EEG Oscillations as a Neural Correlate for Brightness Enhancement of Flickering Stimuli

By

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Abstract

Perception is to sensation what illusion is to the actual state of the world. How we sense information varies greatly from how we ultimately perceive and understand that information - a result of top-down and bottom-up processes at work. Work from over 100 years ago (Brucke, 1864) found an exaggerated display of this discrepancy when the rate at which a light flickered affected its perceived brightness. While the true luminance, or sensation, of the flickering light remained constant across frequencies, the perceived brightness, or perception, of an 8 to 10 Hz flickering light varied up to double the brightness of a constant light. Here, we sought to replicate and extend this finding: first, to make comparisons between two flickering stimuli and second, to explore if there were neural signatures of brightness enhancement observable through electroencephalography (EEG). We hypothesized that this frequency-dependent brightness enhancement should result from the dynamics of entraining neural oscillations in the brain at different frequencies. Specifically, given the historical results, we postulated that this divergence of sensation and perception would lie in the phasic properties of 8 to 10 Hz alpha oscillations, similar to the link between the phase of oscillatory alpha and visual detection by Mathewson et al., 2009. To test these ideas, we carried out two experiments. Experiment 1 (E1) collected behavioural reports from participants (n = 29) making brightness judgements about all possible pairs of 5 frequencies: 0 Hz (no flicker), 4 Hz, 9 Hz, 13 Hz, and 17 Hz. Experiment 2 (E2) (n = 23) included EEG and used a reduced set of frequencies (4 Hz, 9 Hz and 13 Hz) which had the greatest behavioural effects in E1. Both E1 and E2 provided strong behavioural evidence of the greatest brightness enhancement occurring from a 4 Hz stimulus, where 4 Hz looked brighter than all other frequency stimuli upwards of 80% of the time. Critically, all stimuli had the same physical luminance, meaning this brightness enhancement was entirely generated from

perception and not sensation. Our EEG analysis showed that this 4 Hz brightness enhancement occurred together with an increase in the amount of 4 Hz inter trial phase coherence (ITC), or phase consistency. We further tested the link between brightness enhancement and ITC in the 4 Hz band by binning the trials by the brightness judgment, rather than experimental condition (as was done with the other ITC analyses). Specifically, we examined trials where there were two of the same frequency stimuli on the screen (e.g. 4 Hz versus 4 Hz) and found a significant difference between the amount of 4 Hz ITC in the hemisphere contralateral to the 4 Hz stimulus chosen as brighter as opposed to the 4 Hz stimulus not chosen as brighter. The same pattern was not observed for the 9 Hz and 13 Hz stimuli, which had shown only slight phase locking in the previous analysis. This demonstrates that 4 Hz ITC could predict which stimulus was chosen as brighter even when it was identical in both frequency and luminance. We suggest that this brightness enhancement effect is a result of optimal transfer of the brightness information to higher order areas via an information transferring rhythm that resides around 4 Hz. Specifically, we posit that the theta rhythm, around 4 Hz, is the necessary oscillation for broadcasting visual information to areas responsible for brightness discrimination. In this experiment, we provide an exogenous entraining rhythm at or close to that of the endogenous theta rhythm, aligning the natural rhythm in a way that boosts the information transfer to higher areas responsible for decision making. This process results in brightness enhancement. We speculate that our original hypotheses regarding brightness enhancement residing in the alpha band would have been correct had this been a detection rather than a discrimination task. Thus, future experiments will see if the frequency of maximum brightness enhancement shifts to the alpha range if a simpler task is required. Further, we also hope to test if this entrainment of theta will enhance other percepts relying on higher-order processing, like motion coherence or visual search.

Preface

This thesis is an original work by Jennifer K. Bertrand. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Research Ethics Board, Project Name “ACE 1”, Pro00038718, 04/18/2013.

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Glossary of Terms

ANOVA: Analysis of variance
cm: Centimeter
CSD: Current source density
EEG: Electroencephalography
EOG: Electro-oculogram
ERP: Event-related potential
GUI: Graphical user interface
Hz: Hertz
ITC: Inter trial phase coherence
ITI: Inter trial interval
KOhm: kiloohmn
LGN: Lateral geniculate nucleus
ms: Millisecond
MT: Middle temporal visual area, or V5
RMANOVA: Repeated measures analysis of variance
VEP: Visual evoked potential
V1: Primary visual cortex
V2-V4: Visual cortex areas

1.0 – Introduction

Reading this document, whether on printed paper or from a computer screen, does not feel like an elaborate process. We don't need to consciously separate the background paper from the letters of the foreground, nor do we need to make an effort to recognize each letter individually from its shape and sharp edges. With ease we can read a string of letters as a word, and derive meaning from a series of words, all while relating these phrases to our lived experiences and the environment around us. However, the seemingly effortless and efficient way in which we take in visual information should not mislead us in thinking the system processing this information is simple and straightforward, but in fact should make evident just how complex and intricate the visual processing system must be to make the reading and understanding of these words undeniably automatic.

Continuing to read this document, we don't question what we are perceiving; we assume that our eyes provide us with a true and correct picture of the outside world. However, the distinction between the information our eyes receive and our experience of that information is important. The sensation of light entering the eye is understandably related to our visual perception, but critically different – while we are exposed to the same sensation of light hitting our retinae from these words, our experience can be vastly different. Scanning this document for one key word as opposed to reading through, captivated by the content, provides identical sensations, but very different experiences. Though it may seem unsettling, as if our eyes deceive us, the brain and eyes' ability to process the world around us with such efficiency allows us to not become visually overwhelmed, to remain alert and safe, and to process only the most critical of information from our surroundings. Typically, this process is highly automatic, where we don't consider why a certain word on this page stands out, or why we might have to read a paragraph over again for lack of attention. These processes are subconscious and we don't consider that the sensory experience is different from our subjective perceptual experience. Optical illusions, for example, are instances where this division is more obvious, contrasting the real, true world, and our subjective world.

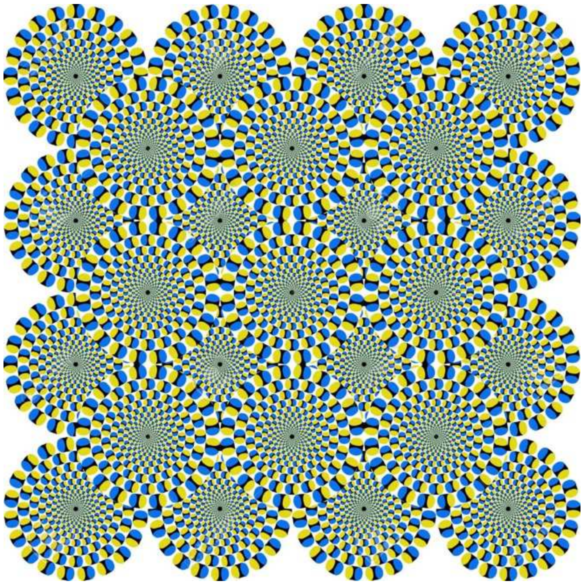

Figure 1.1: An example of an optical illusion that provides apparent motion perceptions, though the true light sensations from the image are not moving. Reprinted from These Optical Illusions Trick Your Brain with Science, in *Wired*, by N. Stockton, 2014, Retrieved March 5, 2017, from https://www.wired.com/2014/11/optical-illusion-science/. Copyright 2014 by Conde Nast.

While Figure 1.1, an optical illusion, may provide the perception of movement, we know that the ink on the paper could not possibly afford this apparent motion. Here, it is easier to divide the perceptual experience from the sensation that produced it – we can understand that some other influence is at play beyond only the qualities of the printed image. This other influence is a product of complex pathways in our brain that combine bottom-up information like the physical attributes of Figure 1, with top-down information from the brain, like the implication of the contrasting of colours and the contouring of the shapes. Taken together, this provides a perception of motion, a subjective experience that differs from the true input from the outside world.

Optical illusions are surely interesting and thought-provoking, but their value extends far beyond their marvel, as advocated by Von Helmholtz (1881):

> "The study of what are called illusions of the senses is however a very prominent and important part of the physiology of the senses; for just those cases in which external impressions evoke conceptions which are not in accordance with reality are particularly instructive for discovering the law of those means and processes by which normal perceptions originate."

In this thesis, I explore one particular illusion, considering how brightness perception differs from the sensation of luminance. Investigating this deviation from reality, where certain stimuli look brighter than others while their true luminance remains constant, will allow for a better understanding of the "means and processes" of perception, just as Helmholtz's encouraged.

1.1 – Eye to brain: Bottom-up visual processing and sensation (Luminance)

Absorbing information from the world around us never feels overly exhausting or onerous. Assuming a functioning neurological system, not much more is necessary than the opening of our eyes to carry out effective bottom-up visual processing. This bottom-up processing is what supplies the brain with a sensation, like the sensation of luminance which is the particular case of interest for this thesis. Of course, it is wildly ignorant to reduce the bottom-up pathway of visual processing to a simple opening of the eyes, and thus it is important to outline the elaborate and powerful bottom-up visual pathway.

All visual processing begins with light and our primary understanding of the visual system is one that takes light information from the outside world and processes it in the brain, a bottom-up pathway. At the broadest level of description, this information enters each of the retinae, makes its way through the optic nerve, combines some left retina and right retina visual information through a cross-over in the optic chiasm, and carries on through the optic tract

(Kandel, Schwartz, Jessell, Siegelbaum, & Hudspeth, 2013). Axons from the retina project to the axons of the lateral geniculate nucleus of the thalamus, which then carry the retinal information to the primary visual cortex and beyond (Kandel et al., 2013). Other bottom up pathways also exist to aid in the mechanics of vision.

1.1.1 – Visual processing before visual cortex

In more detail from Kandel et al. (2013), absorption by the retina of a photon of light energy begins a biochemical process in both types of photoreceptors - the rods and the cones. These rods and cones are unevenly distributed throughout the retina, with only cones in the central fovea, the area at the centre of our gaze, and a less dense collection of photoreceptors moving outward from the central fovea. The functional contributions of the rods and cones align with their physical orientation: cones provide daylight vision because of their diminished sensitivity to light, and rods provide low-light or night vision by way of their high sensitivity to light (can be easily saturated). It is after the activation of the retina's photoreceptors by light that we find the first instance of low-level visual processing, scaling down the information from 100 million rods and 6 million cones to only 1% as many axons in the optic nerve. This substantial reduction of data is essential for an efficient and effective visual pathway, relaying only essential information to the optic nerve. Retinal ganglion cells, and their corresponding receptive fields on the retina, are either ON or OFF cells, firing if illuminated (ON) or not (OFF). Outside the ON or OFF centre area lies an opposite surround region, allowing for spatial contrast and detection of edges of two different luminance intensities. These ganglion cells also provide temporal information, with firing rates of different ganglion cell types coding fast and slow changes in light intensity. It is also at the level of the photoreceptor, specifically in cone pathways, that colour vision is present. However, it is interesting that only 10% of neurons are associated with colour contrast as opposed to luminance contrast - highlighting the immense contribution light makes to our vision. As a system, the retina provides light adaptation, decreasing the sensitivity of changes in light as total illumination increases, and collects relevant information different from large-scale illumination changes. These low-level processing pieces of information become the basis of higher-order processing and represent just the first steps in seeing the whole picture.

The lateral geniculate nucleus (LGN) becomes an intermediate step for the light information moving from the retina to the visual cortex, as described by Kandel et al. (2013). The neurons of the LGN have circular receptive fields like the retinal ganglion cells, and continue to “respond to light-dark contrasts of edges or lines in the visual field”. The six layers of the LGN, residing in the thalamic nucleus, receive information from either the ipsilateral or contralateral eye, and forward the information to the primary visual cortex, creating a “complete neural map of the contralateral visual field”. The LGN preserves the spatial arrangement of the retinal input as a neural, or retinotopic, map of the visual field to relay to the primary visual cortex.

1.1.2 – Visual processing in visual cortex

After progressing through the eye, its photoreceptors, and the LGN, visual information enters the primary visual cortex (V1). Detailed by Kandel et al. (2013), V1 neurons respond selectively to orientation, binocular depth and movement direction, as well as features already processed in the retina and LGN. It is here that properties like orientation specificity and integration of both eyes emerge, where individual neurons first integrate signals from both eyes. V1 is functionally organized in columns, where every visual attribute like “orientation of contours, the colour and direction of movement of objects, and stereoscopic depth" can be analysed for any given particular part of the visual field. This organization allows for a decreased "number of neurons required for analyzing different attributes", explaining another instance of neural volume reduction and efficient processing without the sacrifice of lost information in the visual processing pathway. From V1, pyramidal neurons project to other areas of the cortex, including related visual cortex areas like V2, which concerns object surface properties, V4, an area of integration of colour and object shape, and V5, addressing motion of the spatial domain.

1.1.3 – Visual processing beyond primary visual cortex

Visual information, and the processing of this information, does not terminate in visual cortex. Critically the retinotopic organization of visual information is maintained in regions of the brain beyond strictly visual areas. Multiple frontal and parietal areas have shown retinotopic activity, primarily driven by attention, while the early visual areas show stimuli-driven retinotopic activity (Saygin & Sereno, 2008). Maintenance of these retinotopic representations throughout the processing of visual information, driven originally by the stimulus and then subsequently by attention, suggests different functional roles of these areas during perception and attention (Saygin & Sereno, 2008). Further, areas beyond the early visual cortex, like the lateral temporal cortex, have shown stimuli represented retinotopically without attention (Saygin & Sereno, 2008). These areas are thought to be connected by way of neural fibers that exist parallel to the cortical surface, providing "long-range horizontal connections", that allow for engagement of a large population of neurons to create a "unified percept" (Kandel et al., 2013). These parietal and frontal regions represent the "top" of the bottom-up pathway, a final location for light information originating in the retina after completing its intricate journey through the bottom-up pathway.

1.2 – Brain to eye: Top-down visual processing and perception (Brightness)

Vision’s bottom-up pathway, collecting information from the senses and moving it up into the brain, has long routed our fundamental understanding of sensation. Visual sensation's bottom-up pathway is an obvious one - we can intuitively close and open our eyes, and prevent light from initiating our visual pathway. Historically, it was understood that humans have sensations, like light hitting the retina, a luminance value, but until that sensation is combined with the mental capacity of perception, the light hitting the retina remains only light and not an identified and understood object (Gibson, 1950). This additive theory of sensation combining with perception to form a meaningful visual experience was refined in 1950, when Gibson suggested that while the sensations every person experiences are the same, the perceptual experience is subjective and must reflect individual "peculiarities and past experience[s]" (Gibson, 1950). Here began the still-relevant discussion that visual perception involves a parallel system of coinciding bottom-up and top-down pathways, where the eyes provide information to the brain, but the brain also informs the eyes. Top-down visual processing can provide an explanation for interesting biased visual perceptions, like how a person’s motivational state can affect the processing and categorization of visual stimuli (Balcetis & Dunning, 2006), or how people with schizophrenia and other disorders can have perceptions of a non-existent stimulus – a hallucination (Grossberg, 2000). However, the effects of top-down pathways don’t need to be this overt; top-down pathways are persistently active even when simply reading the words of this document.

1.2.1 – Influences of perception on sensation

Top-down influences on perception exist in different areas throughout the brain, and as the bottom-up pathway moves from the eye to the brain, a reciprocal top-down pathway (comprised of many different pathways) exists. Top-down processing often originates where our discussion of the bottom-up pathways ended, that is, in frontal and parietal areas of the brain. These areas are functionally responsible for a wide range of complex, higher-level cognitive tasks. The frontal area of the brain is concerned with many dimensions of the executive control of behaviour, including goal directed behaviour (Kandel et al., 2013). The parietal area is implicated in general visual attention, with object size and orientation, saccades, and object matching (Culham & Kanwisher, 2001), and visual guidance of motor behaviour (Kandel et al., 2013).

Evidence exists for top-down activity originating in frontal and parietal regions having a direct impact on visual perception including modulating responses in visual cortex. Due to their position at the "pinnacle" of the bottom-up hierarchy and their role in brain-wide modulations, these fronto-parietal areas are widely implicated in attention, which consequently affects visual perception. These frontal and parietal areas have been linked with the modulation of various forms of visual attention: saliency modulation for irrelevant or distracting information or locations (Mevorach, Hodsoll, Allen, Shalev, & Humphreys, 2010; Sylvester, Jack, Corbetta, & Shulman, 2008), anticipatory visual spatial attention or attentional preparation (Bressler, Tang, Sylvester, Shulman, & Corbetta, 2008; Culham & Kanwisher, 2001), and the ignoring of salient distractors (Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006).

Beyond the frontal and parietal areas, some evidence exists for top-down modulation originating from the visual cortex, without input from higher cortical areas. Areas V1, V2, V4 and middle temporal visual area (MT) show "enhancement of neural responses" for spatial attention tasks (Gilbert & Li, 2013). V1 has shown "contour-related facilitation" in detecting a contour in complex scenes, and is also implicated in modulation related to shape expectation of objects. (Gilbert & Li, 2013). The accurate perceiving of low-contrast stimuli can also be predicted by suppression of activity to unattended locations in the visual cortex during anticipation of low-contrast stimuli (Sylvester et al., 2008).

Extending further along the top-down pathway, leaving the cortex, some influence has been affected from structures as far down as the LGN. While we intuitively would assume the bottom-up pathway between the LGN and the cortex may have greater significance in visual processing than its complementary top-down pathway, if the sheer volume of neural projections is used as an indicator of importance, it may be surprising that there are tenfold more top-down connections between the cortex and the LGN as there are bottom-up (Kandel et al., 2013). The LGN has shown modulation by selective attention by way of enhancement of attended stimuli and also suppression of ignored stimuli (O'Connor, Fukui, Pinsk, & Kastner, 2002). The effects of these modulations can then be seen in the visual cortex and onward, making the LGN the first stage of visual processing affected by attention (O'Connor et al., 2002). Attentional modulation appears to exist in two manners (at least in the monkey model): first by LGN activity enhanced by activity in the nearby thalamic reticular nucleus, and a slower, later LGN enhancement possibly from goal-directed attention modulation (McAlonan, Cavanaugh, & Wurtz, 2008). The top-down pathways associated with visual processing can be understood as feedback during the bottom-up pathway, and this feedback to the LGN from the cortex appears to stem from binocular and orientation-selective cells that share corresponding topographically maps (Gove, Grossberg, & Mingolla, 1994).

1.2.2 – Top-down brightness perception

As expected, top-down influences of visual perception exist for the specific perception of brightness. If luminance relates to bottom-up visual processing, brightness, the "perceptual correlate of perceived luminance", is a product of top-down visual processing (Kingdom, 2011). While luminance is a value that could be reduced to a measure at a single point, brightness considers the consequential effects of context and contrast of surrounding points (Kingdom, 2011). Here, it is important to make a distinction between brightness and lightness, two terms used interchangeably in conversation but not in vision science. A brightness judgment and a lightness judgment ask two different questions: brightness judgments ask for the shade of an image, and lightness judgments ask for apparent reflectance of an image (Adelson, 1993). While both these judgments are a result of top-down visual processing this thesis is concerned exclusively with brightness judgments.

Various top-down influences affect brightness perception: priming by way of happy or sad emotional stimuli (Zhang, Zuo, Erskine, & Hu, 2016), the positive or negative valence of music (Bhattacharya & Lindsen, 2016) or the positive or negative affect of words (Meier, Robinson, Crawford, & Ahlvers, 2007) biased brightness judgments in a direction where happy or positive primes produced brighter judgments, and negative or sad primes resulted in darker judgments of the same stimuli. As various visual perceptions are affected by attention, so too is brightness perception, where voluntary attention appears to affect brightness judgments of two overlapping transparent surfaces (Tse, 2004). Other evidence exists for large biases of brightness judgments based on geometrical differences in visual images that should be "inconsequential for low-level mechanisms", suggesting the necessity of top-down pathways to produce such biases (Adelson, 1993). Context and scene also affect luminance judgments about objects that appear to have surface curvature, again suggesting the effects of top-down influence (Knill & Kersten, 1991).

The mechanism of these top-down influences on the specific percept of brightness remain widely unstudied, but it is suggested feedback loops between the LGN and V1, and V1 and V2 play an important role for surface percepts like filled-in brightness (Gove et al., 1994).

1.3 – Flickering stimuli: A case study in luminance sensation and brightness perception differences

Narrowing the focus of visual perception to the topic of this thesis brings us to flicker perception, and specifically how it relates to brightness judgments. This domain appears empirically untouched in more recent years, with the greatest contributions to brightness perception's temporal properties now at least 50 years old. Various classic phenomena associated with brightness perception and brief visual stimuli include Bloch's law, the Broca-Sulzer effect, the critical flicker fusion frequency, the Talbot effect, and most specific to this thesis, the Brücke effect. Bloch's law is an inverse relationship between the duration of "sufficiently brief" (between 1 and 50 milliseconds) stimuli presentations and the amount of visible light energy necessary for a threshold response, such that a very brief stimulus would require greater luminance for it to reach threshold (Baumgardt & Hillmann, 1959; Gorea, 2015). Similarly, the Broca-Sulzer effect illustrates an "overshooting" effect, where for stimulus durations of 50 to 100 milliseconds (ms), apparent brightness increases with the length of stimulus presentation, until a plateau when duration reaches 200 to 250 ms (Raab, 1962; Raab, Fehrer, & Hershenon, 1961). The Broca-Sulzer effect also appears to reverse when a brief flash (56 ms) locks offset with a longer flash (278 ms), where the brief flash then looks brighter

(Eagleman, Jacobsen, & Sejnowski, 2004). Perhaps the most researched temporal characteristics of visual perception involve the critical flicker fusion frequency, a frequency or rate at which a flickering light becomes "steady", around 40 Hertz (Hz), losing its perception of flicker (Simonson & Brožek, 1952). The critical flicker fusion frequency has been shown to increase as illumination of the stimulus increases (Simonson & Brožek, 1952). The Talbot effect then pertains to the perceived brightness of a stimulus at or above the critical flicker fusion frequency, where the brightness value is determined by the time-average luminance of the flickering stimulus (Walker, 1978). For these frequencies at or above the critical flicker fusion frequency, the luminance of a flickering light would need to be two times that of a steady light to appear as bright (Pantle, 1972). Clearly, in various ways, the sensation of flicker produces wide-ranging and biased perceptions of brightness that remain mostly unexplained.

1.3.1 – The Brücke effect

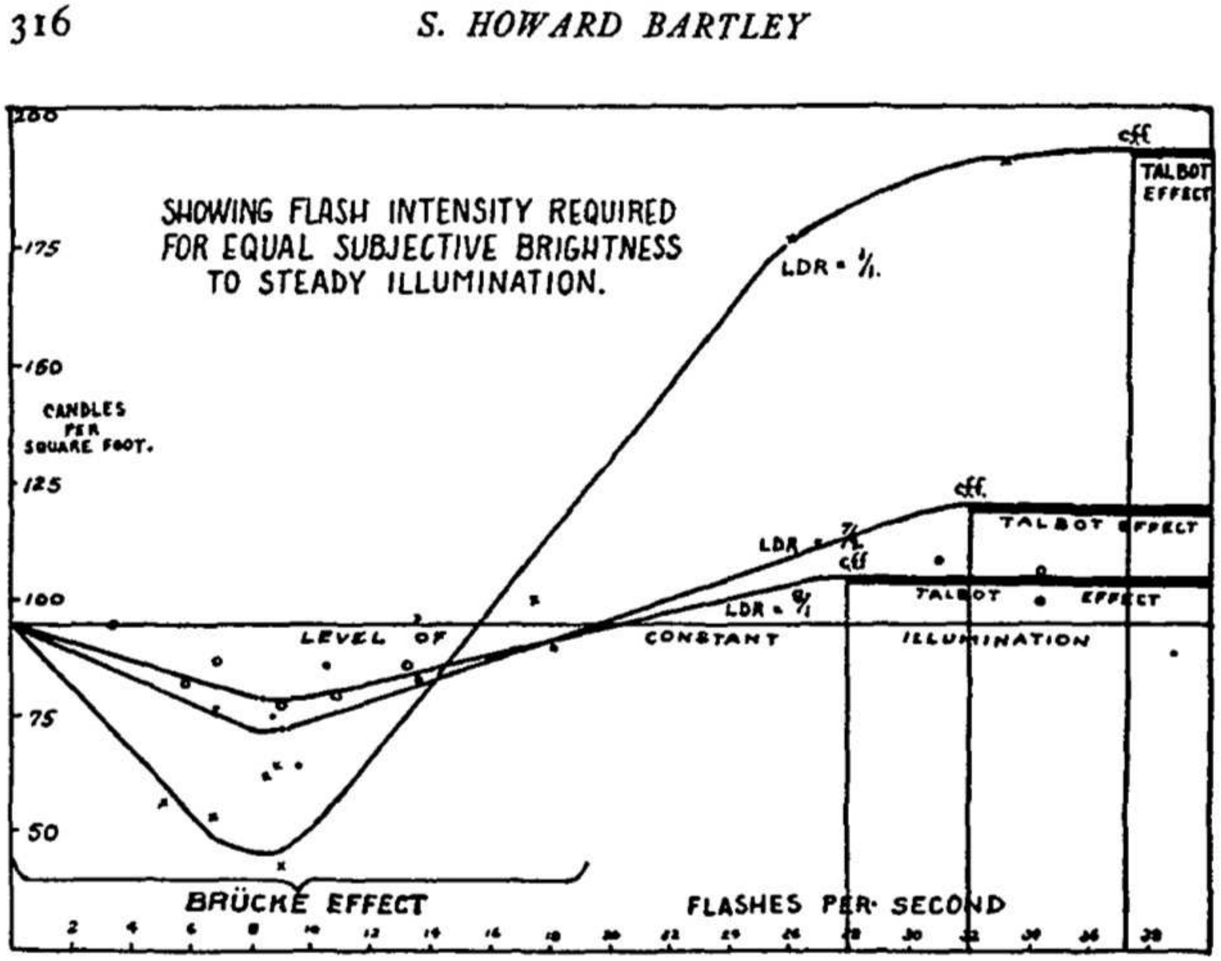

Figure 1.2: Bartley plotted his understanding of the subjective brightness of a flickering light as a function of its frequency. These brightness judgments were compared to the brightness of a light of constant illumination. He coined the brightness enhancement in the lower frequencies the Brücke effect, after Brücke's 1864 German publication, and also recognized a reversing of this effect in the higher frequencies, already known as the Talbot effect. Reprinted from "Subjective brightness in relation to flash rate and the light-dark ratio," by S. H. Bartley, 1938, *Journal of Experimental Psychology, 23*(3), p. 316. Reprinted with permission from APA.

At the heart of this thesis is the fascinating discovery that when the frequency of intermittent or flickering light is below that of the critical flicker fusion frequency, the increased luminance intensity needed to match a constant light decreases, with the relationship critically reversing as the frequency slows to about 10 Hz and lower (Pantle, 1972). This phenomenon, the

Brücke effect, where, at its peak, a flickering stimulus appears twice as bright as a constant stimulus with the same luminance, has become the foundation for the current experiments.

Bartley's (1938) coining of the Brücke effect as the enhancement of brightness by a series of flashes below the critical flicker frequency (Figure 1.2) came by way of much earlier work (1864) by Brücke (Bartley, 1938). Brücke, and subsequently Bartley, tested brightness judgments about a flickering stimulus at a range of frequencies as compared to a steadily illuminated stimulus (Bartley, 1938). Particularly, Bartley was convinced that the Brücke effect occurred as a process "not determined in the eye", and that the flicker rate of greatest brightness enhancement appeared to align with the rate of a centrally-determined cortical rhythm of processing - the alpha rhythm (Bartley, 1938). Bartley bolstered the Brücke effect with examination of the "pulse-to-cycle-fraction", finding, specific to the alpha frequency, the greatest brightness enhancement with a 0.3 pulse-to-cycle-fraction and a decreasing effect with an increasing ratio (Bartley, Paczewitz, & Valsi, 1957). Other related work provided insight on a mismatch between the subjective flash rate and the photic pulse rate near the alpha frequency (Nelson, Bartley, & Bochniak, 1965), and the increasing of brightness enhancement and the frequency at which maximal enhancement occurs by way of increasing the luminance of the stimulus (van der Horst & Muis, 1968). Beyond these contributions, little apparent progress has been made in understanding and elaborating on Brücke's 150-year-old discovery.

1.4 – Neural oscillations as a possible origin of the Brücke effect

Revisiting the Brücke effect 150 years after its first reported discovery is exciting given the technology and tools we now possess to look for a mechanism in the brain that might begin to explain this phenomenon. While the behavioural results of Brücke and Bartley supply an interesting finding to hypothesize about, a study involving electrophysiology may provide answers to how this phenomenon arises. Further, knowing now what we do about visual processing, and the distinction between the sensation of luminance and the perception of brightness, can we find an element of the pathway where the true luminance of a stimuli no longer aligns with its perceived brightness?

As this discussion concerns flickering stimuli, a reasonable preliminary hypothesis should consider the role of neural oscillations as a means for the disconnect between sensation and perception. Bartley's plot of the Brücke effect (Figure 1.2) suggests a brightness perception that varies as a function of the frequency a stimulus flickers. Most notably, the greatest brightness enhancement appears to align with the alpha frequency band, around 8-12 Hz. Given the progress of brain research, we understand the brain to oscillate at many different frequencies as a method of information transfer and communication between areas. The brain is also accepted to realign or reset to external, endogenous frequencies visually. The relationship between flicker frequency and brightness perception may then perhaps be explained by a connection between the frequency of flicker and the frequency of naturally-occurring brain oscillations.

1.4.1 – Overview of neural oscillations

1.4.1.1 – Measuring and characterizing oscillation frequencies

The first known identification of oscillatory activity came about by a Prussian army veteran's assurance in 1929 that telepathy must be facilitated by electrical activity in the brain (Buzsáki, 2006). He found the greatest activity in the occipital area of the human scalp, where large amplitude rhythms oscillated at about 10 waves per second, and faster waves were also present (Buzsáki, 2006). The slower rhythmic activity was named the "alpha" rhythm, as it was the first rhythm he observed (and though prompted by colleagues to name it the Berger rhythm, after himself, he declined), and the faster oscillations were called "beta" waves (Buzsáki, 2006). Discovering these rhythms unfortunately did not support his telepathy hypotheses (as the voltage recorded was so small it could not pass through air), but instead sparked a still-relevant discussion about the brain's rhythms and their functions (Buzsáki, 2006).

As oscillatory activity of other speeds was discovered, they too were provided Greek names and given arbitrary borders of separation to define frequency bands. By 1974, the International Federation of Society for EEG and Clinical Neurophysiology had accepted and documented this classification system, adding the delta, theta, and gamma rhythms to their glossary (Chatrain et al., 1974). This organizational structure still exists today, although greater focus on the dynamics of all frequency activity as a whole appears more relevant than the activity of one frequency band alone.

Today, these frequency bands continue to exist, with greater implications as to what their roles may be in the brain. Slow 1 to 4 Hz activity, the delta rhythm, occurs most prominently during sleep, but also shows links to attention (Buzsáki, 2006; Calderone, Lakatos, Butler, & Castellanos, 2014). Theta (4 – 8 Hz) appears to be involved in exploratory movements and working memory, and is most prominent in hippocampal regions (Wang, 2010). Alpha activity (8 – 12 Hz) correlates best with closed eyes and mental inactivity, and shows an inverse relationship with visual attention (Chatrain et al., 1974). The quick beta activity uncovered by Berger, at 15 to 30 Hz, arises mostly from the primary motor cortex during "preparation and inhibitory control in the motor system" (Wang, 2010). Faster yet, gamma activity (30 – 80 Hz) plays a part in the integration of sensory information, induced by sensory stimulation, and is thought to be involved with attention (Wang, 2010). While classifying this frequency-specific activity in discrete bands, these frequencies are not meant to be understood as existing in isolation, but instead as pieces that contribute to a large scale oscillatory network involving a range of frequencies.

Electrophysiological methods provide evidence of oscillatory activity – some use more direct measures, collecting electrical information directly from the cortex with implanted electrodes, but the most common and least invasive method involves the use of electroencephalography (EEG) at the level of the scalp. This system collects electrical signals from the scalp with high temporal precision, as measured by a relative voltage between a non-cortical reference and scalp electrodes (Cohen, 2014). However, spatial information is limited with surface recordings, and structures and neuron groups responsible for specific activity are relatively impossible to isolate (Buzsáki, 2006). Different techniques exist to analyze and interpret EEG data, including event related potentials and time-frequency approaches. While event related potential (ERP) methods involve a direct comparison of voltage, typically between conditions, time-frequency analyses transform EEG data to centre frequency as a "prominent dimension" (Cohen, 2014). Time frequency methods therefore allow for an interpretation "in terms of neurophysiological mechanisms of neural oscillations", where increased frequency-specific activity reflects an increase of oscillatory activity within that frequency (Cohen, 2014).

Time-frequency analysis, as its name suggests, transforms EEG data to frequency information existing over the time domain with the phase and power of each measured frequency being calculated for each moment in time (Figure 1.3). Phase information provides a measure of position along an oscillation, as visualized as a point on a sine wave, and often described as a circular angle between 0 and 360 degrees, or in radians (Cohen, 2014). Power information is independent of phase information, and describes the amount of energy within an oscillation, computed as the squared amplitude of the sine wave (Cohen, 2014). Separate phase and power measures are available for each frequency, which is the speed of an oscillation, and quantified as the number of cycles of a sine wave per second, or hertz (Cohen, 2014). Together, these measures give a complete picture of time-frequency information, and can be used in further analyses like inter trial phase coherence (ITC) and power spectrums.

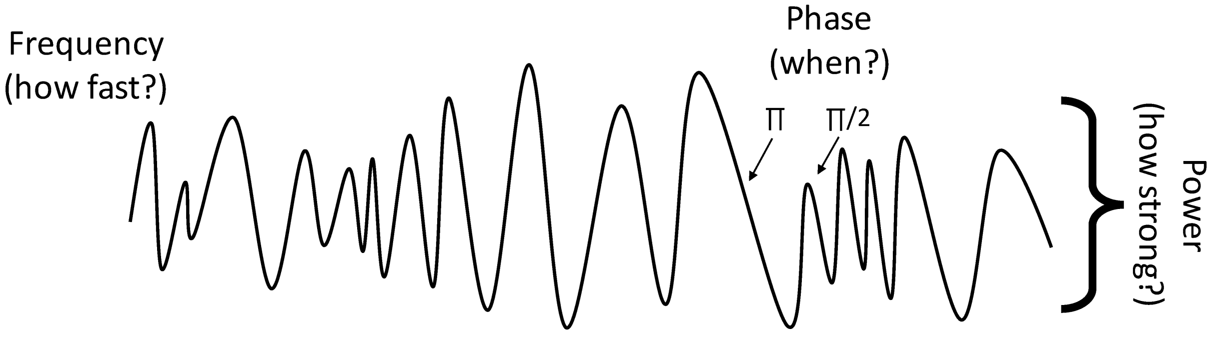

Figure 1.3: A visualization of the three components of time-frequency decomposition: frequency, power, and phase. Adapted from *Analyzing Neural Time Series Data* (p.32), by M.X. Cohen, 2014, MIT Press.

1.4.1.2 – Oscillations in neural networks

Oscillatory activity existing in neuronal networks has been observed in frequencies of 0.05 Hz to 500 Hz, with linearly-progressing frequency bands being referenced to as a way to classify related frequencies (Buzsáki & Draguhn, 2004). These frequency bands, including the common bands mentioned previously, correspond to different activation patterns in the brain, and can compete with other frequency bands, but can also coexist and interact to facilitate processes (Buzsáki & Draguhn, 2004). Oscillatory networks as dynamic and multi-frequency systems test the long-regarded and outdated view of a sole rhythm, the alpha frequency, as only a background, idling signal (VanRullen, 2016). This has since sparked experimentation in not just observation of oscillations, but also the inducing of oscillations, and has evolved our understanding of oscillatory networks as a possible window into perception, memory and consciousness (Buzsáki & Draguhn, 2004).

Oscillations, or synchronous rhythmic activities, are not completely understood. While we expand and strengthen evidence of their existence and correlation with behaviour, we lack a complete understanding about the function and mechanisms oscillations employ in the processing of perception. Evidence suggests that both internal neural connections and stimulus-related signals create an environment for oscillatory activity (da Silva, 1991), disproving the early ideas that oscillations only arise from stimulus-locked synchronization (Uhlhaas et al., 2009). Potential mechanisms for the generation of oscillations in the visual system include: oscillatory input from the lateral geniculate nucleus, like a pacemaker or driving influence, intra-cortical network interactions by way of excitatory synaptic input related to the stimulus, or activity in a subpopulation of cells that are intrinsically oscillatory (Gray, 1994). While cells like the superficial pyramidal neuron have been shown to have pacemaker qualities in visually driven oscillations in the cat brain (Gray & McCormick, 1996), these appear to only be part of the complete story, and are incapable of explaining what function this oscillatory activity serves. Initially, it was thought that these oscillations could not carry information because of their substantial variability in frequency and amplitude (Gray, 1994), however later proposals suggested "temporal signal correlations…, the partial coherence of action potentials within a neural population" might link together areas of the brain during visual processing (Eckhorn et al., 1988). Generally speaking, this hypothesis still exists today, although it has been (and continues to be) elaborated upon.

More recent work has begun to shed light on the mechanisms and functions of oscillatory networks. An increased strength of synchronous activity appears to correlate with more similar neural orientation preferences (Betsch, Einhäuser, Körding, & König, 2004) and related visual features (Singer, 1999). The discovery of zero or near-zero phase lag between cortical regions during neural synchrony, difficult to explain given conduction delays across the cortex, has prompted suggestions that still include the mechanism of an internal oscillator that all rhythms align with, or perhaps an emerging properties mechanism that does not originate from just one point, but is rather an "interaction of elements in the network" (Uhlhaas et al., 2009). Physical properties of cortical interneurons neurons have shown filtering abilities, where a combination of voltage-dependent and time-dependent characteristics of neurons can allow for tuning of preferred input frequencies, "setting network dynamics" (Buzsáki & Draguhn, 2004). And phase-dependent excitability of large, robust, and stable "macroscopic" oscillations appears to have a distinct information transfer phase and an information receiving phase (Buzsáki & Draguhn, 2004). Interpreting the role and means of oscillatory activity in the visual system is not as straightforward as it might have been expected decades after discovery, and points to just how complex these circuits are to disentangle.

1.4.2 – Linking oscillations with sensation and perception

Explaining the combining of top down and bottom up information in the visual process with oscillatory networks will only become fully resolved when oscillations' functions and mechanisms are completely understood, but definite connections exist. Synchronous oscillatory activity in the theta band (~4 Hz) and gamma band (~60-80 Hz) has been linked with bottom-up (feed-forward) influences, and beta band activity (~14-18 Hz) linked with top down (feedback) influences during visual tasks in the primate brain (Bastos et al., 2015). Similar coupling of gamma activity with the phase of alpha activity has proven to be a mechanism of top-down anticipatory gating during visual tasks (Bonnefond & Jensen, 2015), and this coupling also appears to prioritize and order salient unattended stimuli (Jensen, Bonnefond, & VanRullen, 2012). Further, the coupling of the alpha and gamma bands, driven primarily by the power and phase of the alpha rhythm (as it relates to spatial attention) prioritize information processing and carry out parallel processing, where an increase in top down influences, like spatial attention, could increase the firing of neurons in early visual regions within an alpha cycle (Jensen, Gips, Bergmann, & Bonnefond, 2014). In the cat species, cortical synchronizations found necessary for visual processing have been determined to not be only a result of the contribution from the external stimuli, but also from top-down influences liked learned associations and expectations about the stimuli (Von Stein, Chiang, & König, 2000). Again, while not a complete picture, it is clear that oscillations in multiple frequency bands do play a role in visual processing.

1.4.2.1 – Oscillations, discretized processing and how their interaction effects perception

An understanding of synchronous oscillations' role in visual processing would not be complete without acknowledging its part in the rhythmic and discretized nature of visual perception. Unlike a movie streaming over a bad internet connection, we experience no lag or disruptions to our vision, receiving what we feel as a completely continuous stream of visual information. Discussions around perception's discrete or continuous nature have long centered around our subjective experience - we observe, hear, feel, smell, and taste in a continuous way, with no apparent interruption to our sensory experience. However, while not intuitive and still somewhat controversial, it appears that our unwavering visual stream is remarkably the output of a discretized processing system. The discretization of information from our outside world can be understood as brief snapshots that align with a specific phase of an oscillating frequency in the brain (VanRullen, 2016). Periodicities in reaction time and visual threshold as well as relationships between the frequency and phase of brain rhythms and behaviour shed light on a possible connection between periodic or oscillatory processing in the brain and the visual system, and with advances in temporally resolute technology, the idea that perception may be a discrete process, like frames in a movie, became more accepted (VanRullen & Koch, 2003). Upon review, and substantiating perception's discrete nature, oscillatory activity in two specific frequencies, 7 Hz and 11 Hz, across 10 independent EEG studies, appear to show significant amounts of phase-dependent perception during visual perception tasks, where one phase of the oscillation favoured one outcome, and the opposite phase favoured the other outcome (VanRullen, 2016). Discretized visual processing may also explain interesting limits on temporal resolution, with humans showing fast limits, around 50 Hz, like the flicker fusion limit, and slow limits, around 4 Hz, like acceleration perception (Holcombe, 2006).

One specific study demonstrates well the effect of discretized oscillatory activity's role in visual perception. Mathewson, Gratton, Fabiani, Beck, and Ro (2009) presented a single stimulus for 11.7ms, with a backwards mask, and found that detection of the stimulus is directly correlated with the phase and power of alpha activity at the time of stimulus onset. If a trial has high alpha power, the phase of alpha activity can predict if the stimulus will be detected or not (there is no predictive power in low alpha power trials). These phases are opposite to each other, where the average phase angle for a detected stimulus is about 270 degrees, and for undetected trials, 90 degrees. Here, we see an obvious example of naturally occurring rhythms having an effect on visual perception. This finding suggests a "pulsed inhibition" effect, where when alpha activity is present (high alpha power), one phase of the alpha rhythm becomes suppressed or inhibited, while the other remains excitatory, causing targets to only be detected if they fall within the phase of excitation. This supports Koch and VanRullen's 2003 proposal of discretized oscillatory processing, separating the frames in their movie by way of "pulsed inhibition". These alternating phases of excitation and inhibition provide a mode of discretizing visual information and explain how visual perception may be interrupted or altered because of this discrete way of processing.

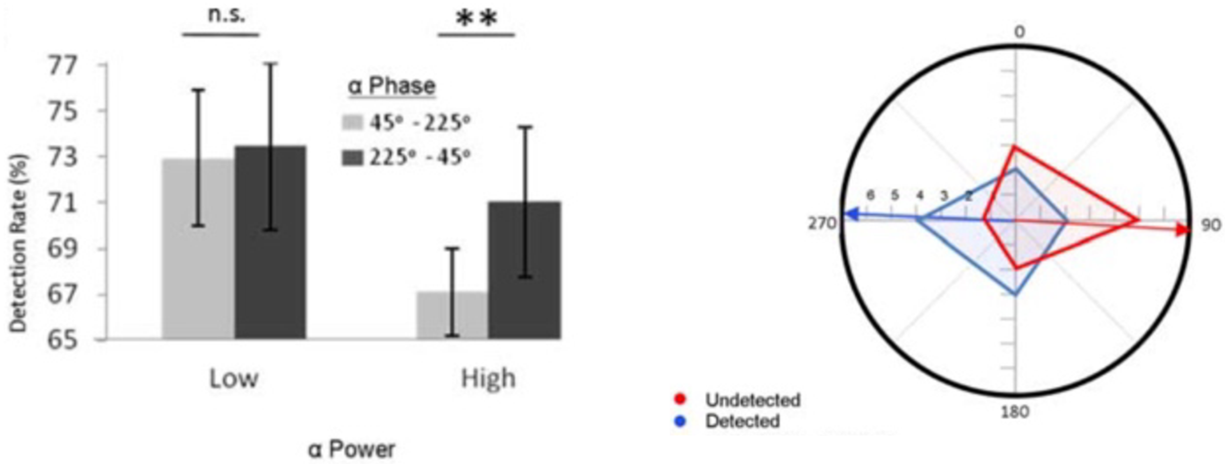

Figure 1.4: Power and phase results from a detection task, where the power and phase of alpha activity could predict whether or not a stimulus was detected. When alpha activity had high power (left), the mean phase angle of the alpha rhythm (right) was completely opposite for detected (blue vector) vs undetected stimuli (red vector) Reprinted from "To See or Not to See: Prestimulus Alpha Phase Predicts Visual Awareness," by K.E. Mathewson et al., 2009, *the Journal of Neuroscience*, *29*(9), p.2729. Copyright 2009 by Society for Neuroscience.

1.4.2.2 – Entraining oscillations to bias perception

In addition to the various naturally-occurring oscillating rhythms, the brain will also synchronize its activity with external rhythms (Figure 1.6). As Calderone et al. (2014) state, "Frequency and timing of ongoing oscillations can be entrained by rhythmic stimuli, aligning the temporal dynamics of neural processing to external patterns". This entrainment can result from transcranial brain stimulation or rhythmic sensory stimulation, including auditory and visual stimulation (Calderone et al., 2014). Entrainment can occur for a range of frequencies of oscillatory activity (Lakatos et al., 2008), and can allow for an optimization of neural excitability during a stimulus presentation (Calderone et al., 2014). Linkages to attention have also been drawn, whereby attending to a rhythm stimulus "enforces phase resetting and entrainment of neuronal excitability oscillations to the relevant stimulus stream" (Lakatos et al., 2008).

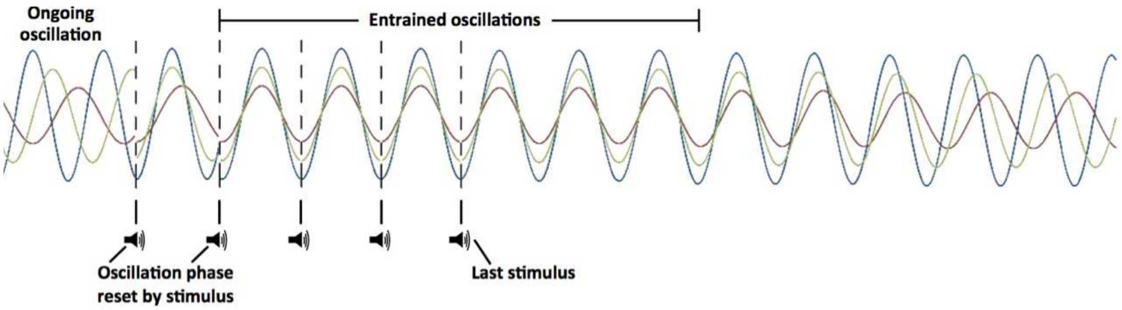

Figure 1.5: A visual of oscillatory entrainment to an auditory stimulus. Ongoing oscillations show a phase resetting and begin to align with the rhythm of the exogenous entrainer. After entrainment, rhythms slowly fall out of the entrained rhythm until they return back to their original oscillatory activity. Adapted from "Entrainment of neural oscillations as a modifiable substrate of attention," by D.J. Calderone et al., 2014, *Trends in Cognitive Science, 18*(6), p. 301. Copyright 2014 Elsevier Ltd.

Mathewson and colleagues extended their original 2009 detection task to include entrainment of the alpha rhythm prior to stimulus presentation (Mathewson et al., 2012). Through entrainment, they manipulated where in the phase of an alpha oscillation the stimulus would be presented. Similar results to the original study were found, where during periods of high alpha power, a pulsed inhibition is again present, creating oscillations of visual perception (Mathewson et al., 2012). Results showed a significantly greater detection rate when the stimulus was presented in phase with the alpha rhythm than when presented out of phase, so long alpha power was high (Mathewson et al., 2012). This controlling of alpha phase, and its subsequent effect on visual perception, demonstrates another example of a biasing of visual perception by exploiting the discretized nature of oscillatory activity.

1.4.3 – Previous attempt to link neural oscillations with Brücke effect

Though it is well reasoned to assume oscillatory activity, with its ability to be entrained and affect various visual percepts, might play a large role in understanding the Brücke effect, we are aware of only one previous study that attempts to link neurophysiological data with Brücke's brightness enhancement phenomenon. Kohn and Salisbury (1966) hypothesized that a frequency-dependent brightness enhancement might arrive by way of increased cortical activity in the frequency of flicker. They first measured frequency-specific activity when a subject was shown a steady light, and then measured the same activity when a flickering light (in the same frequency as measured) was shown. A rotated, sectored disk, with 1/3 of the surface light and 2/3 of the surface dark, was used to provide flickering light at a range of frequency from 5 to 25 Hz. The subjects were shown the flickering light and a steady light in a "hemi-sected bipartite field with a central fixation point", and luminance of the steady light was adjusted until a verbal reporting of matched luminance. Two occipital electrodes were used for EEG recording, and a tuned frequency analyzer reported the amount of oscillatory activity present in the EEG at the tuned frequency.

Kohn and Salisbury (1966) reported behavioural brightness enhancement similar to that of Brücke and Bartley, with enhancement found when the flicker rate was at or below 15 Hz. When the intensity of luminance was varied, it did not appear to affect the range of frequencies providing the brightness enhancement. Using a Chi-square statistical analysis approach, no significant correlations existed between "increased electrical activity in the EEG at a given frequency", or power, and brightness enhancement, and Kohn and Salisbury concluded that "cortical activity at the frequency of the flicker does not play a role in brightness enhancement". This of course may be jumping too quickly to conclusions, considering the limitations of their study include using merely two subjects, recording from only 2 nearby electrodes, and simply considering the amount or power of frequency-specific activity, and not its phase. While this study may therefore be outdated, it does provide an exciting place to begin from, encouraging a revisiting of the Brücke effect using EEG - with upgraded equipment, new frequency analyses, and a more useful understanding of the brain's discretized rhythms.

1.5 – Motivation

The Brücke effect provides a compelling case where brightness perception differs from luminance sensation, yet it appears to have been left in the past, with little reference to it in more modern research. Further, no research included what might happen to brightness judgments if two flickering stimuli were involved, not just a single flickering stimulus as compared to a constant, like the Brücke and Bartley paradigms. Finally, aside from Kohn and Salisbury's failed attempt (1966) to find a relationship between the Brücke effect and brain activity, there has been no study of the neural correlates of the strong behavioural brightness enhancement.

Therefore, Experiment 1 was an attempt to recreate behaviourally the curve of the Brücke effect as illustrated by Bartley in 1938 (Figure 1.2), but this time using two flickering stimuli. This replication would allow us to show perceived brightness of a stimulus relative to its paired stimulus - extending Brücke's relative brightness judgments as compared to a constant light. Experiment 2 was an EEG experiment designed to build off the results of Experiment 1, using only the subset of frequencies found to give the largest behavioural effect to increase EEG power. The main idea behind these experiments was to take a known behavioural effect showing a large separation between luminance sensation and brightness perception, reproduce the behavioural effect with two flashing stimuli, and then understand how the induced bias manifests in the brain.

1.6 – Predictions

For our behavioural results (e.g. the brightness judgment task), though the Brücke effect had not ever been shown to exist for two flickering stimuli, we hypothesized that the brightness enhancement would still be present following the relationship Bartley plotted. This means when a stimulus is flickering at the frequency of greatest brightness enhancement (~10 Hz according to Bartley), and a second stimulus flickers beside it at a frequency of lesser brightness enhancement (say, 5 Hz), the 10 Hz stimulus will still appear brighter than the 5 Hz stimulus, even when not compared to a constant light but instead another flickering stimulus. We predicted a behavioural result that echoed that of Brücke and Bartley with a preservation of 10 Hz as the frequency that would provide the greatest brightness enhancement, regardless of the frequency of flicker of its counter-stimulus. We also hypothesized that we could both replicate Bartley's original plot (using trials where 1 stimulus was "flickering" at 0 Hz – a constant light), and extend the original plot to relative brightness judgments between two flickering stimuli.

The electrophysiological hypotheses were not as clear, as the only comparable study was over 50 years old and found no correlation between frequency-specific activity and brightness enhancement (Kohn & Salisbury, 1966). Despite this earlier failure, given the myriad ways in which oscillatory activity can affect visual perception, the ability of internal oscillations in a range of frequencies to synchronize with external entrainers, and the discretized nature of oscillatory brain activity, we maintain the hypothesis that the Brücke effect, with its frequency dependency, must in some way be related to oscillatory activity. Specifically, given the behavioural prediction that centered around 10 Hz providing the greatest brightness enhancement, we hypothesized that a 10 Hz flickering stimulus may show better entrainment, and in turn enhance its apparent brightness. To measure entrainment, we intend to move away from time frequency approaches of data that rely on power, and instead focus on phase consistency. Thus, we predict that brighter stimuli, in particular those flickering in the alpha range, will be characterized by higher ITC. Importantly, this study differs from many EEG studies in that it uses two stimuli on the screen at the same time. Therefore, we have a secondary hypothesis, unrelated to brightness perception, that our ability to entrain frequency (as measured by higher ITC) will be lateralized, with the best entrainment to a specific frequency stimulus achieved in electrodes contralateral to that stimulus. Finally, for any specific flicker rate showing a correlated behavioural and ITC effect (e.g. we believe that ~10 Hz stimuli should both be perceived as brightest and show better phase locking, as revealed by ITC) we make one final hypothesis: If we analyze our data by comparing those electrodes contralateral to a stimulus perceived as brighter to those electrodes contralateral to a stimulus perceived as dimmer, we hypothesize that stimuli perceived as brighter will show higher ITC.

We also thought that, similar to the Mathewson et al. 2012 findings, if 10 Hz entrains best, it may increase the amount of alpha power in the brain, and induce a pulsed inhibition that could play a role in brightness enhancement. This meant we predicted that the other frequencies of flicker were not as strong of entrainers, and would not be providing the same quality of information as would the 10 Hz rhythm. Further, we also contemplated an inhibitory effect of 10 Hz, where if a 10 Hz stimulus was present, the brains ability to entrain to it would be so powerful that it would also disrupt the brain’s ability to entrain to any other stimulus present. We predicted that this might be why the relationship is U-shaped, with frequencies below and above 10 Hz showing diminished brightness enhancement. These predictions were purposely vague, as there was little evidence to inform educated predictions specific to the Brücke effect. However, we guided all electrophysiological research with the general hypothesis that, given the oscillatory networks of the brain, and the bottom-up and top-down pathways of visual processing, somewhere in the brain’s electrical activity we should find a correlate of brightness perception when its recorded behavioural effects are of such large magnitudes.

2.0 – Materials and Methods

2.1 – Introduction

This study involves two experiments exploring how visual sensation is different than visual perception in the brightness phenomenon known as the Brücke effect. The objective of this study was to find the underlying mechanism for brightness enhancement of flickering stimuli as it might relate to oscillatory activity in the brain. To accomplish this objective, our first experiment cast a large net across different flicker rates to confirm and locate a behavioural effect, and the second experiment focused on those flicker rates giving the greatest behavioural effects and interrogated them using electrophysiological methods.

Experiment 1 was a behavioural experiment, where participants simply made a keyboard press to denote their decision about which, a left or right flickering circle on a monitor, appeared brighter. This experiment involved 5 frequencies of flicker, each paired with every other frequency and itself, creating 25 conditions and allowing for a comprehensive test of a range of frequencies that fell along Bartley's plot (1938, see Figure 1.2) of subjective brightness enhancement. Experiment 1 consisted of a replication of the Brücke effect by using a frequency of 0 Hz (or a constant light, as Brücke used), and also an extension of the original work by comparing a flickering stimulus to another flickering stimulus.

Experiment 2 was informed by the results of Experiment 1 and was designed to test the limited range of frequencies where the greatest and most meaningful brightness discrepancies were found. Critically we incorporated EEG recordings while testing within this narrowed frequency window to examine what neural correlates might be responsible for these large behavioural effects. In this way, Experiments 1 and 2 follow a very similar procedure, with only small variations to allow for the inclusion of EEG. The following methodology describes in detail the procedures used for both experiments in the study in ‘Experiment 1’, with any additional elements specific to the use of EEG placed in ‘Experiment 2’.

2.2 – Experiment 1

2.2.1 – Participants

A total of 30 individuals (11 males) participated in the experiment. All participants self-reported that they were right-handed and had normal or corrected-to-normal vision. One participant was excluded after determining their left-handedness post-experiment setup, resulting in 29 behavioural data sets for analysis. No participant had prior knowledge about the experiment and its objectives. All experimental proceedings were approved by the University of Alberta’s Research Ethics Office.

2.2.2 – Materials and design

Participants sat at a table 50 centimeters (cm) away from a ViewPixx 120 Hz refresh rate monitor, and a keyboard in a dimly lit room (Figure 2.2). The study was designed and carried out with a computer running Windows 7 and the Psychophysics toolbox in Matlab. The stimuli were two circles, one left and one right of the central fixation cross. The stimuli were circles of 2.3° diameter, with 4.6° between the centre of each circle and the centre of the fixation cross (width of 0.4°), as illustrated in Figure 2.1. The stimuli were grey, with a pixel value of [128 128 128], that would flicker between black, the colour of the background, and grey. Stimuli that would “flicker” at a frequency of 0 Hz were presented as a grey circle that remained on the screen for the entire trial.

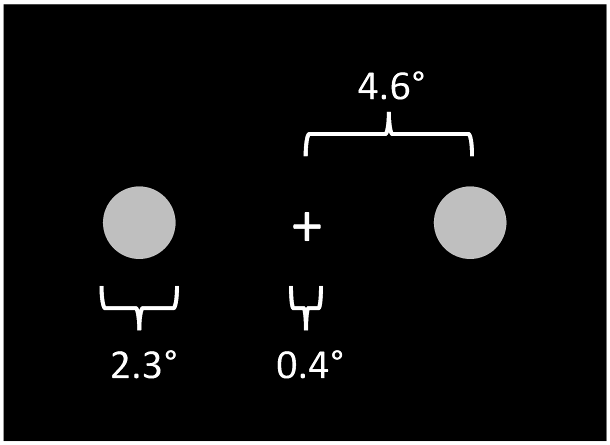

Figure 2.1: Depiction of stimuli sizing for both Experiment 1 and 2.

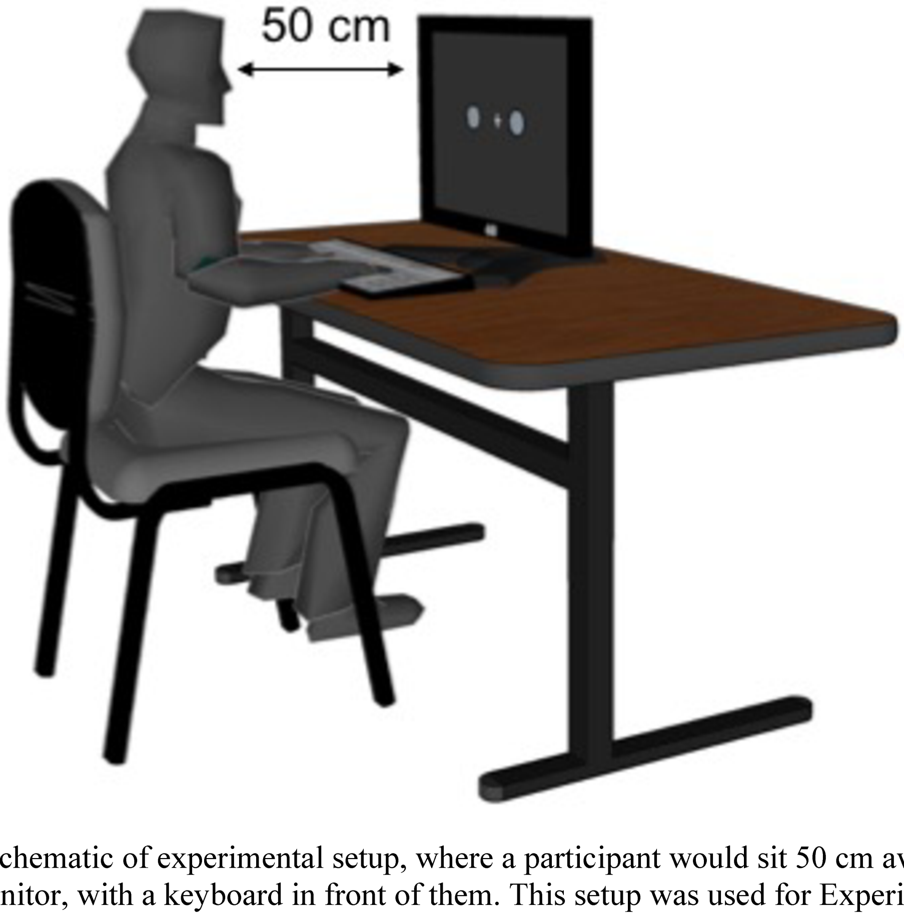

Figure 2.2: Schematic of experimental setup, where a participant would sit 50 cm away from a ViewPixx monitor, with a keyboard in front of them. This setup was used for Experiment 1 and 2.

2.2.3 – Procedure

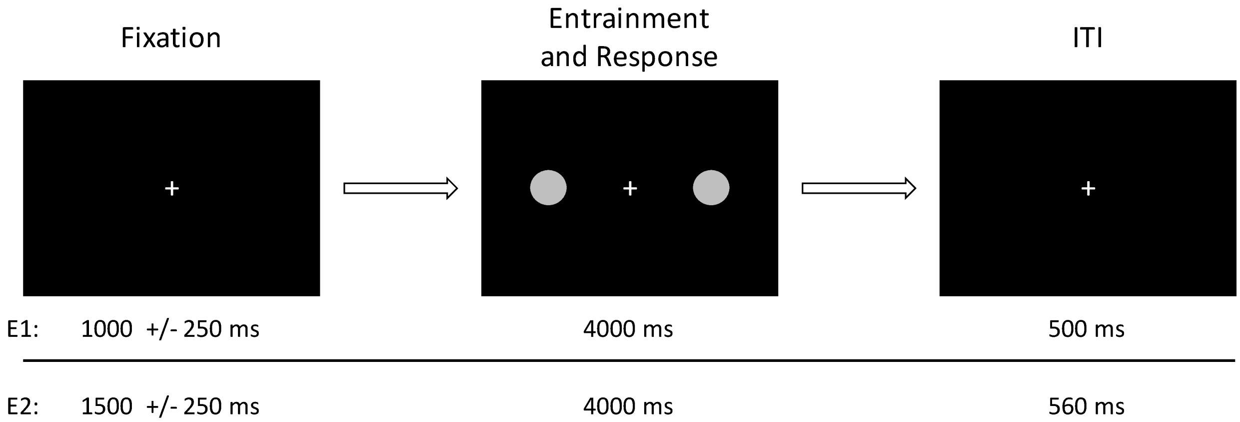

Figure 2.3: The timing of a single trial of Experiment 1 and 2. Experiment 1: fixation was a variable length, randomly jittered between 750 and 1250 ms. Flashing stimuli, the entrainment and response portion, occurred for 4000 ms, and was followed by an inter trial interval of 500 ms until the next trial would begin. The timing of Experiment 2 was similar: fixation was a variable length, randomly jittered between 1250 and 1750 ms and the inter trial interval was 560 ms.

Upon arrival at the testing space, participants filled out a consent form outlining their voluntary participation in the study. Detailed on-screen instructions were supplied, with any necessary clarifications provided by the presiding research assistant. Each trial would start with a small white fixation cross centered in the middle of a black screen, presented for a randomly jittered amount of time between 750 ms and 1250 ms. This fixation cross would remain on the screen the entire trial, and participants were instructed to focus on it for the duration of the trial. Two flashing grey circles would then appear on the screen on either side of the fixation cross for a duration of 4000 ms. Participants were instructed to make a decision, denoted with a left or right shift key button press on a keyboard, about whether the right or left flashing circle looked brighter (or darker, depending on assigned counter-balanced condition). After a decision was made and the 4000 ms of flashing concluded (flashing would occur for the entire 4000 ms, regardless of a decision being made), there would be an inter trial interval of 500 ms, with only the fixation cross on the screen until the next trial would begin. Had a participant failed to make a choice during the 4000 ms of flashing, a fixation cross would remain on the screen until a choice was made, followed by the 500 ms inter trial interval.

A total of 675 trials were presented to each participant, broken into 27 blocks of 25 trials. Participants were instructed that they could self-time breaks between blocks, taking some brief time if they needed. There was a total of 25 conditions consisting of different frequencies of the left and right flashing circles. The frequencies studied were 0 Hz (or no flashing), 4.44 Hz, 9.23 Hz, 13.33 Hz, and 17.14 Hz, with all pairwise comparisons, including paired with itself, creating the 25 conditions. The luminance value of all flickering circles was held constant, flickering to a grey value at a duty cycle of 6 frames per flicker (Figure 2.4). This meant a 4 Hz stimulus would flicker at a rate of 6 frames of grey and the subsequent 21 frames of black (with 4 flickers of grey per second). As the duty cycle was held constant, only the number of frames of black differed to determine frequency, where 9 Hz, 13 Hz, and 17 Hz had 7 frames, 3 frames, and 1 frame of black, respectively, between 6 frames of grey. Participants were assigned to one of two conditions at the beginning of the experiment which informed whether they were asked to make a judgment about the brightness (n = 15) or darkness (n = 14) of the circles.

Upon completion of the 675 trials, participants were thanked for their time, and compensated with either $15 (at a rate of $10 per hour) or provided with 2 hours of credit toward their required research participation for their introductory psychology course.

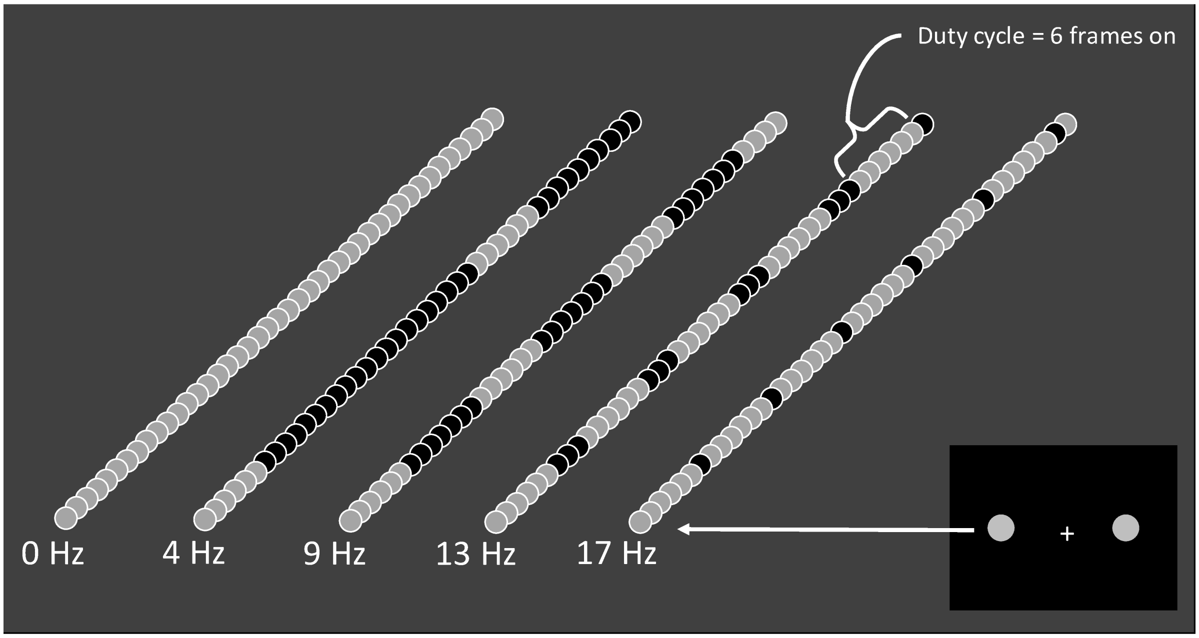

Figure 2.4 Depiction of the duty cycle of stimuli in relation to their frequency. Duty cycle was held constant at 6 frames, meaning every flicker lasted for 6 frames regardless of the frequency of flicker. This depiction only shows 43 frames, and is based on the use of a display with a 120 Hz refresh rate, or 120 frames per second. As duty cycle was held constant at 6 frames, only the amount of black varied to determine the frequency of flicker. While 0 Hz was not flickering, and therefore was grey every frame, 4 Hz, 9 Hz, 13 Hz, and 17 Hz all involved 6 frames of grey, and a subsequent 21, 7, 3, and 1 frame(s) of black, respectively.

2.2.4 – Behavioural Data Acquisition and Processing

For each trial, behavioural data recorded in MATLAB consisted of a reaction time, a response side, a trial condition number, a flag for reaction times faster than 100 ms, and a flag for a collected response. We removed trials with reaction times less than 100 ms or greater than 3 standard deviations above each participant's mean reaction time. For all participants in the darker condition, answers were inverted (ex. a left choice became a right choice) so as to have all data in the form of the brighter condition for ease of analysis.

2.2.5 – Behavioural Measures and Analyses

Reaction Time (ms): time from stimulus onset (appearance of flashing circles) to button press, denoting a response.

Response side: choice of left or right stimulus as the brighter of the two stimuli.

Choice proportion: a measure between 0 and 1 determining, for each pair of frequencies, how often one level frequency is selected as brighter.

For each participant, both reaction time and response side were averaged for each of the 25 conditions. The effects of reaction time and response side were computed in Repeated Measures Analysis of Variance (RMANOVA)s, where left and right frequencies were each considered a factor (2 factors, 5 levels of each), and both factors were within subjects. Multiple comparisons were corrected with Tukey's honest significant difference criterion.

2.3 – Experiment 2

2.3.1 – Participants

A total of 23 individuals (7 males) participated in the experiment, with all participants new to the study, not having participated in Experiment 1. Again, all participants self-reported that they were right-handed and had normal or corrected-to-normal vision, and no participant had prior knowledge about the experiment and its objectives. All experimental proceedings were approved by the University of Alberta’s Research Ethics Office.

2.3.2 – Materials and design

A design identical to that of Experiment 1 was used, supplemented by additional materials for EEG data collection. A BrainVision 32 channel active wet electrode EEG was used, with an actiCHamp amplifier, and an actiCAP electrode cap, operating at a 1000 Hz sampling rate. 4 different sized actiCAP caps were used, measuring the participant's head to select the correct size, though all 4 caps shared the same set of electrodes. Two electro-oculogram (EOG) measures were collected by aligning a pair of bipolar electrodes above and below the left eye (vertical EOG) and on the outside of each eye (horizontal EOG), grounded with their own ground electrode between the eyebrows. EEG and EOG data were recorded using BrainVision Recorder software on a second computer running Windows 7. Both EEG and behavioural data was collected during the study.

2.3.3 – Procedure

An identical procedure to Experiment 1 was followed, except for minor adjustments to the timing and a limiting of frequencies tested to optimize the parameters for high-quality EEG data. One of these adjustments involved adding more time to both the initial fixation period and the inter trial interval (ITI) (see Figure 2.3, and specifically the timing of Experiment 1). This allowed for a time-frequency decomposition (see inter trial phase coherence methods, section 2.3.8.2) that included at least 500 ms before stimulus presentation and the entire duration of flickering (considering a wavelet convolution with 3 Hz as the slowest frequency). The amount of time the flashing circle was on the screen (4000 ms) remained constant between Experiment 1 and Experiment 2. Only 3 frequencies of stimuli were used in Experiment 2. These specific frequencies were chosen after reviewing the results of Experiment 1 so as to choose the most meaningful and prominent subset of frequencies showing brightness discrimination differences. As we were most interested in two flickering stimuli, and had already proven the original Brücke effect (one flickering stimuli, one steady light) replicable in Experiment 1, we eliminated 0 Hz as a frequency for testing, and after finding the greatest brightness enhancement behaviour between 4.44 Hz and the other frequencies, we selected 4 Hz and the next sequential frequencies that we tested that fell along Bartley's curve – 9.23 Hz and 13.33 Hz.

A total of 540 trials was presented to each participant, broken into 20 blocks of 27 trials. Participants were instructed that they could self-time breaks between blocks, taking some brief time if they needed. The frequencies tested were 4.44 Hz, 9.23 Hz, 13.33 Hz, with all pairwise comparisons, including a pairing with itself, creating the 9 conditions. All other qualities about the stimuli were kept consistent with Experiment 1, including holding luminance values constant to a grey value, a 6 frame duty cycle (see Figure 2.4), and 2 experimental counterbalanced groups of brighter (n = 11) or darker judgments (n = 12).

Also, as Experiment 2 incorporated EEG, extra time was taken to set up the cap on the participant, and clean up after the experiment. This made the experiment take approximately 2 hours, as opposed to 1.5 hours for Experiment 1.

Upon completion of the 540 trials, participants were thanked for their time, and compensated with 2 hours of credit toward their required research participation in their introductory psychology course.

2.3.4 – Behavioural Data Acquisition, Processing, and Analyses

Behavioural data was processed in the identical manner as Experiment 1. Besides a reduction in the number of conditions from 25 to 9, all data followed the same cleaning measures and was used to create the same behavioural measures as were established in Experiment 1.

2.3.5 – EEG Data Acquisition

EEG data acquisition occurred in a dimly lit room, identical to the location of Experiment 1. EEG data was sampled at 1000 Hz, with an online anti-aliasing low pass filter at 280 Hz and an online 0Hz DC offset. The data was referenced to an electrode on the right mastoid at the time of collection (online), and then re-referenced to an average of the left and right mastoid channels during data processing (offline). Scalp electrode impedances were held below 10 Kohm using SuperVisc Gel, and all 32 channels were recorded (10-20 system). Pixel-associated triggers on the ViewPixx 120 Hz monitor provided precise temporal markers in the recorded data about experimental condition, stimuli type and onset, and response location and latency.

2.3.6 – EEG Data Processing

EEG data was processed using EEGLAB (Delorme & Makeig, 2004), a graphical user interface (GUI)-based program in Matlab. First, the raw data, initially referenced to the right mastoid electrode, was re-referenced to the average of the left and right mastoid electrodes. Data was then low passed filtered at 30 Hz, and high passed filtered at 0.1 Hz, both with an infinite impulse response Butterworth filter. All triggers in the EEG data, time stamped during recording, were then associated with an event name and numeric code, and epochs were extracted using these events. Epochs were created from the time between 1250 ms before stimulus presentation and 4560 ms after stimulus presentation, creating an epoch with a length of 5810 ms. Visual inspection of a participant's epochs was used to look for any noisy channels involving abnormally large voltage changes or continuously noisy muscular artifact for a sustained amount of time. If a channel was noisy for more than 10% of trials, where those trials would otherwise need to be deleted, the channel would be removed. As the final data analyses were to only involve a subset of electrodes, this channel deletion would allow for more usable data by not deleting epochs because of one or two bad electrodes. Further, because of the application of a current source density (CSD) transformation post-processing, the removed channel was not interpolated, as this interpolation would only provide correlative data, and would add nothing new to the CSD transformed data. Overall, 5 subjects' data required the removal of one channel, and another 2 subjects' data required the removal of two channels. No channels that were removed were part of the subset analysed.

A manual epoch rejection was administered with the goal of removing any epochs that had unconventional artifacts, looking for anything that differed from a stereotypical blink, saccade or muscle artifact that could be easily removed with component analysis. On average, 76, or 14% of epochs were rejected per participant. An independent component analysis was then carried out on the epoched data, with a manual rejection of components that displayed stereotypical artifact and no brain activity. 13 components of 33 were typically removed for each participant. A second epoch rejection was manually completed after artifact components were removed – a final pass of the data to remove any artifact that still existed in the data after the first epoch rejection and component removal. After all data cleaning and processing, an average of 448 epochs of an original 540 per participant, or 83%, remained and were usable for further analysis.

Finally, all EEG data was filtered with a surface Laplacian using CSD toolbox in Matlab (Kayser & Tenke, 2006a, 2006b) removing “spatially broad features of the data” (Cohen, 2014). The last step involved aligning the EEG and behavioural data such that any trials removed during EEG were also removed from the trials for behavioural analysis and vice versa, and resulted in a final data set for each person with an average of 425 trials, or 79% of the original 540 trials.

2.3.7 – Behavioural Measures and Analyses

Behavioural data was analyzed following the same protocol of Experiment 1. Again, reaction time, response side, and choice proportion were the three dependent measures of the behavioural data from Experiment 2, and Repeated Measures ANOVAs were performed, still with 2 factors, but now as a 3x3 design.

2.3.8 – EEG Measures and Analyses

EEG data was analyzed using various techniques. All EEG analyses were completed only on the occipital electrodes of O1 (left) and O2 (right). All analyses were carried out with scripts written and developed in Matlab.

2.3.8.1 – ERPs / VEPs

Processed EEG data was directly used to plot and analyze ERPs, with no additional transformation of the data. Plotting ERPs allowed for an understanding of the electrical activity at specific electrode sites over the course of multiple trials, specific to a condition. This data could then be compared directly, and could show significant differences between conditions. Specifically, we thought ERP analysis would allow us to show that initial activity related to the visually evoked potential (VEP) was not responsible for brightness discrimination differences, where no difference between conditions during the VEP could reflect the behavioural effect perhaps being a product of activity beyond initial bottom-up processing.

First, data was rearranged and averaged together in the form of contralateral and ipsilateral stimuli locations, as opposed to left and right side of space. For example, this reorganization would provide data for a 9 Hz contralateral and a 4 Hz ipsilateral, which would come from an average of the voltage of a left electrode in a 4 Hz left and 9 Hz right trial, and a right electrode in a 9 Hz left and 4 Hz right trial. This was our best option as each condition always involved a pair of frequencies, and could not be reduced to one frequency, but could at least be collapsed over left and right side of space.

Two ERP components, P100 and N100, were analyzed to determine if there were early sensory processing differences across the range of frequencies (Luck, 2014). This would be surprising, given that the first flicker of each stimulus was physically identical, regardless of its subsequent frequency, but was an important first check. Each component was analyzed and tested separately. Both P100 and N100 components were reduced to a mean value derived from a 50 ms window determined by visual inspection of a grand average ERP (averaged over subjects and conditions). The P100 window was between 125 and 175 ms after stimulus onset, and the N100 window was between 175 and 225 ms after stimulus onset. These average values for both the P100 and the N100 windows were tested in separate Repeated Measures ANOVAs, both with 2 factors (Contralateral Frequency and Ipsilateral Frequency) and 3 levels of each factor (4 Hz, 9 Hz, 13 Hz).

2.3.8.2 – ITC

Time frequency analyses involved transforming the original voltage data into frequency-specific information. Again, MATLAB scripts were used, which called upon functions of EEGLAB (Delorme & Makeig, 2004), including ‘newtimef’. The function ‘newtimef’ performed a wavelet transform, between frequencies of 3 Hz to 30 Hz, with a wavelet of 3 cycles for the lowest frequency (3 Hz), where cycles linearly increased with frequency by a rate of 0.5 cycles, reaching a 15 cycle wavelet at the highest frequency (30 Hz). After decomposition, the epoch had a temporal resolution of 400 time points, and ranged from 650 ms before stimulus presentation to 4002 ms after stimulus onset. The output of ‘newtimef’ provided power and phase information about the EEG data.

'Newtimef' provided phase information in the form of ITC. ITC is a measure of the regularity of a specific phase of a certain time and frequency, where, for example, when comparing ITC values between conditions, a higher ITC for one condition would be indicative of more event-related phase-locking in that subset of trials. This function provided ITC values for each subject, for each condition, for each electrode of interest (only O1/O2), for each frequency (3 to 30 Hz, by 0.5 Hz increments) and for each time point (temporal resolution of 400 time points). For all ITC analyses, frequency bands of averaged ITC information were used, as opposed to a single frequency. These bands consisted of the closest frequency to the frequency of entrainment, and the closest frequency below and above it. For example, a 4.44 Hz band was comprised of averaged ITC information from 4.0 Hz, 4.5 Hz and 5.0 Hz.

We analyzed ITC in four ways:

2.3.8.2.1 – Effect of rhythmic flickering stimuli on ITC

First, we wanted to test for entrainment. That is, we wanted to know if there would be an increase of ITC for frequencies that a participant was currently viewing. This would mean internal oscillatory activity in the brain, and specifically in the occipital area, would phase-lock with the frequency of an external rhythm but would show no effect on ITC for frequencies that were not currently being shown. To test this with a Repeated Measures ANOVA, it was necessary to reduce ITC to a single value for each person in each condition of interest. As such we ran a 2 factor, 3x3 ANOVA. The first factor was the frequency band in which we were calculating (referred to as test frequency) ITC and had levels: 4Hz, 9Hz and 13Hz. The second factor explored both the time window in which we were calculating ITC as well as whether the test frequency was on the screen during that window. The three levels were: 1) no entrainment, no test frequency (before flashing appeared on the screen, where only a fixation cross was presented), 2) during entrainment, no test frequency (to see if there were task, but not frequency related increases in ITC in any frequency bands) and 3) during entrainment, with test frequency (this is the critical condition where we expect phase-locking to external stimuli).

The ITC measure during "no entrainment" was taken as an average over a time range of -504 to -197 ms prior to stimuli onset, leaving a buffer of approximately 200 ms before stimuli onset to account for temporal smearing from the time frequency decomposition. For both conditions during entrainment, ITC was averaged over 1002 to 2002 ms. The ITC measure during entrainment with no test frequency was comprised, for example for the 4 Hz measure, of any condition where 4 Hz was not one of the frequencies of entrainment, and then measuring the average amount of 4 Hz in these trials. The ITC measure during entrainment with the test frequency was comprised of finding any condition that included the test frequency and measuring from its contralateral electrode. For example, to find the measure of 4 Hz as the test frequency on a trial of a 4 Hz Right stimulus and a 9 Hz Left stimulus, we would take the ITC measure of 4 Hz (from all trials of this specific condition) from the left, or contralateral electrode. Of note, this final condition, ITC during entrainment with test frequency, is the only one where we specifically measured ITC contralateral to the test-frequency. Since the other two conditions (no entrainment, and, during entrainment, no test-frequency) did not have the test-frequency on the screen, there is no sense in which we can select contralateral electrodes.

2.3.8.2.2 – Effect of different or same frequency stimuli on ITC

In the first ITC RMANOVA described above, the condition, "during entrainment, with test-frequency" collapses across trials in which the test-frequency appears with itself (e.g. a 4Hz left and 4 Hz right trial) and trials in which the test-frequency is paired with a different frequency (e.g. 4Hz left, 9 Hz right). To explore the potential benefit to, or enhancement of, phase-locking caused by having two of the same frequency stimuli on the screen, we conducted a second analysis of ITC contralateral to the test-frequency during the entrainment period. This resulted in a 3x2 RMANOVA of ITC extracted over the same 1002 to 2002 ms window. The first factor was, again, test-frequency (4Hz, 9Hz, 13Hz) and the second factor was same-frequency or different-frequency, with "same" denoting trials where the test-frequency appeared with itself and "different" where the test-frequency appeared with another frequency. For example, a 4 Hz measure for same-frequency stimuli came from an average of only trials where two 4 Hz stimuli were flashing, and collected ITC measures from both electrodes, as they were both contralateral to a 4 Hz stimulus. The 4 Hz measure for different-frequency stimuli came from an average of any condition where 4 Hz was on the screen with either a 9 or 13 Hz stimulus, and measured from the electrode contralateral to the 4 Hz stimulus.

2.3.8.2.3 – Effect of laterality on ITC

Our third ITC analysis was to search for laterality differences in entrainment between frequencies. Here we wondered if entrainment in a certain frequency would show differences between hemispheres when two different frequency stimuli were on the screen. Thus, we furthered narrowed our ITC search and only examined the "different-frequency" trials from the second ITC analysis. Unlike the previous analyses, here we compared data from both the contralateral *and* ipsilateral electrodes on different-frequency trials. To derive a single measure for each condition, we collapsed across the value of the "different" stimuli. That is, a 4Hz measure was taken as being the average of 4Hz when it appeared with 9Hz or 13 Hz. This resulted in a 3x2 RMANOVA with factors test-frequency (4Hz, 9Hz, and 13 Hz) and laterality (contralateral or ipsilateral). For example, a 4 Hz Contralateral measure was the average of the right electrode in the 4 Hz left and 9 Hz right condition, the left electrode in the 9 Hz left and 4 Hz right condition, the right electrode in the 4 Hz left and 13 Hz right condition, and the left electrode in 13 Hz left and 4 Hz right condition.

2.3.8.2.4 – Effect of brightness discrimination on ITC

Our fourth and final test of ITC was prompted by the results of the first three and was the only to test for specific ITC effects when grouping trials by the response behaviour. We wanted to explore if binning by behaviour might provide direct evidence for the use of ITC as a predictive measure of brightness perception. Unfortunately, while the large behavioural results provide a compelling story, it limited our ability to test all conditions because of a lack of power (e.g. if you respond that 4 Hz is brighter more than 80% of the time, the less than 20% where it is perceived as darker is not sufficient to make a bright vs dark comparison). This prompted us to behaviourally bin only the “same-frequency” trials, where response side was near chance (50%) for all frequencies. Binning by behaviour required a secondary time frequency decomposition, where instead of producing an ITC for each person, condition, electrode, frequency, and time point, the "conditions" now became only the same frequency conditions, and within each of those, we separately extracted ITC values for the electrode contralateral to what was chosen as brighter and the electrode contralateral to what was chosen as dimmer (resulting in 6 new "conditions"). Again, to create a single average ITC measure to test, the 1002 to 2002 ms time window was used and then tested with a 3x2, 2 factor Repeated Measures ANOVA with factors frequency (4 Hz, 9 Hz, and 13 Hz) and response (contralateral to bright, contralateral to dim). Given the results from the previous three ITC analyses, we were theoretically motivated to perform a single t-test comparing the amount of 4 Hz ITC contralateral to bright against the 4 Hz ITC contralateral to dim, with the specific a-priori prediction that for 4 Hz, the bright condition would show higher ITC than the dim condition.

3.0 – Results

All statistical analyses followed the same order of testing. First a 2-factor repeated-measures ANOVA was used to test for main effects and interactions. Where there was no interaction, any significant main effect was explored with all possible pairwise comparisons. If a significant interaction was found, simple main effect 1-factor repeated-measures ANOVAs were used to test all levels of one factor at each level of the other factor, and then, where significant, followed up pairwise comparisons. All repeated-measures ANOVA p-values are reported with a Greenhouse-Geiser correction and pairwise comparison tests were corrected using Tukey's Honest Significant Difference method (excluding the case of the single a-priori comparison described above). Significance was set at corrected $p <= 0.05$.

3.1 – Experiment 1

3.1.1 – Behavioural Results

3.1.1.1 – Choice Proportion

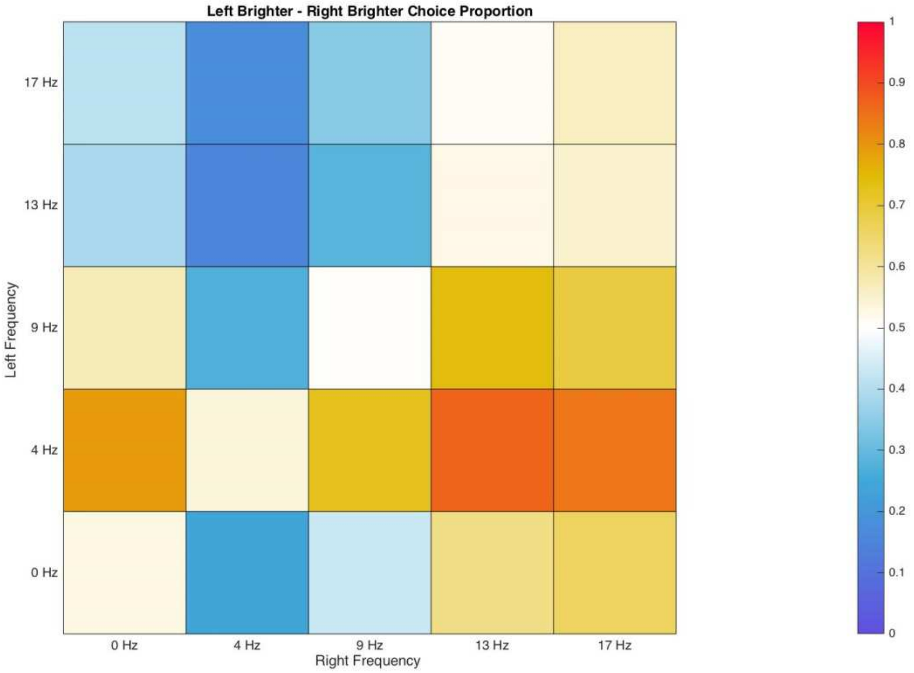

Figure 3.1: Experiment 1 choice proportion of choosing the left stimulus frequency as brighter over the right stimulus frequency (as a subtraction), where white denotes 50% guess to left and right, yellow-red denotes a greater proportion choice of left frequency stimulus, and blue-purple denotes a greater proportion choice of right frequency stimulus.

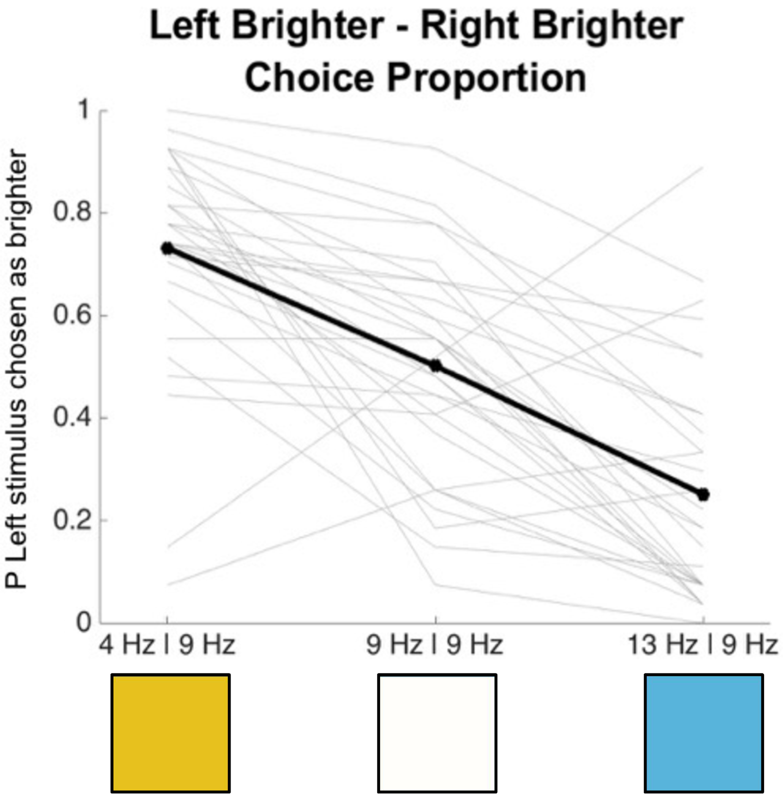

Figure 3.2: A subset of the Experiment 1 5 x 5 choice proportion figure, showing the 29 individual averages as grey lines that contributed to the group choice proportion average (black line, and colour blocks in reference to the colour bar in Figure 3.1). This is highlighted to give an indication of between-participants error, within-participants consistency, and because these frequencies were the ones used in Experiment 2.

Figures 3.1 and 3.2 show the average proportion, as a measure between 0 and 1, that a left stimulus frequency was seen as brighter than a right stimulus frequency. The 5 x 5 repeated-measures ANOVA uncovered a main effect of Left Frequency, F(4,112) = 26.0, *p* = 3.1e-07 and Right Frequency, F(4,112) = 30.3, *p* = 8.7e-09, and no significant interaction between the two factors. Because no interaction was found, multiple comparisons were made for each of the main effects. These multiple comparisons did not account for same frequency stimuli, as the 2 factor design only tested each level within a factor, but five t-tests comparing all of these same-frequency stimuli conditions (e.g. 4 Hz vs 4 Hz on to 17 Hz vs 17 Hz) found that in all cases they did not significantly differ from a 50% guess rate (all *p* values > 0.112). Multiple comparisons for each factor of right and left frequency stimuli found similar results for both factors, and this should be assumed unless otherwise stated. The major finding is that, when paired with a stimulus of any other frequency, 4 Hz stimuli were chosen as brighter more than 80% of the time (all *p* values < .005). Less dramatically, 9 Hz stimuli were chosen as brighter significantly more than 13 and 17 Hz (all *p* values < .005) and 0 Hz stimuli were chosen as brighter more than 17 Hz stimuli (all *p* values < .002). The 0 Hz and 9 Hz (all *p* values > .65) stimuli, and the 13 Hz and 17 Hz (all *p* values > .8) stimuli were not selected at significantly different rates. The only side of space bias existed between 0 Hz and 13 Hz, where only a 0 Hz stimuli on the right was chosen as brighter more often (*p* = .026), while on the left, though 0 Hz was selected as brighter more often, this was not significant (*p* = .108). In general, these results show that a 4 Hz stimulus provided the greatest brightness enhancement as compared to any other stimuli, 0 Hz and 9 Hz stimuli exhibited similar behaviours where a 9 Hz stimulus appears as bright as a constant non-flickering stimulus, and 13 Hz and 17 Hz stimuli appear less bright than all other frequency of stimuli.

3.1.1.2 – Reaction Time

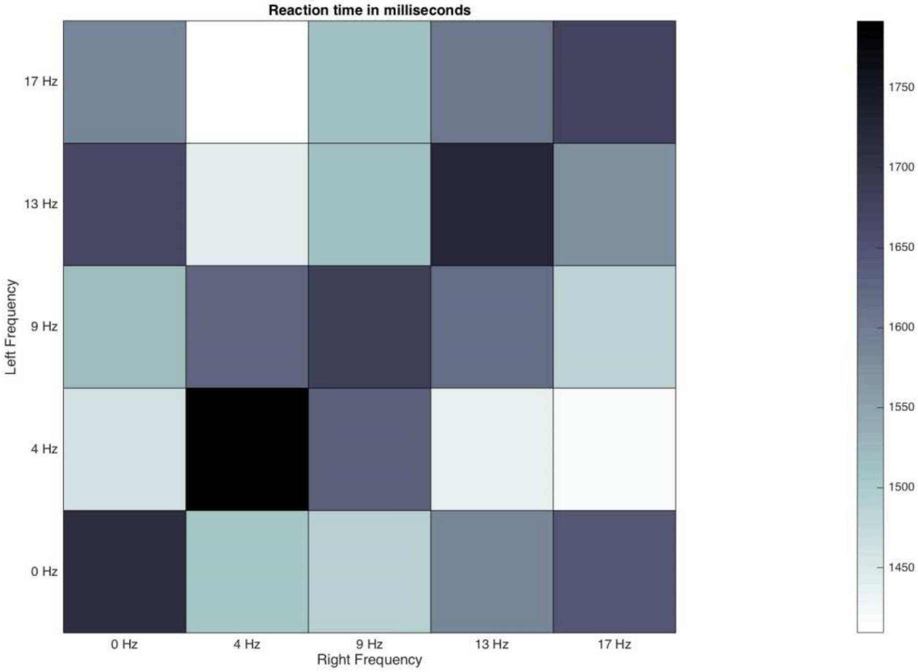

Figure 3.3: Average reaction time of all conditions from Experiment 1. As indicated by the colour bar, white denotes faster reaction times, while black denotes slower reaction times, and all times are in milliseconds.

Reaction time appears to follow from the choice-proportion results, with RTs getting longer as the choice proportion between two stimuli in a pair becomes more similar (e.g. approaches 50%). As visualized with a colour map in Figure 3.3, this results in slower reaction times along the diagonal of the plot, where conditions were that of same frequency stimuli, and yielded close to a 50/50 split in responses. This is consistent with these trials being the most difficult, since participants were being asked to judge which of two identical stimuli were brighter. Faster reaction times appear to correspond with conditions that showed significant response effects (e.g. choice proportions that diverged from 50%), like those involving a 4 Hz stimulus on either the right or left side. Similar to response side analyses, reaction time was analyzed with a 2 factor 5 x 5 repeated-measures ANOVA and though neither Left Frequency or Right Frequency factors were significant, a significant interaction existed, F(16,448) = 9.0, *p* = 3.3e-07. To understand the interaction, simple main effects were tested by holding Left Frequency constant and examining all levels of Right Frequency. All five simple main effects showed a significant effect of Right Frequency (all *p* values < .001), meaning reaction times were significantly different at each level of Left Frequency for all levels of Right Frequency. Multiple comparisons showed that the effect at the level of 0 Hz Left was only driven by a significant difference between a 0 Hz Right and a 9 Hz Right (*p* = .026). At the level of 4 Hz Left, all differences were significant between a 4 Hz Right and all other right frequencies (all *p* values < .013), and also with a 9 Hz Right and all other frequencies (all *p* values < .02). A single significant effect existed with a 9 Hz Left between a 17 Hz Right and 9 Hz Right (*p* = 5.1e-04), and the only significant differences for a 13 Hz Left existed between a 13 Hz Right and both a 4 Hz Right (*p* = .002) and 9 Hz Right (*p* = .002). Finally, for a 17 Hz Left, a 4 Hz Right was different than all other frequencies except 9 Hz Right (all *p* values < .035). Taken together, significant differences existed between reaction times, indicating that the degree of difficulty of choices varied between conditions. This appears to align with the choice proportion results, where, for example, a 4 Hz stimulus, seen as the brightest of the stimuli, has a significantly faster reaction time when a different frequency stimulus is on the screen as compared to another 4 Hz stimulus.

3.2 – Experiment 2

3.2.1 – Behavioural Results

3.2.1.1 – Choice Proportion

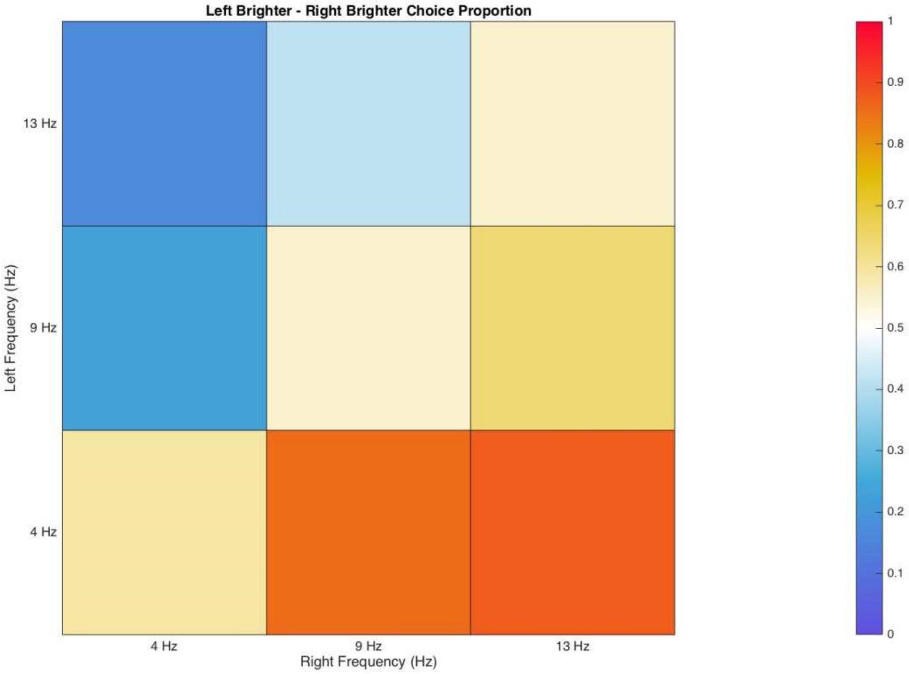

Figure 3.4: Experiment 2 choice proportion, where choice proportion is represented as the amount the left frequency stimulus is chosen over the right frequency stimulus. Colours map as in Figure 3.1.

The 2 factor repeated-measures ANOVA found significant differences for Left Hz, F(2,44) = 59.5, p = 3.2e-11 and Right Hz, F(2,44) = 49.6, p = 4.4e-10, and no significant interaction between the two factors. Multiple comparisons showed that for both the Right and Left factors, 4 Hz was selected as brighter significantly more than 9 Hz or 13 Hz (all p values < 1.5e-07) but, in a slight departure from Experiment 1, although 9 Hz was selected as brighter more often than 13 Hz (M = 0.61 averaging over both conditions involving 9 Hz and 13 Hz) this was close to, but not significantly different (both p values < 0.095). Because this ANOVA isolated Right and Left factors in the same fashion as the tests of Experiment 1, a t-test was used to compare the same frequency stimuli to a guess rate of 50%. This test showed no significant differences between the same frequency stimuli and a guessing rate of 50% when using a significance level of $p < 0.05/3$ to correct for multiple comparisons. Again, similar to Experiment 1, these results support the notion that the frequency of stimulus on the screen affects significantly different choice proportions, where a 4 Hz stimulus look brighter than a 9 Hz stimulus which looks brighter than a 13 Hz stimulus (though this final comparison fails to reach significance).

3.2.1.2 – Reaction Time

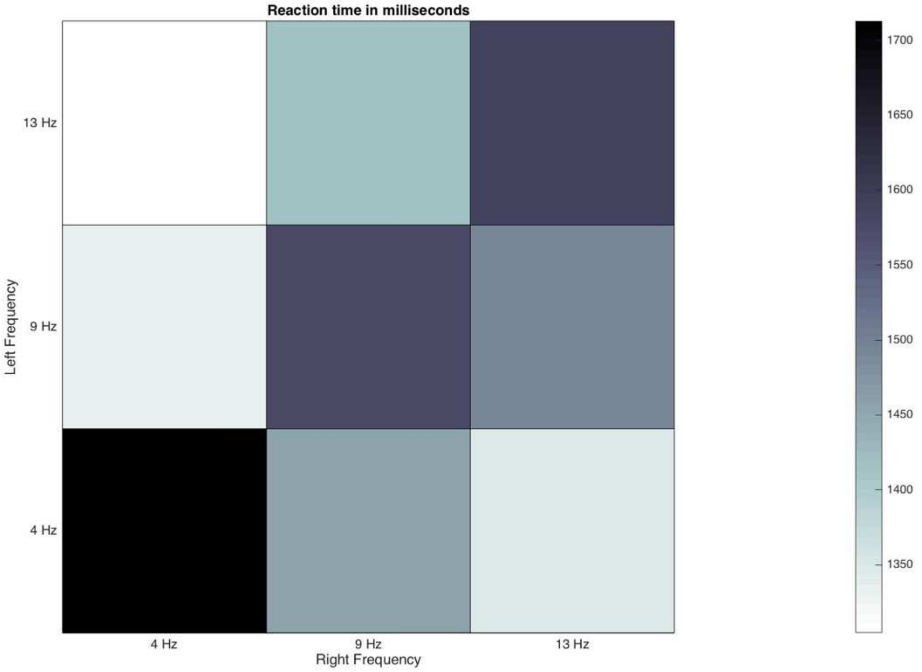

Figure 3.5: Experiment 2 average reaction time for all conditions. As indicated by the colour bar, black indicates a slower reaction time and white indicates a faster reaction time.

Again, a 2 factor repeated-measures ANOVA found that reaction time was not significantly different for the factor of Left Hz (*p* = .162) or the factor of Right Hz (*p* = .481), but an interaction was found between the two factors, F(4,88) = 22.0, *p* = 1.1e-07. The follow up ANOVAs showed that at each level of Left Hz, Right Hz was significantly different (all *p* values < 4.7e-04). Completing multiple comparison tests of these significant effects showed that at the 4 Hz Left level, all differences between Right frequencies were significant (all *p* values < .028), and at both the 9 Hz Left level and 13 Hz Left level, all differences between Right frequencies involving 4 Hz were significant (all *p* values < .028). In summary, the different frequencies of stimuli provided significantly different reaction times in ways similar to that of Experiment 1, where all comparisons involving a 4 Hz stimulus (the stimulus eliciting the greatest brightness enhancement) were significantly faster except when it was paired with itself.

3.2.2 – Electrophysiological Results

3.2.2.1 – ERPs / VEPs

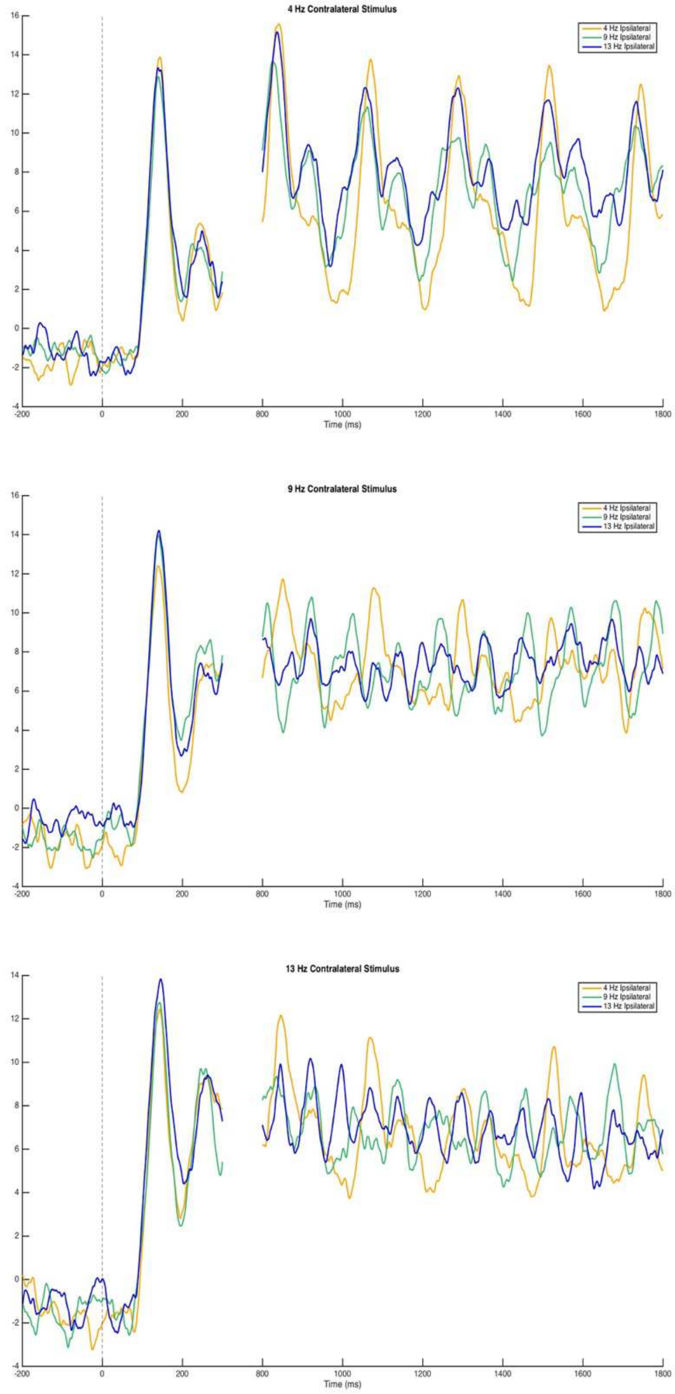

Figure 3.6: ERP components for each of the three frequencies, measured from the contralateral electrode, for a given frequency stimulus on the ipsilateral side to the measured signal. ERPs have broken axes in the time domain to show both the initial VEP and the progression of the ERP over time (approximately the same time used for ITC measures).

Two separate 2 factor repeated-measures ANOVAs were used to test for differences in the P100 component and the N100 component (separately). The P100 RMANOVA showed only a significant effect of Ipsilateral Frequency, F(2,44) = 3.7, *p* = 0.045, but no significant effect of Contralateral Frequency or of an interaction between the two factors. Examining the pairwise comparisons of Ipsilateral Frequency, no significant differences existed between the pairs, though the difference between a 4 Hz Ipsilateral and 13 Hz Ipsilateral was trending to significance (*p* = 0.096). The N100 RMANOVA yielded similar results, where Ipsilateral Frequency was the only significant factor, F(2,44) = 3.7, *p* = 0.033, and pairwise comparisons found no significant differences, though this time both 4 Hz Ipsilateral and 13 Hz Ipsilateral (*p* = 0.093) and 4 Hz Ipsilateral and 9 Hz Ipsilateral (*p* = 0.068) were trending to significance. We believe these results may reflect subtle differences in the ERP components coming from both 9 Hz and 13 Hz stimuli repeating within the P100 and N100 windows, while 4 Hz stimuli can only flicker once during the entire length of both windows. To elaborate, a 4 Hz stimulus flickers every 250 ms, and the windows of interest cover between 125 ms and 225 ms after stimulus onset. In comparison, 9 Hz stimuli flicker approximately every 111 ms, and 13 Hz stimuli flicker every 77 ms. Importantly, the lack of a main effect of contralateral frequency supports the idea that the behavioural brightness enhancement was not a result of the earliest stages of visual processing.

3.2.2.2 – ITC

3.2.2.2.1 – Effect of rhythmic flickering stimuli on ITC

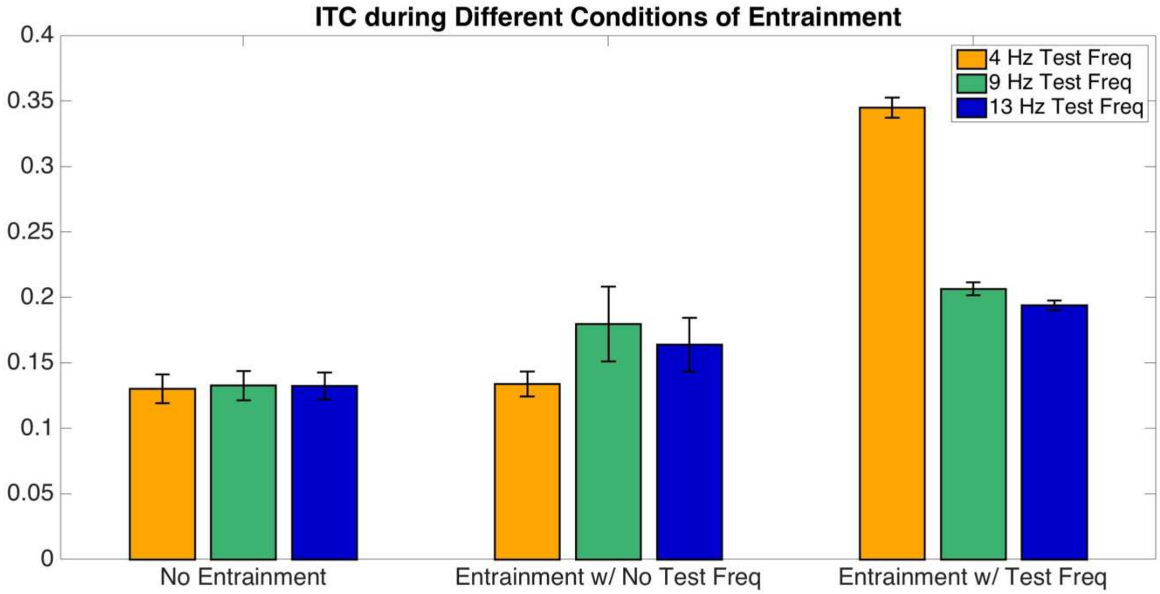

Figure 3.7: ITC within each frequency band during no entrainment, during entrainment of other frequencies, and during entrainment of the frequency tested (measured from the electrode contralateral to the frequency). Error bars represent average within-participant standard error.

A 2 factor 3 x 3 repeated-measures ANOVA was done to test for differences between ITC in the three frequency bands during different conditions of entrainment. These conditions were 1) no entrainment, 2) during entrainment, no test-frequency, and 3) entrainment with test-frequency. Both main effects of Condition (p = 1.9e-08) and Frequency (p = 1.5e-04) were significant, as was their interaction (p = 1.9e-06). Follow up simple main effect RMANOVAs were carried across Frequency at each level of Condition. There was no significant effect of frequency in the no-entrainment Condition (p = .63). Frequency was significantly different for the during entrainment, no test frequency condition (p = 9.7e-07), with both 9 Hz and 13 Hz showing significantly increased levels of ITC relative to 4 Hz (all p values < 7.8e-04). Finally, for the during entrainment with test-frequency condition Frequency also showed a significant effect (*p* = 1.5e-05), and multiple comparisons revealed here that 4 Hz had significantly larger ITC values compared to 9 Hz and 13 Hz (all *p* values < 1.1e-04). Taken together, this indicates a few things: First that at baseline, no frequency naturally has greater phase locking; Second that the task itself appears to elicit an increase of 9 Hz and 13 Hz ITC when those frequencies are not on the screen (possibly task related attention – see discussion), and Third that in general, 4 Hz stimuli show increased ITC values in the respective test-frequency than do the other two frequency stimuli. This fits with our prediction that stimuli perceived as brighter would show higher ITC values.

3.2.2.2.2 – Effect of different or same frequency stimuli on ITC

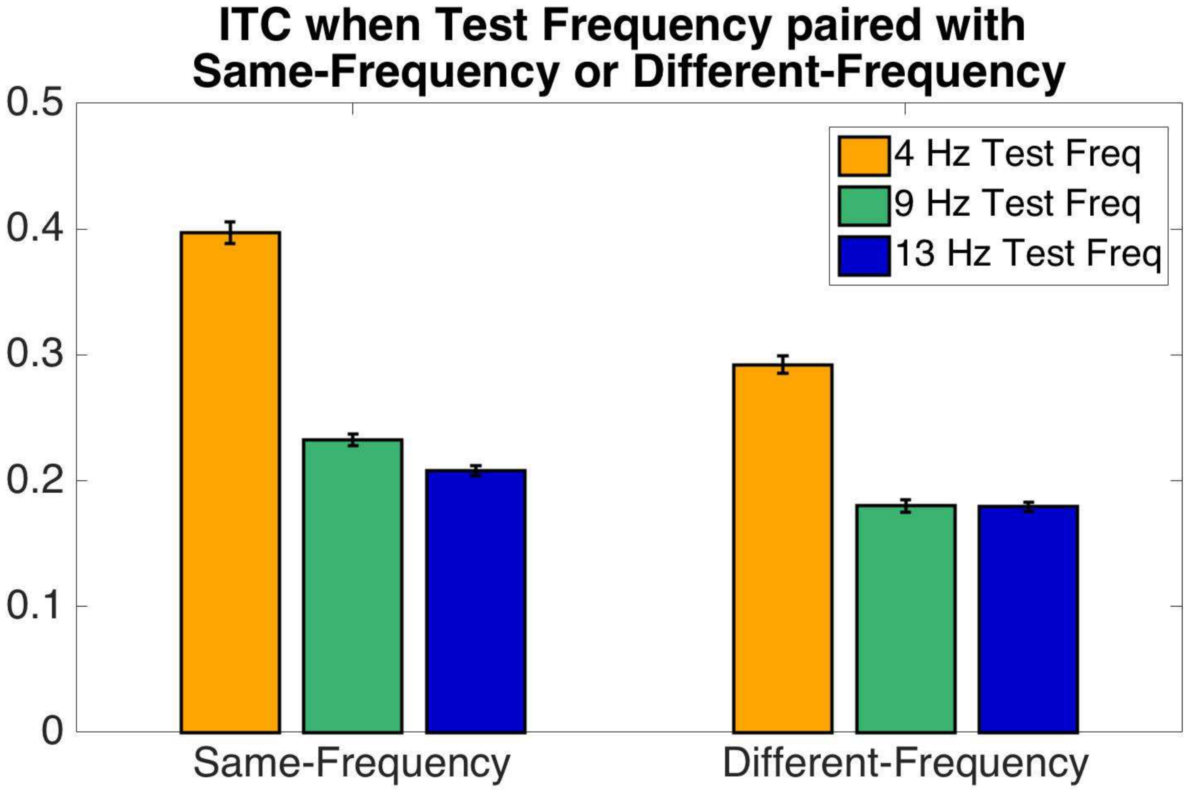

Figure 3.8: The amount of contralateral ITC within each test frequency for conditions where the test frequency was paired with itself, a Same-Frequency, and paired with a different frequency stimulus, Different-Frequency. Error bars represent average within-participant standard error.

A 2 factor 3 x 2 ANOVA was run to compare the amount of ITC contralateral to the test-frequency band when the test-frequency was paired with itself (Same-frequency) or when the test-frequency was paired with another frequency (Different-frequency). Both Stimulus Type, F(1,22) = 32.1, *p* = 1.1e-05, and Frequency, F(2,22) = 27.0, *p* = 1.5e-05, showed significant main effects, as did their interaction, F(2,44) = 11.0, *p* = 4.6e-04. For all levels of Frequency, the effect of Stimulus Type was significant (all *p* values < 0.034). Multiple comparisons were not carried out as there were only 2 levels of the Stimulus Type factor, therefore making the tests redundant. Overall, this shows how two stimuli of the same frequency result in higher ITC values than two stimuli of different frequencies, where if the stimuli ipsilateral to the test frequency is the same frequency as the test frequency, we observe more phase locking.

3.2.2.2.3 – Effect of laterality on ITC

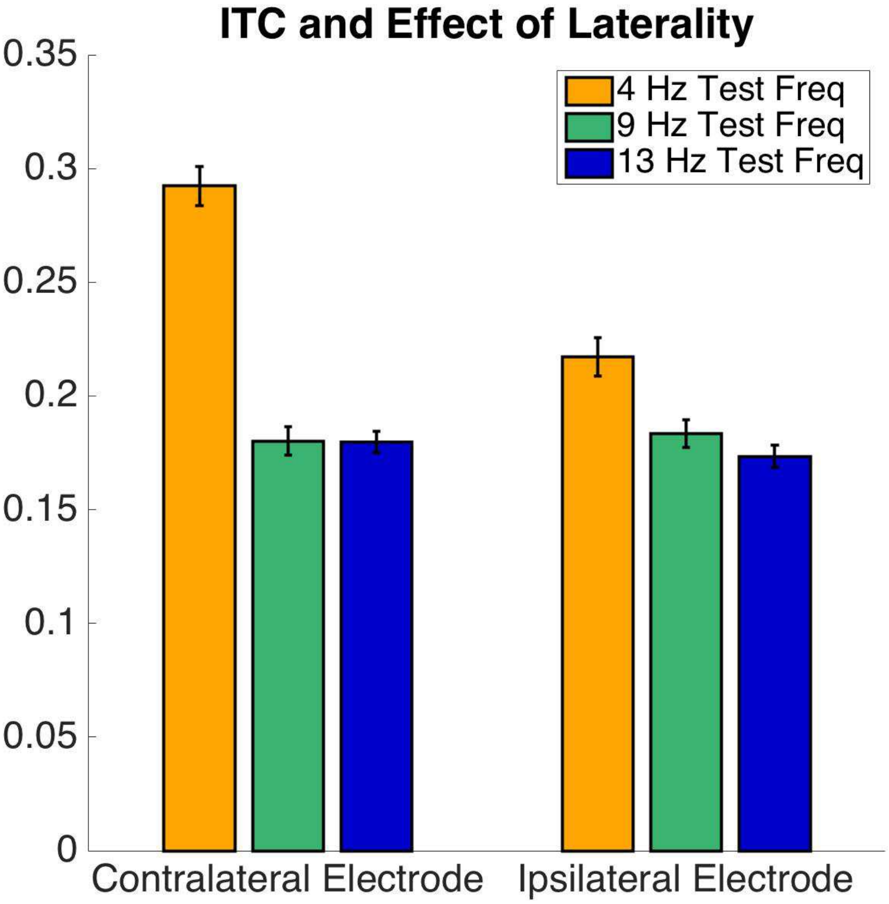

Figure 3.9: ITC within each frequency band at electrode sites contralateral and ipsilateral to the frequency, for conditions only when different frequency stimuli are on the screen. Error bars represent average within-participant standard error.

A 3 x 2, 2 factor repeated-measures ANOVA found main effects for the factors of Frequency, F(2,44) = 20.1, *p* = 5.6e-05 and Side of Electrode, F(1,22) = 16.8, *p* = 4.7e-04, as well as a significant interaction, F(2,44) = 7.3, *p* = .01. The follow-up 1 factor ANOVAs, looking at all levels of Frequency with each level of Side of Electrode found significant effects of

Frequency for each of the Contralateral Electrode (*p* = 2.6e-04) and Ipsilateral Electrode (*p* = .005). These results were explored further with multiple comparisons where again, for both Contralateral and Ipsilateral, Frequency differences were driven by higher 4 Hz ITC values compared to 9 Hz and 13 Hz (all *p* values < .048). Simply, these results indicate a difference in the amount of phase locking between hemispheres only for a 4 Hz stimulus, where 9 Hz and 13 Hz stimulus provide the same amount of phase locking in both hemispheres, regardless of where the stimulus is in relation to the electrode under examination.

3.2.2.2.4 – Effect of brightness discrimination on ITC

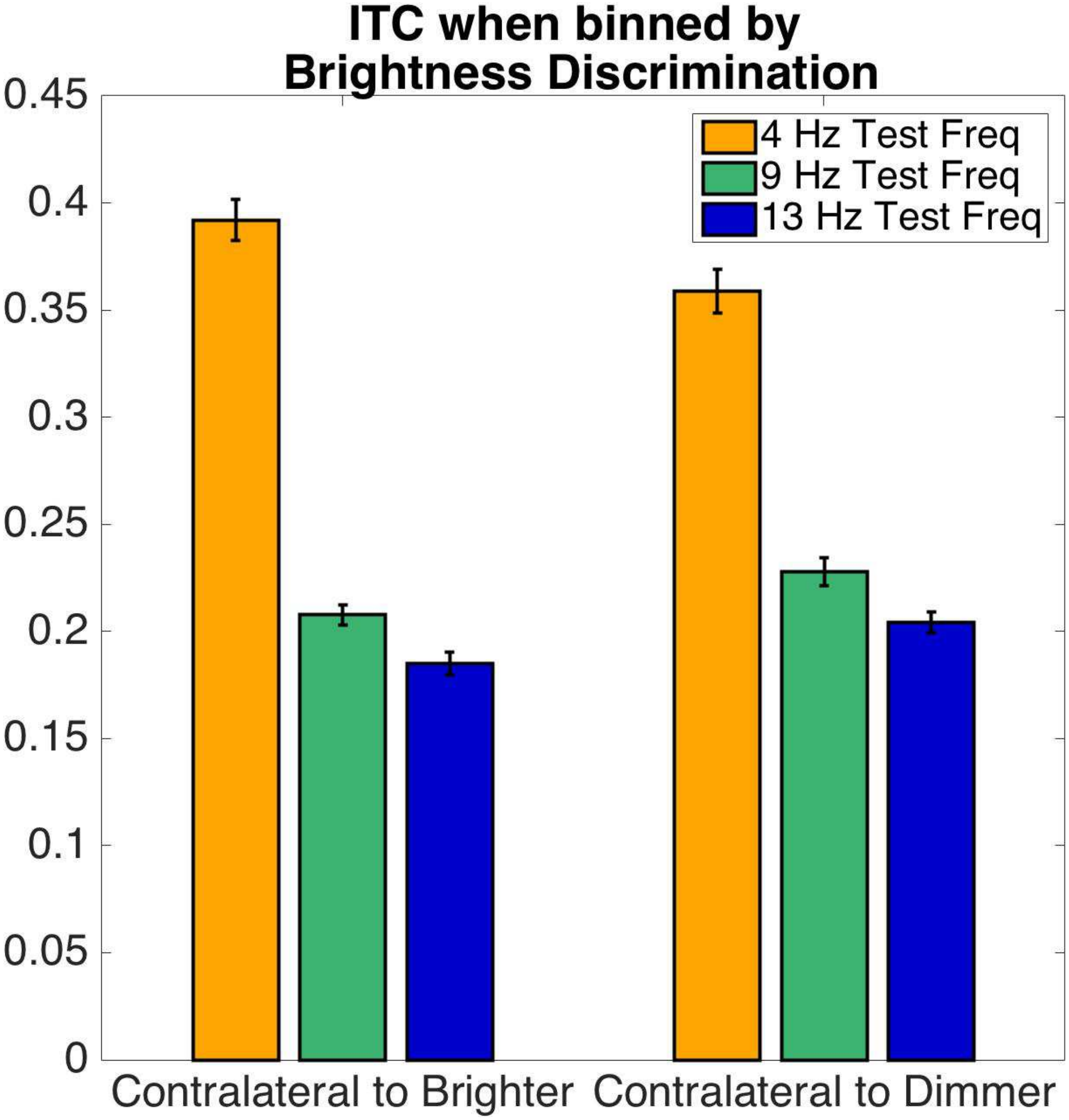

Figure 3.10: ITC within each frequency band when data is binned by behaviour rather than type of stimuli, for only same frequency stimuli. Data represents the amount of ITC within the same frequency stimuli condition of the frequency displayed for the electrode site contralateral to what was chosen as brighter and for the electrode site contralateral to what was not chosen as brighter, or what would be considered dimmer. Error bars represent average within-participant standard error.

A 3 x 2, 2 factor repeated-measures ANOVA was carried out to test for differences in the amount of ITC in same-frequency trials for each frequency band for the electrode contralateral to what a person chose as brighter, and contralateral to what a person chose as dimmer. The results show a significant main effect of Frequency, F(2,44) = 22.7, *p* = 3.1e-05 and a significant interaction between Frequency and Electrode Location, F(2,44) = 4.3, *p* = .023. We tested this interaction by following through on our a-priori prediction that on 4 Hz trials, the ITC values contralateral to what was perceived as brighter would be higher than what was perceived as dimmer. Thus, we performed a single, one-tailed t-test between the amount of 4 Hz ITC in the two levels of Electrode Location, which proved that indeed 4 Hz ITC contralateral to brighter was significantly greater than 4 Hz ITC contralateral to dimmer (*p* = .049). Non-predicted multiple comparisons of 9 Hz and 13 Hz showed no differences due to Electrode Location (both *p* values > 0.103). In sum, this result provides evidence that ITC is greater in the hemisphere contralateral to a stimulus chosen as brighter for the 4 Hz same-frequency stimuli. This supports our hypothesis that, within frequency bands showing brightness enhancement, the contralateral hemisphere with more phase-locking will be chosen as brighter.

4.0 – Discussion

In two experiments, we investigated how the frequency of two flickering stimuli affected brightness perception judgments and how these judgments are related to neural oscillations. We found that a stimulus flickering at 4 Hz was perceived as brighter up to 80% more often than any other flickering stimulus within the 0 - 17 Hz range (Figure 3.1), even though both stimuli were equiluminant. Regarding neural oscillations, which we recorded with EEG in Experiment 2, we focussed on the measure of inter trial phase coherence, or ITC. In general, ITC measures the consistency of phase angles over a subset of trials, as a value from 0 to 1 where a measure of 1 indicates perfect coherence of phase angles in across all trials. During periods of baseline, when no stimuli were on the screen, a restricted set of 3 frequency bands (4, 9 and 13 Hz) showed no difference in ITC between frequencies. As expected, when the flickering stimuli appeared on the screen, the brain showed measurable phase locking, or entrainment, to the flicker rates (Figure 3.7). These entrainment effects were largest in the electrode over occipital cortex contralateral to the flickering stimuli (Figure 3.9), and were strongest when both stimuli flickered at the same rate (Figure 3.8). While all three frequencies showed this ITC boost, the most striking neural finding was that a 4 Hz flickering stimuli elicited much larger increases in ITC than a 9 or 13 Hz stimuli. This ITC advantage was true both when a 4 Hz stimuli appeared on the screen opposite a 9 or 13 Hz stimuli and was especially enhanced when both stimuli oscillated at 4 Hz (Figure 3.8). This finding, which was in accord with the strong behavioural preference to see 4 Hz as brighter, prompted us to directly explore ITC differences sorted not by stimuli in general, but rather, grouped by which stimulus a person chose as brighter. We found in the case of judging the brightness of two 4 Hz stimuli, those stimuli perceived as brighter had significantly greater contralateral ITC than those stimuli perceived as dimmer (Figure 3.10). This represents the most direct evidence in support of our conclusion that the brightness enhancement observed for 4 Hz stimuli is tied to the phase coherence of those stimuli in the brain.

Beyond this critical finding of 4 Hz brightness enhancement and increased ITC, we also found several other interesting results. First, behaviourally, brightness choice proportions appear to generally follow reaction times, where choice proportions closer to 50% resulted in longer reaction times, and vice versa (i.e. harder choices take longer, see Figures 3.3 and 3.5). Second, from EEG, ITC results indicate there to be a 9 Hz task effect. That is, we saw an increase in ITC from baseline in 9 Hz when 9 Hz was not a frequency of entrainment. We attribute this task effect to represent a synchronization of oscillatory activity in the alpha frequency for efficient sampling of the visual information. While both 9 Hz and 13 Hz showed significantly different ITC values when not being directly entrained, we realized post-testing that we had unintentionally selected our 13 Hz frequency as a harmonic frequency of 4 Hz. While a 4 Hz stimulus flickered every 27th frame on our 120 Hz screen, a 13 Hz stimulus flickered every 9th frame. This issue only affects 13 Hz measures with time frequency decomposition, where a 4 Hz sine wave could have the potential to be misinterpreted as a 13 Hz sine wave during wavelet convolution. As such, we believe this increase in 13 Hz ITC when 13 Hz was not the frequency of either stimulus could come from a harmonic effect, as this measure would have included trials involving a 4 Hz stimulus. As an aside, this inadvertently allowed for an interesting comparison of two stimuli that were identical except for 13 Hz's two additional flickers for every one flicker of 4 Hz. As the results indicate, it is intriguing that the 13 Hz, which has 12 more frames of grey (as compared to 4 Hz, where these frames are black) that appear on the screen every ¼ second is perceived less bright more than 85% of the time.

Our original hypothesis, hinging on Bartley's curve of the Brücke Effect (1938) and the attentional effects of oscillations in the alpha frequency, predicted the greatest brightness enhancement to centre around the 9 Hz frequency of flicker. We believed that we would replicate a brightness curve similar to Bartley's, where 8-10Hz appeared to provide the greatest brightness enhancement, and thought this would fit with ideas of the alpha frequency as an internal sampling rhythm by inhibition (Jensen & Mazarehi, 2010; Palva & Palva, 2011; Klimesch, Sausang, & Hanslmayr, 2007). Specifically, we believed Bartley's curve might centre around the alpha frequency because the endogenous alpha rhythm might be best at entraining to external frequencies given the myriad ways in which entrainment of alpha has been successfully employed to alter perception (Mathewson et al., 2012; de Graaf et al., 2013). Instead, it appears our findings match the shape of the Bartley curve, but are shifted, with a peak of brightness enhancement centered somewhere closer to 4 Hz, in the theta frequency band. While this was not the predicted peak frequency, we still believe that our initial reasoning of a match between external stimulus rhythms and internal sampling rhythms offers one explanation for the observed brightness enhancement.

In Experiment 1, the fact that a 4 Hz flickering stimulus was perceived as brighter than a constant (0 Hz) stimulus provides rationale for the label of brightness enhancement in relation to 4 Hz. What remains unclear, however, is whether or not this is truly representing optimal or preferential processing. To explain, regarding Experiment 1, it is interesting to note in Figure 3.1 the similar choice proportions for any 0 Hz and 9 Hz comparison. If 0 Hz stimuli define a “gold-standard”, or baseline measure of brightness perception, then maybe this is evidence that 9 Hz is more “optimally” sampled. Moreover, the similarity between a 0 Hz and 9 Hz stimulus may provide evidence that the constant stimulus is internally sampled at a rhythm around this frequency. Though this in itself is both interesting and informative, and aligns with alpha as an attentional sampling rhythm (VanRullen, Carlson, & Cavanagh, 2007), the remainder of this discussion will focus on how brightness *enhancement* might evolve that resides in a frequency band different from this natural rhythm of attention.

Experiment 2 was specifically designed to understand the large behavioural effect of brightness enhancement at 4 Hz. While behavioural results were consistent with those of Experiment 1 (Figure 3.4), the added EEG data provided insightful information about how this brightness enhancement may evolve in the brain. First, we provide evidence that this brightness enhancement is not attributed to a difference in the earliest sensory response by finding no significant differences in both the N100 and P100 components between all conditions (Figure 3.6). This means the initial visually evoked potential for any frequency stimuli results in the same electrical activity in the occipital area, and can allow us to postulate that this brightness enhancement occurs further along the processing of visual information (i.e. the initial bottom-up visual processing, or the sensation of luminance, is identical for all stimuli). As described above, ITC was used as a measure to provide information about the phase consistency, or success of entraining to a given frequency across trials of the same condition. The phase of oscillatory activity has been shown to affect perception in tasks involving target detection (Mathewson, Gratton, Fabiani, Beck, & Ro, 2009) and discrimination (van Dijk, Schoffelen, Oostenveld, & Jensen, 2008), but these studies have typically analyzed more localized measures of phase at a specific moment just prior to or at stimulus onset. Because the task in this thesis involved a higher-order process – the comparison and decision between two stimuli – and the given null results for differences between VEP components, we believed it was necessary to use a measure capable of representing phase over multiple time points. Thus, our use of ITC allowed us to better understand the dynamics of oscillatory phase unfolding over the same time window (e.g. on the order of a second) that we expected a brightness judgment to arise.

4.1 – What makes 4 Hz special?

To reiterate, our most surprising effect is the difference in the amount of ITC within the three frequency bands of interest. While we demonstrate that all three frequencies are able to show an effect of entrainment (by an increase of ITC from baseline), 4 Hz phase-locks most consistently across trials- much more than 9 Hz or 13 Hz. Here, we offer some speculation of what it might be that makes this frequency band literally stand out.

A 4 Hz oscillation appears in the literature to sit somewhere in the middle of two frequency bands: delta and theta. Though the name and classification of arbitrary frequency bands holds no real scientific value beyond making more generalizable claims (and is perhaps an acknowledgment of the poor spatial resolution of time-frequency decomposition), for the purposes of this thesis, 4 Hz will be characterized as a theta rhythm following the majority of the literature. We do however suggest that these effects might be even larger had the frequency of entrainment been slightly faster and more in the middle of the theta range described in literature (approximately 5 Hz to 6 Hz).

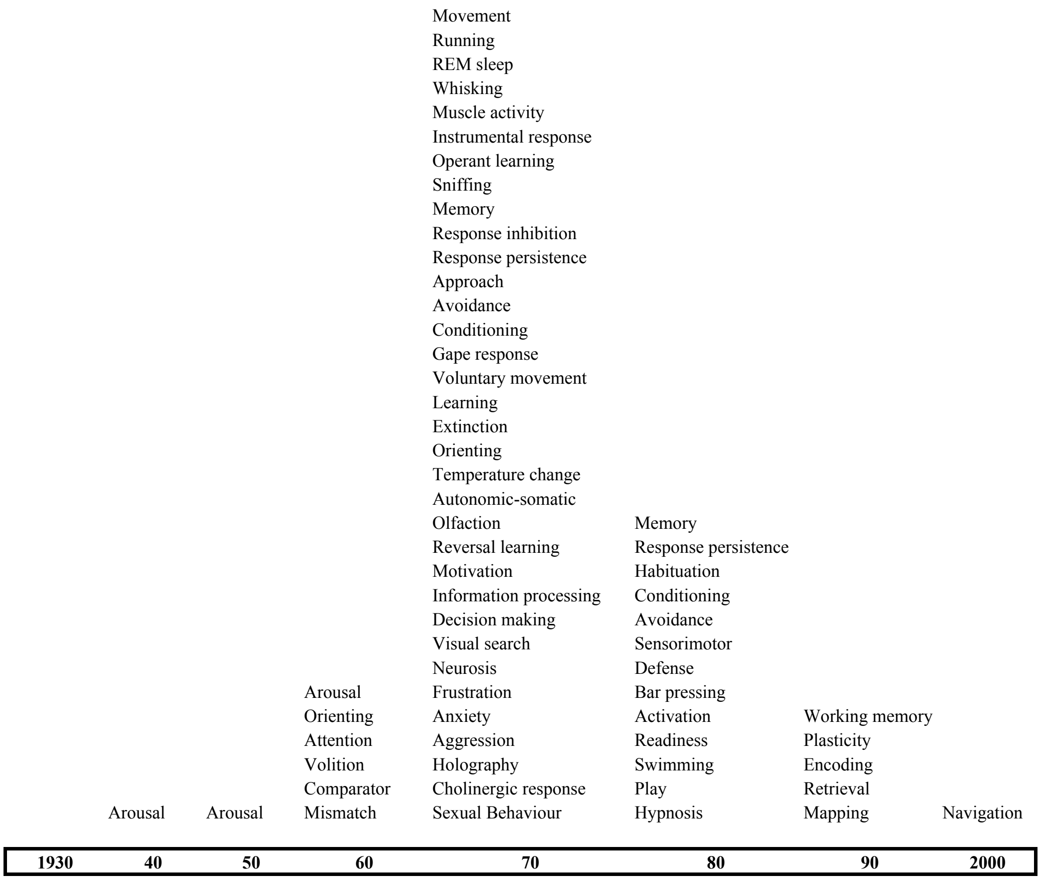

Figure 4.1: Hypotheses about the role of theta as a neural correlate of behaviour throughout time. Adapted from *Rhythms of the Brain* (p. 20), by G. Buzsáki, 2006, New York, NY: Oxford University Press. Copyright 2006 by Oxford University Press, Inc.

Theta oscillations are unique from other oscillations as they are a "sustained rhythm" continuously occurring in the brain (Buzsáki, 2006). Oscillations in the theta band were originally found in the hippocampus and correlated with heading (e.g. which way you are facing), but the "role" of the theta band has been and continues to be contested, challenged, and reassessed (Figure 4.1). Though vague and broad, the conclusion seems to be that theta is the frequency responsible for aspects of movement coordination and attention. To best understand the role this frequency band and how its phase coherence may affect the discussion of brightness enhancement, only literature involving theta's role in visual tasks will be discussed here.

Theta's role in visual perception can be classified by either its state prior to the onset of a stimulus, or its state during the processing of a stimulus. The phase of pre-stimulus theta has been associated with predicting success for attentional search tasks (Dugué, Marque, & VanRullen, 2015), and contrast gain has been shown to depend on the phase of ~4 Hz oscillatory activity just prior to stimulus onset (Cravo, Rohenkohl, Wyart, & Nobre, 2013). Theta oscillations after stimulus onset have also been reported to play a role in visual perception. Greater power and consistency of phase in the theta frequency have been associated with successful attentional search (Dugué et al., 2015), and increased theta power in the contralateral hemisphere during stimuli presentation has been shown to be predictive of colour preference (Kawasaki & Yamaguchi, 2012). Increased oscillatory activity of theta has also been evoked by conjunction search tasks (Dugué, Xue, & Carrasco, 2017), where these authors consider the frequency to play a role in what they call "attentional deployment", and a review on studies using Transcranial Magnetic Stimulation (TMS) suggests theta to be the rhythm of "attentional exploration" (Dugué & VanRullen, 2017). Further, theta's role in visual perception also appears to link with movement, where the initiation of an action can result in ~5 Hz oscillations in the behaviour of visual contrast sensitivity (Benedetto, Spinelli, & Morrone, 2016). This visual contrast sensitivity fluctuating at a theta rhythm has even been shown to precede action, during motor planning stages (Tomassini, Spinelli, Jacono, Sandini, & Morrone, 2015).

With respect to the role of theta oscillations and brightness perception, two recent studies by Han and VanRullen (2016, 2017) have produced exciting results that are very relevant to the current thesis. Like this thesis the first experiment by Han and VanRullen (2016) was a purely behavioural brightness judgment task. Here, they demonstrated that the brightness of a grey disc was enhanced when the disc contained a line drawing (e.g. known shape) when compared against a grey disc containing random lines. They concluded this brightness enhancement was the result of superior predictive coding signals that occur only when the stimulus contains a meaningful shape that can be predicted. Importantly, in a follow-up study, Han and VanRullen (2017) employed the same task while recording EEG. Here they found that the pre-stimulus phase of theta oscillations over frontal cortex, and beta (~16 Hz) oscillations over occipital cortex, were associated with trials in which the line-drawing patch was seen as brighter. The authors suggest that these two frequency bands provide different information for the formation of a brightness judgment, with the slower theta oscillation providing "'top-down control" from higher areas, while faster frequency activity playing a role in more low-level feed-forward processes. Of particular relevance here is the point that the slower theta oscillations are putatively carrying the information necessary for predictive coding – that is, theta oscillations are required in order to compare one representation (in this case a predictive template) against another representation (in this case, the observed stimulus). Moreover, the phase of these theta oscillations is in turn affecting the brightness, very similar to the conclusion we reach in this thesis.

Another domain of luminance judgments that have been shown to be affected by theta oscillations are contrast judgments, and here, one recent study (Zhu et al, 2016) has employed flickering stimuli to observe frequency effects. Importantly, this work is one of few studies to examine how theta oscillations at the time of stimulus processing affect behaviour where the critical dimension of interest is based on the luminance pathway. Zhu, Drewes and Melcher (2016) employed a contrast breakthrough paradigm where a stimulus flickering in one eye is thought to suppress, or mask, the perception of whatever is being shown to the other eye until its contrast is sufficiently large to “break-through” the mask and be reported as visible. In this study a range of frequencies from 0-32 Hz for the mask was used, and a greyscale image increasing in contrast from 0 to 100% over a 6 second interval served as the “breakthrough” stimulus. The main empirical motivation was to see if different frequency masks would result in different breakthrough contrast values. Indeed, they reported that a 6 Hz flickering mask was found to provide the greatest contrast suppression, meaning participants needed higher stimulus contrast to recognize the “breakthrough” image when a 6 Hz mask flickered than any other frequency (Zhu et al., 2016). Most interesting is the U-shaped curve (Figure 4.2) that follows, centering on ~6 Hz for the greatest contrast suppression - a curve that resembles our brightness enhancement. The authors attribute this finding to theta oscillations being a sampling rhythm of the visual system, where a mask "slightly faster than the perceptual cycle" would optimally disrupt the processing of the stimulus. Importantly, this result again suggests that a frequency somewhere slightly less than 6 Hz might be critical in the successful transfer of information across brain regions.

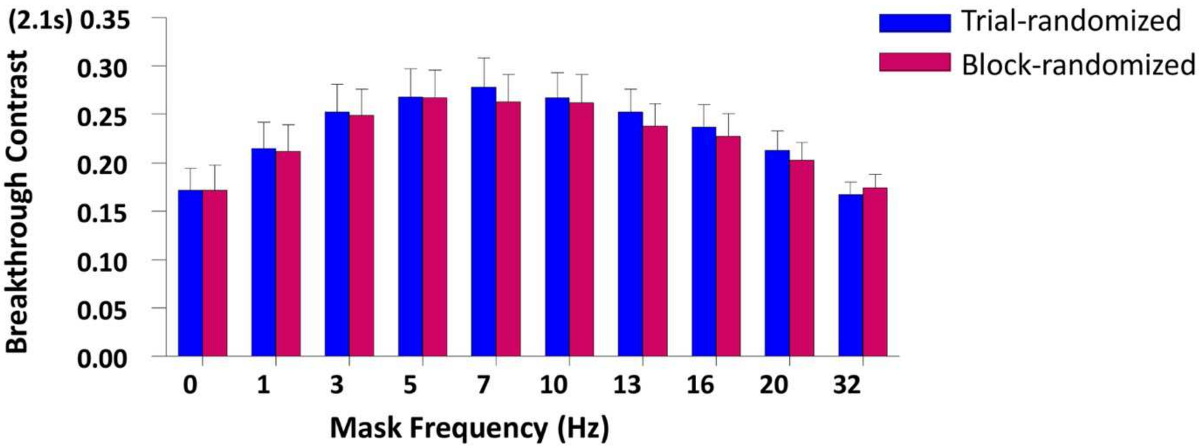

Figure 4.2: The amount of time it takes to reach Breakthrough Contrast for different frequencies of masks in two experimental conditions. Reprinted from “Time for awareness: the influence of temporal properties of the mask on continuous flash suppression effectiveness,” by W. Zhu, J. Drewes, and D. Melcher, 2016, *PLoS ONE, 11*(7), p. 7. Copyright 2016 by Zhu et al.

Finally, theta oscillations appear to play an important role in a variety of cognitive functions including those that extend beyond simple visual perceptual judgments. For example, Kawasaki and Yamaguchi (2012) have found evidence of theta activity as a predictor of subjective colour preference, where increased theta activity was found in the hemisphere contralateral to a preferred colour between 0 and 500 ms after stimulus presentation. Also, alpha de-synchronization followed in the subsequent 500 ms. They believe this theta and alpha activity shows "unconscious attention-related changes induced by subjective preferences", and again, similar to Han and VanRullen (2016, 2017), propose theta as a rhythm responsible for connecting task-dependent regions of the brain by way of "long-range synchronizations". Therefore, we support a theory of theta oscillations as critical not for first-order visual perceptions (e.g. detection tasks), but rather as essential for higher-order perceptual judgments, where the comparison of two stimuli, or a stimulus to a remembered or predicted target is required.

4.2 – A proposed mechanism for theta entrainment leading to visual enhancement

As discussed, theta oscillations appear to play an important role in a very diverse number of cognitive functions. From attention, to movement, to memory, experts in the field are reluctant to assign or narrow theta's role in the brain to one or two dominant features. Perhaps this ambiguity arises because theta is an excellent rhythm for facilitation and communication of various kinds of information, like a carrier wave as alluded to by Agarwal et al. (2014). To be clear, a carrier wave (most notably, when you tune your radio to a station) is a frequency that carries the information, but it is modulations to this wave (e.g. amplitude modulation, or AM, or sideband frequency modulation or FM) that actually contain the information. That is, perhaps theta oscillations are oscillations that allow across-brain information transfer, like a train continuously travelling across the country, where cargo, information, can be loaded and unloaded as necessary wherever its destination may be. Critically, theta still displays phasic properties in both the drop off and pick up of information, like a train that can only receive and give cargo from every other train car. The spacing out of information or cargo allows for an efficient system that does not suffer from a bottleneck, overload or exhaustion. Further, while the train runs continuously once started, it is still possible for it to be controlled by an outside schedule via a reset of its start time. For the endogenous theta rhythm, we believe it can be reset and entrained by an exogenous source, in our case, every flicker of a visual stimulus. For both the train and the theta rhythm, reset signals that arrive too fast (or not at all) might disrupt the most efficient transfer of cargo/information. Finally, as alluded to before, theta is the sole rhythm in the brain that is always sustained, with acetylcholine and GABA-receptive cells in the basal forebrain physiologically capable of maintaining a theta frequency of action potentials, much like a pacemaker (Buzsáki, 2006). Thus, this rhythm appears well-positioned to provide the service of information receiver and deliverer, aligning well with the discretized processing by oscillations described by VanRullen (2016).

Our initial hypothesis assumed alpha oscillations were responsible for supplying a sampling rhythm, whereby visual information was periodically extracted from the world, and that entrainment at this sampling rhythm would enhance brightness. We now propose that in addition to this sampling rhythm (alpha) there also exists a transfer rhythm (theta), and entrainment at this transfer rhythm can also enhance brightness. Importantly, we argue that the kind of task will influence which rhythm is most related to behaviour. In detection tasks (e.g. Mathewson et al., 2009) success is based almost exclusively on whether or not you acquired the low-level, bottom-up visual information from the outside world. Thus, it makes sense that the world-sampling rhythm, alpha, is most relevant. However, in higher-order tasks, like the discrimination task used in the current experiment, where it is necessary to store and/or compare information, we argue that the transfer rhythm, or theta, is most relevant. This also explains some of the above-mentioned studies of other higher-cognitions, like valuation or context-dependent judgments, where theta has been implicated. We believe that theta entrainment creates the most optimal information transfer by way of aligning the naturally-occurring endogenous theta rhythm to a temporally strict and precise schedule. This optimal information transfer then results in a brightness enhancement for 4 Hz stimuli, but not 9 Hz or 13 Hz as the other frequencies do not elicit an optimal alignment of rhythm reset to its highest throughput of information. Returning to the train metaphor, the 9 Hz and 13 Hz stimuli cause start schedule resets too fast, therefore, the train gets pulled back to the station before effectively arriving at its first point of delivery. In the brain, this means that each flash that occurs too quickly interferes with the ability for the theta wave to carry information. It appears as if we have two “trains” in the brain – rhythms that have different but complementary purposes. The alpha train collects cargo from the world, moving about various (visual) local locations picking up information and organizing the load. Only when required by the task, the theta train take the collected cargo on a non-stop cross-country delivery. That is, theta is responsible for distributing the information to the appropriate brain areas (including important feedback information which can arrive at the location where the information first arose, or is expected to arise) when the task requires that level of coordination. The system relies on the alpha train to provide the correct, methodically-packed cargo, or for alpha oscillations to provide high-quality sensory information, and the theta train to provide a reliable express delivery of the cargo, or for theta oscillations to provide efficient information transfer.

Interestingly, the relationship between theta and alpha oscillations appears in the literature to be a reciprocal one, where synchronization of the theta rhythm, or an increase of power, is associated with a de-synchronization of the alpha rhythm, or a decrease of power, and vice versa (Klimesch, 1999; Kawasaki & Yamaguchi, 2012). We propose this relationship may exist as a function of top-down control carried by the theta rhythm, where an unaroused and resting brain with high alpha power is interrupted with a higher-level brain area's anticipation of an event. This top-down control from this brain area is transferred by the theta rhythm, requiring a synchronization of theta activity, and results in a desynchronization of alpha activity.

In terms of our novel findings, simplified, this could mean a 4 Hz flickering stimulus is perceived the brightest because the stimulus closely aligns the endogenous theta rhythm and reduces the noise of the natural rhythm that would exist when a 4 Hz flicker is not present. It's as though a 4 Hz flicker keeps the theta train on a perfect schedule as it crosses the country, where no time is wasted waiting for crossing arms to go down or a track to be switched since the train is flawlessly on time at every moment. The initial first flash sets the schedule for the train of theta, and from there, all flickers align with the transferring rhythm and the information is passed along most efficiently. Further, given evidence of theta's role in feedback from higher-order areas (Han and VanRullen, 2016, 2017), perhaps entrainment at this frequency increases synchronization between these areas and aids in the facilitation of these brightness discrimination judgments more than the other stimuli frequencies.

4.3 – Discrepancy between these results and original report (Bartley, 1938)

One outstanding question is why the greatest brightness enhancement was found in 4 Hz for our study, while Bartley found approximately 8-9 Hz as the frequency of flicker with the greatest brightness enhancement as compared to a constant light (1938). One intuition is that the display technology is so different that this might impact the results, but, Bartley found the maximum of the Brücke effect was independent of the luminance of flash, and found that the frequency of maximal brightness enhancement did not change over varying light-to-dark ratios (although a 1:1 ratio provided the greatest brightness enhancement across frequencies). Impressively, almost 80 years later, Bartley's prediction that "the brain mechanism whose rhythmic activity determines the rate of cortical responses produces the Brücke effect" appears still completely valid today – but, the discrepancy between our 4 Hz and the historical 8-9 Hz as maximally bright is puzzling. Of course, the empirical methods were not as rigorous in the 1938 report - the number of trials is limited in Bartley's sample, and it appears that he may have only tested himself in the study (no clear description of subjects is given, besides a reference to the overtness of the brightness enhancement for even a 12-year-old who's results "compared favourably with the author's"). With respect to the original findings, then, we have no systematic reason to explain the difference in the peak frequency of brightness enhancement, but given the known individual differences in other naturally occurring brain rhythms (e.g. variability of alpha frequency band, see Klimesch, 1999) it is possible that Bartley's report was idiosyncratic to him. Recall that one additional study by Kohn and Salisbury (1966) did attempt to look for neural correlates of flicker brightness enhancement, and perhaps here we actually find more agreement with our behavioural results. Upon revisiting Kohn and Salisbury's attempt to record 2-electrode EEG from 2 subjects while following the same paradigm as Bartley, their behavioural results show some of the largest brightness enhancement occurring at approximately 5 Hz. That is, despite not finding any measurable EEG effects, they did however find a behavioural effect that appeared to have the largest brightness enhancement at 5 Hz, not 9 Hz, which is more consistent with what we found. Moreover, as described above, Zhu et al. looked at continuous contrast suppression with rhythmic stimuli, and make a strong claim for a curve similar to Bartley's but centered around a value just under 6 Hz (2016). Therefore, it appears that the more contemporary work converges on flicker enhancement effects that fall in the theta range, with a peak somewhere from 4-6 Hz. Finally, there is always the chance that some specific feature of the experimental design can account for the discrepant findings. Here, it must be considered that Bartley's curve was created only from tests of one flickering stimulus compared to a constant light, and although Experiment 1 also involved these judgments (e.g. had some trials with one non-flickering stimulus), Experiment 2 only involved 2 flickering stimuli. A comparison between two flickering stimuli seems different than a comparison between a constant stimulus and a flickering stimulus, which could be reduced to the evaluation of only one stimulus, and therefore may not require higher-order areas for brightness discrimination (and in turn result in findings like Bartley's as opposed to ours). Although the dynamics of two flickering stimuli could possibly play a role on the discrepancies between Bartley's study and ours, this seems unlikely as 4 Hz was still chosen as the brightest stimulus even when compared to a 0 Hz, or constant, stimulus. It is also possible that the number of trials in a given experiment plays a role. In Bartley's results are from 125 total trials, but over two sittings, while our experiments had 540 and 625 trials experienced in one sitting. Given the relatively uncharted territory that is the dynamics of oscillatory activity in the brain, it is ignorant to think that a difference of at least 315 trials of entrainment may not have some effect on complex oscillatory activity over time. Moreover, it is similarly naive to think that the demands of one sitting versus the changes induced across two sittings might also play a role. Despite the differences to Bartley's original finding, our ability to replicate the 4 Hz enhancement across two separate experiments, with a total of 52 subjects gives us confidence is the veracity of our results.

4.4 – Conclusion

In summary, we can understand the brightness enhancement we report by returning back to the difference between sensation and perception. We propose that the sensation of light entering the eye from different frequency flickering is generally consistent across frequencies. However, our perception of this light varies, and relates directly to the frequency of the rhythms of exogenous flicker. While the entrainment of an alpha rhythm (9 Hz in this case) was the hypothesized source of the generation of a perception different from sensation, it now appears that is it the entrainment of the theta rhythm, our proposed information-transfer rhythm, that provides this brightness enhancement. Further, our understanding of theta's role as a transferring rhythm includes not only bottom-up processing, moving the visual information collected by the sampling rhythm to the brain, but also top-down processing. We suggest that the entrainment of the theta rhythm would facilitate both bottom-up and top-down processing, where a 4 Hz flickering stimulus appears brighter both because the information is transferred to a brightness discrimination area of the brain most optimally, but also because top-down control is engaged most favourably, readying and maintaining the visual system to collect the best possible information. Entrainment at a frequency at or near the frequency of information transfer creates a reduction of noise in the endogenous theta rhythm and allows for the best possible parallel processing, providing a perception that deviates the most from sensation and ultimately results in a 4 Hz flicker appearing the brightest.

The role that theta oscillations play in understanding the enhancement of brightness perception is complex and far from fully understood. The consistency of phase angles, or the strength of phase-locking, in the theta rhythm appears to be a correlate of brightness enhancement. New behavioural correlates related to perception, action, and memory appear to be associated with theta activity regularly. Our study adds another perception to the list of behaviours correlated with theta activity, perhaps compounding on to the complexity of the discussion, and highlighting the work still needed for a complete understanding of this mysterious and pervasive rhythm. As this finding appears to be, as Bartley describes, “not determined in the eye” (1938), this 4 Hz enhancement effect should extend to other higher-order judgments, like thresholds for motion coherence, visual search tasks, or object categorization - going beyond purely a brightness phenomenon. Future work is also needed in understanding how theta is associated with so many different functions, or if it plays more of a facilitating role in ways similar to a carrier wave.

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