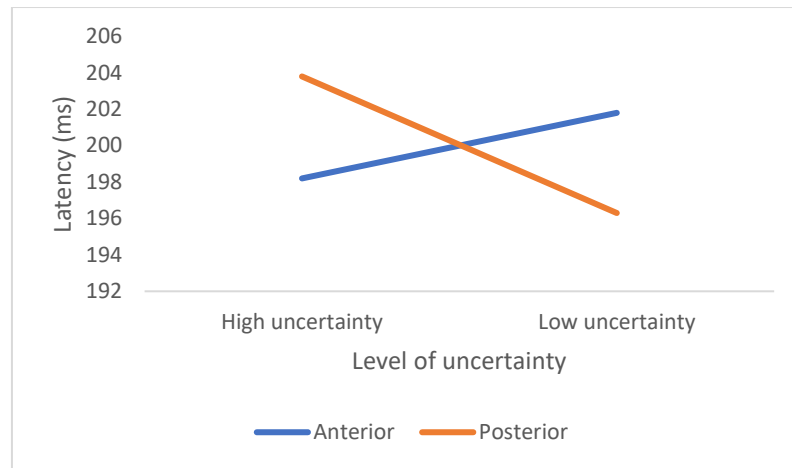


Figure 4.16 Latencies for uncertainty and A-P electrodes.

4.5 Discussion

The current study examined brain activity during a task that looked at the effects of elicited alpha activity under conditions of high and low spatial uncertainty. As a measure of EEG activity, we used four measurements based on peak or minimum alpha power within two-time windows (max1, min1, max2, min2). In this section, we will discuss patterns observed across four measurements and how they relate to the behavioural results. By allocating four consecutive time windows where we observed LofEAP, we aimed to see how alpha neuronal dynamics develop in time. As elaborated in chapter one and discussed by Herring, Thut, Jensen, & Bergmann, (2015); Herrmann, (2001); Spaak et al., (2014), the effect of the alpha visual entrainment lasts only for a few cycles after offset of the last entrainer, Thus we were interested in how alpha entrainer affects consecutive time windows (TW) which start 100 or 150ms after the last visual prime onset. Table 4.6 shows that max1 temporal window achieved the highest number of significant results. Other TWs achieved less significant results (two, three, three consecutively). However, it is difficult to draw any conclusions based on these limited observations. Therefore, were treated all TW as equal observation points.

The picture which emerges from the analysis of LofEAPs is complex, but here we discuss clear patterns in the results and discuss them in the context of the established hypothesis. Hence, interactions involving

spatial uncertainty, which provides the primary motivation for this experiment will be discussed first.

Table 4.6 summarises the significant interactions for LofEAP measurements and behavioural data.

Table 4.6 Significant main effects and interactions for mid alpha power peak latencies and behavioural significance. Empty cells indicate a lack of significance, N/A indicates the interaction which was not conducted in behavioural analysis.

	MAX1	MIN1	MAX2	MIN2	BEHAVIOURAL
A-P LOCI	0.024				N/A
HEMIFIELD STIM, SU	0.021				SIGNIFICANT
HEMIFIELD STIM, ISI	0.032		0.022	0.006	SIGNIFICANT
HEMIFIELD STIM, SU, ISI			0.035		N/A
HEMIFIELD STIM, SU, HEMISPHERE RECORDED	0.013	0.003			N/A
HEMIFIELD STIM, ISI, HEMISPHERE RECORDED			0.02	0.004	N/A
SU, A-P LOCI				0.035	N/A
ISI, HEMISPHERE RECORDED, A-P LOCI	0.028	0.017			N/A
ISI					SIGNIFICANT

The significant difference in max1 between anterior and posterior electrodes suggests the visually entrained alpha waves propagate from the posterior towards anterior locations. As the experiment consisted of visual stimuli and as both bottom-up and top-down alpha was present, on average the bottom-up alpha communication dominated (Kawaguchi et al., 1993). The average posterior-anterior direction of the alpha signal, suggests that bottom-up alpha neuronal communication was a dominant one when we consider the average direction of the signal on the A-P axis, regardless of other conditions. However, this only validates that the alpha signal first arrived in posterior locations and later was detected in anterior locations, which is the typical observation for visual stimuli.

Also, the following interaction effects across all four temporal windows and behavioural measurements are now considered: hemifield stimulated and SU; anterior-posterior loci and SU; hemifield stimulated,

SU and hemisphere recorded; hemifield stimulated and ISI; hemifield stimulated and ISI and hemisphere recorded.

There were significant interactions for the hemifield stimulated and SU for both max1 and the behavioural results. Behavioural results and neuroimaging dynamics followed opposite tendencies (see fig. 4.4 and 4.6). Specifically, in behavioural measures in high SU condition people were performing similarly regardless of the side from which the stimuli arrived. In max1 LofEAP was similar for stimuli arriving from the left and the right hemifield in low SU conditions. Hence, the behavioural results might suggest that people were probing the space evenly while searching for a spatially unguided target. However, it led into substantial phase shift when compared neuronal activity for uncertain targets spotted on the left or the right side.

There were significant interactions for the Anterior - posterior loci electrodes and SU in min2 (fig. 4.17). Behavioural results cannot be directly compared as A-P loci IV could not be included in the behavioural design. The results are engaging in the light of the stated hypothesis about the role of bottom-up and top-down neuronal communication of neuronal tasks characterised by high and low level of SU. Namely, figure 4.17 clearly illustrates alpha power dynamics for arrow (low SU) and non-arrow (high SU) conditions. When participants are pre-guided to the specific location LofEAP, bottom-up dynamics are dominant, because the LofEAP mean across posterior electrodes is detected before that measure is detected across anterior electrodes; which suggest that the alpha oscillations on average propagate from the back towards the front of the cortex and probably another type of tasks involving more working memory and internal processes without visual stimuli would make top down alpha to dominate. That suggests dominant bottom-up communication. However, when participants must actively monitor both possible spatial locations, top-down alpha neuronal dynamics dominate which is indexed by the initial detection of LofEAP peak by anterior electrodes followed by the posterior electrodes. Above results might suggest that alpha as many argue (see chapter one) play a role in top-down and bottom-up neuronal communication. The above results show that in more perceptual, bottom-up tasks, alpha neuronal dynamics follows the bottom-up pattern. On the other hand, for a task involving spatial searching where the target location is uncertain the top-down direction of alpha neuronal dynamics dominates.

A significant hemifield stimulated, SU and hemisphere recorded interaction was observed for both max1 (figure 4.8) and min1 (figure 4.10). The pattern of LofEAP measurement interactions alternates on two levels: between max1 and min1 as well as between left hemifield (LHF) stimulation and right hemifield (RHF) stimulation. Specifically, for max1 LHF stimulation and min1 RHF stimulation in high SU tasks, LofEAP is faster in the left than right hemisphere, but for low SU tasks, the LofEAP is faster in the right than the left hemisphere. The opposite effect is observed for max1 RHF and min1 LHF. Namely, in max1 RHF stimulation and min1 LHF stimulation for high SU tasks, LofEAP is slower in the left than right hemisphere, but for low SU tasks, the LofEAP is slower in the right than the left hemisphere. That explicit alternating LofEAP behaviour for SU manipulation, for stimuli arriving from left and the right, might suggest that alpha neuronal dynamics gate discrete perception by snapshotting the information from the external world in different phases depending on the level of SU as well as the hemifield where the information originates. However, this speculation requires more research focused specifically upon it.

We now consider the interactions that do not involve SU. For the interaction of hemifield stimulated and ISI, results achieved significance in max1 (fig. 4.7), max2 (fig. 4.12), min2 (fig 4.15) and behaviourally (fig 4.4). Max1, min2 and behavioural measures follow the same patterns. Specifically, in the ISI 100 condition, people are better at target detection, and the LofEAP is later when the stimuli arrive from the left than from the right hemifield. The opposite result is observed for stimuli originating from the right hemifield; i.e. for ISI 150 people are better in target detection and LofEAP is longer when the stimuli arrive from the right than from the left hemifield (see fig.4.7, 4.15, 4.4). On the other hand, LofEAP in max2 achieved opposite results to the above. Namely: for ISI100 LofEAP is longer when the stimuli arrive from the right than from the left hemifield. The opposite scenario is observed for stimuli originating from the left hemifield. For ISI 150 LofEAP is longer when the stimuli arrive from the left than from the right hemifield (see fig 4.26).

Finally, for hemifield stimulated, ISI and hemisphere recorded significant interactions were detected in max2 (figure 4.14) and min2 (figure 4.16). In this interaction (similar to the interaction of hemifield stimulation, SU and hemisphere recorded), alternating LofEAP behaviour between max2 (see fig. 4.14) and min2 (see fig. 4.16) was observed. Namely, for the max2, when stimulation originated from the left

hemifield (4.14A) in 100 ISI condition, LofEAP observed in left hemisphere was higher than in the right hemisphere. However, for ISI150 LofEAP observed in the left hemisphere was lower than in the right hemisphere. Also, in min2 alternating patterns were observed between tasks with left and right hemifield stimulation (entrainer plus target) (see fig. 4.16). It is another example of alpha power phase displaying alternating behaviour. However, this effect is not the main focus of this thesis and these observations could indicate a need for future research in this matter.

In summary, on the behavioural level an interaction between hemifield where the visual prime and the target originates, and the level of SU is evident. Also, on the neuronal dynamics level, that relation can be observed: the direction where the stimuli originate affects the alpha phase position (measured in LofEAP) in low and high SU tasks and both hemispheres differently (figures:4.17). The level of spatial uncertainty of the presented target significantly affected the alpha phase position when we focus on LofEAP anterior-posterior dynamics. In other words, these effects differ depending upon where in the scalp you measure them -Hence, for the tasks, where the visual search and prefrontal cortices are more involved (high SU tasks), alpha peak phase (measured by LofEAP) is initially detected by averaged anterior electrodes; and subsequently (~6ms later) is detected by posterior electrodes. However, for tasks with low SU, where the arrow pre-guided the neuronal resources to a specific location, the alpha peak phase (measured by LofEAP) was initially detected by posterior electrodes and subsequently (~4ms later) is detected by anterior electrodes. It might indicate that depending on the level of spatial uncertainty alpha phase shows the top-down or bottom-up direction of neuronal communication served by that low-frequency band (figure 4.17).

On the neuronal dynamics level, the direction from which the alpha prime and the target originate and temporal position of the target (whether the target was presented in or out of phase of the alpha prime) affects the alpha phase position on anterior-posterior axis (measured in LofEAP) and both hemispheres differently (figure 4.14, 4.16). It might suggest that the alpha phase after the target onset is significantly different for the task which originates from the left or the right hemifield and for targets presented in and out of phase with the alpha prime. These results are in line with our current understanding of the hemispheric specialisation. For example, it might be related to the suggestion that right hemisphere

focuses on more global than local aspects of the scene and the left hemisphere specialises in interpreting more local features of the scene (Navon, 1977; Volberg, Kliegl, Hanslmayr, & Greenlee, 2009b).

Functional hemispherical differences influence how perceptual and attentional mechanisms gather information from left and right visual fields. One of the interesting examples is research on the hemispheric specialisation in processing local and global features of the object (Navon, 1977). Several studies investigated the dominating tendency of the left hemisphere to process local features and the right hemisphere to process the global features of the image (Fink, Marshall, Halligan, & Dolan, 1998; Fink et al., 1997; Volberg & Hübner, 2004; Weissman & Woldorff, 2005).

Let us consider a significant interaction between SU and hemifield where the stimuli originated in time window max1 (see fig. 4.6). We can assume that left hemisphere processes the majority of the right hemifield stimuli (and vice-versa) and that high SU stimuli place a higher load of global perception whilst low SU stimuli are resolved by local perception. On this basis we observe that stimuli arriving from left hemifield which are processed by right hemisphere (fig. 4.6 blue line), when it is characterised by low SU the LofEAP is detected significantly earlier, compared to when it is characterised by high SU. As the right hemisphere is involved in global processing the latency of alpha phase (LofEAP) processed by that hemisphere was detected earlier for low SU tasks than for high SU tasks, which seems to be counterintuitive. As you could expect that stimuli with high load of global perception (high SU) would be processed more efficiently – faster than low SU stimuli by the ‘global hemisphere’, which was clearly not the case. On the other hand, stimuli arriving from the right hemifield and mainly processed by the left hemisphere (local perception hemisphere) had similar LofEAP times for both high and low SU tasks. Therefore, the tasks charged with global and local features were processed with the same speed (hence, efficiency) by the left hemisphere which predominantly processes local information.

It is likely that in the congruent condition, (where arrow guides attention towards the location of the target) local perception dominates hence left hemisphere also dominate. On the other hand, in the incongruent condition (where the lack of guiding arrow makes participants to observe the entire image) global perception dominate and the right hemisphere might lead the information processing. Taking together the evidence from the behavioural results (significant lateralised differences) and presented

evidence on lateralised information processing of objects with global and local perceptual features; it was decided that lateralised neuroimaging results will be presented below.

In conclusion, it seems to be plausible to assume that alpha oscillations play an intricate role in human perception and more general cognition by managing top-down and bottom-up communication channels depending on the tasks requirements, controls information flow differently depending on the level of its spatial uncertainty and direction where it originates.

Chapter 5 General Discussion

This thesis investigated the role of alpha frequency neuronal oscillations both in inhibitory control and the coordination of top-down and bottom-up information flow. This was investigated by using flickering stimuli to elicit alpha frequency oscillations in neural activity and then measure the behavioural and neuronal effects. The experiments systematically investigated how an externally induced rhythmic visual signal/prime might influence ongoing neuronal oscillatory activity during various cognitive and perceptual tasks. This discussion is organised in two main sections; the first section (after a brief introduction) links together all the experiments and their outcomes; the second part considers experimental conclusions according to existing research on alpha oscillations (both previous experimental work and theoretical proposals). Directions for future research are outlined across the whole discussion. The chapter finishes with a discussion of the limitations of the studies and a general summary of the main conclusions.

Across all the experiments, rhythmic visual entrainment was applied to entrain distributed oscillatory alpha networks. In the first three experiments, sinusoidal, then on-off visual primes were applied, as it was observed that the majority of studies use the latter method. Photic driving was chosen to influence neuronal dynamics, as it is a relatively simple, cost-effective and a widely used way of entraining neurons (Barlow, 1960; Kawaguchi, Jijiwa, & Watanabe, 1993; Sato, 2013). Each experiment attempted to answer a specific question about the possible role of alpha oscillations in perception/cognition. The first three experiments asked about an alpha role in long-range neuronal communication using tasks with conditions that place different demands on long-range communications. The following experiments investigated the alpha role in gating and blocking information flow in neighbouring neuronal representations, and the last behavioural experiment explored the role of alpha oscillation's temporal structure, where the phase of ongoing oscillation allows snapshots of different types of percepts. The second experimental paradigm was further investigated using EEG to examine the underlying neuronal dynamics.

This thesis confirmed that within the alpha frequency band, 10Hz mid alpha activity plays a vital role in controlling discrete perception and attention. As the most robust observable oscillation (Herrmann, 2001; Jensen & Mazaheri, 2010; Mierau, Klimesch, & Lefebvre, 2017) propagating across the entire cortex,

mid-alpha has been proposed to play a central role in network communication (Bonfond, Kastner, & Jensen, 2017; Daume, Gruber, Engel, & Fries, 2017; Lobier, Palva, & Palva, 2018). Otherwise, nature would not invest scarce energy to sustain it during phylogenesis and ontogenesis.

Although some suggest that there are individual differences between people and establishing an a priori, the specific frequency might limit the scope of the investigation (Grandy et al., 2013; Ruhnau et al., 2016; Wan et al., 2016). However, there is a vast number of studies cited in this thesis which do not adjust the frequency to the individual alpha resting state, and they achieved valid results, (e.g. Mathewson et al., 2011; Mathewson, Basak, et al., 2012; Spaak et al., 2014).

The first three experiments (chapter two) investigated how an alpha frequency flicker prime might influence the effectiveness of long-range neuronal communication required to resolve conflicting information. The first experiment (section 2.2) focused on examining whether visual entrainment of low alpha (8Hz) compared with low theta (4Hz), low beta (16Hz) frequencies and a no flicker baseline attenuated the Stroop effect, which contrasts high conflict and low conflict conditions. The results did not confirm the hypothesis that alpha flicker would enhance long-range communication, but an 8Hz visual prime did make participants significantly faster in responding to stimuli in all conditions (possibly indicating increased visual salience and attention in this condition). The second experiment (section 2.3) assessed whether manipulating the phase and amplitude of an 8Hz visual prime might produce the proposed attenuation of the Stroop effect, i.e. whether optimal parameters for amplitude and phase could be identified. It was assessed using an 8Hz visual prime presented with three ISIs between the offset of the prime and presentation of the stimulus (phase manipulation) and three levels of stimulus brightness (amplitude manipulation). None of the combinations of amplitude and phase significantly diminished the Stroop effect. However, two observations can be drawn from this study; people respond significantly faster when a) exposed to brighter flicker compared to darker flicker (104cdm^2 vs 52cdm^2 and 208cdm^2 vs 52cdm^2) and b) the onset of the task stimulus is in phase compared to other ISI conditions. This is in line with number of previous studies (Busch & VanRullen, 2010; Busch, Dubois, & VanRullen, 2009; Jaegle & Ro, 2014; Mathewson et al., 2011; Mathewson, et al., 2012; Romei et al., 2010; Romei et al., 2012).

The third experiment (section 2.4) was designed to see whether the activity at other low frequencies might be of more importance to the Stroop effect. Specifically, this experiment examined the effect of 6Hz, 8Hz and 10Hz flicker primes at three different ISIs preceding the Stroop task. There was no interaction between frequency and congruency; the Stroop effect was not differently modulated by any of the tested frequencies. So, no conclusions about a diminished Stroop effect and a role for alpha or delta in long-range (interbrain area) communication were supported by this study. However, this experiment did show that people exposed to 10Hz flicker were significantly faster, compared to 6Hz and 8Hz. It is consistent with the proposal by Herrmann (2001) that 10Hz may be a frequency of special importance due to increased neural responses produced to lights flickering at 10Hz compared with closely adjacent frequencies. As a consequence, subsequent experiments in the thesis concentrated on using 10 Hz flicker stimulation.

The fourth experiment (section 3.3) investigated whether the external alpha entrainment limits information processing in the neuronal representation associated with the spatial location where the entrainment is applied. This has been previously established at the interhemispheric scale as visual entrainment of the left hemifield inhibits information processing in the right hemisphere (which processes the flicker) and enhances it in the left hemisphere (Marshall, O'Shea, Jensen, Bergmann, 2015; Rihs, Michel, & Thut, 2007; Romei et al., 2010; Thut & Miniussi, 2009). The fourth experiment examined whether such a mechanism might also take place on a retinotopically smaller scale (2-4 visual degrees) within a hemisphere.

The study examined whether stimulating the target location or an adjacent mask, differentially effected detection with flicker phase. This was formulated as a possible explanation for the discrepancy in results between Mathewson et al., (2012) (who stimulated both the location of a mask that surrounded their target and the target location itself) and Spaak et al., (2014) (who stimulated only the target location). Specifically, it was theorised that when neural activity at the location of the mask is stimulated the salience of the mask is inhibited at time points when the primed alpha activity is high, and this will make the target easier to detect at those times. In contrast, when neural activity at the location of the target is directly stimulated the detection of the target is inhibited at time points when the primed alpha activity is high and

facilitated when it is low. Hence, the same mechanism for the phasic inhibition of spatial areas could produce both conflicting results.

The results showed that people performed significantly differently depending on whether the target or mask locations were stimulated; however the hypothesised reversal effect was not achieved and so this manipulation could not account for differences between Mathewson et al., (2012) and Spaak et al., (2014). Thus, the spatial inhibition observed on the interhemispheric scale,- i.e. high alpha amplitude in a hemisphere limits perception and improves its processing in the opposite hemisphere, was not apparent on a more localised spatial scale.

In the next study, we focussed on differential demands on spatial attention. Every visual task which we do requires us to allocate spatial attention to a specific location in space. At the same time, we monitor our surroundings for things which might be more important, so we can swiftly switch attention to new important locations. Some researchers suggest that attentional mechanisms try to predict the place in space where the salient event might occur, and then allocate neuronal resources to that location (Bubic, Yves von Cramon, & Schubotz, 2010). Alpha phase dynamics, which control discrete perception/attention (e.g. GBI hypothesis) might play a key role in fast switching neuronal resources to stream information from predicted location (when alpha in peak phase state) and from uncertain, unpredicted location (alpha trough phase state).

That idea was tested in the fifth experiment (section 3.4). In other words, this experiment tested the influence of spatial uncertainty of the target in modulating the relationship between the phase of alpha activity and perception. The author was interested in whether high and low uncertainty regarding target locations could lead to a different relationship in the time course of visually induced alpha oscillations and target detection. It was theorised that for the highly uncertain target locations, the optimal moment for perceiving it would be out of phase with the entrained alpha prime. However, for the target whose spatial location is cued and so leads to automatic allocation of attention (low spatial uncertainty), the optimal time window for perceiving it would be in phase with the entrained alpha oscillation. The idea originated from observing discrepancies in the results of Mathewson et al., (2012) and Spaak et al., (2014) (details in section 3.1). This effect was expected as the first author always presented targets in one place, so its spatial location was highly predicted and participants were best when the target was presented

in phase with entrained alpha. The latter author presented targets randomly in one of two possible locations and participants were best when target was presented out of phase.

The results confirmed the hypothesis and showed that when participants were exposed to spatially uncertain targets, they were the most likely to perceive it when it was presented at a time point out of phase of with the timing of the alpha prime. On the other hand, when the same participants were exposed to a cued target location, they were the most likely to spot the target when it is presented in phase with ongoing alpha. This experiment presented a plausible explanation for the central idea that opposite alpha phases are optimal for tasks characterised by low and high spatial uncertainty.

Finally, a sixth experiment (chapter 4) investigated the neuronal dynamics behind the behavioural finding that spatial uncertainty interacts with alpha phase to modulate visual detection. To examine this, specifically the mid-latency of extrema alpha power (LofEAP) was measured using EEG to quantify the alpha neuronal dynamics and to compare the effects of two different levels of target's spatial uncertainty. It was hypothesised that when the target location is uncertain – top-down alpha neuronal dynamics are engaged in monitoring multiple locations and switching attentional resources. However, when the target location was cued (pre-guided), attentional resources are automatically allocated to a specific region of visual space. In this instance, there are fewer demands for higher attentional processing, and so the bottom-up alpha neuronal dynamics dominate. The EEG results supported the existence of these mechanisms. For highly uncertain targets, the latency of extrema alpha power (LofEAP) was detected earlier in anterior electrodes rather than posterior electrodes. The opposite result was observed for targets at spatially cued locations. Thus, it seems plausible to suggest that alpha oscillations play a role in both local (bottom-up) and inter-area (top-down) neuronal communications. The dominance of specific communication pathways depends on the task demands, which is either more local (perceptual) or it involves recruiting top-down guided processes (i.e. directing visual attention and decision making).

These observed alpha dynamics are in line with the findings by Kawaguchi et al., (1993). The authors observed the phase relationships between cortical areas during alpha photic driving and argued that there is a substantial phase shift in elicited activity between occipital and frontal regions (see also Herrmann, 2001). Li, Gratton, Yao, & Knight, (2010) proposed control of bottom-up and top-down attention depends on differential contributions from parietal and frontal alpha (and other low frequency) activity. It might

indicate the presence of two sources of alpha generators, which project in a top-down and bottom-up direction and are engaged by differential task demands. In one condition (high SU) top down generators may dominate while in the second condition (low SU) the bottom-up generators may dominate.

The findings of the EEG experiment about the top-down and bottom-up dynamics is also supported by a study on the role of alpha oscillations in the top-down control in attentional selection (Foxe & Snyder, 2011). These authors concluded that when the brain is involved in the attentionally challenging task, it is beneficial to direct attention to the expected stimulus location so that the brain can allocate neuronal resources in a specific location before the arrival of the stimulus. The authors proposed that alpha neuronal dynamics were involved in this process. Specifically, neuronal representation of the visual space where the target is expected is characterised by lower-alpha amplitude and higher gamma frequency activity (in line with ITH). Meanwhile, other neuronal representations are 'flooded' with high alpha amplitudes, which restricts information processing and limits perception (Foxe & Snyder, 2011).

Such a mechanism of information gating was also reported by Fu et al., (2001) and is in line with ITH (Klimesch et al., 2007). Specifically, Fu et al. (2001) suggested that alpha oscillations in the inferior parietal cortex are implicated in the engagement and maintenance of visual attention. It is also in line with Smith (2005) and Cooper, Croft, Dominey, Burgess, & Gruzelier, (2003) where the authors discuss switching between external sensory and internal mental processing via alpha phase dynamics.

Hanslmayr and colleagues (2007) suggest that the level of alpha phase coherence correlates with perceptual performance. Specifically, increased alpha phase coherence shifts information processing towards internal representations and decreased alpha coherence guides processing towards external stimuli. Similar observations were reported by Todd & Fougner (2005), who observed that a high level of memory load causes inattention blindness. Both studies suggest that high alpha coherence (resulting in high alpha amplitude) in occipital regions limits perception from the external world focusing resources towards internal representations; and opposite low alpha occipital coherence allows efficient processing of external stimuli. Therefore, possibly, this thesis focuses on the latter case, as in all experiments, participants were asked to focus on external visual representations. Hence, if it can be extrapolated that external stimulation drives low posterior and high anterior alpha amplitude dynamics, it would be beneficial to control that in the future experiments. Also, it would be interesting to investigate whether

the same phase dynamics as achieved in the current experiment would exist if opposite to assumed amplitudes (low-posterior, high-anterior) dynamics would be induced (by rTMS instead of visual prime). Also, research by Dugue (see section 1.2.3) indicated that anterior and posterior alpha oscillations momentary sensitivity for information processing are at opposite alpha phases (anterior in-phase; posterior out of phase of ongoing alpha). These are consistent with observations by Herrmann (2001), who also found opposite alpha phase dynamics between occipital and frontal electrodes using external visual stimulation to elicit alpha oscillatory dynamics. It is also consistent with opposing phase relationships in the fifth and in behavioural results of the sixth experiment.

Subsequently, when stimulation originates from top-down or bottom-up, the alpha phases detected in anterior and posterior regions are opposite (two out of three authors researched 10Hz – mid alpha). These findings appear to be reflected in the EEG results in the current thesis. In our case, highly spatially uncertain tasks have dominant top-down mid alpha dynamics, but spatially certain targets lead to dominant bottom-up neuronal dynamics.

In our spatially certain, bottom-up alpha dynamics dominant task, people were the best in detecting the target in phase with visually induced alpha. Interestingly, Dugue, Marque, & VanRullen (2011), when alpha phase dynamics were induced using TMS in the right occipital region, people were more likely to report phosphenes occurring out of phase with the elicited activity. It may be consistent with the proposal that the spatially uncertain condition of our task is dependant upon top-down alpha activity and the **time required to propagate the signal between cortical areas results in a phase shift**. Hence, in both Dugue and our study, visual processing was dependent upon higher processing to either shift attention or generate an illusory percept.

However, there are several factors which might arguably make that direct comparison questionable. The same alpha phases are not compared in the current thesis and the above paper. We determined our alpha phase position based on the timing of the visual entrainer; i.e., the onset of the last alpha visual prime was our point of reference for the target onset time and subsequently for behavioural performance. In contrast, Dugue et al., (2011) used TMS induced phosphene to create signal input; that signal avoided delays caused by transmission between the retina and visual regions. So, it introduced the temporal variable and made

a direct comparison between studies difficult. On the other hand, several studies suggest that delay is about 100ms which is the one cycle of 10Hz alpha, which was used for entrainment in elaborated experiments (Amano et al., 2006; Masquelier, Albantakis, & Deco, 2011; van der Helm, 2017). So, if that is taken into account, arguably comparisons can be considered legitimate.

Each experiment in this thesis has probed different aspects of alpha oscillations' role in the control of inhibition and top-down/bottom-up neuronal dynamics. First, the three experiments (section 2.2, 2.3, 2.4) in chapter two were focused on alpha oscillations as a facilitator of global long-range communication, which is engaged in complex cognitive tasks (to be precise, all the experiments in this thesis with certain scope, investigated the role of alpha oscillations in cross cortex neuronal communication).

The fourth experiment shifted towards an alpha role in gating perception and explored the role of ITH hypothesis, by examining if alpha could lead to highly spatially localised inhibition. The fifth (see section 3.4) experiment focused on exploring the GBI hypothesis as it was interested in the optimal alpha phase position for perceiving spatially certain and uncertain targets. Which crucially, investigated long-range versus local neuronal communication. That experiment also brought together the idea about the role of alpha in long-range neuronal communication (top-down) and perception (bottom-up), which was subsequently tested using EEG.

The findings of the last two experiments (fifth and sixth) broaden our understanding of how mid-alpha phase might participate in controlling the detection of objects depending on their spatial uncertainty characteristics. Hence, perception depends not only on the internal neuronal alpha dynamics but also on the type of visual task, which participant was undertaking. This difference may highlight the role of two various neuronal alpha sources which dominate in both scenarios. When the target location is uncertain, top-down alpha dynamics dominate, and visual search and decision making prefrontal driven processes are engaged. However, when the target location is pre-guided, bottom-up alpha dynamics dominate as short, more local posterior alpha networks are possibly engaged.

So far, this discussion focused mainly on the fifth and sixth experiment; however, previous experiment four (section 3.3) shows us how ITH and GBI hypothesis are interlinked. Romei et al. (2010) previously demonstrated that ITH (high alpha power inhibits perception and low – enhances it) and GBI (peak alpha

phase inhibits perception and trough enhances it) could not be considered in separation. In their research, target visibility was significantly modulated by TMS alpha stimulation, relative to both alpha amplitude and phase. Alpha stimulation selectively impaired visual detection in the visual field opposite to the stimulated hemisphere, while enhancing detection ipsilaterally, which is in line with ITH. Targets were easily detected when they were processed in the neuronal representation characterised by low alpha amplitude and in phase. On the other hand, targets detection was impaired when they were processed in the neuronal representation characterised by high alpha amplitude and in phase.

Another study shows that when TMS is applied centrally (between hemispheres – in a middle of a coronal plane) to the posterior parietal (or ACC) cortex and the target is also presented centrally, the best detection is achieved when the stimulus is presented out of alpha phase with the stimulating pulse and the worst detection is reported in phase with the stimulation (Jaegle & Ro, 2014). That result closely reflects the outcome of the fourth experiment and also Mathewson et al., (2012) experimental design and results. In both the Jaegle & Ro (2014) and Mathewson et al. (2012) studies, stimuli were presented centrally. Hence based on this limited comparison, it can be suggested that alpha applied centrally might drive distinct alpha phase/perception dynamics compared to lateral entrainment. Hence, a valid question for the further investigation may be asked: how both: 1) central versus lateral presentation of the brief target 2) alpha high vs low amplitude and alpha in phase vs out of phase target presentation, may influence discrete perception. This thesis only partially investigates the above, by investigating the role of amplitude on a small retinotopic scale in centrally presented paradigm (section 3.3) and by manipulating alpha phase in laterally presented paradigms (section 3.4 and chapter four). It would be beneficial if the future research could approach the problem of 1) central vs lateral presentation, 2) alpha amplitude and 3) alpha phase globally; as current research has only been focusing on individual elements of the problem. Probing all elements of the jigsaw might broaden our understanding of the role of alpha oscillations in discrete perception and attention.

In retrospect, several elements of the experimental design could be improved. Alpha oscillations could be elicited in different ways, such as visual, magnetic or electric stimulation. Magnetic and electric

stimulation relatively directly influence neuronal dynamics; however, they are invasive and expensive. Visual entrainment, especially within mid alpha frequency is robust and cost-effective. On the other hand we do not know what the extent of the visual prime influence on the neural network is and whether there are certain conditions, which alleviate or block that process. The author of this thesis did not find any studies which directly compared visual, magnetic and electric entrainment and how they differently influence neuronal dynamics.

Another potential limitation is related to the individual variability of the mid-alpha resting state. It might be beneficial in future studies to adjust the entrainment frequency to the individual mid alpha resting state. A number of studies have linked the function of alpha to individual variations, hence they adjusted alpha entrainment to the individual frequency (Grandy et al., 2013; Christoph Herrmann, Rach, Neuling, & Strüber, 2013; Neuling, Rach, & Herrmann, 2013). Mathewson, for example, in recent experiments shifted to adjusting mid alpha to unique individual frequency (Mathewson et al., 2014; Sayeed et al., 2017). Nonetheless, individual adjustment is likely to have no impact if we consider Herrmann (2001) study on resonant frequencies. The author used 10Hz entrainment across all subjects and achieved a strong resonant neuronal response.

In the EEG study, we tried to capture in four-time windows, the neuronal dynamics related to the external photic entrainment and internal neuronal top-down alpha oscillatory response. Four 150ms temporal windows were taken from the onset of the target, which was, depending on the condition 100ms or 150ms **after** the onset of the last entrainer. In retrospect, it would be interesting to see what is happening regarding neuronal dynamics in that period just before the onset of the last entrainer, how the visual entrainment is building up neuronal synchrony with that external flicker. Hence, future studies should consider extending the observation of neuronal dynamics into the pre-target period. Additionally, the arrow was presented during the last 100ms of the visual prime, which was 100 or 150ms before the target. It might allow participants to change their gaze and potentially contaminate foveal with parafoveal perception/vision. That design could be potentially reconsidered as well.

On the other hand, participants were asked to keep their eyes focused on the cross and spread their attention to both possible locations. Thus, we attempted to control unnecessary gazing; however, it would

be safer to control eye movement by using the eye tracker to eliminate trials where participant gazed away from the central cross.

LofEAP was used as an indicator of alpha oscillation dynamics. Initially, we attempted to analyse 9.5-10.5 bandpass event-related potentials. However, the baseline was unstable, so we decided to calculate the LofEAP instead. It theoretically shifted minima (see fig. 4.2) which in theory does not constitute a problem, however, a good practice is to minimise the number of interventions in the data to avoid interference of uncontrolled factors which might influence the results. Also, in retrospect, we could use phase-locking index PLI or phase-locking value, which is the most currently used to estimate functional connectivity between regions instead of LofEAP (Lopes da Silva, 2013).

In this thesis, we mainly focused on investigating the role of the alpha phase. We used alpha flicker in order to establish for a very brief period the position of the alpha phase. Which in consequence, virtually (signal conduction delay) allowed us to present targets in expected timepoints, (e.g. in or out of phase). After the second experiment, we did not directly manipulate alpha amplitude, and we did not measure the consequences of that manipulation. However, ITH allows us to draw theoretical assumptions about the alpha amplitude dynamics. In the 5th experiment testing spatial uncertainty (section 3.4) only one hemifield was stimulated with regular alpha prime (the second was always stimulated with the sham), hence the neuronal representation of that hemifield, (e.g. right hemisphere), had theoretically information processing limited as it was flooded with induced high alpha amplitudes (Klimesch et al., 2007). Hence, the other hemisphere probably was characterised by low alpha amplitude. However, this is only theoretical speculation as current study did not investigate that. Hence, it would be interesting to see how manipulation of the alpha amplitude and also phase together might influence neuronal dynamics and behaviour. Therefore, the experiment investigating directly how mid alpha phase and amplitude are interlocked together in coordinating perceptual and attentional processes would benefit our understanding of how the brain allocates resources for the efficient perception.

Behavioural results of the EEG experiment (see 4.3.1) are intriguing in the light of our knowledge about neuronal underpinnings of local and global perception - Nevon figure (Fink et al., 1997; Navon, 1977). Global features tend to be processed by the right and local features by the left hemisphere. It can be argued

that high SU tasks where a participant has to observe two possible locations in wide visual field angle employ global perception. On the other hand, in low SU tasks where participant has to observe only one pre-suggested location, employ more local perception. Therefore someone might suggest that high SU tasks involve dominance of global - right hemisphere and low SU tasks might involve dominance of more local – left hemisphere perception. Hence, we are interested whether SU level might influence performance in both hemispheres differently. If we accept that left hemifield stimulation is predominantly processed by the right hemisphere and vice versa, we can draw the following observations. A significant interaction between SU and hemifield in chapter four behavioural results (see figure 4.4) show that level of SU significantly influenced performance in both hemispheres differently. People in low SU task (more local perception) were better in detecting right than left hemifield presented targets. So, the right hemifield stimuli were predominantly processed in the left hemisphere, and the advantage of the left hemisphere in processing the local features might cause that difference in performance between low and high SU tasks. Therefore, the cognitive load of local and global features in both high and low SU could also potentially influence the interhemispheric dynamics of the above task.

This interesting observation should be further investigated. It would be interesting to design a similar experiment where participants instead of detecting the briefly presented dots as targets, would be instructed to detect local and global features in Navon figure. That would test whether specific properties of alpha phase and amplitude might preferentially process tasks, where either global or local features are targeted. That experiment could also test alpha interhemispheric power dynamics. For example it could be hypothesised that right hemisphere low alpha power would be the most efficient in processing left hemifield displayed tasks which are engaging global features; and vice versa, left hemisphere low alpha power would be the most efficient in processing right hemifield tasks engaging local features.

Another interesting factor worth considering here are the differences between original Mathewson et al., (2012) paradigm and low SU paradigm in the fifth experiment (section 3.4), which was designed to emulate Mathewson et al., (2012) paradigm. However, there were points of variation between the two paradigms. In the first one, participants were always required to look at one point in space where the target **always** appeared. In the latter, displayed arrow cue directed participant's attention to the location of the target; so cue is a bottom-up signal which automatically directs attention to the location where the

target may be presented, but unlike the original paradigm it is equally likely to appear in the opposite location. However crucially, low SU paradigm, which used low level, bottom-up attentional signal, successfully replicated Mathewson's paradigm. That might support the notion that Mathewson's task is critically dependent on attention being allocated to a location prior to the appearance of a target. Interestingly, the short ISIs in the current paradigm allow little time for disengaging attention and reallocating it. It is possible if the ISIs were longer the absence of certainty in the appearance of the target at the location might have caused a divergence from Mathewson's paradigm.

In summary, this thesis has shown that mid alpha (around 10Hz) oscillations play a unique role in neuronal communication, as the brain would not invest scarce energy to make that bandpass the most energetically dominant. Also, we confirmed that mid-alpha phase determines the probability of detection of a briefly presented target. Also, it was shown here that the optimal alpha phase for detecting briefly presented targets differs depending on the level of spatial uncertainty of that target. Targets at non-predictable locations were more likely to be detected at a trough in the phase of alpha activity while those at cued locations were most likely to be detected in-phase. Hence, the likelihood of detecting briefly presented object depends not only on the internal neuronal alpha dynamics but also on the type of visual task. This difference may highlight the role of two different neuronal alpha sources which dominate in the different scenarios. When the target location was uncertain, top-down alpha dynamics dominate. However, when the target location is pre-guided, bottom-up alpha dynamics dominate. Also, we confirmed Hanslmayr's suggestion that alpha oscillations play a role in attentional and perceptual mechanisms (Hanslmayr et al., 2005). We confirmed that neuronal oscillations (within alpha range) play a role in information processing in the human brain, they conduct information across the cortex and create momentary temporal windows optimal for visual information to enter the cognitive system.

In the fourth experiment (section 3.3), we tried to replicate findings of interhemispheric alpha role in managing information flow/perception into centrally presented on a small retinotopically scale paradigm. There was no evidence in the current study that stimulated a small area in the visual field led to expected reverse detection accuracy of the target when the target vs surround of the target was entrained visually.

Although the interaction effect between ISI and entrainer type (superimposed vs adjacent to target) did not produce expected reverse effect, it was significant. Besides, in one condition entrainer and the mask were spatially superimposed on the other they were adjacent. Hence, it is interesting whether the adjacent mask in one of the conditions could influence the target sensitivity. As there were no significant differences in the rate of errors for each type of entrainer (entrainer type main effect), there is no evidence that this effect existed.

Brain networks have a different function depending on the time and their configuration. That function is controlled by low-frequency neuronal oscillations. Meaning of an alpha signal within these networks depends on the function of the network. If the function of the network is to direct attention either more focally or diffusely, that means that alpha possibly regulates the network in that way. Alpha is always doing the same: inhibition or release, but the way how it expresses itself depends on the function of the network at specific point in time. That alpha mechanism operates in motor functions (mu rhythm) which regulate inhibition and release; as well as in cognitive functions where it directs resources towards external world, or internal cognitive processes. This thesis proposes additional cognitive regulatory alpha role. Neuronal network controlled by alpha directs resources to either spatially certain point in space or monitor another location for possible salient information. Therefore, what alpha is doing in the neuronal network depends on the function of the network. This thesis attempted to investigate that alpha contribution in neuronal network dynamics and further, in understanding human cognition.

References

- Adjamian, P. (2014). The Application of Electro- and Magneto-Encephalography in Tinnitus Research – Methods and Interpretations. *Frontiers in Neurology*, 5, 228. <https://doi.org/10.3389/fneur.2014.00228>
- Adrian, E. D., & Matthews, B. H. C. (1934). The berger rhythm: Potential changes from the occipital lobes in man. *Brain*, 57(4), 355–385. <https://doi.org/10.1093/brain/57.4.355>
- Akam, T. E., & Kullmann, D. M. (2012). Efficient “Communication through Coherence” Requires Oscillations Structured to Minimize Interference between Signals. *PLoS Computational Biology*, 8(11). <https://doi.org/10.1371/journal.pcbi.1002760>
- Babiloni, C., Binetti, G., Cassarino, A., Dal Forno, G., Del Percio, C., Ferreri, F., ... Rossini, P. M. (2006). Sources of cortical rhythms in adults during physiological aging: A multicentric EEG study. *Human Brain Mapping*, 27(2), 162–172. <https://doi.org/10.1002/hbm.20175>
- Barlow, J. S. (1960). Rhythmic activity induced by photic stimulation in relation to intrinsic alpha activity of the brain in man. *Electroencephalography and Clinical Neurophysiology*, 12(2), 317–326. [https://doi.org/10.1016/0013-4694\(60\)90005-5](https://doi.org/10.1016/0013-4694(60)90005-5)
- Bartels, A., & Zeki, S. (2006). The temporal order of binding visual attributes. *Vision Research*, 46(14), 2280–2286. <https://doi.org/10.1016/j.visres.2005.11.017>
- Bartley, S. H. (1937). The neural determination of critical flicker frequency. *Journal of Experimental Psychology*, 21(6), 678–686. <https://doi.org/10.1037/h0061043>
- Başar, E., Başar-Eroglu, C., Karakaş, S., & Schürmann, M. (2000). Brain oscillations in perception and memory. *International Journal of Psychophysiology*, 35(2–3), 95–124. [https://doi.org/10.1016/S0167-8760\(99\)00047-1](https://doi.org/10.1016/S0167-8760(99)00047-1)
- Bauer, F., Cheadle, S. W., Parton, A., Muller, H. J., & Usher, M. (2009). Gamma flicker triggers attentional selection without awareness. *Proceedings of the National Academy of Sciences*, 106(5), 1666–1671. <https://doi.org/10.1073/pnas.0810496106>
- Bench, C. J., Frith, C. D., Grasby, P. M., Friston, K. J., Paulesu, E., Frackowiak, R. S. J., & Dolan, R. J. (1993). Investigations of the functional anatomy of attention using the stroop test. *Neuropsychologia*, 31(9), 907–922. [https://doi.org/10.1016/0028-3932\(93\)90147-R](https://doi.org/10.1016/0028-3932(93)90147-R)
- Benedek, M., Bergner, S., Könen, T., Fink, A., & Neubauer, A. C. (2011). EEG alpha synchronization is related to top-down processing in convergent and divergent thinking. *Neuropsychologia*, 49(12), 3505–3511. <https://doi.org/10.1016/j.neuropsychologia.2011.09.004>
- Benedek, M., Jauk, E., Beaty, R. E., Fink, A., Koschutnig, K., & Neubauer, A. C. (2016). Brain mechanisms associated with internally directed attention and self-generated thought. *Scientific Reports*, 6. <https://doi.org/10.1038/srep22959>
- Benedek, M., Schickel, R. J., Jauk, E., Fink, A., & Neubauer, A. C. (2014). Alpha power increases in right parietal cortex reflects focused internal attention. *Neuropsychologia*, 56(1), 393–400. <https://doi.org/10.1016/j.neuropsychologia.2014.02.010>
- Berry, L. A. (1964). Wave hop theory of long distance propagation of low-frequency radio waves. *RADIO SCIENCE Journal of Research NBSjUSNC-URSI*, 68(12), 1275–1284. Retrieved from http://nvlpubs.nist.gov/nistpubs/jres/68D/jresv68Dn12p1275_A1b.pdf
- Beverina, F., Palmas, G., Silvoni, S., Piccione, F., & Giove, S. (2003). User adaptive BCIs: SSVEP and P300 based interfaces. *PsychNology Journal*, 1(4), 331–354.
- Billah, K. Y., & Scanlan, R. H. (1991). Resonance, Tacoma Narrows bridge failure, and undergraduate physics textbooks. *American Journal of Physics*, 59(2), 118–124. <https://doi.org/10.1119/1.16590>

- Bollimunta, A., Chen, Y., Schroeder, C. E., & Ding, M. (2008). Neuronal Mechanisms of Cortical Alpha Oscillations in Awake-Behaving Macaques. *Journal of Neuroscience*, 28(40), 9976–9988. <https://doi.org/10.1523/JNEUROSCI.2699-08.2008>
- Bollimunta, A., Mo, J., Schroeder, C. E., & Ding, M. (2011). Neuronal Mechanisms and Attentional Modulation of Corticothalamic Alpha Oscillations. *Journal of Neuroscience*, 31(13), 4935–4943. <https://doi.org/10.1523/JNEUROSCI.5580-10.2011>
- Bonnefond, M., & Jensen, O. (2013). The role of gamma and alpha oscillations for blocking out distraction. *Communicative and Integrative Biology*, 6(1), 2–5. <https://doi.org/10.4161/cib.22702>
- Bonnefond, M., & Jensen, O. (2015). Gamma activity coupled to alpha phase as a mechanism for top-down controlled gating. *PLoS ONE*, 10(6), e0128667. <https://doi.org/10.1371/journal.pone.0128667>
- Bonnefond, M., Kastner, S., & Jensen, O. (2017). Communication between Brain Areas Based on Nested Oscillations. *Eneuro*, 4(2), ENEURO.0153-16.2017. <https://doi.org/10.1523/ENEURO.0153-16.2017>
- Botvinick, M. M., Carter, C. S., Braver, T. S., Barch, D. M., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, 108(3), 624–652. <https://doi.org/10.1037/0033-295X.108.3.624>
- Boyle, M. R., & Frohlich, F. (2013). EEG feedback-controlled transcranial alternating current stimulation. *International IEEE/EMBS Conference on Neural Engineering, NER*, 140–143. <https://doi.org/10.1109/NER.2013.6695891>
- Bressler, S. L., & Menon, V. (2010). Large-scale brain networks in cognition: emerging methods and principles. *Trends in Cognitive Sciences*, 14(6), 277–290. <https://doi.org/10.1016/j.tics.2010.04.004>
- Busch, Dubois, J., & VanRullen, R. (2009a). The phase of ongoing EEG oscillations predicts visual perception. *Journal of Neuroscience*, 29(24), 7869–7876. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/19535598>
- Busch, N. A., Dubois, J., & VanRullen, R. (2009b). The Phase of Ongoing EEG Oscillations Predicts Visual Perception. *Journal of Neuroscience*, 29(24), 7869–7876. <https://doi.org/10.1523/JNEUROSCI.0113-09.2009>
- Busch, & VanRullen. (2010). Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proceedings of the National Academy of Sciences*, 107(37), 16048–16053. <https://doi.org/10.1073/pnas.1004801107>
- Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science*, 315(5820), 1860–1864. <https://doi.org/10.1126/science.1138071>
- Buzsáki, G. (2009). *Rhythms of the Brain*. *Rhythms of the Brain*. <https://doi.org/10.1093/acprof:oso/9780195301069.001.0001>
- Buzsáki, G., & Draguhn, A. (2004). Neuronal oscillations in cortical networks. *Science*, 304(5679), 1926–1929. <https://doi.org/10.1126/science.1099745>
- Canolty, R. T., Edwards, E., Dalal, S. S., Soltani, M., Nagarajan, S. S., Kirsch, H. E., ... Knight, R. T. (2006a). High gamma power is phase-locked to theta oscillations in human neocortex. *Science* (Vol. 313). <https://doi.org/10.1126/science.1128115>
- Canolty, R. T., Edwards, E., Dalal, S. S., Soltani, M., Nagarajan, S. S., Kirsch, H. E., ... Knight, R. T. (2006b). High gamma power is phase-locked to theta oscillations in human neocortex. *Science*, 313(5793), 1626–1628. <https://doi.org/10.1126/science.1128115>

- Canolty, Ryan T., & Knight, R. T. (2010). The functional role of cross-frequency coupling. *Trends in Cognitive Sciences*, 14(11), 506–515. <https://doi.org/10.1016/j.tics.2010.09.001>
- Cohen, M. X., & Ridderinkhof, K. R. (2013). EEG Source Reconstruction Reveals Frontal-Parietal Dynamics of Spatial Conflict Processing. *PLoS ONE*, 8(2). <https://doi.org/10.1371/journal.pone.0057293>
- Compton, R. J., Huber, E., Levinson, A. R., & Zheutlin, A. (2012). Is “conflict adaptation” driven by conflict? Behavioral and EEG evidence for the underappreciated role of congruent trials. *Psychophysiology*, 49(5), 583–589. <https://doi.org/10.1111/j.1469-8986.2012.01354.x>
- Cooper, N. R., Croft, R. J., Dominey, S. J. J., Burgess, A. P., & Gruzelier, J. H. (2003). Paradox lost? Exploring the role of alpha oscillations during externally vs. internally directed attention and the implications for idling and inhibition hypotheses. *International Journal of Psychophysiology*, 47(1), 65–74. [https://doi.org/10.1016/S0167-8760\(02\)00107-1](https://doi.org/10.1016/S0167-8760(02)00107-1)
- Cooper, R., & Mundy-Castle, A. C. (1960). Spatial and temporal characteristics of the alpha rhythm: A toposcopic analysis. *Electroencephalography and Clinical Neurophysiology*, 12(1), 153–165. [https://doi.org/10.1016/0013-4694\(60\)90068-7](https://doi.org/10.1016/0013-4694(60)90068-7)
- Corballis, M. C., Miller, A., & Morgan, M. J. (1971). The role of left-right orientation in interhemispheric matching of visual information. *Perception & Psychophysics*, 10(6), 385–388. <https://doi.org/10.3758/BF03210315>
- Cvetkovic, D., Simpson, D., & Cosic, I. (2006). Influence of sinusoidally modulated visual stimuli at extremely low frequency range on the human EEG activity. *Conference Proceedings : ... Annual International Conference of the IEEE Engineering in Medicine and Biology Society. IEEE Engineering in Medicine and Biology Society. Conference*, 1, 1311–1314. <https://doi.org/10.1109/IEMBS.2006.259565>
- D’Angelo, E., Mazzarello, P., Prestori, F., Mapelli, J., Solinas, S., Lombardo, P., ... Congi, L. (2011). The cerebellar network: From structure to function and dynamics. *Brain Research Reviews*, 66(1–2), 5–15. <https://doi.org/10.1016/j.brainresrev.2010.10.002>
- Daume, J., Gruber, T., Engel, A. K., & Frieze, U. (2017). Phase-Amplitude Coupling and Long-Range Phase Synchronization Reveal Frontotemporal Interactions during Visual Working Memory. *The Journal of Neuroscience*, 37(2), 313–322. <https://doi.org/10.1523/JNEUROSCI.2130-16.2017>
- de Graaf, T. A., Gross, J., Paterson, G., Rusch, T., Sack, A. T., & Thut, G. (2013). Alpha-Band Rhythms in Visual Task Performance: Phase-Locking by Rhythmic Sensory Stimulation. *PLoS ONE*, 8(3), e60035. <https://doi.org/10.1371/journal.pone.0060035>
- De Tré, G., & Zdrożny, S. (2015). *Soft computing in database and information management*. (J. Kacprzyk & W. Pedrycz, Eds.), *Springer Handbook of Computational Intelligence*. Berlin, Heidelberg: Springer Berlin Heidelberg. <https://doi.org/10.1007/978-3-662-43505-2>
- Del Percio, C., Brancucci, A., Bergami, F., Marzano, N., Fiore, A., Di Ciolo, E., ... Eusebi, F. (2007). Cortical alpha rhythms are correlated with body sway during quiet open-eyes standing in athletes: A high-resolution EEG study. *NeuroImage*, 36(3), 822–829. <https://doi.org/10.1016/j.neuroimage.2007.02.054>
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>
- Di Marzo Serugendo, G., Foukia, N., Hassas, S., Karageorgos, A., Mostéfaoui, S. K., Rana, O. F., ... Van Aart, C. (2004). Self-Organisation: Paradigms and Applications (pp. 1–19). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-540-24701-2_1
- Doesburg, S. M., Green, J. J., McDonald, J. J., & Ward, L. M. (2009). From local inhibition to long-

- range integration: A functional dissociation of alpha-band synchronization across cortical scales in visuospatial attention. *Brain Research*, 1303, 97–110.
<https://doi.org/10.1016/j.brainres.2009.09.069>
- Draper, I. T. (1974). *the Working Brain (an Introduction To Neuropsychology)*. *Journal of neurology, neurosurgery, and psychiatry* (Vol. 37). Penguin books. <https://doi.org/10.1136/jnnp.37.3.361-b>
- Dugue, L., Marque, P., & VanRullen, R. (2011). The Phase of Ongoing Oscillations Mediates the Causal Relation between Brain Excitation and Visual Perception. *Journal of Neuroscience*, 31(33), 11889–11893. <https://doi.org/10.1523/JNEUROSCI.1161-11.2011>
- Durup, G., & Fessard, A. (1935). I. L'électrencéphalogramme de l'homme. Observations psychophysiologicals relatives à l'action des stimuli visuels et auditifs. *L'année Psychologique*, 36(1), 1–32. <https://doi.org/10.3406/psy.1935.30643>
- Ekstrom, A. D., Caplan, J. B., Ho, E., Shattuck, K., Fried, I., & Kahana, M. J. (2005). Human hippocampal theta activity during virtual navigation. *Hippocampus*, 15(7), 881–889.
<https://doi.org/10.1002/hipo.20109>
- Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., & Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Cognitive Brain Research*, 20(3), 376–383. <https://doi.org/10.1016/j.cogbrainres.2004.03.009>
- Ermentrout, G. B., Galán, R. F., & Urban, N. N. (2008, August 1). Reliability, synchrony and noise. *Trends in Neurosciences*. Elsevier Current Trends. <https://doi.org/10.1016/j.tins.2008.06.002>
- Fan, J., Flombaum, J. I., McCandliss, B. D., Thomas, K. M., & Posner, M. I. (2003). Cognitive and brain consequences of conflict. *NeuroImage*, 18(1), 42–57.
<https://doi.org/10.1006/nimg.2002.1319>
- Feldman, J. (2013). The neural binding problem(s). *Cognitive Neurodynamics*, 7(1), 1–11.
<https://doi.org/10.1007/s11571-012-9219-8>
- Field, A. (2012). *Discovering statistics using SPSS* (third edit).
- Fink, A., & Benedek, M. (2014). EEG alpha power and creative ideation. *Neuroscience and Biobehavioral Reviews*, 44(100), 111–123. <https://doi.org/10.1016/j.neubiorev.2012.12.002>
- Fink, G. R., Marshall, J. C., Halligan, P. W., & Dolan, R. J. (1998). Hemispheric asymmetries in global/local processing are modulated by perceptual salience. *Neuropsychologia*, 37(1), 31–40.
[https://doi.org/10.1016/S0028-3932\(98\)00047-5](https://doi.org/10.1016/S0028-3932(98)00047-5)
- Fink, G. R., Marshall, J. C., Halligan, P. W., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1997). Hemispheric specialization for global and local processing: The effect of stimulus category. *Proceedings of the Royal Society B: Biological Sciences*, 264(1381), 487–494.
<https://doi.org/10.1098/rspb.1997.0070>
- Flanagan, J. A. (1996). Self-organisation in Kohonen's SOM. *Neural Networks*, 9(7), 1185–1197.
[https://doi.org/10.1016/0893-6080\(96\)00038-X](https://doi.org/10.1016/0893-6080(96)00038-X)
- Flint, A. C., & Connors, B. W. (1996). Two types of network oscillations in neocortex mediated by distinct glutamate receptor subtypes and neuronal populations. *Journal of Neurophysiology*, 75(2), 951–957. <https://doi.org/10.1152/jn.1996.75.2.951>
- Forel, A., & Meynert, T. (2014). The origins of EEG. In *Seventh Annual Meeting of the International Society for the History of the Neurosciences (ISHN)* (pp. 2–3).
- Forrest, M. D. (2014). Intracellular calcium dynamics permit a Purkinje neuron model to perform toggle and gain computations upon its inputs. *Frontiers in Computational Neuroscience*, 8(August), 1–19. <https://doi.org/10.3389/fncom.2014.00086>

- Foxe, J. J., & Snyder, A. C. (2011). The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Frontiers in Psychology*, 2(JUL), 1–13. <https://doi.org/10.3389/fpsyg.2011.00154>
- Freedman, N. L. (1963). Bilateral differences in the human occipital electroencephalogram with unilateral photic driving. *Science*, 142(3592), 598–599. <https://doi.org/10.1126/science.142.3592.598>
- Fries, P. (2005). A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, 9(10), 474–480. <https://doi.org/10.1016/j.tics.2005.08.011>
- Fries, P. (2009). Neuronal Gamma-Band Synchronization as a Fundamental Process in Cortical Computation. *Annual Review of Neuroscience*, 32(1), 209–224. <https://doi.org/10.1146/annurev.neuro.051508.135603>
- Fries, P. (2015). Rhythms for Cognition: Communication through Coherence. *Neuron*, 88(1), 220–235. <https://doi.org/10.1016/j.neuron.2015.09.034>
- Fu, K. M. G., Foxe, J. J., Murray, M. M., Higgins, B. A., Javitt, D. C., & Schroeder, C. E. (2001a). Attention-dependent suppression of distracter visual input can be cross-modally cued as indexed by anticipatory parieto-occipital alpha-band oscillations. *Cognitive Brain Research*, 12(1), 145–152. [https://doi.org/10.1016/S0926-6410\(01\)00034-9](https://doi.org/10.1016/S0926-6410(01)00034-9)
- Fu, K. M. G., Foxe, J. J., Murray, M. M., Higgins, B. A., Javitt, D. C., & Schroeder, C. E. (2001b). Attention-dependent suppression of distracter visual input can be cross-modally cued as indexed by anticipatory parieto-occipital alpha-band oscillations. *Cognitive Brain Research* (Vol. 12). [https://doi.org/10.1016/S0926-6410\(01\)00034-9](https://doi.org/10.1016/S0926-6410(01)00034-9)
- Fuchs, S., Andersen, S. K., Gruber, T., & Müller, M. M. (2008). Attentional bias of competitive interactions in neuronal networks of early visual processing in the human brain. *NeuroImage*, 41(3), 1086–1101. <https://doi.org/10.1016/j.neuroimage.2008.02.040>
- Ganzetti, M., & Mantini, D. (2013). Functional connectivity and oscillatory neuronal activity in the resting human brain. *Neuroscience*, 240, 297–309. <https://doi.org/10.1016/j.neuroscience.2013.02.032>
- GIBSON, J. J. (1958). Visually Controlled Locomotion and Visual Orientation in Animals. *British Journal of Psychology*, 49(3), 182–194. <https://doi.org/10.1111/j.2044-8295.1958.tb00656.x>
- Girolami, M. (1999). Self-Organising Neural Networks (pp. 47–75). Springer, London. https://doi.org/10.1007/978-1-4471-0825-2_4
- Goffaux, V., Mouraux, A., Desmet, S., & Rossion, B. (2004). Human non-phase-locked gamma oscillations in experience-based perception of visual scenes. *Neuroscience Letters*, 354(1), 14–17. <https://doi.org/10.1016/j.neulet.2003.09.029>
- Goldberg, M. E. (2000). *The control of gaze. Principles of neural science*. <https://doi.org/10.1036/0838577016>
- Goldberg, M. E., Kandel, E. R., Schwartz, J. H., & Jessell, T. M. (2000). *The Control of Gaze. Principles of Neural Science* (Vol. 3). <https://doi.org/10.1036/0838577016>
- Goldman, R., Stern, J., Jr, J. E., & Cohen, M. (2002). Simultaneous EEG and fMRI of the alpha rhythm. *Neuroreport*, 13(18), 2487–2492. <https://doi.org/10.1097/01.wnr.0000047685.08940.d0.Simultaneous>
- Goodman, R. (2012). William James. <https://doi.org/10.1093/oxfordhb/9780199219315.003.0004>
- Grandy, T. H., Werkle-Bergner, M., Chicherio, C., Lövdén, M., Schmiedek, F., & Lindenberger, U. (2013). Individual alpha peak frequency is related to latent factors of general cognitive abilities.

- NeuroImage*, 79(2013), 10–18. <https://doi.org/10.1016/j.neuroimage.2013.04.059>
- Gray, C. M., & Singer, W. (1989). Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex. *Proceedings of the National Academy of Sciences*, 86(5), 1698–1702. <https://doi.org/10.1073/pnas.86.5.1698>
- Gray, Charles M., König, P., Engel, A. K., & Singer, W. (1989). Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature*. <https://doi.org/10.1038/338334a0>
- Gregoriou, G. G., Paneri, S., & Sapountzis, P. (2015). Oscillatory synchrony as a mechanism of attentional processing. *Brain Research*, 1626, 165–182. <https://doi.org/10.1016/j.brainres.2015.02.004>
- Gross, J., Schmitz, F., Schnitzler, I., Kessler, K., Shapiro, K., Hommel, B., & Schnitzler, A. (2004). Modulation of long-range neural synchrony reflects temporal limitations of visual attention in humans. *Proceedings of the National Academy of Sciences*, 101(35), 13050–13055. <https://doi.org/10.1073/pnas.0404944101>
- Gross, Joachim, Schmitz, F., Schnitzler, I., Kessler, K., Shapiro, K., Hommel, B., & Schnitzler, A. (2004). Modulation of long-range neural synchrony reflects temporal limitations of visual attention in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 101(35), 13050–13055. <https://doi.org/10.1073/pnas.0404944101>
- Grossberg, S. (1976). Adaptive pattern classification and universal recording, II: Feedack. expectation, olfaction, and illusions. *Biological Cybernetics*, 23(23), 187–202.
- Gruzelier, J. (2009). A theory of alpha/theta neurofeedback, creative performance enhancement, long distance functional connectivity and psychological integration. *Cognitive Processing*, 10(1 SUPPL.), 101–109. <https://doi.org/10.1007/s10339-008-0248-5>
- Gulbinaite, R., van Viegen, T., Wieling, M., Cohen, M. X., & VanRullen, R. (2017). Individual alpha peak frequency predicts 10 Hz flicker effects on selective attention. *The Journal of Neuroscience*, 1163–17. <https://doi.org/10.1523/JNEUROSCI.1163-17.2017>
- Haegens, S., Nacher, V., Luna, R., Romo, R., & Jensen, O. (2011). α -Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmic inhibition of neuronal spiking. *Proceedings of the National Academy of Sciences*, 108(48), 19377–19382. <https://doi.org/10.1073/pnas.1117190108>
- Haenschel, C., Linden, D. E., Bittner, R. A., Singer, W., & Hanslmayr, S. (2010). Alpha phase locking predicts residual working memory performance in schizophrenia. *Biological Psychiatry*, 68(7), 595–598. <https://doi.org/10.1016/j.biopsych.2010.06.013>
- Händel, B. F., Haarmeier, T., & Jensen, O. (2011). Alpha oscillations correlate with the successful inhibition of unattended stimuli. *Journal of Cognitive Neuroscience*, 23(9), 2494–2502. <https://doi.org/10.1162/jocn.2010.21557>
- Händel, B., & Haarmeier, T. (2009). Cross-frequency coupling of brain oscillations indicates the success in visual motion discrimination. *NeuroImage*, 45(3), 1040–1046. <https://doi.org/10.1016/j.neuroimage.2008.12.013>
- Hanslmayr, S., Gross, J., Klimesch, W., & Shapiro, K. L. (2011). The role of alpha oscillations in temporal attention. *Brain Research Reviews*, 67(1–2), 331–343. <https://doi.org/10.1016/j.brainresrev.2011.04.002>
- Hanslmayr, S., Klimesch, W., Sauseng, P., Gruber, W., Doppelmayr, M., Freunberger, R., ... Birbaumer, N. (2007). Alpha phase reset contributes to the generation of ERPs. *Cerebral Cortex*, 17(1), 1–8. <https://doi.org/10.1093/cercor/bhj129>

- Hanslmayr, S., Klimesch, W., Sauseng, P., Gruber, W., Doppelmayr, M., Freunberger, R., & Pecherstorfer, T. (2005). Visual discrimination performance is related to decreased alpha amplitude but increased phase locking. *Neuroscience Letters*, *375*(1), 64–68. <https://doi.org/10.1016/j.neulet.2004.10.092>
- Hanslmayr, S., Pastötter, B., Bäuml, K. H., Gruber, S., Wimber, M., & Klimesch, W. (2008). The electrophysiological dynamics of interference during the stroop task. *Journal of Cognitive Neuroscience*, *20*(2), 215–225. <https://doi.org/10.1162/jocn.2008.20020>
- Hanslmayr, S., Volberg, G., Wimber, M., Dalal, S. S., & Greenlee, M. W. (2013). Prestimulus oscillatory phase at 7 Hz gates cortical information flow and visual perception. *Current Biology*, *23*(22), 2273–2278. <https://doi.org/10.1016/j.cub.2013.09.020>
- Hebb, D. O. (1949). The first stage of perception: growth of the assembly. *The Organization of Behavior*, (4), 60–78. [https://doi.org/10.1016/0301-0082\(84\)90021-2](https://doi.org/10.1016/0301-0082(84)90021-2)
- Hela, I. (1986). *The organisation of*. *EMBO Journal* (Vol. 5). <https://doi.org/10.1038/104006a0>
- Helfrich, Knepper, H., Nolte, G., Strüber, D., Rach, S., Herrmann, C. S., ... Engel, A. K. (2014). Selective Modulation of Interhemispheric Functional Connectivity by HD-tACS Shapes Perception. *PLoS Biology*, *12*(12). <https://doi.org/10.1371/journal.pbio.1002031>
- Hemmen, J. L. van, & Sejnowski, T. J. (2005). 23 Problems in Systems Neuroscience (Computational Neuroscience Series), 1–6. Retrieved from <http://www.amazon.ca/exec/obidos/redirect?tag=citeulike09-20&path=ASIN/0195148223%5Cnhttp://www.amazon.de/exec/obidos/redirect?tag=citeulike01-21&path=ASIN/0195148223%5Cnhttp://www.amazon.fr/exec/obidos/redirect?tag=citeulike06-21&path=ASIN/019514>
- Herring, J. D., Thut, G., Jensen, O., & Bergmann, T. O. (2015). Attention Modulates TMS-Locked Alpha Oscillations in the Visual Cortex. *Journal of Neuroscience*, *35*(43), 14435–14447. <https://doi.org/10.1523/JNEUROSCI.1833-15.2015>
- Herrmann, C. S. (2001). Human EEG responses to 1-100 Hz flicker: Resonance phenomena in visual cortex and their potential correlation to cognitive phenomena. *Experimental Brain Research*, *137*(3–4), 346–353. <https://doi.org/10.1007/s002210100682>
- Herrmann, Christoph S., Rach, S., Neuling, T., & Strüber, D. (2013). Transcranial alternating current stimulation: a review of the underlying mechanisms and modulation of cognitive processes. *Frontiers in Human Neuroscience*, *7*(June), 1–13. <https://doi.org/10.3389/fnhum.2013.00279>
- Herrmann, Christoph S., Strüber, D., Helfrich, R. F., & Engel, A. K. (2016). EEG oscillations: From correlation to causality. *International Journal of Psychophysiology*, *103*, 12–21. <https://doi.org/10.1016/j.ijpsycho.2015.02.003>
- Herzog, M. (2009). Binding Problem. *Encyclopedia of Neuroscience*, 388–391. https://doi.org/10.1007/978-3-540-29678-2_626
- Hipp, J. F., Engel, A. K., & Siegel, M. (2011). Oscillatory synchronization in large-scale cortical networks predicts perception. *Neuron*, *69*(2), 387–396. <https://doi.org/10.1016/j.neuron.2010.12.027>
- Huang, S., Rossi, S., Hämäläinen, M., & Ahveninen, J. (2014). Auditory conflict resolution correlates with medial-lateral frontal theta/alpha phase synchrony. *PLoS ONE*, *9*(10), e110989. <https://doi.org/10.1371/journal.pone.0110989>
- Hutchison, R. M., Womelsdorf, T., Allen, E. A., Bandettini, P. A., Calhoun, V. D., Corbetta, M., ... Chang, C. (2013). Dynamic functional connectivity: Promise, issues, and interpretations. *NeuroImage*, *80*, 360–378. <https://doi.org/10.1016/j.neuroimage.2013.05.079>

- Hwang, A. D., Higgins, E. C., & Pomplun, M. (2009). A model of top-down attentional control during visual search in complex scenes. *Journal of Vision*, 9(5), 25–25. <https://doi.org/10.1167/9.5.25>
- Inouye, T., Shinosaki, K., & Yagasaki, A. (1983). The direction of spread of alpha activity over the scalp. *Electroencephalography and Clinical Neurophysiology*, 55(3), 290–300. [https://doi.org/10.1016/0013-4694\(83\)90207-9](https://doi.org/10.1016/0013-4694(83)90207-9)
- Jaegle, A., & Ro, T. (2014). Direct control of visual perception with phase-specific modulation of posterior parietal cortex. *Journal of Cognitive Neuroscience*, 26(2), 422–432. https://doi.org/10.1162/jocn_a_00494
- Jasper, H. H. (1936). Cortical excitatory state and variability in human brain rhythms. *Science*, 83(2150), 259–260. <https://doi.org/10.1126/science.83.2150.259>
- Jasper, H., & Penfield, W. (1949). Electrocorticograms in man: Effect of voluntary movement upon the electrical activity of the precentral gyrus. *Archiv für Psychiatrie Und Nervenkrankheiten*, 183(1–2), 163–174. <https://doi.org/10.1007/BF01062488>
- Jaušovec, N., & Jaušovec, K. (2014). Increasing working memory capacity with theta transcranial alternating current stimulation (tACS). *Biological Psychology*, 96(1), 42–47. <https://doi.org/10.1016/j.biopsycho.2013.11.006>
- Jensen, & Mazaheri, A. (2010). Shaping Functional Architecture by Oscillatory Alpha Activity: Gating by Inhibition. *Frontiers in Human Neuroscience*, 4(November), 186. <https://doi.org/10.3389/fnhum.2010.00186>
- Jensen, O. (2002). Oscillations in the Alpha Band (9–12 Hz) Increase with Memory Load during Retention in a Short-term Memory Task. *Cerebral Cortex*, 12(8), 877–882. <https://doi.org/10.1093/cercor/12.8.877>
- Jensen, Ole, Bonnefond, M., & VanRullen, R. (2012). An oscillatory mechanism for prioritizing salient unattended stimuli. *Trends in Cognitive Sciences*, 16(4), 200–205. <https://doi.org/10.1016/j.tics.2012.03.002>
- Jensen, Ole, & Colgin, L. L. (2007). Cross-frequency coupling between neuronal oscillations. *Trends in Cognitive Sciences*, 11(7), 267–269. <https://doi.org/10.1016/j.tics.2007.05.003>
- Jensen, Ole, Gips, B., Bergmann, T. O., & Bonnefond, M. (2014). Temporal coding organized by coupled alpha and gamma oscillations prioritize visual processing. *Trends in Neurosciences*, 37(7), 357–369. <https://doi.org/10.1016/j.tins.2014.04.001>
- Jensen, Ole, Kaiser, J., & Lachaux, J. P. (2007). Human gamma-frequency oscillations associated with attention and memory. *Trends in Neurosciences*, 30(7), 317–324. <https://doi.org/10.1016/j.tins.2007.05.001>
- Kanai, R., Chaieb, L., Antal, A., Walsh, V., & Paulus, W. (2008). Frequency-Dependent Electrical Stimulation of the Visual Cortex. *Current Biology*, 18(23), 1839–1843. <https://doi.org/10.1016/j.cub.2008.10.027>
- Kashiwase, Y., Matsumiya, K., Kuriki, I., & Shioiri, S. (2013). Temporal dynamics of visual attention measured with event-related potentials. *PloS One*, 8(8), e70922. <https://doi.org/10.1371/journal.pone.0070922>
- Kaufmann, L., Koppelstaetter, F., Delazer, M., Siedentopf, C., Rhomberg, P., Golaszewski, S., ... Ischebeck, A. (2005). Neural correlates of distance and congruity effects in a numerical Stroop task: An event-related fMRI study. *NeuroImage*, 25(3), 888–898. <https://doi.org/10.1016/j.neuroimage.2004.12.041>
- Kawaguchi, T., Jijiwa, H., & Watanabe, S. (1993). The dynamics of phase relationships of alpha waves during photic driving. *Electroencephalography and Clinical Neurophysiology*, 87(3), 88–96.

[https://doi.org/10.1016/0013-4694\(93\)90115-C](https://doi.org/10.1016/0013-4694(93)90115-C)

- Keitel, C., Quigley, C., & Ruhnau, P. (2014). Stimulus-Driven Brain Oscillations in the Alpha Range: Entrainment of Intrinsic Rhythms or Frequency-Following Response? *Journal of Neuroscience*, 34(31), 10137–10140. <https://doi.org/10.1523/JNEUROSCI.1904-14.2014>
- Keitel, Christian, Andersen, S. K., & Müller, M. M. (2010). Competitive effects on steady-state visual evoked potentials with frequencies in- and outside the alpha band. *Experimental Brain Research*. <https://doi.org/10.1007/s00221-010-2384-2>
- Keitel, Christian, Thut, G., & Gross, J. (2017). Visual cortex responses reflect temporal structure of continuous quasi-rhythmic sensory stimulation. *NeuroImage*, 146, 58–70. <https://doi.org/10.1016/j.neuroimage.2016.11.043>
- Kelly. (2006). Increases in Alpha Oscillatory Power Reflect an Active Retinotopic Mechanism for Distracter Suppression During Sustained Visuospatial Attention. *Journal of Neurophysiology*, 95(6), 3844–3851. <https://doi.org/10.1152/jn.01234.2005>
- Kerns, J. G., Cohen, J. D., MacDonald, A. W., Cho, R. Y., Stenger, V. A., & Carter, C. S. (2004). Anterior Cingulate Conflict Monitoring and Adjustments in Control. *Science*, 303(5660), 1023–1026. <https://doi.org/10.1126/science.1089910>
- Kingdom, F. A. A., & Prins, N. (2010). *PSYCHOPHYSICS A PRACTICAL INTRODUCTION*. Academic Press Elsevier (Vol. 6).
- Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences*, 16(12), 606–617. <https://doi.org/10.1016/j.tics.2012.10.007>
- Klimesch, W., Freunberger, R., & Sauseng, P. (2010, June). Oscillatory mechanisms of process binding in memory. *Neuroscience and Biobehavioral Reviews*. <https://doi.org/10.1016/j.neubiorev.2009.10.004>
- Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews*, 53(1), 63–88. <https://doi.org/10.1016/j.brainresrev.2006.06.003>
- Klimesch, W., Sauseng, P., Hanslmayr, S., Gruber, W., & Freunberger, R. (2007). Event-related phase reorganization may explain evoked neural dynamics. *Neuroscience and Biobehavioral Reviews*, 31(7), 1003–1016. <https://doi.org/10.1016/j.neubiorev.2007.03.005>
- Kopell, N., Kramer, M. A., Malerba, P., & Whittington, M. A. (2010). Are Different Rhythms Good for Different Functions? *Frontiers in Human Neuroscience*, 4(1). <https://doi.org/10.3389/fnhum.2010.00187>
- Kosslyn, S. M., Pascual-Leone, A., Felician, O., Camposano, S., Keenan, J. P., Thompson, W. L., ... Alpert, N. M. (1999). The role of area 17 in visual imagery: Convergent evidence from PET and rTMS. *Science*, 284(5411), 167–170. <https://doi.org/10.1126/science.284.5411.167>
- Kraft, U. (2006). Train your Brain: Mental exercises with neurofeedback may ease symptoms of attention-deficit disorder, epilepsy and depression--and even boost cognition in healthy brains. *Scientific America: Mind*, (February).
- Kroger, W. S., & Schneider, S. A. (1959). An electronic aid for hypnotic induction: A pret, immary report. *International Journal of Clinical and Experimental Hypnosis*, 7(2), 93–98. <https://doi.org/10.1080/00207145908415812>
- Lakatos, P. (2005). An Oscillatory Hierarchy Controlling Neuronal Excitability and Stimulus Processing in the Auditory Cortex. *Journal of Neurophysiology*, 94(3), 1904–1911. <https://doi.org/10.1152/jn.00263.2005>
- Lakatos, Peter, Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of

- neuronal oscillations as a mechanism of attentional selection. *Science*, 320(5872), 110–113. <https://doi.org/10.1126/science.1154735>
- Landau, A. N., & Fries, P. (2012). Attention samples stimuli rhythmically. *Current Biology*, 22(11), 1000–1004. <https://doi.org/10.1016/j.cub.2012.03.054>
- Lange, J., Keil, J., Schnitzler, A., van Dijk, H., & Weisz, N. (2014). The role of alpha oscillations for illusory perception. *Behavioural Brain Research*, 271, 294–301. <https://doi.org/10.1016/j.bbr.2014.06.015>
- Laufs, H., Kleinschmidt, A., Beyerle, A., Eger, E., Salek-Haddadi, A., Preibisch, C., & Krakow, K. (2003). EEG-correlated fMRI of human alpha activity. *NeuroImage*, 19(4), 1463–1476. [https://doi.org/10.1016/S1053-8119\(03\)00286-6](https://doi.org/10.1016/S1053-8119(03)00286-6)
- Leij, A. R. Van Der, Sligte, I. G., Lamme, V. A. F., & Scholte, H. S. (2016). Bottom-up and top-down attention are independent Yair Pinto, 13(2013), 1–14. <https://doi.org/10.1167/13.3.16>
- Leonardo Chelazzi Earl Miller, John Duncn, R. D. (1993). A neural basis for visual search in inferior temporal cortex. *Nature*, 363(2–3), 345–347. <https://doi.org/10.1038/363345a0>
- Lewis, G. J., & Bates, T. C. (2013). The long reach of the gene. *Psychologist*, 26(3), 194–198. <https://doi.org/10.1162/jocn>
- Li, L., Gratton, C., Yao, D., & Knight, R. T. (2010). Role of frontal and parietal cortices in the control of bottom-up and top-down attention in humans. *Brain Research*, 1344, 173–184. <https://doi.org/10.1016/J.BRAINRES.2010.05.016>
- Linkenkaer-Hansen, K. (2004). Prestimulus Oscillations Enhance Psychophysical Performance in Humans. *Journal of Neuroscience*, 24(45), 10186–10190. <https://doi.org/10.1523/JNEUROSCI.2584-04.2004>
- Liotti, M., Liotti, M., Woldorff, M. G., Woldorff, M. G., Perez III, R., Perez III, R., ... Mayberg, H. S. (2000). An ERP study of the temporal course of the Stroop colour-word interference effect. *Neuropsychologia*, 38, 701–711. [https://doi.org/10.1016/S0028-3932\(99\)00106-2](https://doi.org/10.1016/S0028-3932(99)00106-2)
- Lisman, J. E., & Jensen, O. (2013). The Theta-Gamma Neural Code. *Neuron*, 77(6), 1002–1016. <https://doi.org/10.1016/j.neuron.2013.03.007>
- Lobier, M., Palva, J. M., & Palva, S. (2018). High-alpha band synchronization across frontal, parietal and visual cortex mediates behavioral and neuronal effects of visuospatial attention. *NeuroImage*, 165(July 2017), 222–237. <https://doi.org/10.1016/j.neuroimage.2017.10.044>
- Lopes da Silva, F. (2013). EEG and MEG: Relevance to neuroscience. *Neuron*, 80(5), 1112–1128. <https://doi.org/10.1016/j.neuron.2013.10.017>
- Lorincz, M. L., Kékesi, K. A., Juhász, G., Crunelli, V., & Hughes, S. W. (2009). Temporal Framing of Thalamic Relay-Mode Firing by Phasic Inhibition during the Alpha Rhythm. *Neuron*, 63(5), 683–696. <https://doi.org/10.1016/j.neuron.2009.08.012>
- Luria, A. R. (1932). *The nature of human conflicts or emotion, conflict and will: An objective study of disorganisation and control of human behaviour* (Vol. 7). Liveright. <https://doi.org/10.1097/00001888-193211000-00036>
- Luriiia, A. R. (Aleksandr R. (1973). *The working brain: an introduction to neuropsychology*, [by] A. R. Luria; translated [from the Russian MS.] by Basil Haigh. Basic Books.
- MacDonald, A. W., Cohen, J. D., Andrew Stenger, V., & Carter, C. S. (2000). Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science*, 288(5472), 1835–1838. <https://doi.org/10.1126/science.288.5472.1835>
- Makeig, S., Westerfield, M., Jung, T. P., Enghoff, S., Townsend, J., Courchesne, E., & Sejnowski, T. J.

- (2002). Dynamic brain sources of visual evoked responses. *Science*, 295(5555), 690–694. <https://doi.org/10.1126/science.1066168>
- Maris, E., Fries, P., & van Ede, F. (2016). Diverse Phase Relations among Neuronal Rhythms and Their Potential Function. *Trends in Neurosciences*, 39(2), 86–99. <https://doi.org/10.1016/j.tins.2015.12.004>
- Markela-Lerenc, J., Schmidt-Kraepelin, C., Roesch-Ely, D., Mundt, C., Weisbrod, M., & Kaiser, S. (2009). Stroop interference effect in schizophrenic patients: An electrophysiological approach. *International Journal of Psychophysiology*, 71(3), 248–257. <https://doi.org/10.1016/j.ijpsycho.2008.10.005>
- Marshall, T. R., O’Shea, J., Jensen, O., & Bergmann, T. O. (2015). Frontal Eye Fields Control Attentional Modulation of Alpha and Gamma Oscillations in Contralateral Occipitoparietal Cortex. *Journal of Neuroscience*, 35(4), 1638–1647. <https://doi.org/10.1523/JNEUROSCI.3116-14.2015>
- Martens, U., & Hübner, R. (2013). Functional hemispheric asymmetries of global/local processing mirrored by the steady-state visual evoked potential. *Brain and Cognition*, 81(2), 161–166. <https://doi.org/10.1016/j.bandc.2012.11.005>
- Mathewson, Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To See or Not to See: Prestimulus Phase Predicts Visual Awareness. *Journal of Neuroscience*, 29(9), 2725–2732. <https://doi.org/10.1523/JNEUROSCI.3963-08.2009>
- Mathewson, K. E., Basak, C., Maclin, E. L., Low, K. A., Boot, W. R., Kramer, A. F., ... Gratton, G. (2012). Different slopes for different folks: Alpha and delta EEG power predict subsequent video game learning rate and improvements in cognitive control tasks. *Psychophysiology*, 49(12), 1558–1570. <https://doi.org/10.1111/j.1469-8986.2012.01474.x>
- Mathewson, K. E., Lleras, A., Beck, D. M., Fabiani, M., Ro, T., & Gratton, G. (2011). Pulsed out of awareness: EEG alpha oscillations represent a pulsed-inhibition of ongoing cortical processing. *Frontiers in Psychology*, 2(MAY), 1–15. <https://doi.org/10.3389/fpsyg.2011.00099>
- Mathewson, Prudhomme, C., Fabiani, M., Beck, D. M., Lleras, A., & Gratton, G. (2012). Making waves in the stream of consciousness: Entraining oscillations in EEG alpha and fluctuations in visual awareness with rhythmic visual stimulation. *Journal of Cognitive Neuroscience*, 24(12), 2321–2333. https://doi.org/10.1162/jocn_a_00288
- Mazaheri, A., Nieuwenhuis, I. L. C., Van Dijk, H., & Jensen, O. (2009). Prestimulus alpha and mu activity predicts failure to inhibit motor responses. *Human Brain Mapping*, 30(6), 1791–1800. <https://doi.org/10.1002/hbm.20763>
- Mierau, A., Klimesch, W., & Lefebvre, J. (2017). State-dependent alpha peak frequency shifts: Experimental evidence, potential mechanisms and functional implications. *Neuroscience*, 360, 146–154. <https://doi.org/10.1016/j.neuroscience.2017.07.037>
- Millett, D. (2001). Hans Berger: From Psychic Energy to the EEG. *Perspectives in Biology and Medicine*, 44(4), 522–542. <https://doi.org/10.1353/pbm.2001.0070>
- Milner, P. M. (1974). A model for visual shape recognition. *Psychological Review*, 81(6), 521–535. <https://doi.org/10.1037/h0037149>
- Milton, A., & Pleydell-Pearce, C. W. (2016). The phase of pre-stimulus alpha oscillations influences the visual perception of stimulus timing. *NeuroImage*, 133, 53–61. <https://doi.org/10.1016/j.neuroimage.2016.02.065>
- Mora-Cortes, A., Ridderinkhof, K. R., & Cohen, M. X. (2018). Evaluating the feasibility of the steady-state visual evoked potential (SSVEP) to study temporal attention. *Psychophysiology*, 55(5). <https://doi.org/10.1111/psyp.13029>

- Moratti, S., Clementz, B. A., Gao, Y., Ortiz, T., & Keil, A. (2007). Neural mechanisms of evoked oscillations: Stability and interaction with transient events. *Human Brain Mapping*, 28(12), 1318–1333. <https://doi.org/10.1002/hbm.20342>
- Murta, T., Leite, M., Carmichael, D. W., Figueiredo, P., & Lemieux, L. (2015). Electrophysiological correlates of the BOLD signal for EEG-informed fMRI. *Human Brain Mapping*, 36(1), 391–414. <https://doi.org/10.1002/hbm.22623>
- Nadasdy, Z. (2010). Binding by asynchrony: The neuronal phase code. *Frontiers in Neuroscience*, 4(SEP), 1–11. <https://doi.org/10.3389/fnins.2010.00051>
- Nakasaki, H., Clausen, H., Hakomori, S. itiroh, Mitomi, T., Noto, T., Ogoshi, K., ... Makuuchi, H. (1989). Mosaicism in the Expression of Tumor-associated Carbohydrate Antigens in Human Colonic and Gastric Cancers. *Cancer Research*, 49(13), 3662–3669. <https://doi.org/10.3389/neuro.07>
- Navon, D. (1977). *Forest before trees: The precedence of global features in visual perception. Cognitive Psychology* (Vol. 9). [https://doi.org/10.1016/0010-0285\(77\)90012-3](https://doi.org/10.1016/0010-0285(77)90012-3)
- Neuling, Rach, S., & Herrmann, C. S. (2013). Orchestrating neuronal networks: sustained after-effects of transcranial alternating current stimulation depend upon brain states. *Frontiers in Human Neuroscience*, 7(April), 161. <https://doi.org/10.3389/fnhum.2013.00161>
- Neuling, Rach, S., Wagner, S., Wolters, C. H., & Herrmann, C. S. (2012). Good vibrations: Oscillatory phase shapes perception. *NeuroImage*, 63(2), 771–778. <https://doi.org/10.1016/j.neuroimage.2012.07.024>
- Niedermeyer, E., & Lopes da Silva, F. H. (2005). *Electroencephalography : basic principles, clinical applications, and related fields*. Lippincott Williams & Wilkins. Retrieved from [https://books.google.co.uk/books?hl=en&lr=&id=tndqYGPHQdEC&oi=fnd&pg=PR11&dq=\(Niedermeyer+%26+da+Silva+Electroencephalography:+basic+principles,+clinical+applications,+and+related+fields&ots=GOBi682cqA&sig=FcSOii7Rhv41IZX91kvCQnuB41I#v=onepage&q=\(Niedermeyer+%26+da+Silva+Electroencephalography%3A+basic+principles%2C+clinical+applications%2C+and+related+fields&f=false](https://books.google.co.uk/books?hl=en&lr=&id=tndqYGPHQdEC&oi=fnd&pg=PR11&dq=(Niedermeyer+%26+da+Silva+Electroencephalography:+basic+principles,+clinical+applications,+and+related+fields&ots=GOBi682cqA&sig=FcSOii7Rhv41IZX91kvCQnuB41I#v=onepage&q=(Niedermeyer+%26+da+Silva+Electroencephalography%3A+basic+principles%2C+clinical+applications%2C+and+related+fields&f=false)
- Nikulin, V. V., & Brismar, T. (2006). Phase synchronization between alpha and beta oscillations in the human electroencephalogram. *Neuroscience*, 137(2), 647–657. <https://doi.org/10.1016/j.neuroscience.2005.10.031>
- Noël, M. (2016). Influence des systèmes de notation des nombres sur les mécanismes d'encodage et de traitements numériques, *91*, 581–607.
- Nombela, C., Nombela, M., Castell, P., García, T., López-Coronado, J., & Herrero, M. T. (2014). Alpha-Theta effects associated with ageing during the Stroop test. *PLoS ONE*, 9(5), 1–7. <https://doi.org/10.1371/journal.pone.0095657>
- Norcia, A. M., Appelbaum, L. G. G., Ales, J. M. J. M., Cottareau, B. R. B. R., & Rossion, B. (2015). The steady-state visual evoked potential in vision research: a review. *Journal of Vision*, 15(6), 4. <https://doi.org/10.1167/15.6.4>
- Notebaert, W., Gevers, W., Verbruggen, F., & Liefoghe, B. (2006). Top-down and bottom-up sequential modulations of congruency effects. *Psychonomic Bulletin and Review*, 13(1), 112–117. <https://doi.org/10.3758/BF03193821>
- Nunez, P. L. (1974). Wave-like properties of the alpha rhythm., (6).
- Nunez, P. L., & Srinivasan, R. (2010). Scale and frequency chauvinism in brain dynamics: Too much emphasis on gamma band oscillations. *Brain Structure and Function*, 215(2), 67–71. <https://doi.org/10.1007/s00429-010-0277-6>

- Oehrn, C. R., Hanslmayr, S., Fell, J., Deuker, L., Kremers, N. A., Do Lam, A. T., ... Axmacher, N. (2014). Neural Communication Patterns Underlying Conflict Detection, Resolution, and Adaptation. *Journal of Neuroscience*, *34*(31), 10438–10452. <https://doi.org/10.1523/JNEUROSCI.3099-13.2014>
- Okamoto, Y., & Nakagawa, S. (2011). Comparison of MEG responses to the sinusoidal flicker and the envelope of amplitude-modulated flicker. *Neuroscience Letters*, *487*(2), 207–210. <https://doi.org/10.1016/j.neulet.2010.10.024>
- Omata, K., Hanakawa, T., Morimoto, M., & Honda, M. (2013). Spontaneous Slow Fluctuation of EEG Alpha Rhythm Reflects Activity in Deep-Brain Structures: A Simultaneous EEG-fMRI Study. *PLoS ONE*, *8*(6), 1–12. <https://doi.org/10.1371/journal.pone.0066869>
- Op De Beeck, H., Wagemans, J., & Vogels, R. (2001). Can neuroimaging really tell us what the human brain is doing? The relevance of indirect measures of population activity. *Acta Psychologica*, *107*(1–3), 323–351. [https://doi.org/10.1016/S0001-6918\(01\)00027-0](https://doi.org/10.1016/S0001-6918(01)00027-0)
- Palva, S., & Palva, J. M. (2007). New vistas for α -frequency band oscillations. *Trends in Neurosciences*, *30*(4), 150–158. <https://doi.org/10.1016/j.tins.2007.02.001>
- Palva, S., & Palva, J. M. (2011). Functional roles of alpha-band phase synchronization in local and large-scale cortical networks. *Frontiers in Psychology*, *2*(SEP), 1–15. <https://doi.org/10.3389/fpsyg.2011.00204>
- Pansky, A., & Algom, D. (2002). Comparative Judgment of Numerosity and Numerical Magnitude: Attention Preempts Automaticity. *Journal of Experimental Psychology: Learning Memory and Cognition*, *28*(2), 259–274. <https://doi.org/10.1037/0278-7393.28.2.259>
- Perkel, D. H., & Bullock, P. H. (1968). Neural coding. *Neurosci. Res. Prog. Sum*, *3*, 405–527.
- Pfurtscheller, G., Neuper, C., & Mohl, W. (1994). Event-related desynchronization (ERD) during visual processing. *International Journal of Psychophysiology: Official Journal of the International Organization of Psychophysiology*, *16*(2–3), 147–153. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/8089033>
- Pockett, S., Bold, G. E. J., & Freeman, W. J. (2009). EEG synchrony during a perceptual-cognitive task: Widespread phase synchrony at all frequencies. *Clinical Neurophysiology*, *120*(4), 695–708. <https://doi.org/10.1016/j.clinph.2008.12.044>
- Pocock, P. V. (1980). The spatial and temporal distribution of alpha activity and their modification during motor preparation. *Rhythmic EEG Activities and Cortical Functioning*, 135–149. Retrieved from https://scholar.google.pl/scholar?hl=pl&as_sdt=0%2C5&q=Pocock+The+spatial+and+temporal+distribution+of+alpha+activity+and+their+modification+during+motor+preparation.+In%3A+G.+Pfurtscheller%2C+P.+Buser%2C+F.H.+Lopes+da+Silva+and+H.+Petsche+%28Eds.%29%2C+R
- Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*, *32*(1), 3–25. <https://doi.org/10.1080/00335558008248231>
- Raghavachari, S. (2006). Theta Oscillations in Human Cortex During a Working-Memory Task: Evidence for Local Generators. *Journal of Neurophysiology*, *95*(3), 1630–1638. <https://doi.org/10.1152/jn.00409.2005>
- Rana, K. D., & Vaina, L. M. (2014). Functional roles of 10 Hz alpha-band power modulating engagement and disengagement of cortical networks in a complex visual motion task. *PLoS ONE*, *9*(10), e107715. <https://doi.org/10.1371/journal.pone.0107715>
- Rihs, T. A., Michel, C. M., & Thut, G. (2007). Mechanisms of selective inhibition in visual spatial attention are indexed by β -band EEG synchronization. *European Journal of Neuroscience*, *25*(2), 603–610. <https://doi.org/10.1111/j.1460-9568.2007.05278.x>

- Rizzuto, D. S., Madsen, J. R., Bromfield, E. B., Schulze-Bonhage, A., Seelig, D., Aschenbrenner-Scheibe, R., & Kahana, M. J. (2003). Reset of human neocortical oscillations during a working memory task. *Proceedings of the National Academy of Sciences*, *100*(13), 7931–7936. <https://doi.org/10.1073/pnas.0732061100>
- Romei, Gross, J., & Thut, G. (2010). On the Role of Prestimulus Alpha Rhythms over Occipito-Parietal Areas in Visual Input Regulation: Correlation or Causation? *Journal of Neuroscience*, *30*(25), 8692–8697. <https://doi.org/10.1523/JNEUROSCI.0160-10.2010>
- Romei, V., Gross, J., & Thut, G. (2012). Sounds reset rhythms of visual cortex and corresponding human visual perception. *Current Biology*, *22*(9), 807–813. <https://doi.org/10.1016/j.cub.2012.03.025>
- Ronconi, L., Oosterhof, N. N., Bonmassar, C., & Melcher, D. (2017). Multiple oscillatory rhythms determine the temporal organization of perception. *Proceedings of the National Academy of Sciences*, *114*(51), 201714522. <https://doi.org/10.1073/pnas.1714522114>
- Ruhnau, P., Neuling, T., Fuscì, M., Herrmann, C. S., Demarchi, G., & Weisz, N. (2016). Eyes wide shut: Transcranial alternating current stimulation drives alpha rhythm in a state dependent manner. *Scientific Reports*, *6*(December 2015), 1–6. <https://doi.org/10.1038/srep27138>
- Sadaghiani, S., Scheeringa, R., Lehongre, K., Morillon, B., Giraud, A.-L., D'Esposito, M., & Kleinschmidt, A. (2012). Alpha-Band Phase Synchrony Is Related to Activity in the Fronto-Parietal Adaptive Control Network. *Journal of Neuroscience*, *32*(41), 14305–14310. <https://doi.org/10.1523/JNEUROSCI.1358-12.2012>
- Sato, N. (2013). Fast entrainment of human electroencephalogram to a theta-band photic flicker during successful memory encoding. *Frontiers in Human Neuroscience*, *7*(May), 208. <https://doi.org/10.3389/fnhum.2013.00208>
- Sauseng, P. (2012). Brain oscillations: Phase-locked EEG alpha controls perception. *Current Biology*, *22*(9), R306-8. <https://doi.org/10.1016/j.cub.2012.03.029>
- Sauseng, P., & Klimesch, W. (2008). What does phase information of oscillatory brain activity tell us about cognitive processes? *Neuroscience and Biobehavioral Reviews*, *32*(5), 1001–1013. <https://doi.org/10.1016/j.neubiorev.2008.03.014>
- Sauseng, P., Klimesch, W., Schabus, M., & Doppelmayr, M. (2005). Fronto-parietal EEG coherence in theta and upper alpha reflect central executive functions of working memory. *International Journal of Psychophysiology*, *57*(2), 97–103. <https://doi.org/10.1016/j.ijpsycho.2005.03.018>
- Schack, B., Chen, A. C. N., Mescha, S., & Witte, H. (1999). Instantaneous eeg coherence analysis during the Stroop task. *Clinical Neurophysiology*, *110*(8), 1410–1426. [https://doi.org/10.1016/S1388-2457\(99\)00111-X](https://doi.org/10.1016/S1388-2457(99)00111-X)
- Schmid, M. C., Singer, W., & Fries, P. (2012). Thalamic Coordination of Cortical Communication. *Neuron*, *75*(4), 551–552. <https://doi.org/10.1016/j.neuron.2012.08.009>
- Shaw, J. C., & McLachlan, K. R. (1968). THE ASSOCIATION BETWEEN ALPHA RHYTHM PROPAGATION TIME AND LEVEL OF AROUSAL. *Psychophysiology*, *4*(3), 307–310. <https://doi.org/10.1111/j.1469-8986.1968.tb02772.x>
- Siegel, M., Donner, T. H., & Engel, A. K. (2012). Spectral fingerprints of large-scale neuronal interactions. *Nature Reviews Neuroscience*, *13*(2), 121–134. <https://doi.org/10.1038/nrn3137>
- Siever, D. (2006). The Application of Audiovisual Entrainment for the Treatment of Seniors' Issues , Part 2. *Biofeedback Magazine*, *34*(2), 69–72. Retrieved from http://www.resourcenter.net/images/AAPB/Files/Biofeedback/2005/BIOF3303_109-113.pdf
- Singer. (2010). Temporal Coherence: A Versatile Code for the Definition of Relations. *The Senses: A*

- Comprehensive Reference*, 2, 1–9. <https://doi.org/10.1016/B978-012370880-9.00287-5>
- Singer, W. (1990). The formation of cooperative cell assemblies in the visual cortex. *The Journal of Experimental Biology*, 153, 177–197.
- Singer, Wolf. (2009). Distributed processing and temporal codes in neuronal networks. *Cognitive Neurodynamics*, 3(3), 189–196. <https://doi.org/10.1007/s11571-009-9087-z>
- Singer, Wolf. (2013). Cortical dynamics revisited. *Trends in Cognitive Sciences*, 17(12), 616–626. <https://doi.org/10.1016/j.tics.2013.09.006>
- Smith, D. (2015). *The oxford handbook of attention*. (Anna C. Nobre, Ed.), *Perception* (Vol. 44). Oxford: Oxford University Press. <https://doi.org/10.1093/oxfordhb/9780199675111.001.0001>
- Sokal, F. A., & Text, S. (2006). BARBARA T UCHAŃSKA O Sokalu z Bricmontem , Latourze i o tym , co z tego (nie) wynika, (Sokal 2004), 93–111.
- Spaak, E., de Lange, F. P., & Jensen, O. (2014). Local Entrainment of Alpha Oscillations by Visual Stimuli Causes Cyclic Modulation of Perception. *Journal of Neuroscience*, 34(10), 3536–3544. <https://doi.org/10.1523/JNEUROSCI.4385-13.2014>
- Stam, C. J., & van Straaten, E. C. W. (2012). The organization of physiological brain networks. *Clinical Neurophysiology*, 123(6), 1067–1087. <https://doi.org/10.1016/j.clinph.2012.01.011>
- Stevenson, E. (2010). *oxford Dictionary of English*. Oxford University Press.
- Suffczynski, P., Kalitzin, S., Pfurtscheller, G., & Lopes Da Silva, F. H. (2001). *Computational model of thalamo-cortical networks: Dynamical control of alpha rhythms in relation to focal attention*. *International Journal of Psychophysiology* (Vol. 43). [https://doi.org/10.1016/S0167-8760\(01\)00177-5](https://doi.org/10.1016/S0167-8760(01)00177-5)
- Sun, W., & Dan, Y. (2009). Layer-specific network oscillation and spatiotemporal receptive field in the visual cortex. *Proceedings of the National Academy of Sciences*, 106(42), 17986–17991. <https://doi.org/10.1073/pnas.0903962106>
- SUZUKI, H. (1974). *Phase Relationships of Alpha Rhythm in Man*. *The Japanese Journal of Physiology* (Vol. 24). <https://doi.org/10.2170/jjphysiol.24.569>
- Tartar, V. (2013). *The Biology of Stentor: International Series of Monographs on Pure and Applied Biology: Zoology*. Retrieved from <https://books.google.com/books?id=KRPLBAAAQBAJ&pgis=1>
- Taylor, P. C. J., Nobre, A. C., & Rushworth, M. F. S. (2007). FEF TMS affects visual cortical activity. *Cerebral Cortex*, 17(2), 391–399. <https://doi.org/10.1093/cercor/bhj156>
- Ter Huurne, N., Onnink, M., Kan, C., Franke, B., Buitelaar, J., & Jensen, O. (2013). Behavioral consequences of aberrant alpha lateralization in attention-deficit/hyperactivity disorder. *Biological Psychiatry*, 74(3), 227–233. <https://doi.org/10.1016/j.biopsych.2013.02.001>
- Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature*, 381(6582), 520–522. <https://doi.org/10.1038/381520a0>
- Thut. (2006). -Band Electroencephalographic Activity over Occipital Cortex Indexes Visuospatial Attention Bias and Predicts Visual Target Detection. *Journal of Neuroscience*, 26(37), 9494–9502. <https://doi.org/10.1523/JNEUROSCI.0875-06.2006>
- Thut, G., & Miniussi, C. (2009). New insights into rhythmic brain activity from TMS-EEG studies. *Trends in Cognitive Sciences*, 13(4), 182–189. <https://doi.org/10.1016/j.tics.2009.01.004>
- Thut, G., Schyns, P. G., & Gross, J. (2011). Entrainment of perceptually relevant brain oscillations by non-invasive rhythmic stimulation of the human brain. *Frontiers in Psychology*, 2(JUL), 1–10.

<https://doi.org/10.3389/fpsyg.2011.00170>

- Thut, G., Veniero, D., Romei, V., Miniussi, C., Schyns, P., & Gross, J. (2011). Rhythmic TMS causes local entrainment of natural oscillatory signatures. *Current Biology*, *21*(14), 1176–1185. <https://doi.org/10.1016/j.cub.2011.05.049>
- Tiesling-Rusch, A., Dimond, A., & College, B. (2012). Stroop Effect Differences of Native and Non-Native Japanese. *Undergraduate Research Journal for the Human Sciences*, *11*.
- Toman, J. (1941). Flicker Potentials and the Alpha Rhythm in Man. *Journal of Neurophysiology*, *4*(1), 51–61. <https://doi.org/10.1152/jn.1941.4.1.51>
- Toosy, A. T., Werring, D. J., Plant, G. T., Bullmore, E. T., Miller, D. H., & Thompson, A. J. (2001). Asymmetrical activation of human visual cortex demonstrated by functional MRI with monocular stimulation. *NeuroImage*, *14*(3), 632–641. <https://doi.org/10.1006/nimg.2001.0851>
- Tovee, M. J., & Tove, M. J. (1996). *An Introduction to the Visual System - e. Theorizing Visual Studies*. Cambridge University Press. <https://doi.org/10.1097/00006324-199710000-00013>
- Townsend, R. E., Lubin, A., & Naitoh, P. (1975). Stabilization of alpha frequency by sinusoidally modulated light. *Electroencephalography and Clinical Neurophysiology*, *39*(5), 515–518. [https://doi.org/10.1016/0013-4694\(75\)90053-X](https://doi.org/10.1016/0013-4694(75)90053-X)
- Uhlhaas, P. J. (2013). Dysconnectivity, large-scale networks and neuronal dynamics in schizophrenia. *Current Opinion in Neurobiology*, *23*(2), 283–290. <https://doi.org/10.1016/j.conb.2012.11.004>
- Uhlhaas, P. J., & Singer, W. (2006). Neural Synchrony in Brain Disorders: Relevance for Cognitive Dysfunctions and Pathophysiology. *Neuron*, *52*(1), 155–168. <https://doi.org/10.1016/j.neuron.2006.09.020>
- Valdes-Sosa, P. A., Sanchez-Bornot, J. M., Sotero, R. C., Iturria-Medina, Y., Aleman-Gomez, Y., Bosch-Bayard, J., ... Ozaki, T. (2009). Model driven EEG/fMRI fusion of brain oscillations. *Human Brain Mapping*, *30*(9), 2701–2721. <https://doi.org/10.1002/hbm.20704>
- Valera, F. J., Toro, A., Roy John, E., & Schwartz, E. L. (1981). Perceptual framing and cortical alpha rhythm. *Neuropsychologia*. [https://doi.org/10.1016/0028-3932\(81\)90005-1](https://doi.org/10.1016/0028-3932(81)90005-1)
- van der Tweel, L. H., & Verduyn Lunel, H. F. E. (1965). Human visual responses to sinusoidally modulated light. *Electroencephalography and Clinical Neurophysiology*, *18*(6), 587–598. [https://doi.org/10.1016/0013-4694\(65\)90076-3](https://doi.org/10.1016/0013-4694(65)90076-3)
- van Dijk, H., Schoffelen, J.-M., Oostenveld, R., & Jensen, O. (2008). Prestimulus Oscillatory Activity in the Alpha Band Predicts Visual Discrimination Ability. *Journal of Neuroscience*, *28*(8), 1816–1823. <https://doi.org/10.1523/JNEUROSCI.1853-07.2008>
- van Driel, J., Gunseli, E., Meeter, M., & Olivers, C. N. L. (2017). Local and interregional alpha EEG dynamics dissociate between memory for search and memory for recognition. *NeuroImage*, *149*(October 2016), 114–128. <https://doi.org/10.1016/j.neuroimage.2017.01.031>
- Van Rullen, R., & Thorpe, S. J. (2001). Rate coding versus temporal order coding: What the retinal ganglion cells tell the visual cortex. *Neural Computation*, *13*(6), 1255–1283. <https://doi.org/10.1162/08997660152002852>
- van Straaten, E. C. W., & Stam, C. J. (2013). Structure out of chaos: Functional brain network analysis with EEG, MEG, and functional MRI. *European Neuropsychopharmacology*, *23*(1), 7–18. <https://doi.org/10.1016/j.euroneuro.2012.10.010>
- VanRullen, R. (2016). Perceptual Cycles. *Trends in Cognitive Sciences*, *20*(10), 723–735. <https://doi.org/10.1016/j.tics.2016.07.006>
- VanRullen, R., & Koch, C. (2003). Is perception discrete or continuous? *Trends in Cognitive Sciences*,

7(5), 207–213. [https://doi.org/10.1016/S1364-6613\(03\)00095-0](https://doi.org/10.1016/S1364-6613(03)00095-0)

- Varela, F. J., Lachaux, J.-P., Rodriguez, E., & Martinerie, J. (2001). The BrainWeb: Phase large-scale integration. *Nature Reviews. Neuroscience*, 2(April), 229–239. <https://doi.org/10.1038/35067550>
- Verstraeten, E., & Cluydts, R. (2002). Attentional switching-related human EEG alpha oscillations. *NeuroReport*, 13(5), 681–684. <https://doi.org/10.1097/00001756-200204160-00029>
- Vialatte, F. B., Maurice, M., Dauwels, J., & Cichocki, A. (2010). Steady-state visually evoked potentials: Focus on essential paradigms and future perspectives. *Progress in Neurobiology*, 90(4), 418–438. <https://doi.org/10.1016/j.pneurobio.2009.11.005>
- Volberg, G., & Hübner, R. (2004). On the role of response conflicts and stimulus position for hemispheric differences in global/local processing: An ERP study. *Neuropsychologia*, 42(13), 1805–1813. <https://doi.org/10.1016/j.neuropsychologia.2004.04.017>
- Volberg, G., Kliegl, K., Hanslmayr, S., & Greenlee, M. W. (2009a). EEG alpha oscillations in the preparation for global and local processing predict behavioral performance. *Human Brain Mapping*, 30(7), 2173–2183. <https://doi.org/10.1002/hbm.20659>
- Volberg, G., Kliegl, K., Hanslmayr, S., & Greenlee, M. W. (2009b). EEG alpha oscillations in the preparation for global and local processing predict behavioral performance. *Human Brain Mapping*, 30(7), 2173–2183. <https://doi.org/10.1002/hbm.20659>
- Voloh, B., & Womelsdorf, T. (2016). A Role of Phase-Resetting in Coordinating Large Scale Neural Networks During Attention and Goal-Directed Behavior. *Frontiers in Systems Neuroscience*, 10(March), 1–19. <https://doi.org/10.3389/fnsys.2016.00018>
- Von Der Malsburg, C. (1999). The what and why of binding: The modeler's perspective. *Neuron*, 24(1), 95–104. [https://doi.org/10.1016/S0896-6273\(00\)80825-9](https://doi.org/10.1016/S0896-6273(00)80825-9)
- von der Malsburg, Christoph. (1981a). The Correlation Theory of Brain Function. *Models of Neural Networks II*, (July 1981), 1–26. <https://doi.org/10.1109/CVPR.2007.383092>
- von der Malsburg, Christoph. (1981b). The Correlation Theory of Brain Function, (July 1981), 1–26. <https://doi.org/10.1109/CVPR.2007.383092>
- von Stein, A., Chiang, C., & Konig, P. (2000). Top-down processing mediated by interareal synchronization. *Proceedings of the National Academy of Sciences*, 97(26), 14748–14753. <https://doi.org/10.1073/pnas.97.26.14748>
- Von Stein, Astrid, & Sarnthein, J. (2000). Different frequencies for different scales of cortical integration: From local gamma to long range alpha/theta synchronization. *International Journal of Psychophysiology*, 38(3), 301–313. [https://doi.org/10.1016/S0167-8760\(00\)00172-0](https://doi.org/10.1016/S0167-8760(00)00172-0)
- Waagan, K. (2014). *Low-frequency long-range atmospheric noise propagation modelling with the PE method*.
- Wach, C., Krause, V., Moliadze, V., Paulus, W., Schnitzler, A., & Pollok, B. (2013). The effect of 10 Hz transcranial alternating current stimulation (tACS) on corticomuscular coherence. *Frontiers in Human Neuroscience*, 7(August), 1–10. <https://doi.org/10.3389/fnhum.2013.00511>
- Wacker, M., Galicki, M., Putsche, P., Milde, T., Schwab, K., Haueisen, J., ... Witte, H. (2011). A time-variant processing approach for the analysis of alpha and gamma MEG oscillations during flicker stimulus generated entrainment. *IEEE Transactions on Biomedical Engineering*, 58(11), 3069–3077. <https://doi.org/10.1109/TBME.2011.2160640>
- Wahid, H., Ahmad, S., Nor, M. A. M., & Rashid, M. A. (2017). *Prestasi kecekapan pengurusan kewangan dan agihan zakat: perbandingan antara majlis agama islam negeri di Malaysia*. *Jurnal Ekonomi Malaysia* (Vol. 51). <https://doi.org/10.1017/CBO9781107415324.004>

- Waldhauser, G. T., Johansson, M., & Hanslmayr, S. (2012). Alpha/Beta Oscillations Indicate Inhibition of Interfering Visual Memories. *Journal of Neuroscience*, *32*(6), 1953–1961. <https://doi.org/10.1523/JNEUROSCI.4201-11.2012>
- Walter, D. O., Rhodes, J. M., Brown, D., & Adey, W. R. (1966). Comprehensive spectral analysis of human EEG generators in posterior cerebral regions. *Electroencephalography and Clinical Neurophysiology*, *20*(3), 224–237. [https://doi.org/10.1016/0013-4694\(66\)90087-3](https://doi.org/10.1016/0013-4694(66)90087-3)
- Wan, F., Da Cruz, J. N., Nan, W., Wong, C. M., Vai, M. I., & Rosa, A. (2016). Alpha neurofeedback training improves SSVEP-based BCI performance. *Journal of Neural Engineering*, *13*(3), 036019. <https://doi.org/10.1088/1741-2560/13/3/036019>
- Ward, L. M. (2003, December). Synchronous neural oscillations and cognitive processes. *Trends in Cognitive Sciences*. <https://doi.org/10.1016/j.tics.2003.10.012>
- Weiss, Y., & Freeman, W. T. (2007). What makes a good model of natural images? *2007 IEEE Conference on Computer Vision and Pattern Recognition*, (July 1981), 1–8. <https://doi.org/10.1109/CVPR.2007.383092>
- Weissman, D. H., & Woldorff, M. G. (2005). Hemispheric asymmetries for different components of global/local attention occur in distinct temporo-parietal loci. *Cerebral Cortex*, *15*(6), 870–876. <https://doi.org/10.1093/cercor/bhh187>
- West, R. (2003). Neural correlates of cognitive control and conflict detection in the Stroop and digit-localisation tasks. *Neuropsychologia*, *41*(2003), 1122–1135.
- Wilson, E. (1975). *Sociobiology : the new synthesis*. Belknap Press of Harvard University Press.
- Womelsdorf, T., & Fries, P. (2007). The role of neuronal synchronization in selective attention. *Current Opinion in Neurobiology*, *17*(2), 154–160. <https://doi.org/10.1016/j.conb.2007.02.002>
- Wong, A. a, Read, S. J., The Mendeley Support Team, Tendra, M., Aboyans, V., Bartelink, M.-L., ... Wijdicks, E. F. M. (2011). 2011 ASA/ACCF/AHA/AANN/AANS/ACR/ASNR/CNS/SAIP/SCAI/SIR/SNIS/SVM/SVS guideline on the management of patients with extracranial carotid and vertebral artery disease. A report of the American College of Cardiology Foundation/American Heart Association Task F. *European Heart Journal*. London: Mendeley Ltd. <https://doi.org/10.1161/CIR.0b013e31820d8c98>
- Wu, Z. (2014). Studying modulation on simultaneously activated SSVEP neural networks by a cognitive task. *Journal of Biological Physics*, *40*(1), 55–70. <https://doi.org/10.1007/s10867-013-9335-7>
- Wutz, A., Weisz, N., Braun, C., & Melcher, D. (2014). Temporal Windows in Visual Processing: “Prestimulus Brain State” and “Poststimulus Phase Reset” Segregate Visual Transients on Different Temporal Scales. *Journal of Neuroscience*, *34*(4), 1554–1565. <https://doi.org/10.1523/JNEUROSCI.3187-13.2014>
- Xie, S., Liu, C., Obermayer, K., Zhu, F., Wang, L., Xie, X., & Wang, W. (2016). Stimulator Selection in SSVEP-Based Spatial Selective Attention Study. *Computational Intelligence and Neuroscience*, *2016*. <https://doi.org/10.1155/2016/6410718>
- Yin, X., Zhang, J., & Wang, X. (2004). *Sequential injection analysis system for the determination of arsenic by hydride generation atomic absorption spectrometry*. *Fenxi Huaxue* (Vol. 32). <https://doi.org/10.1017/CBO9781107415324.004>
- Zumer, J. M., Scheeringa, R., Schoffelen, J. M., Norris, D. G., & Jensen, O. (2014). Occipital Alpha Activity during Stimulus Processing Gates the Information Flow to Object-Selective Cortex. *PLoS Biology*, *12*(10). <https://doi.org/10.1371/journal.pbio.1001965>

Appendix 1: Ethics approval behavioural experiments

**ETHICAL MATTERS MUST BE CONSIDERED BEFORE ANY RESEARCH TAKES PLACE
FAILURE TO FOLLOW THE CORRECT ETHICAL PROCEDURES OR CONDUCTING
RESEARCH WITHOUT ETHICAL APPROVAL WHERE IT IS REQUIRED MAY LEAD TO
DISCIPLINARY ACTION**

Guidance

This Ethics Checklist has been designed to help determine the level of risk or harm to participants' welfare entailed in a proposed study. It also contains a sample consent form and information leaflet checklist that you can use/adapt as appropriate.

NB: If your research requires NHS ethics approval, you should not complete this form. Please provide the School with a copy of your letter of NHS approval once you receive this.

Who Completes the Checklist?

The Principal Investigator (PI) is the main researcher and can be a student. The PI (or where the PI is a student, the supervisor) is responsible for exercising appropriate professional judgement in this review.

Underpinning Codes of Ethics

Before completing this checklist, you must refer to the University [Code of Research Ethics](#) as well as the relevant code of ethics for your discipline. These are listed in the Useful Links section at the end of this guidance. It is your responsibility to follow these Codes of Research Ethics in the conduct of your study. This includes providing appropriate documentation and ensuring confidentiality in the storage and use of data (see section 3.3.2 of the University Code of Research Ethics).

The Checklist

This Checklist is in two parts:

Part 1: This must be completed by all students and staff undertaking research. This section aims to confirm that there are no ethical or risk assessment issues related to your research.

Part 2: This is for all Principal Investigators who identify that there are ethical and/or risk assessment issues in their proposed research.

YOU MUST HAVE YOUR APPLICATION, CONSENT FORM AND INFORMATION SHEET APPROVED BY YOUR DEPARTMENTAL ETHICS COORDINATOR (OR IF APPROPRIATE, UNIVERSITY ETHICS COMMITTEE) BEFORE YOU START YOUR RESEARCH AND APPROACH POTENTIAL PARTICIPANTS.

What do I have to do if I need to complete the University Research Ethics Committee Application Form?

You will need to complete and submit this via BBL. In most cases, the School will be able to review and approve the ethics form. If the research needs University level approval, your form will be submitted to the University Research Ethics Committee by the Research Office.

Risk Assessment

All Principal Investigators (and their supervisor where relevant) are required to consider matters of risk and conduct a risk assessment as part of the University's Health and Safety Policy. If issues of risk are identified, a risk assessment is required and must be attached to this form. For further information about Risk Assessments and guidance on how to undertake one, see the document 'RISK ASSESSMENT – FAQs' which can be found in the School of Social Sciences Ethics Organisation, under my Organisations in BBL.

Disclosure and Barring Service (formerly Criminal Record Bureau) Checks

If your research involves vulnerable persons, you are required to follow University guidelines for Disclosure and Barring Service (DBS) checks. If you need a DBS check please contact the DBS Administrator in Admissions who will send you the information you need to make a DBS application.

How to submit Checklist and appendices on Blackboard Learn

Stage 1: Log into BBL

Stage 2: Click on the School of Social Sciences Research Ethics Organisation, under the My Organisations list on the right hand side

Stage 3: Download the Ethics Checklist from the folder on the homepage titled 'Research Ethics Application Form'.

Stage 3: Click on your appropriate department folder

Stage 4: Click on the Ethics Checklist Submission Assignment Tool

Stage 5: Upload your Ethics Checklist and appendices eg consent form, information leaflet, using the Browse My Computer link, and ensure you have uploaded the correct documents

Stage 6: Once you have confirmed they are the correct documents, click submit

Stage 7: You will receive an email receipt of your submission to your Brunel email account

Stage 8: Click on the My Grades link in the School of Social Sciences Research Ethics Organisation to find the outcome and feedback once it has been reviewed by your Departmental Ethics Coordinator.

Further information about how to submit is available in the School of Social Sciences Ethics Organisation, under My Organisations, in BBL.

What happens after I have received ethical approval?

Once you have received ethical approval, you can start your research.

Students are required to retain a copy of the approved Checklist, consent form and information leaflet and submit these with their research report/dissertation/thesis.

All undergraduate and postgraduate work submitted/conducted without ethical approval may be subject to academic penalties and disciplinary action.

If your research is delayed and will extend beyond the dates stated on your form, please contact your Departmental Ethics Coordinator to seek approval for an extension.

Useful Links and Resources

University Research Code of Ethics [LINK](#)

UREC website - [LINK](#)

Code of Ethics – Anthropology [LINK](#)

Code of Ethics – Economics and Finance (Use University Research Code of Ethics)

Code of Ethics – Politics and History (Use University Research Code of Ethics)

Code of Human Research Ethics – Psychology [PDF](#)

Code of Ethics – Sociology and Communications - [LINK](#)

Risk Assessment – FAQs – School of Social Sciences Ethics Organisation, under my Organisations in BBL.

Contacts

Anthropology Ethics Coordinator:

Dr Isak Niehaus

Economics and Finance Ethics Coordinator:

Professor Frank Skinner

Politics and History Ethics Coordinator:

Dr John MacMillan

Psychology Ethics Coordinator:

Dr Achim Schutzwohl/ Dr Bridget Dibb

Sociology and Communications Ethics Coordinator: Dr Simon Weaver

Research Ethics Administrator: Ms Amreen Malik

SSS Research Ethics Review Checklist – Part 1

Section I: Project details

1. Project title: Influence of flicker cueing with various spatial and temporal properties on reaction time and visual discrimination of near threshold masked object.	
2. Proposed start date:21/01/15	3. Proposed end date:21/05/15
Section II: Applicant details	
4. Name of researcher (applicant)	Karol Wereszczynski
5. Student Number	0826848
6. Status	PGR Student
7. Department	Psychology
8. Brunel e-mail address	karol.wereszczynski@brunel.ac.uk
9. Telephone number	
Section III: For students only	
10. Module name and number:	Psychology PhD
11. Supervisor's name:	dr. Andrew Parton
12. Brunel supervisor's e-mail address:	andrew.parton@brunel.ac.uk

	Yes	No
13. Does this research involve human participants?	<input checked="" type="radio"/>	<input type="radio"/>
14. Does this research raise any ethical or risk concerns as set out in the University Code of Research Ethics or relevant disciplinary code?	<input type="radio"/>	<input checked="" type="radio"/>
15. Risk Assessment – are there any elements of risk related to the proposed research? (See Risk Assessment – FAQs)	<input checked="" type="radio"/>	<input type="radio"/>

If you have answered **Yes** to any of questions 13-15, you must **complete Part 2** of this form.

Students: If you have answered No, please email this document to your supervisor who will confirm that the research does not involve ethical issues. Once electronically signed by your supervisor, please submit Part 1 of this form via BBL within 1 week. Please keep a copy for yourself and bind it into your dissertation/thesis as an appendix.

Staff: If you have answered No, please sign below and submit your form via BBL. Please keep a copy for yourself.

If your research methodology changes significantly, you must submit a new form.

For Supervisor's/Staff e- signature

I confirm that there are no ethical or risk issues relating to this research and the applicant can proceed with the proposed research.

e-signature/ Date:

SSS Research Ethics Review Checklist – Part 2

Section IV: Description of project

Please provide a short description of your project:

Recently there is an increased interest in the literature about photic driving and its effects on visual discrimination. More specifically, there are two recent papers by Mathewson et al (2010) and Eelke et al (2014) reporting apparently opposing results.

Mathewson found that in the regular 12 Hz condition thresholds were best when the IS was in-phase and worst when out of phase. This contrasts with the study by Eelke and colleagues that finds enhanced thresholds following a flicker prime for targets presented out of phase compared with other time lags.

Whilst there are several methodological differences between the paradigms, i.e. (1) masked super threshold targets vs. unmasked threshold target, 2) central presentation vs. lateralised presentation, 3) frequency of entrainment 12Hz (Mathewson) vs 10 (Eelke) etc.). The basic principle of measuring thresholds after flicker stimulation remains the same and so we investigate possibilities that might offer simple explanations for the difference.

The current study focus upon the possibility that the results reflect a difference in entraining neurones spatially aligned with the mask (Mathewson) vs. those aligned with the target (Eelke). In simple terms by flickering in the area of the mask Mathewson enhanced the effectiveness of the mask (diminishing detection rates) and Eelke that of the target (enhancing detection rates).

I try to find out what causes the differences between both authors results. I will use variants of the Mathewson paradigm to focus on whether stimulating target area vs mask area by flicker can influence visual discrimination in phase / out of phase presented target.

Therefore, I propose a variant of the paradigm in which the flicker stimulus is visibly different from the target and mask, e.g. using a mid-grey flicker prime instead of black.

All four conditions are going to be conducted three ISIs in-phase and counter-phase before and after in-phase time.

The research will contribute into better understanding of mechanisms of human perception,, especially relation between entrained frequency and level of facilitation in particular time points after the entrainment.

The experiment will be conducted using DMDX software.

Section V: Research checklist

Please answer each question by ticking the appropriate box:

	YES	NO
1. Does the project involve participants who are particularly vulnerable or unable to give informed consent (e.g. children/ young people under 18, people with learning disabilities, your own students)?	<input type="radio"/>	<input checked="" type="radio"/>

	YES	NO
2. Will the research involve people who could be deemed in any way to be vulnerable by virtue of their status within particular institutional settings (e.g., students at school, residents of nursing home, prison or other institution where individuals cannot come and go freely)?	<input type="radio"/>	<input checked="" type="radio"/>
3. Will it be necessary for participants to take part in the study without their knowledge and consent (e.g., covert observation of people in non-public places)?	<input type="radio"/>	<input checked="" type="radio"/>
4. Will the study involve discussion of sensitive topics (e.g., sexual activity, drug use) where participants have not given prior consent to this?	<input type="radio"/>	<input checked="" type="radio"/>
5. Will the study involve work with participants engaged in breaking the law?	<input type="radio"/>	<input checked="" type="radio"/>
6. Will the publications/reports resulting from the study identify participants by name or in any other way that may identify them, bring them to the attention of the authorities, or any other persons, group or faction?	<input type="radio"/>	<input checked="" type="radio"/>
7. Are drugs, placebos or other substances (e.g. food substances, vitamins) to be administered to the study participants or will the study involve invasive, intrusive or potentially harmful procedures of any kind?	<input type="radio"/>	<input checked="" type="radio"/>
8. Will the study involve the use of human tissue or other human biological material?	<input type="radio"/>	<input checked="" type="radio"/>
9. Will blood or tissue samples be obtained from participants?	<input type="radio"/>	<input checked="" type="radio"/>
10. Is pain or more than mild discomfort likely to result from the study?	<input type="radio"/>	<input checked="" type="radio"/>
11. Could the study induce psychological stress or anxiety or cause harm or negative consequences beyond the risks encountered in normal life?	<input type="radio"/>	<input checked="" type="radio"/>
12. Will the study involve prolonged or repetitive testing?	<input type="radio"/>	<input checked="" type="radio"/>
13. Will financial inducements (other than reasonable expenses and compensation for time) be offered to participants?	<input type="radio"/>	<input checked="" type="radio"/>

	YES	NO
14. Will the study require the co-operation of another individual/ organisation for initial access to the groups or individuals to be recruited? If yes please attach the letters of permission from them.	<input type="radio"/>	<input checked="" type="radio"/>
15. Will you be undertaking this research as part of a work placement or in conjunction with an external organisation? If Yes and the organisation has conducted its own research ethics review, please attach the ethical approval.	<input type="radio"/>	<input checked="" type="radio"/>

If you have answered 'yes' to any of questions 1-13, you will need to complete the [University Application Form for Research Ethics Approval](#).

Students: If you have answered 'No' to all of questions 1-13, please **sign below and submit this completed Checklist, consent form, information leaflet and any other documents and attachments for your supervisor's approval by email . Once you have received it back from your supervisor you will be able to submit via BBL. Forms that do not have your supervisor's approval will be rejected.**

Staff: If you have answered 'No' to all of questions 1-13, please **sign below and submit this completed Checklist, consent form, information sheet and any other documents and attachments via BBL.**

Please note that it is your responsibility to follow the University's Code of Research Ethics and any relevant academic or professional guidelines in the conduct of your study. **This includes providing appropriate information sheets and consent forms, and ensuring confidentiality in the storage and use of data.** Any significant change in protocol over the course of the research should be notified to the Departmental Ethics Coordinator and may require a new application for ethics approval.

Applicant (Principal Investigator) Name: Karol Wereszczynski
Applicant's e-signature: Karol Wereszczynski
Date: 16/01/15

Supervisor Section (for students only)

Please tick the appropriate boxes. The study should not be submitted until all boxes are ticked:

<input type="checkbox"/>	The student has read the University's Code of Research Ethics
<input type="checkbox"/>	The topic merits further research
<input type="checkbox"/>	The student has the skills to carry out the research
<input type="checkbox"/>	The consent form is appropriate
<input type="checkbox"/>	The participant information leaflet is appropriate
<input type="checkbox"/>	The procedures for recruitment and obtaining informed consent are appropriate
<input type="checkbox"/>	An initial risk assessment has been completed
<input type="checkbox"/>	If there are issues of risk in the research, a full risk assessment has been undertaken in line with the 'School of Social Sciences Risk Assessment– FAQs' document and a risk assessment is attached.
<input type="checkbox"/>	A DBS check has been obtained (where appropriate)
<input type="checkbox"/>	The debriefing form is appropriate (NB for psychology only - please refer to BBL)

Any comments from supervisor:

--

Supervisor or module leader (where appropriate):

E-signature:

Date:

Supervisors: Please **email** this form to the student who will then need to submit it and related appendices via BBL.

Student: Once you have received this form back from your supervisor, submit this completed Checklist, consent form, information sheet and any other documents and attachments via BBL.

Departmental Ethics Coordinator section:

This request for expedited review has been:	<input type="checkbox"/> Approved (No additional ethics form is necessary)
	<input type="checkbox"/> Declined (Full University Ethics Form is necessary)
	<input type="checkbox"/> Declined (Please give reason below)

Departmental Ethics Coordinator Name:
E- signature
Date:

CONSENT FORM

“Influence of flicker cueing with various spatial and temporal properties on reaction time and visual discrimination of near threshold masked object.”

The participant should answer every question

	YES	NO
1. I have read the Research Participant Information Sheet.	<input type="checkbox"/>	<input type="checkbox"/>
2. I have had an opportunity to ask questions and discuss this study.	<input type="checkbox"/>	<input type="checkbox"/>
3. I understand that I am free to withdraw from the study:		
- at any time (Please note that you will unable to withdraw once your data has been included in any reports, publications etc)	<input type="checkbox"/>	<input type="checkbox"/>
- without having to give a reason for withdrawing	<input type="checkbox"/>	<input type="checkbox"/>
4. I agree to my answers being recorded	<input type="checkbox"/>	<input type="checkbox"/>
5. I understand that I will not be referred to by name in any report/publications resulting from this study and all data collected will be kept strictly confidential.	<input type="checkbox"/>	<input type="checkbox"/>
6. I understand that if I have any concerns, or complains I can contact dr. Andrew Parton	<input type="checkbox"/>	<input type="checkbox"/>
7. I declare that I don't suffer (have suffered) epilepsy, severe headaches, or member of my family doesn't have history of epilepsy	<input type="checkbox"/>	<input type="checkbox"/>
8. I understand that research will involve being exposed to blinking/flickering elements of the screen	<input type="checkbox"/>	<input type="checkbox"/>
9. I agree to take part in this study	<input type="checkbox"/>	<input type="checkbox"/>

Research Participant Name:
Research Participant signature:
Date:
Principal Investigator name:
Principal Investigator signature:
Date:

One copy to be kept by the participant and one by the researcher

PARTICIPANT INFORMATION LEAFLET

Study title “Influence of flicker cueing with various spatial and temporal properties on reaction time and perception of near threshold masked object.”

You are invited to take part in the study about influence of external stimuli (flickering light) on human cognitive processes. The purpose of the study is to investigate how different properties of external light modify out perception, attention and cognition in general. You have been invited to freely participate in this study in order to have an opportunity to contribute in scientific research, learn about the process of running behavioural experiments, and expand the knowledge about relation: brain – behaviour.

Do I have to take part?

You will participate as a volunteer and you can withdraw your consent of participation any time, without any further consequences.

What will happen to me if I take part?

Experimenter will ask you to sign consent form, verbally explain to you all procedures and will make sure you understand everything and you feel comfortable. Also you will be given the opportunity to ask questions regarding the experiment, and the experimenter will answer all your questions.

What do I have to do?

You will sit in front of the computer screen and will be asked to solve series of easy judgement tasks, such as spotting the object on the screen. Subsequently, you will be asked to indicate the answer by pressing one of two buttons.

What are the possible disadvantages and risks of taking part?

The experiment is, in general very save, you will see flickering light which sometimes can be irritating, but in general, people do not report any concerns regarding this effect. If you have a history of epilepsy, severe headaches, or someone in your family has got epilepsy history, you cannot take part in this experiment.

What if something goes wrong?

The probability of fatal errors, physical consequences of participation are very low.....

Will my taking part in this study be kept confidential?

Yes it is fully confidential, the data is anonymised, and all documents are kept in locked room.

What will happen to the results of the research study?

The results will be anonymously analysed and used in scientific research. The group results might be publish in scientific journal.

Who is organising and funding the research?

The researcher works as a PhD student, volunteer and is not paid by any organisation to conduct this research

What are the indemnity arrangements?

The Brunel University is responsible for indemnity arrangements

Who has reviewed the study?

The study was reviewed by dr. Andrew Parton and prof Marius Usher

Contact for further information

karol.wereszczynski@brunel.ac.uk

andrew.parton@brunel.ac.uk

(Refer to the short text titled *Research Participant Information Sheet* in the University Research Ethics Handbook for more information about the use of these headings)

CONSENT FORM

“Influence of flicker priming on visual discrimination for spatially cued and uncued targets.”

The participant should answer every question:	YES	NO
10. I have read the Research Participant Information Sheet.	<input type="checkbox"/>	<input type="checkbox"/>
11. I have had an opportunity to ask questions and discuss this study.	<input type="checkbox"/>	<input type="checkbox"/>
12. I understand that I am free to withdraw from the study:		
- at any time (Please note that you will be unable to withdraw once your data has been included in any reports, publications etc.)	<input type="checkbox"/>	<input type="checkbox"/>
- without having to give a reason for withdrawing	<input type="checkbox"/>	<input type="checkbox"/>
13. I agree to my answers being recorded	<input type="checkbox"/>	<input type="checkbox"/>
14. I understand that I will not be referred to by name in any report/publications resulting from this study and all data collected will be kept strictly confidential.	<input type="checkbox"/>	<input type="checkbox"/>
15. I understand that if I have any concerns, or complaints I can contact dr. Andrew Parton	<input type="checkbox"/>	<input type="checkbox"/>
16. I declare that I don't suffer (have suffered) epilepsy, severe headaches, or member of my family doesn't have history of epilepsy	<input type="checkbox"/>	<input type="checkbox"/>
17. I understand that research will involve being exposed to blinking/flickering elements of the screen	<input type="checkbox"/>	<input type="checkbox"/>
18. I agree to take part in this study	<input type="checkbox"/>	<input type="checkbox"/>

Research Participant Name:
Research Participant signature:
Date:
Principal Investigator name:
Principal Investigator signature:
Date:

One copy to be kept by the participant and one by the researcher

DEBRIEFING FORM:

Influence of flicker priming on visual discrimination for spatially cued and uncued targets.

Recently there is an increased interest in the literature about photic driving and its effects on visual discrimination. More specifically, there are two recent papers by Mathewson et al (2010) and Eelke et al (2014) reporting apparently opposing results.

The current study focuses upon the possibility that the results reflect a difference in the level of spatial location certainty and its attentional consequences. In simple terms probably different attentional neuronal strategies are applied when the spatial location of the target is highly predictable (Mathewson), or random (Spaak). I try to find out what causes the differences between both authors results. I will use variants of the Mathewson and Spaak paradigm to focus on whether spatial uncertainty of the near threshold target can influence visual discrimination in phase / out of phase of presented target. We try to find out what causes the differences between both authors results. We use variants of Mathewson and Eelke paradigm to focus on whether stimulating target area vs mask area by flicker can influence visual discrimination in phase / out of phase presented target.

You can find more details about the research in:

“Making Waves in the Stream of Consciousness: Entraining Oscillations in EEG Alpha and Fluctuations in Visual Awareness with Rhythmic Visual Stimulation”

Kyle E. Mathewson, Christopher Prudhomme, Monica Fabiani, Diane M. Beck, Alejandro Lleras, and Gabriele Gratton, 2012.

“Local Entrainment of Alpha Oscillations by Visual Stimuli Causes Cyclic Modulation of Perception”

Spaak Eelke, de Lange Floris, Jensen Ole, 2014.

If you would like to receive a copy of one of the papers please send me an email request.

karol.wereszczynski@brunel.ac.uk

THANK YOU

Appendix 2: Ethics approval EEG study

College of Health and Life Sciences
Life Sciences

Photic driving and visual discrimination – EEG study

RESEARCH ETHICS RISK ASSESSMENT AND MANAGEMENT

This form should be used to support the assessment of risks associated with your research project and their mitigation. This must be completed and submitted where relevant (see questions 43.2 and 44.1 on the Application Form for Research Ethics Approval).

Prior to completion, if there is any aspect of the risks or risk management process associated with your proposed research that you feel unsure about then it is **your responsibility** (as the researcher) to seek further guidance.

For Completion by the Researcher:

Identified Risks	Likelihood	Potential Impact/Outcome	Risk Management/Mitigating Factors
Identify the risks/hazards present	High/Medium/Low	Who might be harmed and how?	Evaluate the risks and decide on the precautions, e.g., Health & Safety

Damage to delicate EEG caps	High	Cost of repair or replacement	All prospective EEG operators receive hands-on supervised training on all procedures.
Electrode gel (if participant has skin break or allergy)	Low	Participant suffers skin irritation, stinging or inflammation	We use only hypoallergenic gel. Briefing and pre-screening allows us to exclude participants at risk.
Cross-infection	Low	Illness of participants or operators	Disinfection of all items in contact with participant after session e.g. electrode caps.
Electrical hazard	Low	Electric shock (to participant or operator)	All equipment in the lab receives a regular electrical safety check (last inspection 17/06/15). EEG equipment is certified to meet relevant EU/UK safety standards. Correct use of equipment is included in training.

Debrief form

“Influence of flicker priming on visual discrimination for spatially cued and uncued targets.”

We would like to say thank you for participating in the study. Below, there is a short description of the basis of the experiment which you have taken part.

Recently there is an increased interest in the literature about photic driving and its effects on visual discrimination. More specifically, there are two recent papers by Mathewson et al (2010) and Eelke et al (2014) reporting apparently opposing results.

The current study focuses upon the possibility that the results reflect a difference in the level of spatial location certainty and its attentional consequences. In simple terms probably different attentional neuronal strategies are applied when the spatial location of the target is highly predictable (Mathewson), or random (Spaak). I try to find out what causes the differences between both authors results. I will use variants of the Mathewson and Spaak paradigm to focus on whether spatial uncertainty of the near threshold target can influence visual discrimination in phase / out of phase of presented target. We try to find out what causes the differences between both authors results. We use variants of Mathewson and Eelke paradigm to focus on how manipulating the spatial uncertainty influence neuronal dynamics in phase and out of phase presented target.

You can find more details about the research in:

“Making Waves in the Stream of Consciousness: Entraining Oscillations in EEG Alpha and Fluctuations in Visual Awareness with Rhythmic Visual Stimulation”

Kyle E. Mathewson, Christopher Prudhomme, Monica Fabiani, Diane M. Beck, Alejandro Lleras, and Gabriele Gratton, 2012.

“Local Entrainment of Alpha Oscillations by Visual Stimuli Causes Cyclic Modulation of Perception”

Spaak Eelke, de Lange Floris, Jensen Ole, 2014.

If you would like to receive a copy of one of the papers, please send me an email request.

karol.wereszczynski@brunel.ac.uk

THANK YOU

College of Health and Life Sciences

Department of Life Sciences

PARTICIPANT INFORMATION SHEET

Study title “Influence of flicker priming on visual discrimination for spatially cued and uncued targets EEG study”

You are invited to take part in the study about influence of external stimuli (flickering light) on human cognitive processes. The purpose of the study is to investigate how different properties of external light modify our perception, attention and cognition. You have been invited to freely participate in this study (which will take approximately 80 minutes) in order to have an opportunity to contribute in scientific research, learn about the process of running neuroimaging experiments, and expand the knowledge about relation: brain – behaviour. Ask us if there is anything that is not clear or if you would like more information. Take time to decide whether or not you wish to take part.

Do I have to take part?

You will participate as a volunteer and you can withdraw your consent of participation any time, without any further consequences.

What will happen to me if I take part?

The experimenter will ask you to sign consent form, verbally explain to you all procedures and will make sure you understand everything and you feel comfortable. Also you will be given an opportunity to ask questions regarding the experiment, and the experimenter will answer all your questions.

EEG is a recording of the electrical activity of the brain. It is a safe, non-invasive procedure. It involves wearing a cap that contains 32 electrodes. Each electrode is a small ceramic disc with a sintered silver coating sitting in a small rubber cup. To make electrical contact with the scalp, saline gel (similar in consistency to hair gel) is squirted into the cup. The gel is hypoallergenic and harmless to normal hair and skin and is certified for this use. However you should not take part if you have any skin problems affecting your scalp or face such as cuts, grazes, spots, inflammation or soreness.

Once the electrodes have been filled, the cap is connected to the recording system to check whether the electrodes will record (impedance testing). There is usually some adjustment of the cap and re-filling of the electrodes to make sure that a good recording can be obtained. In the experiment itself, changing facial expressions are presented briefly (1 sec every 4 secs) and repeatedly (100 times per block), and you will carry out a simple task such as identifying each change as an increase or decrease in happiness, which you indicate by a button press. The tiny electrical signals from your scalp are passed into a powerful amplifier, and a computer records the EEG signal from each electrode. After the experiment, we average the activity to each stimulus to obtain a 3D map (two spatial dimensions plus time) of the brain’s response to the stimulus, known as an event related potential (ERP). Each block would typically last 8 min, and there would be breaks in between the blocks in which you can move around, stretch, talk, drink some water, etc. The experiment part would last about 50 min and the preparation and removal of the EEG cap would last about 30 min making about 80 min for the whole procedure. To remove the gel, it will be necessary to wash your hair soon after the experiment. There is a shower room nearby, with shampoo and a clean towel available, or if you prefer, you can remove most of the gel with a tissue and wash hair when you get home. It is also advisable to wash hair on the morning or night before the experiment for your own comfort and to obtain good recordings. We cannot record from people wearing a hijab or other head covering, with hair extensions, weave, thick plaited hair, or hair styled using wax, hair spray or similar products.

What do I have to do?

You will sit in front of the computer screen in the EEG lab and will be asked to solve series of easy judgement tasks, such as spotting the object on the screen. Subsequently, you will be asked to indicate the answer by pressing one of two buttons. The experiment will

involve observing 4 or 5 blocks of stimuli and pressing buttons while keeping seated, still, relaxed and attentive. Normal activities can resume between blocks.

What are the possible disadvantages and risks of taking part?

The experiment is, in general very safe, you will see flickering light which sometimes can be irritating, but in general, people do not report any concerns regarding this effect. If you have a history of epilepsy, severe headaches, or someone in your family has got epilepsy history, you cannot take part in this experiment. There are no other foreseeable disadvantages in taking part in the experiment apart from the fact that it may take up 80 minutes of your time. However an advantage is that you will be contributing towards psychological research and you will be reimbursed 15 pounds for your time.

What if something goes wrong?

You may stop the experiment at any time. If you have any questions about the study you can contact myself at karol.wereszczynski@brunel.ac.uk or my supervisor at andrew.parton@brunel.ac.uk. If a fire alarm sounds, you will need to leave the building while still wearing the cap.

Will my taking part in this study be kept confidential?

If you take part in the research all information collected from you during the course of the research will be kept strictly confidential. All references to participants in the report and any subsequent publications/presentations will be anonymous. The information will be kept in a secure location, accessible only to the researchers. Also all references to participants in the report and any subsequent publications/presentations will be anonymous.

What will happen to the results of the research study?

The results will be coded (for anonymity) and analysed by the research team before being reported. The results may also be presented in appropriate scientific peer reviewed journals and conferences. If you take part in this research, you can obtain copies of these publications from the research team. The data will be stored by the Supervisor Dr Andrew Parton at Brunel University under conditions specified by the Departmental Data Protection Advisor.

Who is organising and funding the research?

The project does not have any external funding. The running costs are supported by Brunel University. The researcher works as a PhD student and is not paid by any organisation to conduct this research

What are the indemnity arrangements?

Brunel University holds Public liability insurance policies which apply to this study. If you can demonstrate that you experienced harm as a result of you participation in this study, you may be able to claim compensation. Please contact David Anderson-Ford, the Chair of the University Research Ethics Committee (Professor Peter Hobson) if you would like further information about the insurance arrangements which apply to this study.

Who has reviewed the study?

The study has been reviewed the Department of Life Sciences Research Ethics Committee. Brunel University is committed to the UK Concordat on Research Integrity The University seeks to ensure that good practice in research is an integral part of its research strategy and associated policies. This code states that the general principle of integrity should inform all research activities. Honesty should be central to the relationship between the researcher, the participant and other interested parties.

Contact for further information

For further information on the research study please contact Michael.wright@brunel.ac.uk. If you have any complaints or concerns, please contact the chair of the Department of Life Sciences ethics committee, Dr. Richard Godfrey, Richard.godfrey@brunel.ac.uk

Available contacts include:

Karol Wereszczynski (karol.wereszczynski@brunel.ac.uk) Dr Andrew Parton (andrew.parton@brunel.ac.uk; 01895 267326)

College of Health and Life Sciences

Department of Life Sciences

CONSENT FORM

“Influence of flicker priming on visual discrimination for spatially cued and uncued targets.”

The participant should complete the whole of this sheet	
<i>Please tick the appropriate box</i>	
YES	NO
Have you read the Research Participant Information Sheet?	<input type="checkbox"/> <input type="checkbox"/>
Have you had an opportunity to ask questions and discuss this study?	<input type="checkbox"/> <input type="checkbox"/>
Have you received satisfactory answers to all your questions?	<input type="checkbox"/> <input type="checkbox"/>
Who have you spoken to?	<input type="checkbox"/>
Do you understand that you will not be referred to by name in any report concerning the study?	<input type="checkbox"/> <input type="checkbox"/>
Do you understand that you are free to withdraw from the study:	<input type="checkbox"/> <input type="checkbox"/>
• at any time?	<input type="checkbox"/> <input type="checkbox"/>
• without having to give a reason for withdrawing?	<input type="checkbox"/> <input type="checkbox"/>
• (where relevant, adapt if necessary) without affecting your future care?	<input type="checkbox"/> <input type="checkbox"/>
I declare that I don't suffer (have suffered) epilepsy, or severe headaches	<input type="checkbox"/> <input type="checkbox"/>
I understand that research will involve being exposed to	

blinking/flickering elements of the screen	<input type="checkbox"/>
Do you agree to take part in this study?	<input type="checkbox"/> <input type="checkbox"/>
Signature of Research Participant:	
Date:	
Name in capitals:	

Researcher name:	Signature:
Supervisor name:	Signature:

Advertisement

You are invited to take part in the exciting experiment, where your task will be to watch flashing objects on both sides of the screen, and immediately after, in one of the locations (either left or right) there will be presented brief target, which you will have to spot and report it by pressing corresponding button.

Prior to the experiment you will be given clear explanation and you will have the opportunity to do a short training session. As well you will have the opportunity to ask any clarifying questions.

For the reason that the task involves some flashes, participants not suffering epilepsy and severe headaches are invited.