The neural mechanisms of binocular rivalry revealed by oscillatory signals in the electroencephalogram

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Dedication

I dedicate this thesis to my family, mother, father and sister who were a great support throughout my graduate studies. I also dedicate this to anyone interested in understanding the neural basis of awareness and consciousness.

Abstract

This thesis work focuses on understanding the neural mechanisms of vision and visual awareness through the study of binocular rivalry. Binocular rivalry is a perceptual phenomenon which occurs when two different images are shown separately to each eye and perception alternates between the images. The number of investigations on binocular rivalry has risen in recent years due its potential in disentangling the neuronal processes related to ocular competition, perceptual suppression, and the brain basis of perceptual awareness. Although much progress has been made, we still have a limited understanding of where exactly rivalry takes place within the visual system, and further, what mechanisms mediate perceptual suppression. Here, I assess functional roles of alpha oscillations, measured by the electroencephalogram (EEG), as potential neural mechanisms of suppression. I also use EEG to study externally generated steady-state visually evoked potentials (SSVEPs) to address at what level the visual system competes for perceptual dominance. The general conclusions from the alpha oscillation experiments suggest that they can predict individual differences in rivalry behavior, and also that they may mediate ocular suppression during rivalry perceptual transitions. Furthermore, the general conclusions from the SSVEP experiments suggest that stimulus rivalry, a counterpart of binocular rivalry where the stimulus representations are thought to compete instead of the eyes, may be mediated by similar neural processes as binocular rivalry transpiring within early visual cortex.

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INTRODUCTION

General Introduction

The main goal of this dissertation project was to better elucidate the neural mechanisms underpinning binocular rivalry by using large-scale neural population recordings available in the electroencephalogram (EEG). Binocular rivalry is a visual process that occurs when corresponding locations of the retina process dissimilar visual images. Alternation of visual percepts occurs between the two dissimilar images continues indefinitely as long subjects continuously view the images. Binocular rivalry is studied because it is can tell us important information about what neural processes are involved in the generation of visual perception and also binocular vision. Often fascinating the people who experience this visual phenomenon, binocular rivalry has been studied for over 200 years (Blake 2000). Our understanding of this visual process has evolved alongside scientific inquiries beginning with behavioral investigations (Blake 2000), to modern day neuroimaging studies (Tong et al 2006). Binocular rivalry can be grouped into a larger class of visual stimuli which vision scientists term multistable phenomena (or bistable phenomena), characterized by alternating perceptual interpretations when the visual input is ambiguous but remains constant. This dissociation with perception and sensation allows for a clearer understanding of the different types of processes involved in not just sensing the world but also in creating a perceptual representations which allow for flexible behavior in animals. Here, I will discuss the general scientific findings related to the neural mechanisms of binocular rivalry, including current controversies in the field, and finish with contemporary models

of the generation and resolution of rivalry.

Motivation

Apart from its dazzling perceptual nature, there are multiple scientific motivations to better understand binocular rivalry. First, given that the visual display is unchanged, and the inputs to the two eyes remain constant during a binocular rivalry viewing, understanding the neural mechanisms of binocular rivalry can tell us how the brain suppresses information of one whole eyes' input. Secondly, given that this process arises from incompatible visual information, it can tell us how the brain resolves conflicting information in the visual modality, and perhaps more generally, how the cortex resolves conflicting information (Dieter and Tadin 2011). Third, given that sensory stimulation is constant, binocular rivalry reveals the neural processes involved in spontaneous changes in visual awareness, and allow us to study the naturally generated intrinsic dynamics of cortical activity not confounded by the visual task structure. Related to this final note, it has been suggested that rivalry might also be closely related to the neural correlates of consciousness (Crick and Koch 1990). This has spurred a great number of scientific studies aimed at developing a model of rivalry, even though recently this idea has come under scrutiny as to how exactly rivalry contributes to our understanding of consciousness, and its potential limits in accomplishing this task (Blake et al 2014).

History of the Neural Basis of Rivalry

The first neural models of binocular rivalry stressed ocular competition as a

potential mechanism to the spontaneous alternations seen in binocular rivalry (Blake 1989). Reciprocal inhibition of ocular dominance columns provided a substrate for the large-scale eye based suppression seen during rivalry. Much of the evidence from psychophysics converged on this model (Blake 2001). This idea stemmed from studies which showed that swapping the dominant stimulus while it was suppressed caused the dominant eyes' image to reach awareness. Furthermore, removing the dominant stimulus when rivalry was engaged maintained perceptual suppression of the suppressed stimulus for several seconds after removal (de Graaf et al 2017). Finally, probe methods of contrast threshold elevation during rivalry suppression suggest an attenuation of the suppressed eyes' signal (Alais 2011). Overall, these findings suggested that the neural mechanisms of rivalry were closely related to neural systems tied to processing information from each eye.

Single-unit electrophysiological studies then started to shed light on the neural mechanisms of binocular rivalry in monkeys. Single unit firing rates were found to be modulated in the lateral geniculate nucleus (LGN) when dichoptic stimuli were presented, but they were also sensitive to any type of stimulus presented (even the same stimuli), suggesting little involvement with rivalry per say. Furthermore, Layer 4 neurons which are strictly monocular also displayed the same behavior with firing rate (Sengpiel 1997). Thus, the monocular model didn't seem to capture all of the known observations of single unit studies that predicted a higher magnitude of modulation in very early sensory pathways.

Further psychophysical findings also gave way to the idea that perhaps stimuli,

rather than eyes, were competing with the discovery of ‘stimulus rivalry’, where monocular images are swapped between the eyes (Logothetis et al 1996). Other studies with half image amalgamates of two separate images showed that the brain can combine hemifields of two separate images shown to each eye (Kovacs et al 1996). Finally, another case of rivalry called monocular rivalry can indeed occur without any interocular conflict when orientation and color are overlapped to generate a spatial ambiguity (Buckthought et al 2011). Binocular rivalry is also linked to the general realm of bistable perception, given that it has similar distributions with the necker cube and face-face images, which are thought to be related to high-level neuronal processing involved in perceptual interpretation (Leopold and Logothetis 1999). Thus, psychophysical observations show that some high-level perceptual processes may play a role in determining rivalry.

Given the single unit evidence going against the monocular reciprocal inhibition model, investigators turned to other brain regions outside of LGN and early V1 in determining the neural mechanism of binocular rivalry. This was thoroughly investigated by Logothetis and colleagues, in a series of studies looking at monkey single units, they studied binocular rivalry across a spectrum of brain regions. A combination of visual brain areas were sensitive to rivalry percepts, with an increase in the number of single units increasing toward high-level visual areas such as V4 and IT (Logothetis 1998). Recently, they have shown that even prefrontal association areas also show perceptually related modulation (Panagiotaropoulos et al 2012). Thus, a major conclusion from these studies was that many higher-level visually responsive brain areas do indeed modulate

firing rates associated with perceptual changes during rivalry, much more so than early visual areas (Logothetis 1998).

Different Neural Mechanisms of Rivalry

Neurophysiological changes were not confined to firing rates, however, local field potentials which are thought to reflect the summed input to a brain region, also show robust modulations with perceptual transitions. Electrophysiological studies in monkeys focusing on the local field potential suggested that changes occur throughout the brain as a result of the binocular rivalry process, but modulations can be found very early in the visual system. Local field potentials in low frequencies are correlated with perceptual modulations in early visual areas during binocular rivalry in monkeys (Gail 2004). Alternatively, modulations have also been found in lateral prefrontal cortex, with a major component at high frequencies (>50 Hz), and a small component at lower frequencies (20-30 Hz) (Panagiotaropoulos et al 2012). Unfortunately, local field fields have not been measured in IT areas during rivalry, but studies investigating visual attention show that oscillations in the alpha band synchronize across visual brain areas and with spikes when attention is directed to the receptive field of the neuron during a cue period, indicating that oscillatory changes are present in these brain regions (Saalmann et al 2012). A potential question for future rivalry studies is to address how local field potentials change in association areas during rivalry, especially within the pulvinar and temporal/parietal regions.

Given that spiking changes in the LGN were unaffected by rivalry perceptual

dominance, it was difficult to assess what role the thalamus may play during rivalry. Early models incorporated thalamocortical wiring as a major part of the mechanism of rivalry, and anatomy and physiology of the thalamus was strongly in favor of retaining the circuitry important in mediating eye-based suppression. When investigators looked at the LGN of the thalamus during rivalry in fMRI, they found that modulations were indeed correlated with rivalry states (Haynes et al 2005; Wunderlich et al 2005). Furthermore, local field potentials measured in the LGN during perceptual suppression induced by generalized flash suppression showed a 9-30 Hz modulation in the LGN and in the pulvinar nuclei of the thalamus (Wilke et al 2009). Thus, modulations in the LGN are correlated with modulations in visual perception but are a reflection of the population activity or field potential changes likely related to feedback inputs from other cortical areas.

In conclusion, the current model of rivalry posits it to be a combination of low-level and high level neural mechanisms (Blake and Logothetis 2002). However, many questions remain unresolved, and the neural mechanism remains an area of active research. Multiple brain sites seem to fire action potentials in coordination with each other as perceptual states change during rivalry. These include changes in early to late visual areas, and possibly even prefrontal regions and association cortices. On top of the modulations in single unit firing are the local field potential changes which show activity in early visual areas and also the visual thalamic nuclei such as the LGN and the pulvinar. Thus, outstanding questions that remain include how the neurophysiological mechanisms mediating perceptual selection and inhibition of one eyes signals interact across areas.

Also, a related but separate question is how discrepancies between single-units and other electrophysiological studies such as EEG, and fMRI during rivalry can be provided with a unified framework.

Chapter 1 of this thesis will attempt at addressing the first question regarding whether the mechanism of binocular rivalry does indeed involve competition between monocular visual channels, or if it is at the level of stimulus representations much higher in the visual system. The second chapter of the thesis will show how the brains natural oscillations in the alpha band are indeed correlated to transitions in rivalry states and specifically to interocular competition. Given the relationship between alpha oscillations and the thalamus, the second chapter addresses possible mechanisms of the suppressive role alpha oscillations may play during binocular rivalry. Further, it hints at a potential insight into how the brain might utilize oscillations in the visual thalamus and visual cortices without altering changes in spike rate to establish perceptual transitions.

EEG, Oscillations, and Rivalry

As mentioned above, a major component of this thesis is how alpha oscillations are related to binocular rivalry. Generally, the human brain spontaneously produces oscillations which can be measured readily in the electroencephalogram (EEG). Many of these rhythms were initially observed during state changes such as sleep (Achermann and Borbely 1997), or changes in attention (Clayton et al 2015). Figure 1 shows multiple rhythmic frequencies that are produced by the brain, being lumped into frequency bands called delta (<1 Hz), theta (4-8 Hz), beta (15-30 Hz, and gamma (30-100 Hz). Although

the precise function of these oscillations is not fully understood, it is currently a major topic of investigation in neuroscience, and theories about the function of oscillations are currently being developed (Buzsaki and Draguhn 2004).

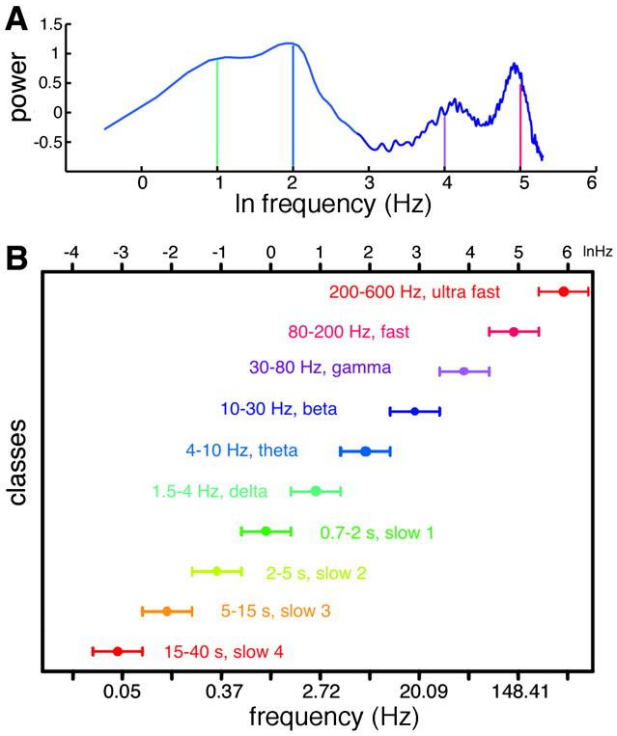

Figure 1: Subdivisions of different frequency bands in neural oscillations research. Adapted from Buzsaki and Draguhn 2004.

One of the most prevalent oscillations in EEG research is the alpha oscillation. It is a high SNR band which is highly modulated during motor commands (ERD/ERS), and also during perceptual and cognitive operations (Mathes et al 2010). One of the first brain rhythms to be discovered, the alpha amplitude was initially inversely correlated with cortical excitability (Lange et al 2014), however, later studies revealed that the level of alpha activity doesn't always linearly relate to the level of cortical inhibition (Palva and Palva 2007). The functions of alpha are still under debate, yet prominent theories still link a major component of alpha oscillation with neural inhibition, or selection of information, as shown in Figure 2 (Pfurtscheller 2003, Klimesch 2012). Thus, the alpha

oscillation is important in neural processing and typically plays an inhibitory role.

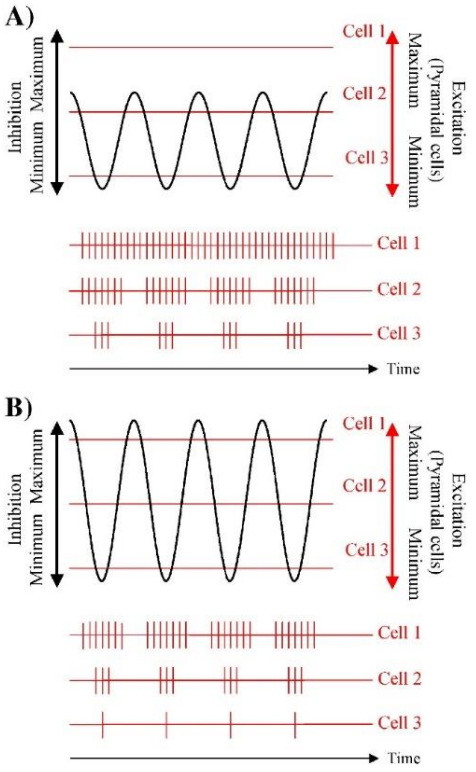

Figure 2: Alpha amplitude may influence neural coding on the single cell level. Adapted from Klimesch et al. 2007.

Multiple studies have implicated alpha activity related to mutistable perception. Approximately 250 ms before a reversal in Necker cube orientation there is a decrease of alpha activity (Isoglu-Alkac et al. 2000). Alpha activity across the whole scalp also seems to decrease prior to changes in dot-quartet bistable perception (Struber and Herrmann, 2002). A summary table including a number of other studies finding oscillatory changes with bistable perception is included in Table 1 (adapted from Kornmeier and Bach 2012). It is clear that a number of researchers have found that changes in awareness during bistable perception have been linked to changes in multiple oscillatory bands. Thus, natural oscillations that the brain produces are linked to the changing perceptual and cognitive states of subjects.

Table 1: Summary of oscillatory changes in the brain during bistable perception

	Peak latency (ms)		Location	Stimuli
	Stimulus onset = 0	Reaction time = 0		
Reversal positivity (RP)	**130**[1–6]	−470	Occipital electrodes[1–3] Primary visual areas[6]	Necker cube[2], Necker lattice[1, 3], old/young woman[4], vase/face stimulus[5], Schroeders staircase[5], Binocular rivalry stimuli[6]
Alpha-power decrease (≈10 Hz)	−400 to +600 (−1400–+600) **130–200**[7]	−**1000** to **0**[8, 10, 20] **(−2000–0)**[8] −470 to −400	Parietally distributed[8] Left-hemispheric, from occipital to frontopolar electrodes[7]	Necker lattice[7], Necker cube[10, 19], SAM[8]
Reversal negativity (RN)	**260**[1–6, 11–14] **(220)**[1, 11, 12, 14]	−340 (−380)	Occipital and parietal electrodes[1, 11–13] Lateral occipital and inferior temporal areas[6, 9]	Necker lattice[1, 3, 7, 12–14], Necker cube[9], face/vase[5], old/young woman[4], Schröder staircase[5], Binocular rivalry stimuli[6]
Late (incl. parietal and frontopolar) positivity	**340**[1, 4, 11–13] **(300)**[1, 11, 12] **470**[1, 3, 4, 11–15] **(400)**[1, 11, 12, 15] 350	−260 (−300) −130 (−200) −**250**[8, 16–18]	Frontopolar electrode[1, 4, 12, 13] Parietal electrodes[1, 4, 12–14], inferior temporal, and superior parietal regions[9] Right parietal electrodes[15–18, 20]	Necker cube[9, 16–18], Necker lattice[7], old/young woman[4], SAM[8, 15], Binocular rivalry stimuli[6]
Beta power increase (14–26 Hz)	**340 (180)**[7]	−260 (−420)	Parietal and central electrodes[7]	Necker lattice[7]
Gamma power increase (≈30–70 Hz)	−400 to +600 −**200**[7] **300 (150)**[7]	−**1000** to **−0**[16, 17, 20, 21] −800 −300 (−450)	Right frontal electrode[20] Right parietal/central electrodes[7] Left-central electrodes[7]	SAM[20, 21], Necker cube[16, 17], Necker lattice[7]
Global field power effects	−**50**[3] −**300**[24]	−650 −900	Right inferior parietal lobe[3, 22]	Necker lattice[3], SAM[24], Binocular rivalry stimuli[22]

Bold indicates raw values, regular type indicates values are translated by a 600-ms reaction time[2, 8, 12].

[1] Kornmeier and Bach (2005), [2] Kornmeier et al. (2011), [3] Britz et al. (2009), [4] Kornmeier and Bach (2004a), [5] Pitts et al. (2007), [6] Britz and Pitts (2011), [7] Ehm et al. (2011), [8] Strüber and Herrmann (2002), [9] Pitts et al. (2009), [10] İşoğlu-Alkaç (2000), [11] Kornmeier et al. (2001), [12] Kornmeier and Bach (2004b), [13] Kornmeier et al. (2007), [14] Pitts et al. (2008), [15] Intaite et al. (2010), [16] Basar-Eroglu et al. (1993), [17] Strüber et al. (2001), [18] Mathes et al. (2006), [19] O'Donnell et al. (1988), [20] İşoğlu-Alkaç and Struber (2006), [21] Basar-Eroglu et al. (1996), [22] Strüber et al. (2000), [23] Britz et al. (2010), [24] Muller et al. (2005).

The phase of alpha oscillations has also been linked to perceptual outcomes in a variety of visual tasks. If a stimulus is presented in the peripheral visual field at threshold, the alpha phase can predict 16% of the variability in detection (Busch et al 2009). The phase of the alpha cycle also makes it more or less likely to induce a TMS phosphene in visual cortex (Dugue et al 2011). Interestingly, an increase in alpha power has been correlated with suppression of subliminal processing in the periphery when stimuli were presented at a 50 percent detection threshold, as seen in Figure 3 (Bereither et al 2014). Thus, the phase, and the specific end (positive or negative) of the alpha cycle is important in determining whether the alpha oscillation suppresses or augments the neural response.

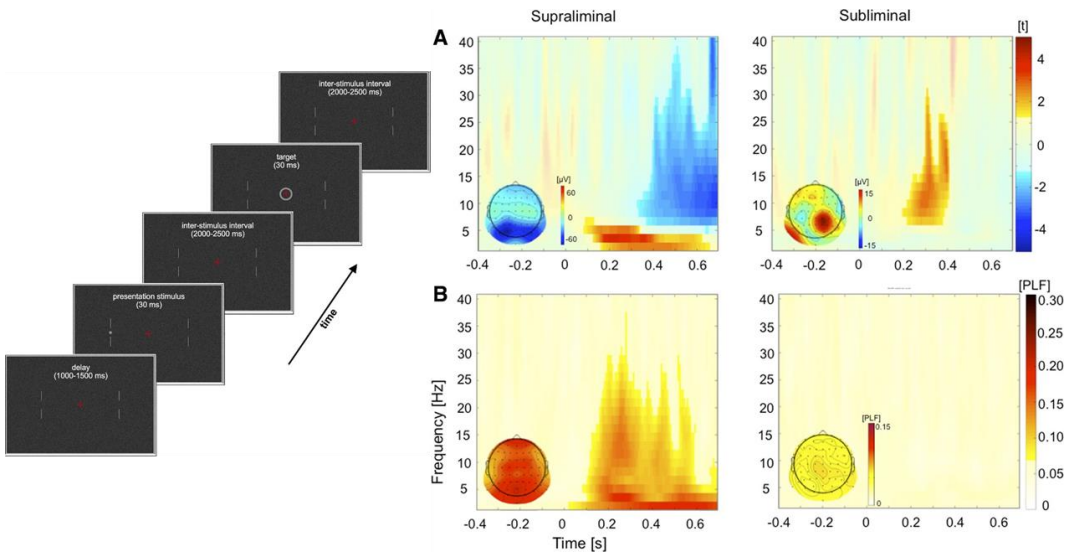

Figure 3: The level of alpha amplitude may increase during processing of subliminal stimuli as opposed to the typically observed decrease in alpha amplitude during supraliminal perception of the same stimulus. Adapted from Bareither et al. 2014.

GENERAL METHODS

Visual Psychophysics

Visual psychophysics is a technique used by vision researchers to infer the underlying physiology of visual processing. As mentioned earlier, many visual phenomena were initially studied using psychophysics and have therefore provided for a large knowledgebase of information on the nature of vision. Typical paradigms include asking subjects to respond to a set of stimuli with carefully designed visual parameters. For this, a visual display toolbox such as psychtoolbox is used to adjust visual parameters like luminance, contrast, stimulus size, location, background luminance, flicker rate, etc. In the treatment conditions, the experimenter can then change one component of the stimulus, e.g. flicker rate, and then assess the change in behavior. An important methodological aside is that the computer monitor must also be carefully selected, especially for flicker rate experiments, given that the monitor flicker rate will limit the available flickering frequencies of the stimuli only a select number of frequency ranges are available. Then, typical measures of behavior include behavioral dwell time (i.e. the proportion of time spent viewing A versus B), duration of the average subject report, histograms of response durations, etc. Much can be inferred about the potential neural mechanisms of a visual phenomenon but care must also be taken in addressing whether it is a limitation of the behavioral response system or the perceptual system when utilizing psychophysics experiments.

Eletroencephalogram (EEG)

Traditionally, the electroencephalogram (EEG) has been used since the 1800s and has taught us about physiological basis of brain rhythms, sleep, and attentive states. Recent discoveries in digital signal processing have allowed for a sophisticated new level of analysis and processing speed to be applied to EEG data which has brought forth a new era of EEG insights (Kennet 2012). Uses of EEG range from research, to clinical applications, especially prevalent in sleep and epilepsy diagnoses, where EEG remains one of the most critical sources of information properly identify these brain disorders. Despite current limitations, EEG is also being developed, alongside its electrophysiological counterpart magnetoencephalography (MEG), to diagnose and identify biomarkers for an increasing number of brain disorders such as Schizophrenia, dementia, and Alzheimers (Enaw and Smith 2014; Georgopoulos et al 2007).

The source of EEG signals is considered to be from large parallel pyramidal cells aligned along the gyri of cortex (Jackson and Bolger 2014). These cells are excitatory and have large apical dendrites which extend into the upper layers of the neocortex and receive a multitude of inputs from a range of cortical and subcortical areas. The standard dogma over the years has been that these synchronized activity of large populations of cells drive electric field changes which are then identified with the electrodes that we place over the scalp of human subjects, establishing the neurophysiological basis of the EEG signal.

The typical analysis pipeline for an EEG experiment is as follows:

1. Re-referencing
2. Removal of dc offset

3. Initial filtering of very low and very high frequencies (e.g. 0.1-150 Hz)
4. Running of ICA
    a. Artefact Identification
    b. Artefact reliability measures and statistics
    c. Artefact removal
    d. Physiological Component Selection and projection into electrode space
5. Filtering of specific frequency band, amplitude estimation, power estimation
6. Event related metrics and relation to behavior
7. Source localization

EEG activity is correlated across electrodes and contains noise and artefact from multiple sources, therefore, prior to any claims about neural activity, a thorough preprocessing analysis must be conducted. First a decision must be made about the type of reference, there is no ideal case for reference. Typically common average reference is used given that it is least sensitive to electrode arrangement, and reduces common noise from electrodes, and can attenuate some forms of artefacts. An online amplifier typically filters data as it is collected and stored on the computer (0.1-200 Hz). From here, the analysis typically divides into what type of signal one is trying to interpret.

Oscillations

EEG allows for the observation of brain rhythms, or oscillations, but there are many potential sources for error when evaluating and properly extracting these from the raw

timeseries. Also worth noting, that the exact nature of these oscillations are still under investigation and thus adds caution when interpreting spectral results.

First, the typical rhythmic oscillation of the delta, theta, alpha and sometimes beta can sometimes be seen in the clean raw EEG timesereies, for the rest of the bands a careful filtering and assessment of artefactual sources is needed, and this is especially true for the gamma band which overlaps with muscle sources (Muthukumaraswamy 2013). Furthermore, other factors may complicate interpretation of an oscillatory spectral power in averages since non-oscillatory waveforms can give rise to power in multiple bands, and furthermore, large amplitude trials may give high amplitude averages when on a trial bases the modulation is low (Jones 2016).

Independent component analysis is a highly valuable tool to remove artefacts from EEG data. The most common of which are eye blinks and muscle artifacts, which without proper removal make it impossible to analyze EEG data given they are much stronger (often an order of magnitude or more) than neurophysiological changes measured at the scalp. This has recently been summarized by a number of authors (Murthukumaraswamy 2013; Keren 2010) which conclude that without ICA, high frequencies above 20 Hz are typically too corrupted by muscle artefacts to be identified. This is also the case for an artifact called the saccadic spike potential, which similarly confounds most gamma bands in studies, and has a time course which follows event-related modulations often seen in visual tasks (Keren 2010). Overall, caution must be used when investigating high frequencies in the EEG, and when interpreting average amplitude or power from oscillatory signals.

The steady-state visual evoked potential (SSVEP)

The steady state visual evoked potential is generated by flickering stimuli at a constant frequency which then causes neurons responsive to one stimulus to fire in groups. The collective electrical activity of many neurons firing can then be measured with EEG recordings at the scalp of the head. One of the most appealing characteristics about the SSVEP signal is that it is robust to noise and artifacts and typically doesn't require much preprocessing to be accurately extracted from EEG data. Methods of extracting the SSVEP amplitude and phase information have evolved over the years, starting with basic band-pass filtering to recursive-least-square (RLS) Filtering (Brown and Norcia 1997). The RLS filter output give coefficients of the instantaneous amplitude and phase of a particular frequency timecourse. It recursively identifies coefficients from a sliding window which minimizes a cost function between an impulse response at the frequency of interest and the estimated response. It is a powerful tool in EEG research and gives one of the most reliable and precise estimates of the SSVEP that is attainable from the data.

Event-related metrics and Source Localization

The brain activity which produces the SSVEP or intrinsic oscillatory signals can then be related to behavior or a particular time locked event of interest. Brain activity can then be investigated across trials or averaged across a session to assess how it is related to the behavior.

In EEG studies, source localization can be conducted to systematically find the neurophysiological sources of the signal in the brain. It is important to note that source localization requires accurate phase information from signals and therefore cannot be done on the amplitude or power data alone. Finally, brain regions contributing to a behavioral event during a visual task are identified with algorithms such as LORETTA or minimum norm. Given the many sources in the brain and possible source combinations which can contribute to a particular scalp activity map, these algorithms find an arrangement of source contributions that mathematically optimizes a particular function of hypothesized relations between source and scalp. Each algorithm differs slightly in the assumptions of source activity and also in the potential contribution each source makes to the scalp activity map. In the end, the final output of source localization is brain activity map determined from the scalp EEG activity.

General Conclusion

This concludes the general methods section, what follows are more specific experiments and scientific questions related to the neural mechanisms of binocular rivalry. The specific methodology used and hypotheses for those experiments are outlined in detail in each of the chapters. Two main questions were addressed: where does binocular rivalry occur, and how does the brain mediate suppression during rivalry? I will then finish with general conclusions and future potential directions from these research studies.

CHAPTER 1: STIMULUS RIVALRY AND BINOCULAR RIVALRY SHARE A COMMON NEURAL SUBSTRATE

INTRODUCTION

In natural viewing, the human visual system fuses the two images from each eye into one representation of the outside world. However, when the images become sufficiently different, a perceptual process known as binocular rivalry may occur, in which one eye's visual information is suppressed while the other eye dominates perception. Reciprocal inhibition of monocular neurons in V1 is considered an important mechanism in the resolution of rivalry (Tong et al. 2006; Blake and Logothetis 2002). Although an important neural mechanism of binocular rivalry (Blake 1989), the reciprocal inhibition of eye specific channels alone does not explain the occurrence of rivalry generated by high-level differences in stimuli which bypass monocular competition (Leopold and Logothetis 1999; Wolf and Hochstein 2011). To account for these findings binocular rivalry is hypothesized to be a hybrid of both binocular pattern-level and monocular eye-level competition (Blake and Logothetis 2002).

However, whether suppression takes place between the eye-specific neurons or between the stimulus representations has yet to be clearly demonstrated (Blake and Logothetis 2002). One primary piece of evidence in favor of stimulus-level competition is a phenomenon known as 'stimulus rivalry,' so called since the stimulus representations are thought to be in competition. Stimulus rivalry occurs when incompatible dichoptic stimuli are swapped between the eyes at a rate of ~3 Hz, such that each eye over time

sees both of the competing stimuli, and the perceptual transitions remain as they do in binocular rivalry (Logothetis et al. 1996). This finding led to the initial suggestion that competition during binocular rivalry is actually between the binocular stimulus representations situated at later visual stages. Thus, it was hypothesized that inhibition could potentially occur between neurons representing incompatible stimulus features in extrastriate regions or beyond (Leopold and Logothetis 1999).

Electrophysiological studies investigating large-scale neural activity suggests that changes occur throughout the brain as a result of the binocular rivalry process, however, modulations can be found very early in the visual system. Local field potentials in low frequencies are correlated with perceptual modulation in early visual areas during binocular rivalry in monkeys (Gail et al. 2004). Furthermore, when stimuli are flickered in order to generate a steady-state visual evoked potential (SSVEP), the signatures of competition can be found in the occipital and medial temporal (MT) visual areas (Zhang et al 2011). Investigations of concurrent SSVEP and fMRI studies suggest involvement of other brain areas in parietal and cingulate regions alongside early visual areas (Roy et al 2017). Thus, early visual areas show competitive interactions, with coordinated activity occurring throughout the visual system as a consequence of resolving rivalry.

The high-level presumption of competition during stimulus rivalry has also recently become less clear. Psychophysical evidence shows a monocular contribution to stimulus rivalry (Brascamp et al 2013), and fMRI evidence suggests that brain networks of stimulus rivalry and binocular rivalry largely overlap, with stimulus rivalry showing the same but generally weaker brain network activation (Buckthought et al 2015). Thus,

although seemingly mediated by high-level processes, a difference in the locus of neural activation between stimulus rivalry and binocular rivalry has yet to be shown.

Do the signatures of competing neural representations differ when the competition is at the level of the stimulus representations compared to when it is between the monocular representations? We tested the hypothesis that stimulus rivalry would show a similar pattern of SSVEP responses as binocular rivalry but among pattern-level representations in higher level brain regions (Leopold and Logothetis 1999). Specifically, we used SSVEP frequency tagging to track the competing neural representations in binocular rivalry and stimulus rivalry. We used two different frequencies which stayed with the stimuli while subjects reported perceptual transitions, and quantified neural competition from the amplitude changes in each frequency tag. We found that competitive neural signatures are localized to occipital brain areas in both binocular rivalry and stimulus rivalry. Thus, contrary to our hypothesis, these results indicate that stimulus rivalry and binocular rivalry competition may be supported by overlapping neural mechanisms located in the occipital brain regions.

EXPERIMENTAL METHODS

-Experimental Paradigm

Subjects began each experiment with a training session composed of each of the three experimental conditions in order to familiarize themselves with the stimulus and reporting procedures. Subjects viewed the stimulus through a mirror stereoscope, and care was taken to ensure that subjects fused both stimuli before training and experimental

sessions began. Once subjects went through on average 2 sessions of practice in reporting the red, green, and mixed percepts (for binocular rivalry, stimulus rivalry and replay, respectively), they were asked if they were confident in reporting each perceptual state. If they were confident in their reports, the experiment began, if not, they went through 1 or 2 more practice sessions.

Subjects performed the experiment in a sound-proof chamber, with lights off, and they initiated continuation of each session with the press of any key, before which subjects could take breaks of variable durations according to their needs. There was a mandatory break halfway between the sessions. Each condition began with 1 run lasting 60 sec) of stimulus rivalry, binocular rivalry and replay. For replay, reported perceptual transitions during binocular rivalry were replayed back to the subjects unless the binocular rivalry run had less than 5 responses total, in which case a standard template of durations was used. Each condition had two types of stimulus dynamics, namely an SSVEP-on case where the stimuli were flickering at a specified frequency (F1=14.4 Hz, red grating; F2=12.0 Hz, green grating), and a non-flickering control condition where the gratings were not flickered. In binocular rivalry, the red and green gratings were shown separately to each eye for the duration of the session, while for stimulus rivalry, the stimuli were swapped at 3.15 Hz. In replay, the same stimulus was always shown to both eyes. Before and after each condition we collected 1 min. baseline where subjects passively fixated on a black box with the same background and fixation as in the experimental conditions. Each 60 second block of flicker on and flicker off was repeated 3 times for each condition in the order of stimulus rivalry, binocular rivalry, and replay.

Subjects sat upright facing a computer screen 55 cm from a chinrest on which they rested their head during the experiment. After we outfitted the proper cap size for subject, each electrode was filled with a conductive gel and to ensure impedance < 10 kOhms. Subjects responded on a computer keyboard and were instructed to report their perceptual state in binocular rivalry by pressing with their right index finger the 'j' key if they saw the red grating, and the 'f' key with their left index finger if they saw the green grating. Transitions between the red and green gratings were reported when less than 75% of the dominant stimulus became suppressed by pressing both the 'f' and 'j' keys together. Subjects were told to hold down the keys for the whole duration of the 3 potential perceptual states.

-Stimuli

Stimuli were orthogonal (+45° and +135°) red/green colored gratings of mean luminance $36.0\frac{cd}{m^2}$. We accounted for gamma correction by making photometer luminance measurements to ensure isoluminance between gratings. Stimulus flicker was 25% contrast modulated, in line with previous studies of stimulus rivalry (Logothetis et al 1996). The background included lines bisecting the screen to help with convergence, along with surround contours around each stimulus, and the fixation cross at the center. Background luminance was $5\frac{cd}{m^2}$. Stimulus flicker frequency was selected based on a pilot series of experiments on 5 subjects in which proportion of behavioral dominance was analyzed at different flicker frequencies ranging from 0-20 Hz. The green stimulus was frequency tagged at 12.0 Hz and the red stimulus was tagged at 14.4 Hz since the

proportion of dominance in binocular rivalry and stimulus rivalry were robust to flickering frequency combination.

-Data Acquisition

Data was collected on a Neuroscan SynAmps 2 setup and Amplifiers with a parallel port triggering system running between the acquisition computer and the amplifier to synchronize button press timing to the EEG data collection. Data was online filtered at 0.1-200 Hz and the sampling rate was 1000 Hz. We used a 64 Channel Neuroscan Quick-Cap EEG, of recommended sizes based on manufacturer specifications after measurement of horizontal head circumference. This cap conforms to the UI10/10 system of channel names and locations (Jurak et al 2007). Ground and reference were on the anterior and posterior central regions of electrodes. Reference was placed between Cz and CPz, and ground was placed between Fz and Fpz. EEG signal at each electrode was collected relative to the reference electrode during the experiment and during offline analysis each electrode's time series was rereferenced to a common average reference. Not all 68 channels were used, scalp electrodes (62 electrodes) were used in the analysis after removing EOG, EKG, VEO (vertical EOG), HEO (Horizontal EOG), M1 (Mastoid 1) and M2 (Mastoid 2). Finally, electrode locations were digitized with a Polhemus Fastrak digitizer relative to the nasion, right pre-auricular, and left pre-auricular anatomical locations for each subject.

-Participants

A total of 40 subjects participated in the behavioral experiment, and a total of 26 subjects of either sex participated in the EEG experiments. All experiments began after subjects signed and gave written consent of being informed of the experimental procedures in compliance with the UMN IRB regulations on human subjects.

-Data Preprocessing

Data were preprocessed with automated custom Matlab scripts. Each stage of the processing pipeline is described, in order, below.

1)*Early Preprocessing*, Subject specific bad channels, if any existed, were interpolated from surrounding 4 electrode timeseries. All data was then re-referenced to a common average reference and then underwent removal of the dc offset for each electrode.

2)*Temporal Filtering*, Resulting timeseries underwent general high/low-pass filtering between 4-30 Hz surrounding the frequency tags: F1=14.4 Hz and F2=12.0 Hz.

3)*SSVEP filtering*, Each SSVEP timecourse was extracted with an RLS-filter (Zhang et al 2011) at the SSVEP frequencies F1 and F2. The RLS-filter was set to an 834 millisecond moving window and frequencies for F1 and F2 were matched to the frequency tags. The resulting coefficients were used to calculate the amplitude and phase of the SSVEPs (Tang and Norcia 1995).

4)*Event-related metrics*, trials were created by taking the estimated ssVEP amplitude timecourse and selecting a window of 2 seconds prior to and 2 seconds after the button press, each separated based on the type of percept (i.e. red or green

grating). Trials were then averaged after removing the mean of each trial for each electrode.

-Response Distributions

We concatenated all dominance times by taking the response durations from all 3 completed sessions of a condition for a particular subject. We then thresholded the responses at a minimum of 20, below that number there was no reliable estimate of the distributions. If the subjects exceeded the threshold then we fit each subjects' distribution to a gamma function. For each subject the *a* and *b* parameter were calculated and then stored for statistical testing.

-SNR

Since harmonics of the swap frequency were close to the SSVEP frequency in stimulus rivalry we decided to use the power spectrum from sessions with the flicker-on divided by the power spectrum from sessions with the flicker-off. This gave us a ratio power spectrum that isolated the neural responses generated by the flickering frequencies, and thus avoided any swapping harmonics in stimulus rivalry.

-Statistics

All statistical t-tests were independent samples t-tests unless otherwise reported.

-Rivalry Index Bootstrapping

To get an idea of whether the computed rivalry indices were significant we used a bootsrapping procedure which utilized the non-flickering control conditions. For example, for each condition, we showed subjects either binocular rivalry, stimulus rivalry, or replay with flickering gratings, and then subsequently the same gratings and condition but without the flicker. We then analyzed the data in exactly the same way as in the flickering condition, and computed rivalry indices for each electrode, subject and condition. We combined both of the rivalry index distributions of the flicker and non-flicker conditions across subjects for each electrode and condition, and randomly sampled to generate a distribution of empirical t-values. We then thresholded at the 95% t-value after 1000 iterations and assessed whether the observed t-value was greater or less than this value. Significant values were greater than the 95% threshold and were colored in the t-value topographies.

-Source Localization

Source Localization was conducted in a manner similar to Zheng et al. 2011 with some slight differences. Phase alignment was used on the button press timing in order to ensure the retention of the SSVEP activity which oscillates at a fast rate and which would otherwise be smeared by differences in button press timing. So for each trial and for the occipital electrode, we searched in a window of 100 ms before and after the button press to find the peak (pi/2) of the oscillation and then shifted the button press time such that the peak corresponded to t=0 ms. We then took the mean of all of the aligned button presses for each of the two frequencies and then took the Hilbert transform of the final

average timecourse for each electrode. We then took the real and imaginary components of the Hilbert transformed timecourse and input them into a minimum norm source localization algorithm to estimate the cortical sources of activity (Hamalainene Ilmoniemi 1994). We specifically localized the time point of the peak of the amplitude of the dominantly perceived SSVEP in the window during perception of the corresponding grating (e.g. the green grating frequency tag at 12 Hz during perception of the green grating). A total of 15001 Sources were used, and extracted from the segmented surface of the standard Colin brain. Sources were then constrained to be perpendicular to the cortical surface. For all subjects a standard template of electrode locations were used. Finally, to get a metric of neural competition, this same time point of the peak amplitude in the perceived SSVEP was also localized for the suppressed stimulus' frequency tag and then subtracted from the original dominant frequency tag source map. The difference source maps were then taken for each subject and normalized via zscore and then the mean values across subjects were plotted on the source map. Identified peaks of the sources corresponded to standard atlas labels of occipital pole (left and right) and middle temporal gyri (left and right) which is in line with previous work on dipole source localization during binocular rivalry and cortical generators of SSVEPs (Zhang et al 2011; Di Russo et al 2007).

RESULTS

RIVALRY STIMULI AND DIFFERENCES IN STIMULUS RIVALRY AND BINOCULAR RIVALRY RESPONSE DISTRIBUTIONS

Our primary aim was to identify whether stimulus rivalry would transpire at higher levels in visual processing and we first investigated perceptual dominance time distributions generated by the subjects' responses to the stimuli. We projected the same flickering red/green isoluminant, orthogonal, gratings to each eye, only changing the presentation: separately to each eye (binocular rivalry), swapping between each eye (stimulus rivalry), or congruently one grating to both eyes (replay) (Figure 4 A). We used red/green colors to enhance the SSVEP power by presumably engaging more neurons sensitive to color in the parvocellular pathway activated by flicker (Vialatte et al 2010), and consequently, the signal-to-noise ratio (SNR) of the frequency tag (Figure 4 B). In addition, previous work indicated that stimuli differing along more than one visual dimension (e.g. frequency or contrast) can potentially enhance the occurrence of stimulus rivalry as opposed to the fast swapping percept of the two stimuli (Denison and Silver 2012; Silver and Logothetis 2007). Furthermore, it is believed that flickering might mask the transients associated with the swap, and helps promote stimulus rivalry in general (Lee and Blake 1999). Thus, we tagged, in all conditions, a particular grating (red grating =f1=14.4 hz; green grating = f2=12.0 hz) with a particular frequency which stayed with that grating for the duration of the session.

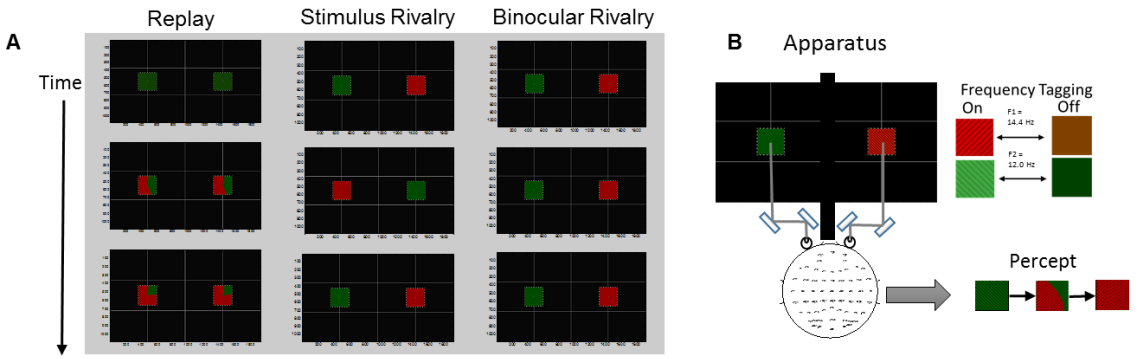

Figure 4. Rivalry Stimuli, Conditions, and Apparatus
(A) Timecourse of stimulus presentation for each conditions. In replay the same stimulus is shown to both eyes and a transition is simulated as a wedge sweeping across the box, or a fading of one color (not shown). In stimulus rivalry, the two stimuli are swapped between the eyes at an interval of 3.1 Hz. In binocular rivalry the stimuli stay constant in each eye. Each session lasted 60 seconds with frequency tag on and frequency tag off, with 3 repetitions of each condition with frequency tag on and off.
(B) Rivalry Stimuli used in the experiment and the apparatus used to generate binocular rivalry. The subjects viewed stimuli through a stereoscope and responded by saying they saw the green grating, red grating, or a piecemeal mixture of the two. Frequency tagging was done with a luminance modulation between high/low (on) and mean luminance (off) states.

Previous studies using orthogonal black and white gratings flickering at 18 Hz showed that binocular rivalry and stimulus rivalry had very similar normalized dominance time distributions which could be estimated by a gamma density function (Logothetis et al 1996). We fit gamma distributions to each subjects' reported dominance time histograms thresholding at a minimum of 20 responses per fit (i.e. for a given subject, 3 sessions of 60 seconds of rivalry needed a minimum of 20 total responses, see methods). A students t-test showed that for the *a* parameter of the gamma function there was a trend for a difference but it was not significant at the 95% confidence level between stimulus and binocular rivalry (red: p=0.062, tstat=-1.898, df=72, n=37; green: p=0.558, tstat=-0.589, df=80, n=41). The *b* parameter, however, showed a significant difference (red: p=3.54e-5, tstat=4.4, df=72, n=37; green: p=0.0058, tstat=2.84, n=41). The gamma distribution from the average *a* and *b* parameters across all subjects is shown in Figure 5 A and B for the red and green percepts, respectively. Thus, our data suggest that subjective perceptual reporting for both binocular rivalry and stimulus rivalry have

significantly different distribution for the scale parameter of the gamma function but not the shape parameter, which each define the curve of the gamma function. Overall, this means subjects responses are faster during stimulus rivalry than during binocular rivalry and highlights differences in neural processing between the two conditions.

Finally, to ensure our frequency tag selection does not change the proportion of dominance distributions, we chose a series of frequency tag combinations between the two stimuli and measured the proportion of dominance time in either binocular rivalry or stimulus rivalry. This is a behavioral measure of the overall clarity of rivalry, with longer proportions of mixed percepts indicative of less clear rivalry and longer proportions red/green proportions indicative of stable rivalry. As can be seen in Figure 5C, the proportion of stable percepts in binocular rivalry varied minimally as a function of frequency tag combination and the same was observed for stimulus rivalry (n=5 subjects). Thus, we chose frequencies F1=14.4 Hz and F2=12.0 Hz to tag each of the stimuli in the subsequent EEG experiments since they minimized subjective flicker and gave reasonably high proportions of stable percepts in both types of rivalry.

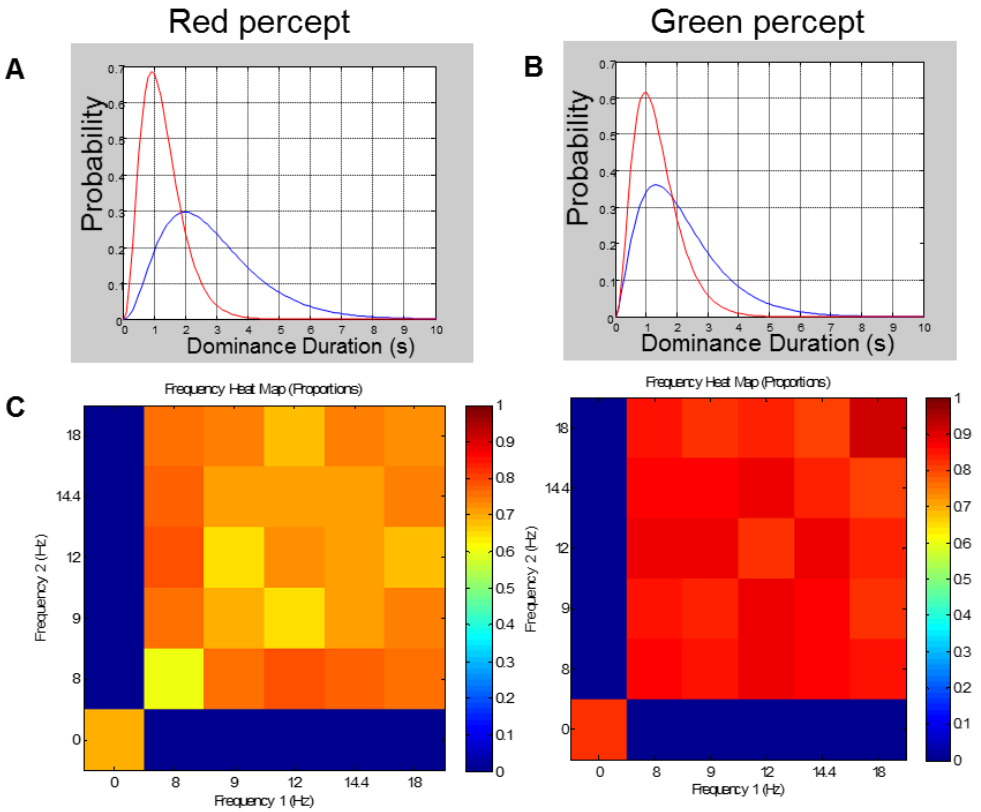

Figure 5. Differences in Stimulus Rivalry and Binocular Rivalry Dominance Distributions and Frequency Heat Map

(A) Dominance duration histograms for the reported perception of the red grating (red-stimulus rivalry, blue-binocular rivalry).

(B) Dominance duration histograms for the reported perception of the green grating (line color same as B).

(C) Proportion of the trial with either a red or green grating dominant in perception, as opposed to a mixed percept. Each box represents a particular combination of the flickering frequency for stimulus 1 (Frequency 1) and stimulus 2 (Frequency 2). Left panel shows the proportion of the trial for stimulus rivalry and right panel shows the proportion for binocular rivalry.

POWER OF SSVEP DIFFERS IN STRENGTH BETWEEN THE TAG FREQUENCIES

We began the investigation of the electrophysiological differences between the types of competition by looking at the power spectra calculated over a given session. This would tell us any prolonged changes in neural response to the flicker that were present during a session of binocular rivalry, stimulus rivalry, or replay. We calculated

the power spectra when the stimuli were flickering and divided each corresponding frequencies power by the power spectra of calculated during sessions without the flicker, giving a ratio power spectrum. This spectrum isolated electrophysiological changes elicited specifically by the flickering stimuli for each condition, and removed any intrinsic oscillations or swap harmonics (particularly for stimulus rivalry).

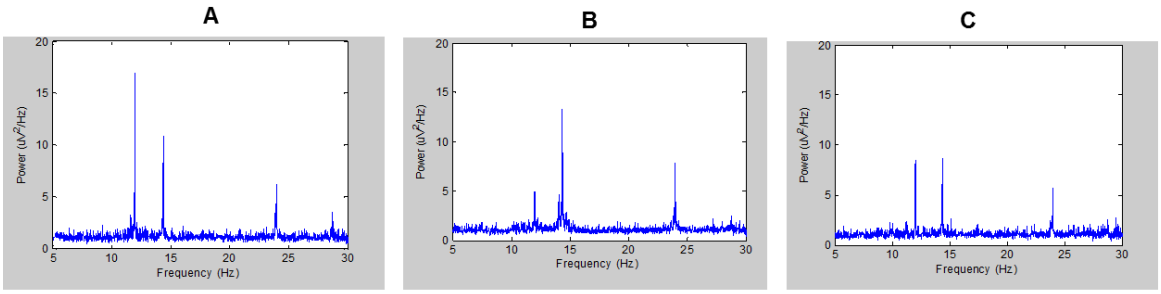

Figure 6. Power Spectra of SSVEPs Differs In Strength Between the Tag Frequencies For Binocular Rivalry and Stimulus Rivalry

(A) The average SSVEP power spectra calculated across n=26 subjects. Spectra with flicker-on were divided by the power observed in a control non-flickering condition. Average of 3 sessions of binocular rivalry each lasting 60 seconds.
(B) Same as A except for replay.
(C) Same as C except for stimulus rivalry.

For all completed binocular rivalry sessions grand averaged across subjects (n=26) the power spectrum for an occipital electrode (Oz) was analyzed since previous studies have suggested reliable SSVEP power at this or nearby electrodes (Zhang et al 2011). The power spectrum revealed the presence of both SSVEP frequencies F1=14.4 Hz and F2=12.0 Hz, and the first harmonic, however the 12.0 Hz SSVEP frequency was higher on average than the 14.4 Hz SSVEP (Figure 6A). For Replay, SSVEP power at both frequencies were also present in the spectrum (Figure 6B), although the 12.0 Hz frequency was now smaller in magnitude compared to binocular rivalry, while the 14.4 Hz frequency stayed unchanged. To evaluate whether this difference was significant, we searched each subjects' time series for the electrode with the maximum Peak and SNR

values for the frequency tag frequencies in the power spectrum. This accounted for any variability across subjects' cap positioning, or underlying anatomical differences, that could change the topography of the SSVEP power spectrum. Comparing the maximum SNR values for replay and binocular rivalry showed that the red stimulus frequency tag at 14.4 Hz was not significantly different in replay and binocular rivalry ($p=0.1264$ $tstat=1.5581$, $df=44$), however, the green stimulus frequency tag at 12.0 Hz showed a larger power during binocular rivalry ($p=0.0041$, $tstat=3.0254$, $df=44$). This suggests that the 12.0 Hz frequency tag was selectively enhanced in the presence of interocular competition as opposed to binocular integration (see discussion).

Finally, we compared the power spectra of binocular rivalry and stimulus rivalry at the same electrode across subjects to assess whether the neural response would change depending on the type of visual competition. We hypothesized a reduction in SNR in stimulus rivalry if the pattern-level competition is more engaged. As can be seen in Figure 6C the magnitude of the power spectrum was larger for binocular rivalry for the 12.0 Hz frequency tag but not the 14.4 Hz frequency tag (Red: $p=0.3183$, $tstat=1.0095$, $df=44$; Green: $p=0.0034$, $tstat=3.099$, $df=44$). Additionally, we noticed the stimulus power was better matched for both frequencies in stimulus rivalry, indicating that swapping between the eyes accounts for any eye-specific preferences of each frequency/stimulus pair. Thus, binocular rivalry showed an enhancement of the 12.0 Hz frequency tag when compared to stimulus rivalry in addition to the same enhancement seen when compared with the replay condition. Overall, this may be due to eye dominance since the stimuli stay presented to one eye for the duration of the binocular

rivalry session. Nevertheless, the power spectra confirm the presence of SSVEP signals generated by the flicker in all conditions.

SPATIAL TOPOGRAPHY OF THE POWER SPECTRA GENERATED FLICKER LOCALIZE TO OCCIPITAL REGIONS IN SENSOR SPACE

To assess how the spatial distribution of the SSVEP power changes across conditions, we then looked at scalp maps of the power at the flicker frequencies. This could tell us if there were regional differences in sensitivity at the level of the scalp to the frequency tag and also if there were regional changes of activation across conditions. As can be seen in Figure 7, the topographical distribution of SSVEP SNR at the frequency tag frequencies, (power spectra peaks divided by the surrounding noise frequencies ±0.5-1 Hz) calculated on the ratio spectrum (as in Figure 6, taking the ratio of flicker and no-flicker conditions), showed an occipital source for all conditions. Furthermore, this source overlapped for both frequency tags in all conditions in the occipital pole, suggesting both frequency tags were processed in the same area. Thus, flickering stimuli generated a reliable signal at the tagged frequencies in all conditions which localized to a similarly located occipital patch across the scalp, highlighting that stimulus rivalry and binocular rivalry at early visual stages might share common stimulus related neural processing to the flickering stimuli.

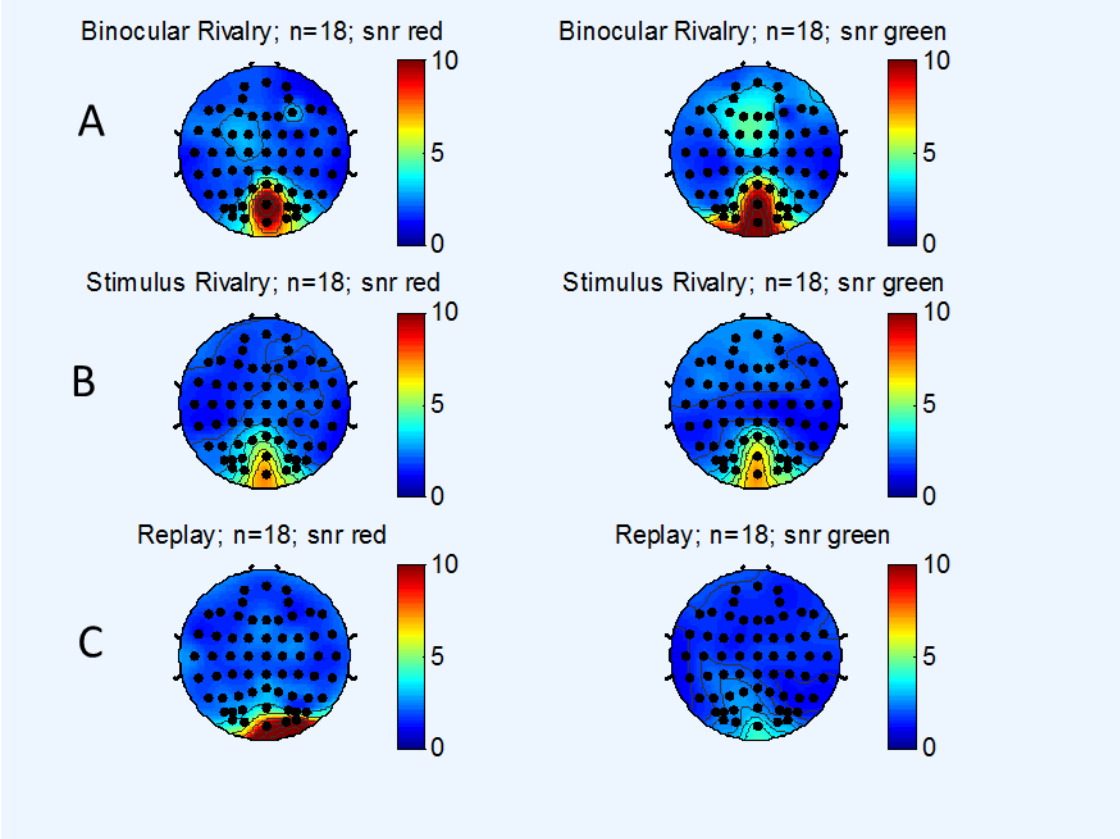

Figure 7. Spatial Topography of the Power Spectra Generated by Flicker Localize to Occipital Regions in Sensor Space
(A) Signal to noise ratio topography of each condition (rows) and each stimulus' frequency tag (columns) for n=26 subjects. Signal to noise ratio was computed on the ratio power spectrum (see text) as the peak divided by the surrounding 1 Hz frequency bins.
(B) Same as (A) except for stimulus rivalry sessions.
(C) Same as (A) except for replay sessions.

RIVALRY INDEX TOPOGRAPHIES SHOW SIGNIFICANT MODULATION IN OCCIPITAL CORTEX

The power spectrum indicated that across the duration of a session, there is little difference in the topographies of binocular rivalry and stimulus rivalry. We then hypothesized that if the competition was between the patterns in stimulus rivalry, then signatures of high-level neural competition might instead be identified at local time-

points during a session. We therefore extracted the time course of modulations of the SSVEP amplitude for the two frequency tags during both stimulus rivalry and binocular rivalry. Previous studies have shown that during binocular rivalry the frequency tag amplitudes show a counterphase relationship with each other, meaning that during the perception of the red grating the SSVEP amplitude is high for the red frequency tag and low for the green grating's frequency tag, and the trend is reversed when the green grating is perceived (Zhang et al 2011). This counterphase behavior is primarily localized around occipital areas for binocular rivalry and replay, and is assumed to be a signature of the competitive neural interactions (Zhang et al 2011).

We tested the hypothesis that stimulus rivalry would show a similar counterphase relationship between the SSVEP signals but among pattern-level representations in higher level brain regions (Leopold and Logothetis 1999). We quantified the counterphase behavior by computing a rivalry index which takes the sum of the absolute differences between the amplitudes of both SSVEP frequencies over the timewindow around a button press (Figure 8A). We assessed statistical significance by computing a rivalry index independently for each electrode and then used permutation statistics to evaluate empirical distributions from the null hypothesis observed during the non-flickering conditions.

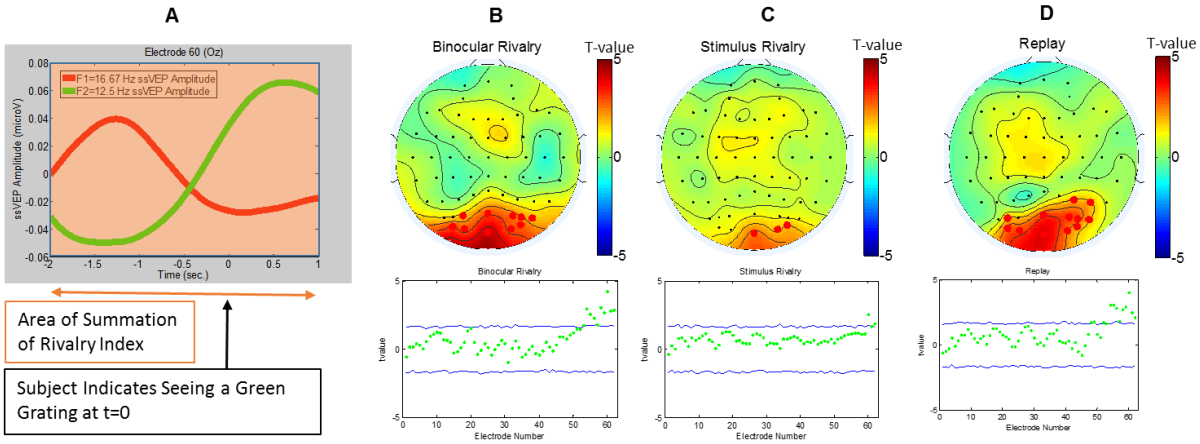

Figure 8. Rivalry Index Topographies Show Significant Modulation in Occipital Cortex
(A) Visual of the rivalry index computation where we sum the absolute difference between the amplitude of two SSVEP signals, effectively measuring the area of counterphase modulation. Windows of 2 seconds before and after were used around each button press for a stabilized percept.
(B) For binocular rivalry, the rivalry index for each electrode in ssVEP and non-flickering control conditions were combined and a 99% confidence interval was computed based on random sampling a subset of rivalry indices from the new distribution. The red dots are significant rivalry indices computed for a particular electrode. Bottom panel shows the t-values in one dimension with electrodes spaced equally on the x axis. Blue lines correspond to the 95% confidence interval of the bootstrap.
(C) Same as in (B) except for stimulus rivalry.
(D) Same as in (B and C) except for replay.

We plotted the observed t-values across the topography of the scalp for each electrode and highlighted the significant ($p<0.05$) p-values with a red dot (Figure 8B-C). We found that the rivalry indices were significant only in an occipital region of the scalp topography ($p<0.05$) in all conditions. Thus, contrary to our hypothesis, these results suggest that both binocular rivalry and stimulus rivalry share dynamic SSVEP-based competitive neural interactions in the early occipital areas at local time-points based on the perceptual state.

TIMECOURSE OF SIGNIFICANTLY MODULATED REGIONS SHOW EQUIVALENT DEPTH OF MODULATION

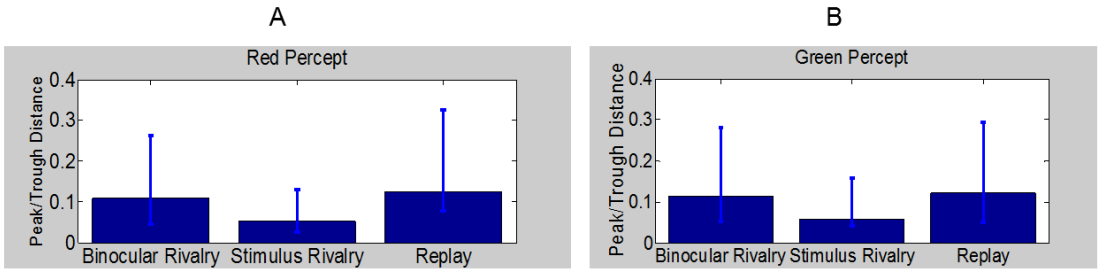

Figure 9. Timecourse of Significantly Modulated Regions Show Similar Depth of Modulation for Binocular Rivalry and Stimulus Rivalry

(A) Peak to trough distance was calculated by finding the maximum and minimum values of the average amplitude of the ssVEP over a subset of occipital electrodes. Electrodes were chosen as the occipital electrodes significantly modulated, as found in the previous section, in terms of rivalry indices.

(B) Same as in A, except for the green grating percept.

We then checked whether the competitive neural interactions are modulated to the same extent for the two different types of rivalry which would give us a measure of the strength of suppression in the occipital area. The depth of counterphase modulation was measured by the peak-to-trough distance of the counterphase SSVEP signals averaged across all occipital electrodes. We measured the peak to trough distance for the two signals' SSVEP amplitude for either the red percept or the green percept within the 2 second peri-time window around the button press. We found that in the occipital electrode the depth of modulation was not significantly different in stimulus rivalry than in binocular rivalry or replay, as seen with the corresponding 95% confidence intervals calculated across subjects (Figure 9). Overall, this result suggests that the early visual areas show similar levels of neural suppression in binocular rivalry and stimulus rivalry, indicating the mechanism of competition engages occipital areas to the same degree for both forms of rivalry.

SOURCE LOCALIZATION ON ALIGNED PEAKS OF RIVALRY TIMECOURSE

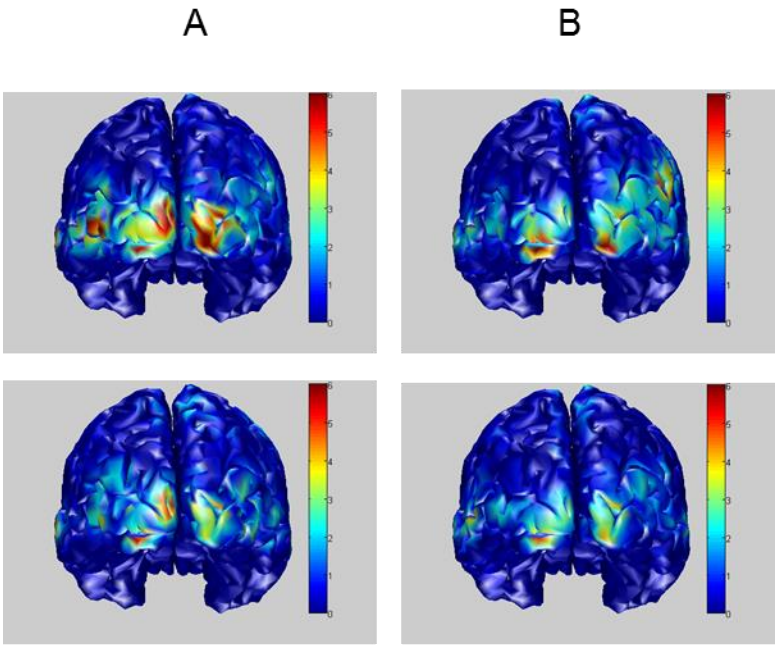

Figure 10. Source Localization on Aligned Peaks of Rivalry Amplitude Timecourse

(A) The difference in the two competing SSVEPs were localized on a standard brain for the green grating percept (Top) and red grating percept (bottom) during binocular rivalry. Subjects (n=5) with clear counterphase amplitude modulation during either stimulus rivalry or binocular rivalry were selected for source localization. SSVEP signals were phase aligned and then localized to a standard brain with standard electrode positions common for all subjects.

(B) Same source localization procedure but for stimulus rivalry.

To get a more precise spatial measure of the sources accounting for the modulations in SSVEP amplitude and account for any effects of volume conduction on the scalp potentials, the competing SSVEP signals in each condition were localized in the source space. We identified 5 subjects with clear counterphase modulation of the SSVEP amplitudes during binocular rivalry and stimulus rivalry and localized the SSVEPs at the time point of the peak of the counterphase modulation (see methods). This corresponds to time point of maximum in ocular suppression and could identify any underlying

differences in suppressive mechanism between stimulus rivalry and binocular rivalry. To take into account the neural competition, we also took the difference in the two SSVEP frequency tag source topographies. Taking the difference in the SSVEP maps generated by Freq(percieved)-Freq(unperceived), it can be seen that the average topography was not different for stimulus rivalry and binocular rivalry (Figure 10). The anatomical label for the peak activations of both conditions corresponded to the right occipital pole and left occipital pole, and an additional source in MT (middle temporal cortex). Thus, source analysis corresponded with the power spectra topographies and the rivalry index topographies, and suggests further that neural competition during stimulus rivalry and binocular rivalry might share a similar substrate in the early occipital cortex.

DISCUSSION

We used EEG frequency tagging to give us SSVEP signals which tracked the timecourse of neural competition between stimuli in binocular rivalry and stimulus rivalry. We evaluated a model of rivalry which posits that competition for stimulus rivalry occurs at the level of stimulus representations in extrastriate regions (e.g. V4 or IT) and found that the SSVEPs instead colocalized in occipital cortex. This was observed for the spectral power which is sensitive to prolonged changes in neural response, the rivalry index which quantifies local processes in time relative to behavior, and source analysis which was performed at the peak in neural competition. Overall these results suggest an early mechanism for stimulus rivalry that is centered in occipital cortex, and supports eye-based models of rivalry, similar to previous findings (Brascamp et al 2013; Buckthought

et al 2015).

DIFFERENCES IN DOMINANCE DISTRIBUTIONS OF BINOCULAR RIVALRY AND STIMULUS RIVALRY

In this study we found a difference in behavioral dominance distributions between binocular rivalry and stimulus rivalry (Figure 5B and C). Previous reports have suggested that binocular rivalry and stimulus rivalry have the same distributions that both conform to a gamma function (Logothetis et al 1996), however, it is worth noting that those distributions were normalized and thus unclear whether they differed in duration. In our study, comparing a large number of subjects (n=40) we found that differences were indeed significant for the shape parameter of the gamma function without normalization of the distribution. Another study looking at individual differences for binocular rivalry and stimulus rivalry found similar distributions between the two conditions but stimulus rivalry dominance durations were typically shorter than binocular rivalry (Patel et al 2015). Overall, our results are consistent with previous results, and suggest that in stimulus rivalry the dominance times seem to be shorter than for binocular rivalry.

INCREASE OF 12 HZ FREQUENCY TAG IN BINOCULAR RIVALRY POWER SPETRUM

We observed a significant increase in the 12 Hz frequency tag in the power spectrum for binocular rivalry compared to stimulus rivalry and replay. One potential reason is that

the 12.0 Hz frequency tag was presented for a shorter duration in the replay condition since one frequency is present at a given moment in that condition. If it was an effect of overall presentation duration, we would expect to see the 14.4 Hz frequency tag reduced as well, which was not the case. Another reason could be that the red stimulus proved to be more salient in replay, than when it was engaged with a competing stimulus in binocular rivalry. However, the behavioral dominance distributions for perception of red and green are similar for binocular rivalry (Fig.5 A and B), and the physical characteristics of the stimuli are matched between conditions (see methods), so it is unlikely to be an inherent stimulus saliency difference that could explain the findings. Another explanation may be that eye dominance enhanced the 12.0 Hz frequency tag since the green grating (flickering at 12.0 Hz) was always presented to the left eye during binocular rivalry. This is in line with the power spectrum data from stimulus rivalry which showed that when the two stimuli are swapped between the eyes the 12 Hz power enhancement goes away and the power at both tagged frequencies is equal. Our speculation is that in the replay condition, since it always followed the binocular rivalry condition, the left eye neurons adapted to the 12.0 Hz flicker and therefore gave a weaker response than the 14.4 Hz neurons which did not adapt in the left eye. Thus, when the 14.4 Hz frequency tag was presented in the left eye in replay, it could generate a larger response than the 12.0 Hz frequency tag since the neurons hadn't adapted as much in the dominant eye.

OVERLAP OF THE POWER SPECTRUM OF BINOCULAR RIVALRY AND

We used a ratio power spectrum to reliably estimate the power of the SSVEP SNR by dividing the power calculated from sessions with flickering stimuli by the power calculated from sessions with the stimuli not flickering. This reduced any intrinsic oscillatory activity from rivalry or other task related oscillations and enhanced the SSVEP power at the tagged frequencies. From the power topographies it was apparent that most of the SSVEP activity generated by the flicker was centralized around occipital areas and it was localized to the same areas for binocular rivalry and stimulus rivalry. Previous studies also showed that SSVEPs are localized in occipital areas for rivalry stimuli (Zhang et al 2011), but our results suggest that swapping the stimuli between the eyes at a rapid rate (3 Hz) activates the SSVEPs in the occipital cortex in a similar manner as when they are not swapped. Thus, there are two interpretations, the first is that the monocular channels can switch their inhibitory activity at 333 ms to activate downstream neurons which then hold one of the stimuli in perception. This would suggest that the SSVEP is being driven by lower layers in the occipital pole. A second interpretation could be that monocular channels are unable to switch their inhibition at 333 ms, and thus binocular neurons integrate information across both eyes. It is unclear which one of the two mechanisms is better suited to explain our findings, given both monocular and binocular neurons overlap in early visual cortex.

RIVALRY INDEX COLOCALIZES TO THE OCCIPITAL CORTEX FOR BOTH STIMULUS RIVALRY AND BINOCULAR RIVALRY

Finally, our metric of neural competition, the rivalry index, was based on the counterphase activity of the SSVEP amplitude of the two competing frequency tags during rivalry. We found an occipital colocalizaiton of the rivalry index calculated across the scalp in all conditions. Source localization on the SSVEPs at the peak of the counterphase modulation showed that sources generating the SSVEPs originated in the occipital pole and in MT. The finding of SSVEP modulation in the occipital pole and MT is similar to previous studies of binocular rivalry in EEG (Zhang et al 2011), MEG (Srinivasan et al 1999), and also consistent with previously identified cortical generators of SSVEPs (Di Russo et al 2007).

Given that the eye swapping in stimulus rivalry is thought to bypass eye specific channels it was expected that the rivalry index for stimulus rivalry would not be high in early visual areas (Logothetis et al 1996; Tong et al 2006). Contrary to this hypothesis, however, we found that the rivalry index and source localization results showed competitive signatures in the occipital pole, a cortical region where monocular and binocular channels reside. This suggests that we cannot rule out that part of the mechanism of stimulus rivalry might incorporate monocular channels. Previous fMRI studies suggest largely overlapping cortical networks when comparing binocular rivalry and stimulus rivalry (Buckthought et al 2015), and behavioral studies of stimulus rivalry suggest that it still incorporates monocular interactions (Blake 2015). Our results are consistent with those findings, and further illustrate an electrophysiological substrate for neural competition in stimulus rivalry is not completely inconsistent with a monocular based explanation.

Although previous results at lower frequencies around 6 and 7 Hz showed similar localization in occipital areas (Zhang et al 2011), the choice of frequency tag can potentially influence the localization given that temporal tuning of visual neurons changes along the visual hierarchy (Gauthier et al 2012). In particular, it may be that higher areas show a modulation with stimulus rivalry but fail to be captured by the 12.0 and 14.4 Hz frequency tags. Hence, future studies should address whether temporal frequency tags at lower frequencies show a similar localization to early visual areas in stimulus rivalry.

We should note that we cannot rule out the effects of attention on influencing part of the rivalry index modulations seen in either stimulus rivalry or binocular rivalry. Previous reports indicate that in the absence of attention the rivalry index drops dramatically for binocular rivalry (Zhang et al 2011), so it is possible that attention may also impact the counterphase modulation for stimulus rivalry. Further studies should address if attention is necessary, or how important it is in generating counterphase modulations of the SSVEP signals during rivalry.

Overall, these results suggest that binocular rivalry and stimulus rivalry show similar neural signatures in the topography of the frequency tag power spectrum, time course of SSVEP amplitude modulations, and source localization topographies. This suggests that part of the mechanism of stimulus rivalry might incorporate early visual cortical mechanisms to resolve the visual conflict which may be similar to the mechanisms involved in binocular rivalry.

CHAPTER 2: CHANGES OF ALPHA OSCILLATIONS DURING BINOCULAR RIVALRY REFLECT NEURAL COMPETITION

INTRODUCTION

During binocular rivalry, visual perception alternates spontaneously between two stable interpretations of a constant sensory stimulus. The neural basis that underlies this competitive interaction includes a large network of brain areas from primary visual areas to prefrontal cortical areas (Panagiotaropoulos et al 2014). The full mechanism of rivalry, however, is still debated, and it is unclear how activity of multiple brain areas are coordinated together for the selection of stimulus specific information (Blake 2001). Along those lines, a striking feature of binocular rivalry is that one eyes whole input is perceptually suppressed during rivalry and major question is how does the brain organize such a large-scale suppression of one eye's information during binocular rivalry?

One proposed mechanism of global stimulus selection is through the thalamocortical system, which connects multiple visual areas to the thalamus and is composed of feedforward and feedback connections (Blake 1989; Jones 2002). Thalamocortical projections from LGN contain information from one eye, and interact with inhibitory interneurons within the LGN and the reticular nucleus of the thalamus, containing some of the major circuitry important in generating large-scale binocular rivalry suppression (Wunderlich et al 2005). Thalamocortical interactions are therefore hypothesized to be involved in the neural competition that gives rise to rivalry (Lehky and Blake 1991). Feedback from V1 to thalamus, where eye-specificity is retained, might also be the source of the large-scale suppression of one eye when ocular

convergence is unattained, and global inhibition is perhaps mediated by the thalamic reticular nucleus (Lehky and Blake 1991). Additionally, in humans, fMRI experiments have demonstrated that the thalamus shows perceptually related suppression and dominance modulation (Haynes et al 2005), and is thus a contributor in establishing rivalry phases.

One mechanism by which to investigate thalamocortical interactions is through the amplitude changes in oscillatory bands of the electroencephalogram (EEG). It has been shown recently that oscillations in the alpha band are thought to, in large part, originate in the thalamus, although corticocortical alpha generation is also possible (Hughes and Crunelli 2005). In line with the thalamus' role as a gatekeeper in relaying sensory information to the cortex, sensory transmission is attenuated in the presence of alpha oscillations called the down state as opposed to when it is in the up state (Palva and Palva 2011). Thus, the state of the thalamus can dramatically impact neural coding, and is indexed, in part, by the level of alpha oscillation amplitude, and the alpha oscillation may play a role during processing of dominant or suppressed stimuli in rivalry.

As of yet, few investigations of human EEG activity during rivalry have focused on the oscillatory changes of intrinsic oscillatory bands and it is thus unclear how oscillations are involved in the binocular rivalry process. Given that spontaneous alpha oscillations generated by the thalamus may serve as a suppressive mechanism of ocular channels during rivalry, here we tested the prediction that they would be involved during ocular suppression phases of rivalry transitions. Specifically we investigated alpha oscillations during binocular integration processes and compared them to ocular

integration processes involved in a simulated replay of binocular rivalry. We found that changes in the alpha band are related to interocular competition in rivalry where there are significant modifications in activity of thalamocortical ocular channels of visual cortex, whereas they failed to track replayed transitions without ocular conflict. The results suggest that alpha oscillations spontaneously arise during alternating perceptual interpretations and reflect neural competition during binocular rivalry.

METHODS

-Experimental Paradigm

Subjects began each experiment with a training session composed of each of the three experimental conditions (one of which was unused in this study) in order to familiarize themselves with the stimulus and reporting procedures. Subjects viewed the stimulus through a mirror stereoscope, and care was taken to ensure that subjects fused both stimuli before training and experimental sessions began. Once subjects went through on average 2 sessions of practice in reporting the red, green, and mixed percepts (for binocular rivalry and replay, respectively), they were asked if they were confident in reporting each perceptual state. If they were confident in their reports, the experiment began, if not, they went through 1 or 2 more practice sessions.

Subjects performed the experiment in a sound-proof chamber, with lights off, and they initiated continuation of each session with the press of any key, before which subjects could take breaks of variable durations according to their needs. There was a mandatory break halfway between the sessions. Each condition had two types of

stimulus dynamics, 1) stimuli were flickering at a specified frequency and 2) a non-flickering condition where the gratings were not flickered. Only the non-flickering sessions were used in this study. Each condition began with 1 run (lasting 60 sec) of binocular rivalry or replay. Each 60 second block of flicker on and flicker off was repeated 3 times for each condition in the order of stimulus rivalry, binocular rivalry, and replay. For replay, reported perceptual transitions during binocular rivalry were replayed back to the subjects unless the binocular rivalry run had less than 5 responses total, in which case a standard template of durations was used. In binocular rivalry, the red and green gratings were shown separately to each eye for the duration of the session, while in replay the same stimulus was always shown to both eyes including the transition. Before and after each condition we collected 1 min. baseline where subjects passively fixated on a black box with the same background and fixation as in the experimental conditions.

Subjects sat upright facing a computer screen 55 cm from a chinrest on which they rested their head during the experiment. After we outfitted the proper cap size for each subject, electrodes were filled with a conductive gel to ensure impedance was < 10 kOhms. Subjects responded on a computer keyboard and were instructed to report their perceptual state in binocular rivalry by pressing with their right index finger the ‘j’ key if they saw the red grating, and the ‘f’ key with their left index finger if they saw the green grating. Transitions between the red and green gratings were reported when less than 75% of the dominant stimulus became suppressed by pressing both the ‘f’ and ‘j’ keys together. Subjects were told to hold down the keys for the whole duration of the 3 potential perceptual states.

-Stimuli

Stimuli were orthogonal (+45° and +135°) red/green colored gratings of mean luminance 36.0 cd/m^2. We accounted for gamma correction by making photometer luminance measurements to ensure isoluminance between gratings. Stimulus were 25% contrast between the light and dark bars. The background included lines bisecting the screen to help with convergence, along with surround contours around each stimulus, and the fixation cross at the center. Background luminance was 5 cd/m^2.

-Data Acquisition

Data was collected on a Neuroscan SynAmps 2 setup and Amplifiers with a parallel port triggering system running between the acquisition computer and the amplifier to synchronize button press timing to the EEG data collection. Data was online filtered at 0.1-200 Hz and the sampling rate was 1000 Hz. We used a 64 Channel Neuroscan Quick-Cap EEG, of recommended sizes based on manufacturer specifications after measurement of horizontal head circumference. This cap conforms to the UI10/10 system of channel names and locations (Jurak et al 2007). Ground and reference were on the anterior and posterior central regions of electrodes. Reference was placed between Cz and CPz, and ground was placed between Fz and Fpz. EEG signal at each electrode was collected relative to the reference electrode during the experiment and during offline analysis each electrode's time series was rereferenced to a common average reference. Not all 68 channels were used, scalp electrodes (62 electrodes) were used in the analysis

after removing EOG, EKG, VEO (vertical EOG), HEO (Horizontal EOG), M1 (Mastoid 1) and M2 (Mastoid 2). Finally, electrode locations were digitized with a Polhemus Fastrak digitizer relative to the nasion, right pre-auricular, and left pre-auricular anatomical locations for each subject.

-Participants

A total of 31 subjects of either sex participated the EEG experiments. All experiments began after subjects signed and gave written consent of being informed of the experimental procedures in compliance with the UMN IRB regulations on human subjects.

-Response Distributions

We concatenated all dominance times by taking the response durations from all 3 completed sessions of a condition for a particular subject. We then thresholded the responses at a minimum of 20, below that number there was no reliable estimate of the distributions. If the subjects exceeded the threshold then we fit each subjects' distribution to a gamma function. For each subject the *a* and *b* parameter were calculated for each percept type and then stored for statistical testing.

-Alpha Algorithm

Six subjects were removed due to poor algorithm performance (i.e. small number of alpha components), small alpha power, or large artifacts that confounded the timeseires.

The remaining 25 subjects were analyzed in the same way with an automated algorithm. Data was preprocessed with custom Matlab scripts in the following order:

5) Data from 3 60 second sessions of rivalry or replay were concatenated after rereferencing to the common average and removal of baseline offset giving an overall timeseries of 62x180,003. A baseline time series of the same duration but with a blank box and no subject responses was then concatenated to both the rivalry and replay time series giving a resulting time series of 62x360,006.

6) *Selection of ssVEP Components*. We then ran ICA on the concatenated timeseries where each IC was independently converted power spectrum. The mean signal power in the theta (<6 Hz) alpha (6-15 Hz) and high-frequency (15-200) bands were calculated and components the highest mean signal power in the alpha band were selected automatically. To account for 1/f spectral distortion we multiplied the power values by the frequency prior to taking the mean value in the band.

7) *Alpha filtering*. The top components with spectral components in the ssVEP were backprojected into each electrode and then filtered for each ssVEP in the alpha band (±5Hz) around 10 Hz.

8) *Alpha amplitude estimation.* We then estimated the alpha amplitude taking the Hilbert transform of the backprojected components. Absolute values of the alpha amplitude were then converted to an event-related time series of 2 seconds before and after each behavioral button press indicated in rivalry or replay.

9) *Averaging.* Event-related time series were then averaged after the mean was removed from each electrode and trial. All trials were averaged across subjects

for group maps.

-Statistics

For determination of statistical significance of each event-related alpha amplitude map, we used a corresponding baseline time series from each subjects experiment. Baselines were collected before each block (e.g. repetitions of 60 seconds of rivalry or replay) and were the same duration as each conditions' session. Baselines were included to ensure robust estimation of alpha components, and further, to allow for accurate estimation of baseline distributions. We used the backprojected time series (see step 2 above) to select time points of 2 seconds around each subjects button press. We selected the corresponding time points except on the baseline time series and then averaged all events in the same way as in the task data. The resulting average time series 62x4,001 was used to build a baseline distribution for which 95% threshold values were calculated to evaluate each pixels statistical significance on the group average task event-related time series.

-Alpha Power Permutation

To get an idea of whether the computed rivalry indices were significant we used a permutation procedure which utilized the baseline control conditions. For each condition, we used alpha power values during either binocular rivalry or replay and then identified the alpha power values during the baseline control condition prior to each block of rivalry or replay. We then analyzed the power values across subjects and for

each electrode and condition separately, and randomly sampled the combined baseline and task distributions to generate an empirical distribution of t-values. We then thresholded at the 95% t-value after 1000 iterations and assessed whether the observed t-value was greater or less than this value. Significant values were greater than the 95% threshold and were colored in the t-value topographies with blue indicating below threshold and red indicating above threshold.

RESULTS

BINOCULAR RIVALRY AND REPLAY DOMINANCE TIME DISTRIBUTIONS AND EXPERIMENT SETUP

We asked subjects to respond to a binocular display of competing oriented colored gratings during binocular rivalry and also a replay version of the gratings where the same grating was presented to each eye. In this replay condition, the response duration for each percept was taken from the previous run and replayed to the subject, and transitions were simulated as a fading grating or an oriented radial sweep. Prior to testing any electrophysiological differences in the EEG, we first wanted to assess whether subject responses were accurately representing the transitions and dominant percepts seen in binocular rivalry. Subjects reported perceptual transitions during binocular rivalry by pressing a button on a keyboard, and we subsequently calculated the duration of each percept by taking the difference between successive time points (Figure 11 A). We plotted the distribution of durations for binocular rivalry, which is known to fit to a

gamma distribution (Blake 2001). Comparing the binocular rivalry distribution to the replay distribution we found that fit parameters were not significantly different for the two gamma distributions (Figure 11 B and C) red percepts (a parameter: p=0.67, tstat=-0.43, df=16, b parameter: p=0.59, tstat=0.59, df=16) or green percepts (a parameter: p=0.29, tstat=-1.1, df=18, b parameter: p=0.98, tstat=0.02, df=18). Thus, subjects respond to the replay condition, which simulates a session of binocular rivalry, very similarly to how they respond to natural binocular rivalry.

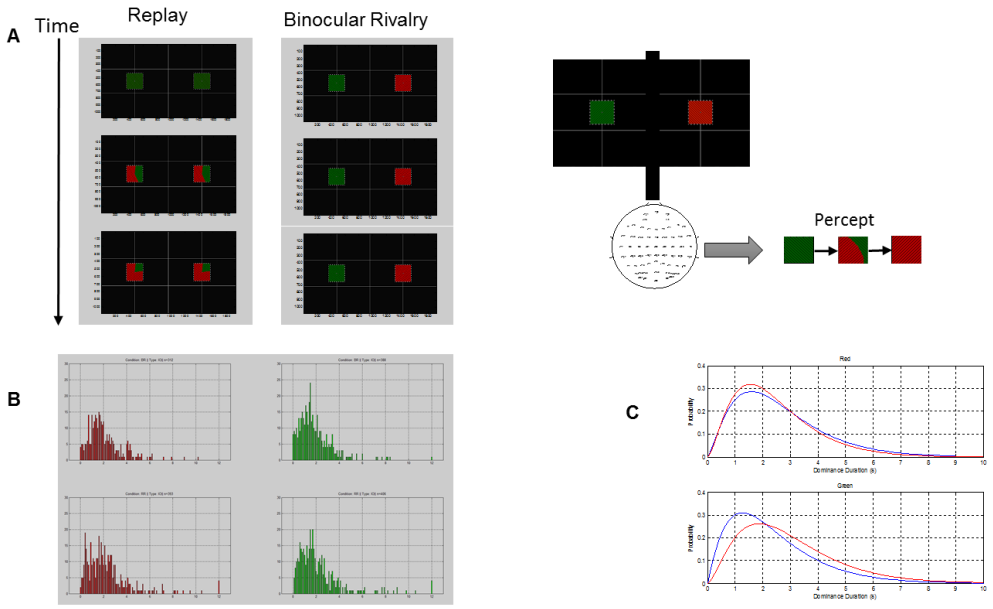

Figure 11. Stimulus Presentation Apparatus and Behavioral Dominance Distributions

(A) Stimulus used during binocular rivalry and replay were the same red/green oriented gratings. Replay incorporated the response durations of binocular rivalry, and also included simulated transitions either being a wedge sweeping across the box or the box fading between colors. Subjects reported their perceptual states as being a red grating, a transition or a green grating.

(B) Histogram of dominance times during a binocular rivalry (top panel) or replay (bottom panel) session (red grating percepts – red bars; green grating percepts – green bars).

(C) Fit histograms to the dominance time distributions averaged across subjects for binocular rivalry (blue) or replay (red). Top panel is red percepts, bottom panel is for green

ALPHA POWER DECREASES DURING BINOCULAR RIVALRY AND REPLAY IN THE OCCIPITAL CORTEX COMPARED TO BASELINE

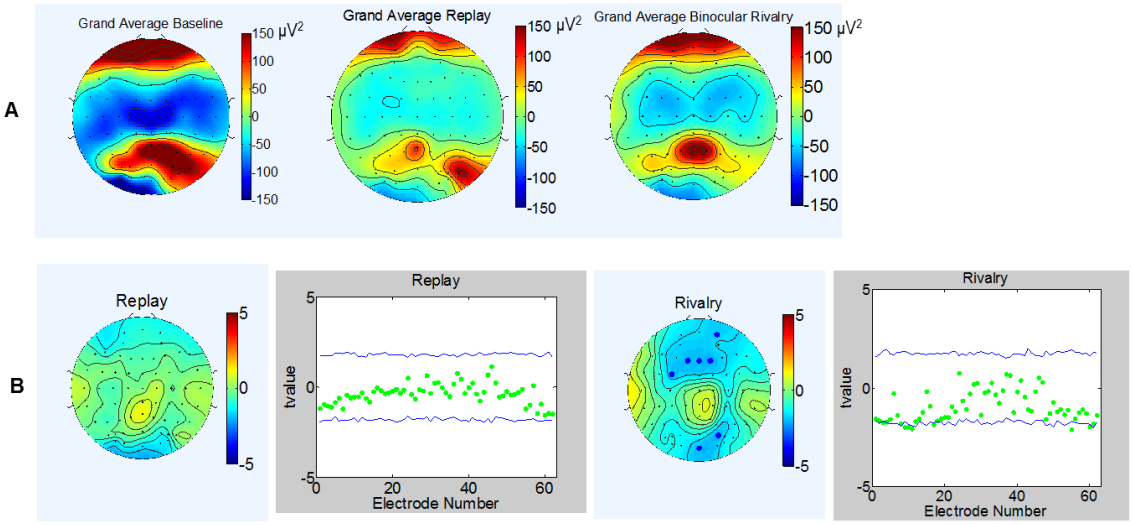

Figure 12. Alpha Power Decreases in Frontal and Occipital areas for Rivalry

(A) Grand average scalp topographies were computed across subjects (n=26 rivalry and baseline, and n=11 replay) showing the alpha power localizes to parietal and frontal areas with a decrease in central and occipital areas common for all conditions (Baseline-left panel, replay-middle panel, rivalry-right panel).

(B) To evaluate significance, a permutation procedure on the alpha power values was carried out across the same subjects for rivalry and replay (n=11) for each electrode indpenedently. Left panel shows replay tvalue topography with no significant electrodes highlighted, right panel showing electrodes instead plotted along the x axis. Blue line is the 95% permutation based confidence interval. Right panel shows the rivalry tvalue topography with significant decreases relative to baseline for occipital and frontal electrodes, right panel similarly shows electrodes along the x axis.

Given our hypothesis that alpha oscillations are involved during binocular rivalry, we assessed whether average power spectra would change in the alpha band during binocular rivalry relative to our replay condition. Taking the power average across the task allowed us to account for any differences in behavioral dynamics of rivalry and instead assess general changes in alpha level during binocular rivalry compared to replay. Maxima in the power spectra in the range of 5-15 Hz were taken across electrodes and computed for all subjects. Grand average power spectrum topographies of both conditions averaged across 26 subject in rivalry and 11 subjects in replay are shown in Figure 12A. There was an observable increase in alpha power in the frontal and central-parietal electrodes relative to the other electrodes across the scalp for all conditions

including the baseline. We used a permutation approach to evaluate significant changes across electrodes during the rivalry period relative to baseline periods prior to the start of any block of our task conditions. We also used the same subjects for both rivalry and replay, constraining the number of subject to the same amount in the replay condition (n=11). There was a significant decrease between the task and baseline alpha power for rivalry (Figure 12B right panel), whereas alpha was trending for a similar decrease during replay but was insignificant versus baseline (Figure 12B, left panel). A decrease in occipital alpha power is indicative of an active engagement of the visual cortex during the rivalry condition. Alternatively, the parietal alpha increase during baseline and task may reflect a sustained attentional alpha component. It should also be noted, that although there is a change in power for the baseline and rivalry, the overall pattern of alpha increase stays similar across all three conditions, indicating the presence of alpha oscillations in frontal and central-parietal areas. The observed frontal alpha oscillations may be related to fatigue of subjects since it is not related to the task and decreases during rivalry (see discussion). These results are consistent with the idea that alpha oscillations are engaged when subjects perform binocular rivalry, and although not significant, a similar trend was observed for the replay condition.

ALPHA OSCILLATION POWER DECREASES DURING THE TRANSITION IN BINOCULAR RIVALRY AND REFLECTS NEURAL COMPETITION

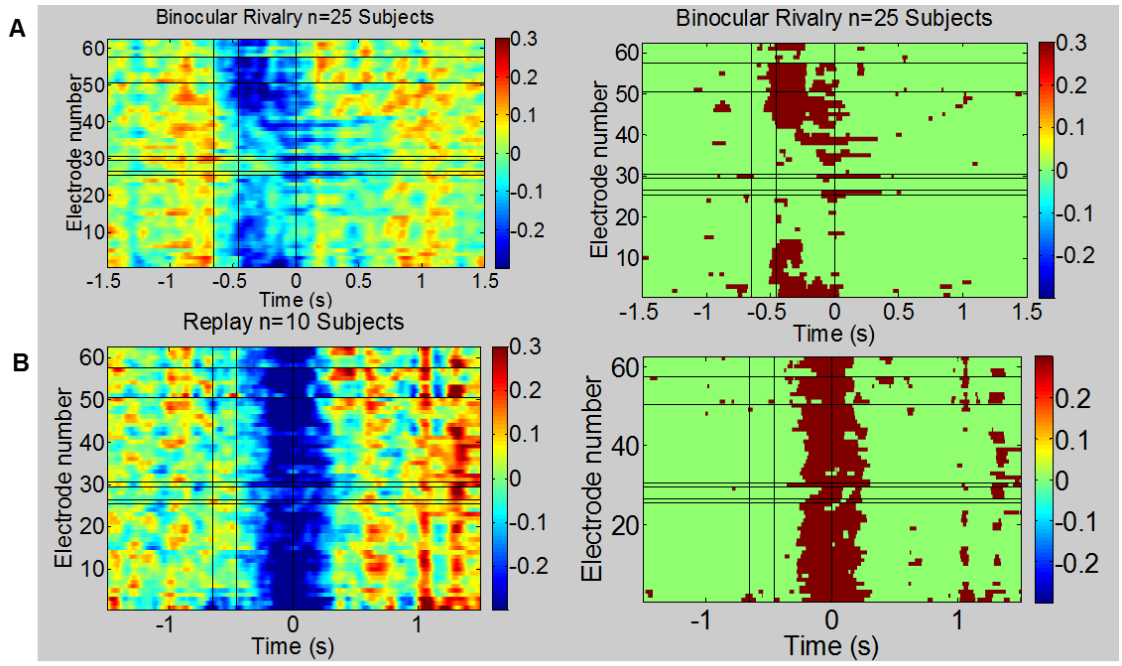

Figure 13. Alpha Power Desynchronization in Binocular Rivalry Precedes Replay

(A) The average alpha amplitude for a window of -1.5 to 1.5 seconds around button press indicating stabilized perception of either a red grating or a green grating during binocular rivalry (n=25 subjects). Vertical black lines indicate different subdivisions of time before the button press common in both conditions, and horizontal lines are markers for occipital electrodes (top), parietal electrodes (middle), and motor electrodes (2 bottom). Right panel shows the pixels that exceeded threshold for 95% significance after permutation testing with a baseline fixation task.

(B) Same as A, except for replay (n=10 subjects). The vertical line at 450 ms before the button press was the measured onset of a presented stable percept shown similarly for binocular rivalry for comparison.

Alpha oscillations have been correlated with perception, working memory, and attention (Basar 2012), and function as an inhibition to neural processing (Klimesch et al 2007). Thus we compared alpha oscillations during competitive interocular neuronal interactions in binocular rivalry with the fascilatory interocular interactions in replay. Based on previous EEG experiments on bistable perception, we expected to see some changes of alpha oscillations around the time of the perceptual transition (Isoglu-Alkac et al 2000; Vanni et al 1999) so we computed the average alpha oscillation amplitude for each electrodes timeseries 2 seconds before and after each button press of a stable percept during binocular rivalry and replay. For each subject we averaged across all button press trials, and then averaged all event-related timeseries across all subjects. A significant

decrease of alpha amplitude was observed for occipital and frontal electrodes up to 600 ms prior to the button press which then progressed to motor electrodes around the time of the button press for binocular rivalry (Figure 13A). On the other hand, in replay the alpha oscillation amplitude decreased globally across the scalp in a window of 600 ms centered on the button press (Figure 13B). To evaluate significance of the occipital alpha decrease, we ran the same analysis on baseline data which was collected before each block of binocular rivalry or replay (see methods). We then used the distribution of this averaged baseline to infer 95% significance thresholds shown in the bottom panels of Figure 13, which further showed that the center of the density preceded the button press in rivalry while being centered on the button press in replay. This suggests that an alpha oscillation decrease may play a role in binocular rivalry competition since the timing of the alpha change corresponds to a transition occurring as perception switches to a new stable state. Furthermore, when compared with replay where there are no interocular interactions, and a simulated visual transition, the alpha oscillation fails to precede the button press around the time of the transition. Thus, the alpha oscillation amplitude decrease during binocular rivalry reflects interocular competition.

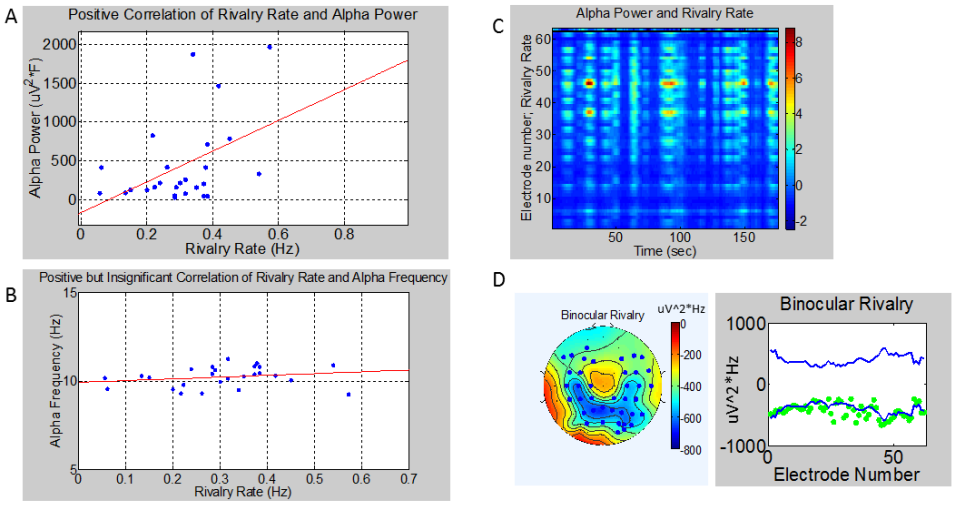

Figure 14. Alpha Power correlates positively with rivalry rate

(A) Correlation of alpha power with the mean response rate across a session of binocular rivalry for each subject (n=26). The maximum value in the alpha band (8-12 Hz) of the power spectrum was found for each electrode, and then the maximum value across electrodes was used for each subject and correlated to the rivalry rate.

(B) The mean frequency across electrodes was also positively but not significantly correlated with rivalry rate.

(C) Example subject timeseries of alpha amplitude for each electrode on the y axis across time on the x axis. The upper most timeseries (above the black line) is the sum of responses for a 5 second moving window. Both timeseries were zscored for comparison on the same axis to show that when alpha bursts occur, the number of responses decreases.

(D) Mean covariance across subjects of each electrodes' timeseries alpha amplitude with rivalry rate. A permutation approach for each electrode, where time-points were shuffled, was used to calculate significance levels for each electrode (Binocular rivalry, n=26). Blue indicates significant decrease relative to a shuffled timeseries. Right panel shows the same data but with the electrodes projected onto the x-axis.

ALPHA OSCILLATION POWER CORRELATES WITH THE RESPONSE RATE DURING BINOCULAR RIVALRY

We then asked whether the average alpha power during a binocular rivalry session would correlate with behavioral rivalry rates of the subject given that both metrics are intrinsic for each subject, and also since they may be used as potential markers for individual differences between subjects. We found a significant correlation for the power in the maximum electrode (e.g. electrode with the highest alpha power), and the rivalry rate, with a correlation of R=0.44 [0.05, 0.71] (p=0.028, n=25). However, the mean alpha frequency for each subject had no significant correlations with the response rate (p=0.2, n=25). Thus, the amount of alpha oscillations for a subject is positively related to

the rate such that higher switch rates are associated with higher alpha power.

We then looked within subjects and assessed whether alpha amplitude and rivalry rate would be correlated during a rivalry session. Using a 5 second moving window with a 1 second step size, we measured the local number of stable percepts in the window. We also then summed the alpha power for each electrode within the same window, and found that at some electrodes, the rivalry rate showed an inverse relationship with bursts of alpha activity, such that an increase in alpha amplitude corresponded to a decrease in the rivalry rate within a session for a given subject (Figure 14C).

In Figure 14D we covaried each electrodes' alpha amplitude with the local rivalry rate, and then plotted the topography of the average covariation across all subjects (left panel). We found that in parietal central regions and occipital posterior regions the rivalry rate was negatively correlated with the alpha amplitude, along with the electrodes situated over sensorimotor cortex. A random permutation of the covariance values calculated by shuffling the timepoints of the alpha amplitude and repeatedly covarying the same responses obtained binocular rivalry. This random shuffling approach showed that the sensori-motor and posterior parietal electrodes significantly negatively covaried with behavior ($p<0.05$, Figure 14D). Given that motor electrodes show an event-related decrease during button presses this is expected, however, electrodes in posterior central areas were also significant indicating that this region may be dynamnically involved in determinining the rivalry rate. Overall, this suggests that for a given subject, alpha can indeed predict rivalry switch rates along shorter timescales, along with the expected motor covariance, posterior parietal electrodes might be related to the short term

modulations in alpha amplitude perhaps playing a role in the level of attention payed to the stimuli which can change rivalry switch rates.

DISCUSSION

In this study we investigated the oscillatory changes in the alpha band during binocular rivalry and found that decreases in alpha amplitude were timelocked to perceptual transitions reflecting interocular competition. We also showed that alpha power changes across a session are sensitive to visual tasks, and that alpha power may predict behavioral characteristics of rivalry such as the rivalry switching rate.

FUNCTIONAL ROLE FOR ALPHA OSCILLATIONS DURING RIVALRY

Our findings suggest that alpha oscillations are related to interocular interactions, and that a change in alpha may be important in the processes involved during interocular competition. Specifically, when we saw lowest alpha power (during the transition) this corresponded to the lowest levels of interocular inhibition, whereas when the alpha power rebounded to a high level the corresponding level of interocular suppression was also the highest. Overall, this corresponds with previous functional models of alpha oscillations which have been linked with an inhibition of neural information processing (Klimesch et al 2007), and in our case it was specifically related to ocular inhibition. Thus, alpha oscillations may be a critical inhibitory component in maintaining stable states during binocular rivalry.

The mechanism of alpha action on neurons is summarized elsewhere (Klimesch et

al 2012) but the overall hypothesis is summarized as follows: high levels of oscillation in the alpha band can feedback onto neural firing by filtering the input such that the neurons output is suppressed, and at intermediate levels it can facilitate output by making the membranes more excitable at specified phases of the alpha cycle. Thus, the neural firing patterns are influenced by changes in the local field amplitude of the alpha oscillation which can play an inhibitory role at high levels such as during the stable phase of rivalry, or establishing optimal time-windows for neural coding at intermediate levels such as during the transition phase of rivalry. In line with this view, alpha phase can predict whether stimulus will be perceived in the periphery of visual stimuli at threshold of perceptions (Busch et al 2009), and it phase of the alpha cycle has been linked to numerous optical illusions (VanRullen 2016). Thus, the overall level of alpha oscillation in visual cortex may, during binocular rivalry, guide network activity by altering communication between ocular channels and downstream visual regions or the thalamus.

PREVIOUS STUDIES ON BISTABLE PERCEPTION

Previous neurophysiological evidence also strongly favors that alpha oscillations change during bistable perception, where visual awareness changes while stimuli remain constant. It is apparent from bistable stimulus experiments that alpha activity decreases when subjects perceive changes in awareness during ambiguous figures (Struber and Herrmann 2002; Isoglu-Alkac et al 2000; Vanni et al 1999). It has also been shown that alpha oscillation amplitude can increase when stimuli presented at threshold but remain unperceived (Bareither et al 2014), indicating that increases may be related to the

suppressed information. These findings in the visual domain extend to illusions in other modalities where alpha oscillation amplitude plays a similar role (Lange et al 2014). Thus, even in the absence of changes in sensory stimulation, alpha oscillations are sensitive to changes in the state of perceptual interpretations and modulations of perceptual suppression as we have also identified. Our study further suggests that changes of alpha oscillations arise from interocular competition that is a component of binocular rivalry.

FRONTAL ALPHA OSCILLATIONS

We observed an increase in frontal alpha power during our rivalry, replay and baseline conditions. The fact that alpha increased in frontal areas during baseline suggests that it reflects a general alpha response not specific to the particular visual task we employed. One possibility is that frontal alpha activity reflects sleepiness of subjects, however, previous studies show a negative correlation between frontal alpha power and sleepiness (Strijkstra et al 2003). A more plausible explanation is that subjects were perhaps involved in creative ideation during baseline and also, but to a lesser degree, during both of the replay and binocular rivalry tasks (Fink and Benedek 2014). Related to this notion, is that frontal alpha power increases when attention is directed internally which may be high during baseline conditions due to the absence of any stimuli (Aftanas and Golocheikine 2001). Finally, others have noted that the frontal alpha activity could be considered an index for motivational behavior (Coan and Allen 2003) indicating subjects may have been motivated to do the experiment. Given that these tasks were very simple

and mastered by subjects early in the experiment, it is not unlikely that subjects engaged in creative thinking and directed attention internally during the experiment. Thus, we attribute the observation of frontal alpha to a combination of creative thinking, internally directed attention, and motivated behavior.

NEUROPHYSIOLOGICAL MECHANISMS OF RIVALRY AND ALPHA OSCILLATIONS

As previous studies have indicated, the thalamus may be an important node in the rivalry neural network. Thalamus interconnects many regions of visual cortex and contains monocular channels from each eye. Thus, the thalamus may be a major site of suppression in rivalry, and the proportion of cells having the strongest impact on the primary visual cortex may determine the dominant stimulus. However, single unit studies have failed to show large modulations in thalamic neuron spiking during rivalry (Logothetis 1998), and contradict the thalamic model of selection or suppression. As discussed previously, neurophysiological mechanisms of signal generation may account for some of the discrepancy between single unit studies and fMRI activity (Boynton et al 2011), and thus doesn't rule out the potential impact of the thalamus during rivalry. As suggested by our results, it may be that the oscillatory state of the thalamus at the alpha range could play part of the role as a selection mechanism while spikes remain unchanged in the thalamus.

The selective properties of the thalamus during attention shifts have recently been highlighted for alpha oscillations arising in the pulvinar (Saalmann et al 2012), and thus

may LGN may serve an analogous role for perceptual selection during rivalry. Previous studies investigating oscillatory changes in the LGN during perceptual suppression showed that alpha oscillations decrease in low frequency bands around the alpha frequency in monkeys in the absence of spiking changes (Wilke et al 2009), and others studies have shown similar findings that the oscillatory field potential at low frequencies (<30 Hz) in V1 follow perception without changes in spiking in non-human primates (Gail et al 2004). Thus, it is plausible that alpha changes in the thalamus may gate perceptually relevant neural activity indirectly, not observed in the spiking changes, but instead through oscillatory field state of the neural population which may indirectly alter the spikes' postsynaptic effect.

One argument for the thalamus as a substrate for suppression in rivalry is that a subset of alpha oscillations has been shown to synchronize in the alpha frequency range via gap junctions, which might allow for large scale suppression of one whole eyes input at monocular channels in the thalamus (Hughes et al 2004). Another important factor to note is that even though visual stimulation has been shown to shift cortical firing from synchronous to asynchronous state (Tan et al 2014), in our results the stimuli remain constant, so a decrease of alpha oscillation during transitions in visual cortex would be expected if thalamus were driven by corticothalamic feedback mechanisms. Finally, as discovered during state transitions in the sleeping brain, the thalamus is thought to be a major modulator and inductor of sleep which results in unawareness and disconnection from the external sensory world, and adds further support to the notion that thalamus has the required circuitry to suppress ocular information (Palva and Palva 2007).

It should also be noted that cortical mechanisms may also generate alpha oscillations (Bollimunta et al 2008) and may thus be responsible for the changes that we observed in the alpha band. In particular, layer 5 neurons can repetitively fire at 10 hz to generate an alpha oscillation (Silva et al 1991), while areas such as V2, V4 and IT have alpha generators in multiple layers (Bolluminta et al 2008). Although feedback from layer 6 to LGN is thought to be a potential source for rivalry related modulations, nonspecific feedback from layer 5 may also guide genesis of alpha oscillations synchronization (Jones 2002), which remains within the scope of thalamic and early visual cortex based rivalry models (Bake 1989; Lehky 1988). On the other hand, it should be noted that cortical genesis of alpha oscillations are primarily thought to reflect cognitive influences of memory or attention (Saalmann et al 2012; Klimesch 1999; Klimesch et al 2006), which have little influence on the occurrence and independence of rivalry transitions (Meng and Tong 2004; Fox and Herrmann 1967; Blake 2001). Thus, the modulations we observed in occipital cortex during the transition may be specifically related to modulation occurring in LGN and gives credence to its contribution during rivalry, in coordination with its thalamocortical and corticothalamic interactions with the primary visual cortex, a neural network structure similar to that originally proposed by Blake 1989.

Taken together, the alpha oscillation amplitude changes during binocular rivalry reflect a potential mechanism of interocular inhibition that may be mediated in part by the interacting geniculostriate and corticothalamic feedback loops.

CONCLUSION

Externally Induced Oscillations

Externally induced oscillations were studied by using a paradigm called frequency tagging which generates a steady-state visually evoked potential (SSVEP). This is an oscillating response at the stimulus frequency and allows us to trach changes in the neural processing of a stimulus. We used this approach to see if binocular rivalry, a low-level competitive process, was similar to stimulus rivalry, a proposed high-level counterpart. We found that both types of competition shared mechanisms in early visual areas and further suggested that perceptual awareness is perhaps closely related to the activity of the sensory visual cortical areas.

Intrinsically generated oscillations

Looking at intrinsic oscillations, with a particular focus on the alpha band due to its high SNR and high power during sessions, we investigated what role it may play during rivalry. Also, given that alpha oscillations seem to play a role in selection and attention, we assessed how they are modulated during binocular rivalry perceptual states. We showed that a particular alpha component derived from ICA seemed to be consistently modulated, and further, that this modulation was closely related to the timing of the transition during binocular rivalry. It was also distinct from a non-competitive control condition where we replayed transitions to subjects, suggesting that alpha oscillations were related to competitive interactions during perceptual suppression in binocular rivalry.

General Conclusion

In conclusion, binocular vision and binocular rivalry can tell us a great deal about how the brain generates visual perception. From the introduction it was clear that despite a great wealth of knowledge we have much to learn about the neural mechanisms of binocular rivalry. From this thesis work, we can make a few speculative claims about the potential neural mechanisms that this series of experiments have suggested. First, the set of experiments in the SSVEP chapter point to the early visual cortex as a major site of modulation of the SSVEP amplitudes during rivalry. Thus, part of the mechanism of binocular rivalry likely includes the early visual cortex. It is more difficult to address which layer of early visual cortex given that the SSVEP signal can be generated by monocular neurons in layer 4 or by binocular cells in layer 2/3. From the second chapter we can speculate that alpha oscillations, long hypothesized to serve an inhibitory role in the neural processing of brain regions, may play a role in suppression of interocular information during binocular rivalry transitions. It is therefore possible that this may be a form of attentional modulation that is feedback to the thalamus and supports the dominance of the perceived stimulus while suppressing the non-dominant eye, making it a potential neural mechanism of binocular rivalry inhibition.

Future

Future studies should examine whether this component in the alpha band that gets modulated during rivalry is related to attention, and what the timing of changes in this

band reflect relative to the timing changes in the alpha band. It would also be important to do an SSVEP study on stimulus rivalry with stimuli of lower frequency and perhaps that tag higher level areas. This is hard to do, however, given that the minimum frequency is 3 Hz, and that most of the high level neurons are only sensitive to a flicker around or below 6 Hz. It would be better to adapt the stimulus rivalry paradigm into an intermittent form of binocular rivalry and stimulus rivalry so that there can be both a low frequency flicker but also swapping of the two stimuli.

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