THE EFFECT OF ATTENTION ON BINOCULAR RIVALRY: AN OKN APPROACH

By

Cheng Qian

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Psychology --- Doctor of Philosophy

2019

ABSTRACT

THE EFFECT OF ATTENTION ON BINOCULAR RIVALRY: AN OKN APPROACH

By

Cheng Qian

Binocular rivalry (BR) is observed when the two eyes receive conflicting information, leading to perceptual switches between the eyes' images. Previous computational models and empirical evidence were inconsistent in their account of the effect of moderate attention withdrawal on the switch frequency of BR. One concern with the empirical work in question, however, is that the observers reported BR dominance while performing a secondary attention task: a dual task design that might have produced unreliable data. To avoid this potential concern, we reexamined the effect of moderate attention withdrawal on binocular rivalry by using optokinetic nystagmus to track perceptual switches of a task-irrelevant rivalry stimulus (foveally presented dot fields moving in opposite directions in the two eyes), while observers performed an auditory attention task.

Our results showed that switch frequency decreased as a function of increasing attention load, confirming the existing empirical finding with our new method that does not share the original method's potential shortcomings. Furthermore, our results showed an increased proportion of non-exclusive percepts as a function of increasing attention load, coupled with the decreased switch frequency. This suggests that attention may modulate the switch frequency of BR by modulating perceptual grouping. Specifically, attention may modulate switch frequency of BR by binding the dominant rivalry percept

across space; hence the increased proportion of piecemeal rivalry accompanying attention withdrawal. We developed a mathematical model that implements this proposed mechanism of altered binding across space, to examine whether it can account for the empirical patterns. Attention implemented as an overall gain modulation of lateral facilitation can account for the observed change in the proportion of exclusive percepts with attention load, but still the predicted effect on switch frequency is in the wrong direction; the same shortcoming we observed in existing, non-spatial, models. Other aspects of attentional modulation might help fitting the model to both aspects of empirical findings.

TABLE OF CONTENTS

LIST OF FIGURES

1 General Introduction

1.1 BR and visual awareness

With a seamless three-dimensional scene floating in front of our eyes, we often ignore the non-resting work from our brain that joins together the two eyes' inputs constantly. However, when the two eyes are presented with incompatible images, our brain decides to resolve conflicting information by an alternation between the two images, which is called binocular rivalry (BR) (Blake, 1989; Blake & Logothetis, 2002). BR can be seen as a compromise of the brain due to the bandwidth of conscious processing. Thus, BR has been a popular tool to investigate visual awareness, considering the subjective experience fluctuations in the absence of physical input change (Crick & Koch, 1998, 2003).

BR is thought to be one of the most important experimental methods in the search of the neural correlates of consciousness (Blake, Brascamp, & Heeger, 2014; Crick & Koch, 1998). Recent empirical evidence showed that rivalry can proceed in the absence of conscious awareness (Zou, He, & Zhang, 2016), which induced skepticism on whether BR can inform us with the neural correlates of consciousness (Giles, Lau, & Odegaard, 2016). Admittedly, BR might not be able to disentangle the problem of the conscious states, as whether an individual is awake or in coma, but it still remains a good tool for understanding visual awareness, especially how the brain resolves conflicting input from the two eyes to accommodate for the processing bandwidth imposed by the awareness system.

1.2 Attention and BR

It is intuitively clear, and generally agreed (Bayne, 2012; Revonsuo, 1999), that one key factor shaping visual awareness or conscious experience is attention: what one experiences is usually that which is at the focus of attention, while unattended items often remain outside of one's awareness. The exact relation between attention and awareness, however, remains intensely debated (Boxtel, Tsuchiya, & Koch, 2010; Cohen, Cavanagh, Chun, & Nakayama, 2012). This proposal focuses on the effect of attention on fluctuations of the conscious experience, specifically, the attentional modulation of BR.

The history of studying the relationship between attention and BR dates back to when BR first drew researchers' interest (von Helmholtz, 1859, 1910; Wheatstone, 1838). A historical debate started between von Helmholtz and Hering (Hering, 1879) on what drives the wax and wane of the percepts: attention or the stimulus strength. Several researchers revisited this topic (Ooi & He, 1999; Paffen & Alais, 2011; Paffen, Alais, & Verstraten, 2006) and some found that the full attention withdrawal from rivalry stimuli prevents the normal rivalry situation in which one percept dominates over the other, as shown by behavioral evidence (J. W. Brascamp & Blake, 2012) and neuroimaging work (Lee, Blake, & Heeger, 2007; P. Zhang, Jamison, Engel, He, & He, 2011). Considering this converging evidence, researchers have reached a general consensus on the necessity of attention for BR (Dieter, Brascamp, Tadin, & Blake, 2016; R. Zhang, Engel, & Kay, 2017), which is also further supported by a study using language processing index as the measurement of processing (Eo, Cha, Chong, & Kang, 2016). However, the mechanism behind BR's requirement of attention remains unknown. To explore it here, we started with an in-depth review of the original work on the effect of full attention withdrawal on BR.

Zhang et al. (2011) tested whether rivalry proceeds in the absence of attention with an Electroencephalography (EEG) based frequency tagging technique. Participants were presented with two dichoptically presented images (see Figure 1a), which flickered at two different and non-harmonic frequencies. The amplitude profiles of the frequencies corresponding to the two images were extracted as the indices of processing (see Figure 1b). The amplitude profile for BR with attention is two waves that wax and wane in counter phase, which matches with participants' subjective percept report (shaded areas in Figure 1b). However, when attention is withdrawn from the rivalry stimuli with a demanding task in the fovea, the amplitude profile of the two images collapses to the same level without differential properties (Figure 1b bottom panel). The authors concluded that the representations of the conflicting inputs do not keep switching in dominance in the absence of attention; instead, both sources of input are processed almost equally.

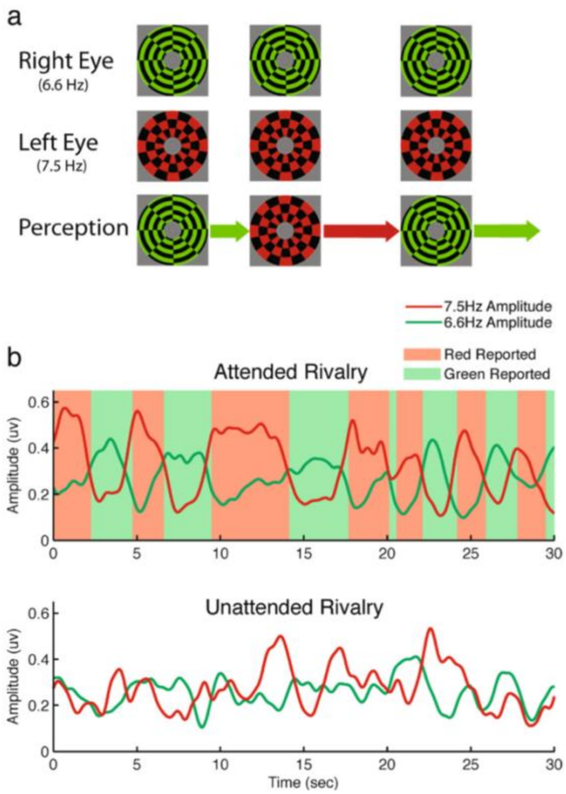

Figure 1. The design and processing indices of attended and unattended binocular rivalry.

(a) The BR stimuli. Two flickering incompatible images were presented to two eyes. In the attended condition, observers saw perceptual alternations. In the unattended condition, observers performed a demanding feature conjunction task at fixation. (b) The EEG frequency-tagging results of attended and unattended BR. In the attended condition, participants' perceptual report (shaded red and green) aligned with the processing indices acquired via EEG. In the unattended condition, the anti-correlated rivalry signature was not found. Instead, the processing indices seem to be collapsed to be the average value of the two eyes' indices in normal rivalry condition. The figure was adapted from Zhang et al. (2011)[1].

In addition to this evidence from neural activity, a behavior study investigated the consequence of attended and unattended BR on the subsequent perceptual experience

---

[1] Reprint from Neuron, 71, Zhang, Jamison, Engel, He & He, Binocular Rivalry Requires Visual Attention, 362-369, Copyright (2011), with permission from Elsevier.

of an attended BR stimulus, thus drawing the conclusion that unattended BR does not produce the same perceptual history as attended BR (J. W. Brascamp & Blake, 2012). Specifically, this study relies on the priming effect of flash suppression, a variant of BR stimuli that induce one predominant percept (Wolfe, 1984). After the priming of attended rivalry stimuli, observers tend to report one percept more than the other, following the wax and wane of the established rivalry dynamics (see Figure 2a). However, if attention is withdrawn from the rivalry stimuli with a demanding task immediately following the priming stimulus, the probability of seeing either of the images in rivalry following attention withdrawal is the same (see Figure 2b). In the absence of attention, the two images do not cause dominance switches as in attended BR (Figure 2a) but it is similar to the stimulus absent condition (Figure 2c).

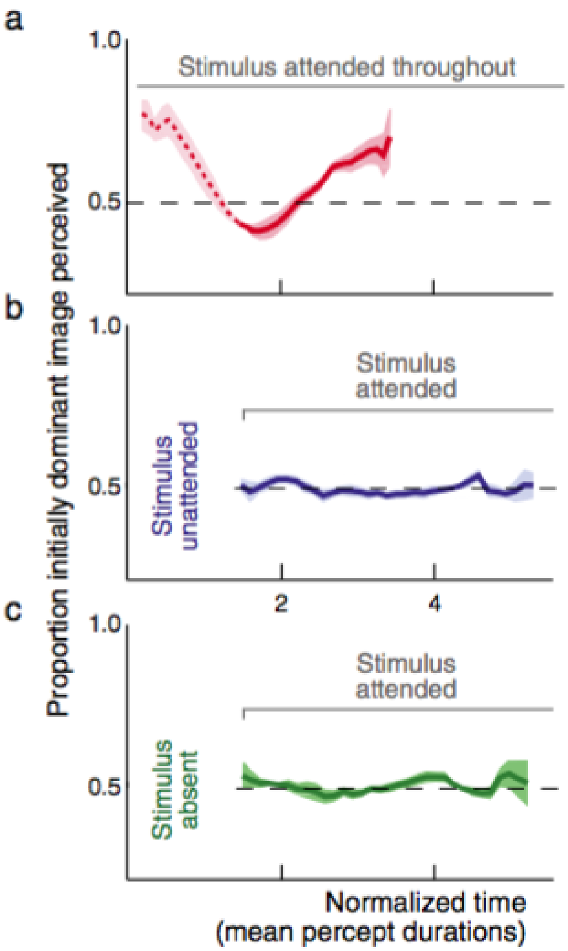

Figure 2. The perceptual consequences of attended BR, unattended BR, and stimulus absent.

(a) After the priming of attended BR (dashed red line), the probability of seeing one of the images of BR was first below chance and then above chance (red line), indicating a signature of rivalry. (b) However, when attention was withdrawn from the BR stimuli, the probability of seeing that image was at chance. (c) The inattention condition turned out to be similar to stimulus absent condition. The figure was adapted from Brascamp and Blake (2012)[2].

---

[2] Reprint from Psychological Science, 23, Brascamp & Blake, Inattention Abolishes Binocular Rivalry, 1159-1167, Copyright (2012), with permission from SAGE Publications.

Zhang et al. (2011) and Brascamp et al. (2012) provided converging evidence that BR requires attention to proceed. Even though this finding has been corroborated with several other studies (Eo et al., 2016; Moradi & Heeger, 2009) and became a consensus in the field, the mechanism behind this phenomenon is far from clear (Dieter et al., 2016). Here, computational models of BR might provide an approach to understanding the mechanism of both BR and the effect of attention on BR.

1.3 Modeling work of BR

The computational modeling of the BR process has been developed substantially (J. Brascamp, Sohn, Lee, & Blake, 2013; Dayan, 1998; Laing & Chow, 2001; Seely & Chow, 2011; Wilson, 2003, 2007), which may shed light on the explanation why BR is abolished in the absence of attention. Shpiro and colleagues (2007) have noted that, despite the variations of the models, the typical BR model usually implements neuronal competition by reciprocally inhibitory populations (Laing & Chow, 2001; Wilson, 2003). Even though only one paper incorporated attention as the factor in such a neuronal competition model (H.-H. Li, Rankin, Rinzel, Carrasco, & Heeger, 2017), the general behaviors of the model and the topology of the parameter space are shared across neuronal competition models. As such, models without an attention factor can still be analyzed in the context of attentional modulation by evaluating the consequences of changing various parameters, under the hypothesis that attention might alter these parameters.

The general topology of the parameter space of all the neuronal competition models is featured with three parameter regions: the equilibrium regime, rivalry or oscillation regime, and winner-take-all (WTA) regime (see Figure 3)(Laing & Chow, 2001; H.-H. Li et al., 2017; Wilson, 2003). The rivalry (or oscillation) regime refers to the two populations of neurons showing counter phase fluctuations, corresponding to the perceptual alternations in behavioral results as well as matching neuroimaging work using EEG frequency tagging (P. Zhang et al., 2011), fMRI (Engel & Tong, 2001; Tong, Nakayama, Vaughan, & Kanwisher, 1998), and monkey physiology (Xu et al., 2016). The simulated oscillation regime legitimized the neuronal competition models to be a common choice of models of BR. In the equilibrium regime the signals of the two populations of neurons reach the same steady level. In the WTA regime one population of neurons reaches a certain level of activity and the other population of neurons cannot take over dominance. Even though rivalry ceases in both the equilibrium state and WTA state, inattention is expected to land the system in the equilibrium regime as previous studies suggested both representations to be equally active during inattention (J. W. Brascamp & Blake, 2012; Eo et al., 2016; P. Zhang et al., 2011). Li et al.’s (2017) model, indeed, walks from the oscillation regime to the equilibrium regime with the decrease of attentional modulation, consistent with the empirical evidence reviewed in the last section (see Figure 3b green arrow).

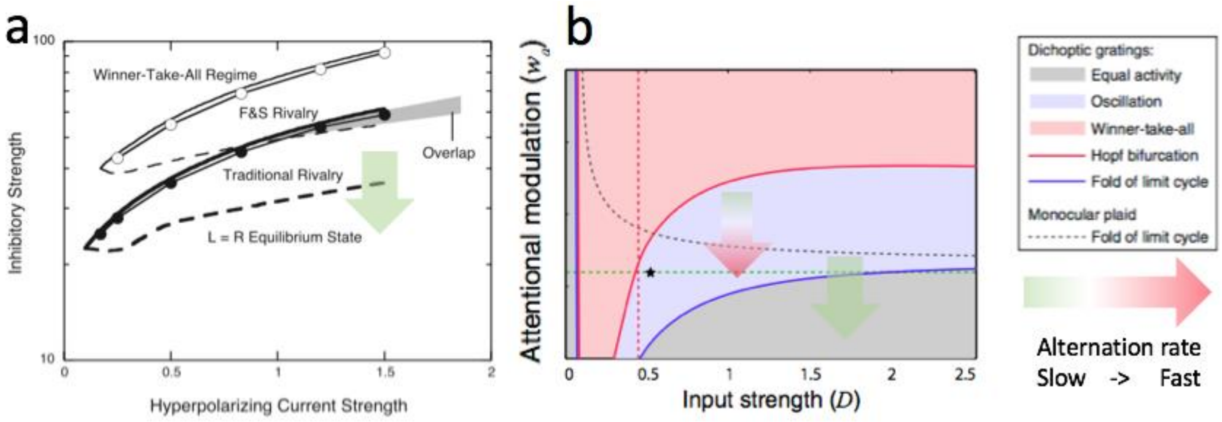

Figure 3. The parameter space of two BR models.

Both models include three parameter spaces: equilibrium/equal activity, rivalry/oscillation, and winner-take-all. (a) The parameter space of Wilson (2003)[3]. (b) The parameter space of Li et al. (2017)[4]. The green arrows in both figures shows that the models have the oscillation or rivalry regime connected with the equal activity regime. In figure b, the attentional modulation decrease is associated with the status change from the oscillation to equal activity. The gradient and direction of the arrow denotes the increase of the alternation rate. With the decrease of the attentional modulation, the alternation rate becomes faster.

As explained in the previous paragraph, BR models are consistent with the empirical evidence in the sense that full attention withdrawal can abolish BR. How about moderate attention withdrawal? All BR models based on neuronal competition predict that the switch frequency in the oscillation regime increases when approaching the

---

[3] Reprint from PNAS, 100, Wilson, Computational Evidence for a Rivalry Hierarchy in Vision, 14499-14503, Copyright (2003), with permission from PNAS.

[4] Reprint from PNAS, 114, Li, Rankin, Rinzel, Carrasco, & Heeger, Attention Model of Binocular Rivalry, E6192-E6201, Copyright (2017), with permission from PNAS.

equilibrium regime. In Li et al. (2017)'s model, it means the switch frequency increases with less attention (see Figure 3b). However, available empirical evidence suggests otherwise: Paffen and colleagues (2006) showed that reduced attention slows binocular rivalry. The current study will verify this inconsistency on the effect of moderate attention withdrawal on BR.

1.4 Eye movement as a measure of BR switches

Studies on BR with attention manipulation are faced with the challenge to achieve the manipulation of attention and the perceptual report simultaneously. Studies focusing on the switch frequency of BR usually require subjective report as the way of obtaining the perceptual switch measure. However, when asked to report the percept, observers automatically attend to the rivalry stimuli, which makes it difficult to manipulate the amount of attention allocated to the rivalry stimuli. Paffen et al. (2006) used a dual task method in which observers alternated between pressing keys for the attention load task and for the perceptual report task, which may have invited a strategy of shifting attention back and forth between the binocular rivalry stimulus and the secondary stimulus related to the attention task. It is thus difficult to interpret whether their switch frequency difference was due to a moderate attention withdrawal as they claimed or constantly interrupted full attention withdrawal. The current experiment was designed to circumvent this methodological challenge by changing the dual task to a single attention task.

This study measured perceptual dominance with eye movement patterns. Eye movements can reflect the processing of the visual stimuli, even in the absence of observers’ awareness (Spering, Pomplun, & Carrasco, 2011), making it one of the best ways to study binocular rivalry with attention manipulations. If the binocular rivalry stimuli were rendered to be two stimuli moving in opposite directions, the optokinetic nystagmus (OKN) can reveal the direction of the perceived stimulus (Fox, Todd, & Bettinger, 1975; Sun, Tong, Yang, Tian, & Hung, 2002). Indeed, previous research has used this method and found an effect of active reporting on the switch frequency of BR (Frässle, Sommer, Jansen, Naber, & Einhäuser, 2014; Naber, Frässle, & Einhäuser, 2011). This method was then examined to be robust across age groups, autism patients, borderline personality disorders, and other groups with disability to accurately report their perceptual experience in BR (Aleshin, Jochen-Braun, Kovács, & Gergő Ziman, 2018).

2 Experiments and Simulations

2.1 Pilot Experiment

This experiment is to ensure the feasibility of measuring the perceptual switch rate with eye movements. Observers reported their percept in a classical binocular rivalry condition, as well as a replay of the rivalry key press report obtained from the same observer. The accuracy of inferring switches from eye movement was then examined against the key press report. To ensure that the eye movement patterns are equally informative when not reporting the perceptual switches, participants also performed a percept-irrelevant task in both rivalry and replay conditions.

2.1.1 Participants.

Seven participants were included in the data analysis (4 females and 3 males; age: *M* = 25.29, *SD* = 6.92, range 20-40). Two of the participants were involved in the experimental design (C.Q. and J.B.), while the remaining participants were students of Michigan State University who were naive to the purpose of the experiment. All naive participants were compensated at the rate of $10/hour and signed a consent form before participation. All experimental protocols were approved by the Human Research Protection Program at Michigan State University.

2.1.2 Materials.

The experimental apparatus was a variant of the classical mirror stereoscope (J. W. Brascamp & Naber, 2016; Qian & Brascamp, 2017; Wheatstone, 1838), consisting of two mirrors (45° relative to participants' midline) reflecting stimuli from two screens facing each other (62 cm away from the midline of the participant). A head rest stabilized the alignment of participants to view the reflection of one mirror with each eye.

Visual stimuli were displayed on two 24-inch flat-screen monitors (60-Hz refresh; mean luminance 31.8 cd/m^2) as the only source of illumination in a dark testing room. All the stimuli were presented on a gray background. All aspects of the experiment were generated in Python with the Psychopy (Peirce, 2007, 2009) running on a Mac Mini. Eye movements were recorded by an EyeLink 1000 eye tracker (SR Research, Ontario, Canada) at a sampling rate of 1000 Hz.

2.1.3 Stimuli.

The stimuli of the experiment were designed to optimize the signal of OKN. In the binocular rivalry condition, one eye was presented with a colored dot field (field size: 14° in diameter; dot size: 1°; dot number: about 156 dots in the field; dot color: grey dots with either 20.0 cd/m^2 or 45 cd/m^2) moving left (speed: 7.5 °/s) and the other eye was presented with a different colored dot field moving right. The assignment of the dot fields was randomized. In the replay presentation, both eyes were presented with the same stimuli depending on participants' reported percepts. The replay of the mixture consisted of the two dot fields each subtending the top or bottom half of the space. During the presentation of the dot fields, the size of the dots changed (duration: 500ms) in both of the dot fields, serving as an attention task (see Procedure for further details).

2.1.4 Procedure.

At the start of each block, participant performed 9-point calibration and validation of the eye tracker. Every trial started with a drift correction for three attempts. If the drift correction failed for all three attempts, another calibration and validation were conducted.

Each participant finished one block of a percept report task and one block of an attention task in both the rivalry and replay conditions. In the percept report task, observers were given three keys to indicate percept change to moving left, moving right, and a mixture of both in the percept report condition. In the attention task, observers reported the size change of the dots. The size change was modulated with a staircase for observers to reach 75% accuracy.

The binocular rivalry condition with the percept report task was the first block for participants in order to obtain the sequence information needed for the replay, and the order of other blocks were assigned randomly. Each block has 32 trials of 40-second trials and takes about 30 minutes to finish. Participants were encouraged to take rests between trials as needed.

2.1.5 Results.

The perceptual switch rate for all conditions were inferred from the pursuit eye movement patterns. The direction of smooth pursuit phases in OKN typically corresponds to the motion direction that dominates the perceptual appearance (Frässle et al., 2014; Fujiwara et al., 2017). Here, we first removed the blinks, saccades, signal losses and artefacts to acquire a concatenated signal of smooth pursuit. Then we identified the periods of smooth pursuit that matches the direction and the speed of the moving stimuli and interpolated the other periods according to the periods before and after.

The perceptual switch rate from the key press report and that inferred from the OKN were analyzed (see Figure 4). The inferred switch rate was not different from the reported switch rate for both the rivalry condition (reported active rivalry: *M* = 16.50, *SD* = 11.02; inferred active rivalry: *M* = 17.79, *SD* = 6.09; *t* (6) = 0.60, *p* = 0.57) and the replay condition (reported active replay: *M* = 16.93, *SD* = 11.22; inferred active replay: *M* = 16.07, *SD* = 9.52; *t* (6) = 0.88, *p* = 0.41). The reported rivalry and reported replay conditions also did not show significant difference (*t* (6) = 1.00, *p* = 0.36). The inferred replay conditions have indifferentiable rate of perceptual switches (paired sample t-test: *t* (6) = 0.80, *p* = 0.46), showing that the number of switches inferred from the eye movements were not influenced by the tasks. Then a repeated measures ANOVA was conducted to compare the inferred switch frequency with the stimuli factor (rivalry or replay) and the task factor (report percept or report dot size). We found a task main effect and the interaction being close to significant (task factor: *F* (1,6) = 21.16, *MSE* = 2.00, *p* = 0.004; stimuli factor: *F* (1,6) = 0.06, *MSE* = 12.72, *p* = 0.82; interaction: *F* (1,6) = 29.01, *MSE* = 5.39, *p* = 0.05). The switch rate of the rivalry condition with attention task was lower than the rivalry condition with report task (*t* (6) = 3.33, *p* = 0.02), probably because the attention to perceptual switches, compared to attention to a different attribute of the rivalry stimuli, accelerates the perceptual switches more.

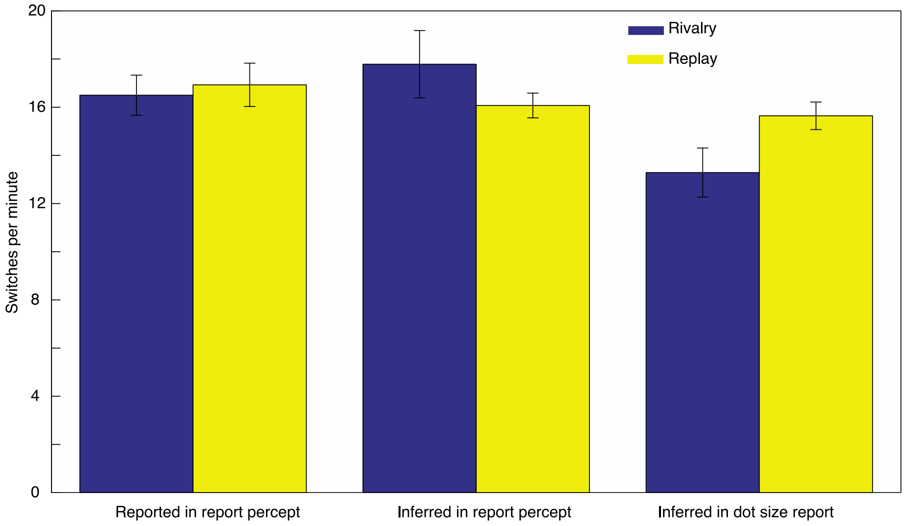

Figure 4. The switch frequency results of the pilot experiment.

2.1.6 Discussion.

The pilot experiment has confirmed the feasibility and validity of using eye movement to infer the perceptual switches. Interestingly, the perceptual switch frequency decreased when participants' attention was directed to a feature of the rivalry stimuli that is irrelevant to the percept identification, indicating that feature-based attention on the percept-defining features can facilitate the rivalry switch frequency.

2.2 Main Experiment

The general methodology of the main experiment is similar to the pilot experiment except that the attention allocated to the visual stimuli were designed more systematic to understand the effect of attention withdrawal on BR.

2.2.1 Participants.

Ten participants have finished their participation of this experiment (4 male and 6 females; age: *M* = 24.09, *SD* = 3.11, range 20-30). All the participants were students of Michigan State University who were naive to the purpose of the experiment. They were compensated at the rate of $10/hour and signed a consent form before participation. All experimental protocols were approved by the Institutional Review Board at Michigan State University.

2.2.2 Stimuli.

The visual stimuli have been slightly modified but kept generally similar to the pilot experiment. The number of dots presented were halved to be 78 and the color of the dots were changed (magenta for one eye and blue for the other with equal luminance) to increase the visibility of the perceptual switches. Both the binocular rivalry condition and the replay condition share the same visual stimuli with the pilot experiment.

The auditory stimuli consisted of pure tones (frequency: 200 Hz; duration: 200ms) and sound pips (frequency: 10000 Hz; duration: 200ms). Target pure tones were louder than normal pure tones (10 percent of the maximum volume) and occurred randomly once every 6 seconds. The target pure tones were not presented after another target pure tone. The sound pips were played between two pure tones randomly on average once every 3 seconds. In 50% of the instances, the sound pip occurred right after a target pure tone. All the auditory stimuli had a maximum sound pressure level at 74 dB.

2.2.3 Procedure.

At the start of each block, participant aligned the stimuli on the two computer screens and performed 9-point calibration and validation of the eye tracker. The instruction screen appeared to remind the participants about which task they are performing for the current block. Every trial started with a drift correction for three attempts. If all three attempts failed, another calibration and validation were conducted.

Participants' tasks were designed as a modulation of attention on the rivalry or the replay stimuli: active percept report task, passive viewing task, and the distraction attention task. In the active report task, same with the pilot experiment, observers pressed one of the three keys to indicate percept change to moving left, moving right, and a mixture of both in the percept report condition. In the passive viewing task, participants were exposed to the visual and auditory stimuli. According to previous literature, actively reporting the perceptual changes can increase the perceptual switch rate (Naber et al., 2011). In the distraction attention task, observers reported when hearing the pure tone louder than the other tones. The loudness difference was staircased at 75% accuracy in the attention condition.

The binocular rivalry condition with the percept report task was the first block for participants in order to obtain the sequence information needed for the replay, and the order of other blocks were assigned randomly. Each block has 24 trials with random durations (range 20-60 seconds, average 40 seconds). It took about 25 minutes to finish one block including the rests, which participants were encouraged to take between trials.

At the end of each trial, participants reported the percept they experienced at the end of the trial by pressing one of three keys to indicate the dot field moving to the left, the dot field moving to the right, and the mixture of the two motion. Then they reported the confidence of the percept judgement on the scale of 1-7. Participants were explicitly instructed to guess the percept with equal chance if they did not identify or remember the percept. This discouraged observers to report mixture when they are not sure about the percept but encouraged them to indicate their low confidence in the proceeding confidence report task. The trial durations were randomized to avoid observers shifting their attention on the perceptual experience in preparation of the percept report task.

Data Analysis and Results for the incomplete dataset of Part I.

The perceptual switches in the rivalry conditions were inferred with the same methods in the pilot experiment. The reported switch frequency and the inferred switch frequency were similar in both the active rivalry condition (t (9) = 1.62, p = 0.14) and the active replay condition (t (9) = 1.46, p = 0.17), confirming the consistency between reported switch rate and the inferred switch rate. Furthermore, the replay conditions in all three attention conditions had indistinguishable level of switch frequency (repeated measures ANOVA with the attention factor: F (2,18) = 2.77, MSE = 5.41, p = 0.09), providing further evidence on the accuracy of the switch frequency inference from the OKN (see Figure 5).

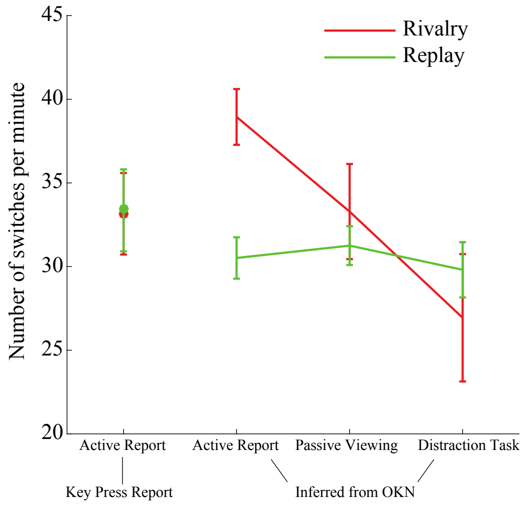

Figure 5. The reported and inferred switch frequency of both the rivalry and replay conditions as a function of attention conditions: active report of percept, passive viewing of the stimuli, and distraction task condition.

A repeated-measures ANOVA was conducted to test the effect of attention (active report, passive viewing, and distraction task) and stimuli (rivalry and replay) on the inferred switch frequency (Stimuli: *F* (1,18) = 0.82, *MSE* = 170.43, *p* = 0.39; Attention: *F* (2,18) = 9.46, *MSE* = 22.92, *p* = 0.002; Interaction: *F* (2,18) = 6.11, *MSE* = 29.36, *p* = 0.02). The attention effect was majorly driven by the rivalry conditions: the attention rivalry condition had a switch frequency significantly lower than that of the active rivalry condition (*p* = 0.029 with Bonferroni correction) as well as the switch frequency of the passive rivalry condition (*p* = 0.030 with Bonferroni correction). The interaction showed that the trend of the switch frequency of rivalry conditions is different from that of the replay conditions (see Figure 5). Specifically, the active rivalry condition had a higher switch frequency than the active replay condition (*t* (9) = 3.14, *p* = 0.012).

The number of mixture percept reported at the end of each trial was analyzed with repeated-measures ANOVA. Participants reported more mixture percepts by the end of the trial in rivalry conditions than replay conditions (Stimuli: F (1,18) = 5.98, MSE = 15.67, p = 0.037; Attention: F (2,18) = 1.12, MSE = 6.38, p = 0.35; Interaction: F (2,18) = 0.58, MSE = 8.56, p = 0.58). To further understand the difference between rivalry and replay conditions, paired sample t-tests were conducted between rivalry and replay conditions with the same attention manipulation. There was significantly more report of mixture percepts in the rivalry distraction task condition than that of the replay distraction task condition (t (9) = 2.58, p = 0.03), while the other two attention conditions did not show difference between rivalry and replay.

2.2.4 Discussion for Part I, and an alternative to the existing model account.

Our experiment managed to reduce the interference between the measurements of perceptual experience and the manipulation of the attention task by using OKN to infer the perceptual switches. The perceptual switch rate decreased with the increase of attentional load, verifying previous empirical work (Alais, van Boxtel, Parker, & van Ee, 2010; Paffen et al., 2006). Thus, the computational models were not accurate in the moderate withdrawal of attention and need modifications.

The computational models in question usually simplify the BR system as two units selective to two features (e.g. left tilted grating and right tilted grating), which represents the two images presented to two eyes (J. Brascamp et al., 2013; Dayan, 1998; Laing & Chow, 2001; Seely & Chow, 2011; Wilson, 2003). As a result, the spatial aspect of BR is not explicitly represented, which means that at least the piecemeal type of mixture percept, where observers see complementary parts of the two eyes' images, is ignored in these models. BR is unique in the spatial layout compared to other forms of perceptual bistability: a simultaneous appearance of two percepts in different regions of visual space (Kovács, Papathomas, Yang, & Fehér, 1996) only appears in BR but not in other forms of bistabilities. BR also appears to be the only form of bistabilities that can be abolished by inattention and the mechanism remains unexplained (Dieter et al., 2016). Considering the concordance of BR's standing in the bistable phenomena, the spatial aspect of BR is hypothesized here to be where attention moderates BR.

As an alternative to existing model accounts, it is hypothesized here that BR occurs relatively independently in different spatial units in the absence of attention, and that attention facilitates the perceptual synchrony between these units of binocular rivalry (see Figure 6). One prediction from this hypothesis is that mixture percepts will occur more often when there is less amount of attention applied to BR stimuli, which was tested in the following analysis. Indeed, the mixture percept reported at the end of the trial was more prevalent in the rivalry distraction condition than the replay distraction condition.

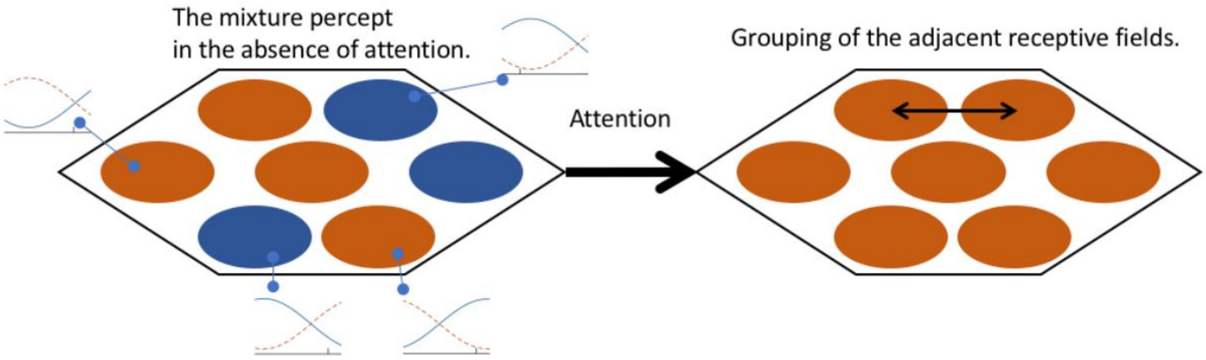

Figure 6. Graphic illustration of the proposed mechanism of attention in binocular rivalry.

Rivalry occurs relatively independently before the application of attention. Attention facilitates the perceptual grouping between adjacent units of BR.

The examination of the proportion of mixture percept under attention withdrawal is difficult to achieve, but previous studies has examined this property of BR in patient populations including attention deficit and hyperactivity disorder (ADHD). The perceived proportion of mixture percept was positively correlated with the severity of the ADHD symptoms (Jusyte, Zaretskaya, Höhnle, Bartels, & Schönenberg, 2018). A degraded attentional state due to the pathological reasons can increase the proportion of mixture percepts, so it is reasonable to infer that moderate attention withdrawal might have a similar consequence.

2.2.5 Data Analysis and Results Part II.

The hypothesis that attention facilitates binding across space of the BR percept would predict that the proportion of exclusive percepts should decrease with the increase of attention load. A distribution analysis of the pursuit eye movement velocity was conducted for each participant to identify the proportion of exclusive percepts in each condition. Based on the presented stimuli in the active replay conditions, the distributions of the pursuit eye movement velocity were obtained for both exclusive percepts and mixture percept. These distributions were standardized to be density functions (i.e. scaled such that the sum of their enclosed areas equaled 1). A regression model was fitted with the density functions of the velocity distribution of all the other conditions as the target variable and the three density functions corresponding to three percepts as the predictors (see equation 1).

$$observedDistribution = \beta_1 rightP + \beta_2 leftP + (1 - \beta_1 - \beta_2) mixtureP \tag{1}$$

$\beta_1, \beta_2 \geq 0 \; and \; \beta_1 + \beta_2 \leq 1$

The beta weights of the regression models could then be interpreted as the dominance proportions of the three possible percepts. β_1 and β_2 are the beta weights corresponding to the two exclusive percepts, thus their sum represents the proportion of exclusive perception. $\beta_1 + \beta_2$ was analyzed across different attention conditions, as a measurement of the proportion of exclusive percepts (see Figure 7a). As suggested in the data (see Figure 7a), with the increase of the attention load, both rivalry and replay conditions showed decreased proportion of exclusive percepts. Trend in the replay conditions, where the on-screen proportion of mixed perception did not actually differ, suggests that the attention load also changed the quality of eye movements, causing an apparent change in the proportion of mixtures. Accordingly, the ratio of rivalry over replay was analyzed to compare the effect in rivalry conditions while accounting for the difference in the replay conditions. A repeated measures ANOVA was conducted to examine the effect of attention on the ratio of the proportion of exclusive percepts (rivalry over replay). A significant attention effect was found (*F* (2,18) = 6.02; *MSE* = 0.07; *p* = 0.01) and the post hoc comparison showed that the difference between active report and distraction task condition was statistically significant (*p* = 0.015 with LSD correction). The data showed that the proportion of the exclusive percepts decreased with the increase of attention load after accounting for the difference in the replay condition. Although the other two pairs of comparisons did not reach statistical significance (active report and passive viewing: *p* = 0.097 with LSD correction; passive viewing and distraction task: *p* = 0.077 with LSD correction), the numerical trend of the effect followed the tentative conclusion.

The variance explained by the regression analyses was higher than 90% for all the rivalry and replay conditions, indicating that our methods can account for most of the variance in the velocity distribution.

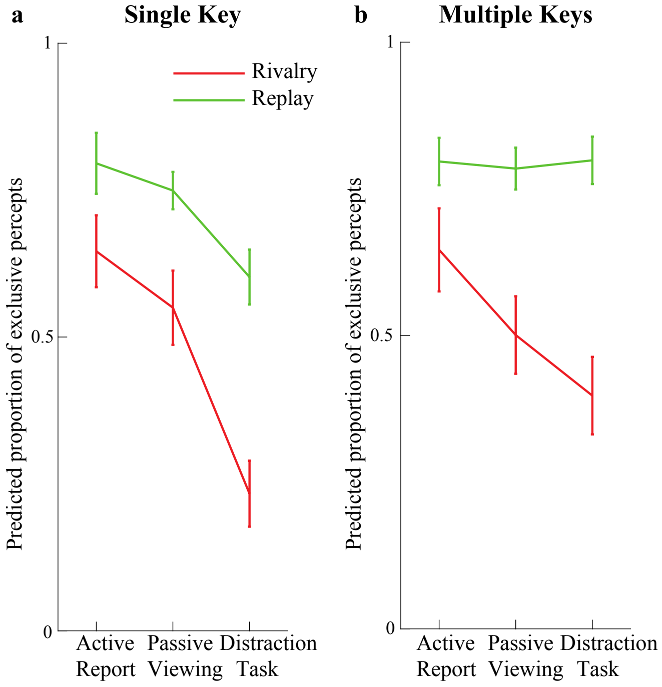

Figure 7. The estimated proportion of exclusive percepts from the regression models.

(a) The estimated proportion of exclusive percepts. (b) Ratio of rivalry over replay conditions of the estimated proportion of exclusive percepts. It is intended for comparing the difference between rivalry conditions accounting for the difference in the replay conditions.

Considering that the attention task might change the eye movement quality, we conducted the same analysis again, now using the corresponding replay conditions as the predictors in explaining each rivalry condition. In other words, the inference of the proportion of percepts during rivalry under a particular attention manipulation was based on the eye movement velocity distributions from the replay condition under the same attention manipulation. This analysis thus controlled for changes in eye movement quality under the influence of attention manipulation.

A repeated-measures ANOVA was conducted to test the effect of attention (active report, passive viewing, and attention distraction task) and stimuli (rivalry and replay) on the inferred proportion of exclusive percepts (Stimuli: F (1,18) = 14.46, MSE = 0.10, p = 0.004; Attention: F (2,18) = 9.46, MSE = 0.02, p = 0.01; Interaction: F (2,18) = 6.86, MSE = 0.02, p = 0.006; see Figure 7b). The replay conditions have higher proportion in the inferred exclusive percepts than the inferred proportion of the exclusive percepts of the rivalry conditions. Paired sample t-tests were conducted to understand the interaction. The active rivalry condition was found to have significantly higher inferred proportion of exclusive percepts than both the passive rivalry conditions (t (9) = 3.17; p = 0.01) and the distraction task conditions (t (9) = 2.85; p = 0.02). The three replay conditions did not differ from each other on the inferred proportion of exclusive percepts, confirming that the attentional effect in the rivalry conditions was not due to the change in eye movement quality. In conclusion, the inferred proportion of exclusive percepts decreased with the increase of attention load for the rivalry conditions but not for the replay conditions.

2.2.6 Discussion for Part II.

Our experiment managed to minimize the interference between the measurements of perceptual experience and the manipulation of the attention task, thus, confirmed the effect of moderate attention on BR (Alais et al., 2010; Paffen et al., 2006): the perceptual switch frequency decreased with the increase of attentional load. More importantly, the results showed that the decreased switch frequency can be attributed to the increased duration of mixture percept according to our distribution separation analyses, which supports the hypothesis we proposed earlier. Here, the hypothesis is further generalized to explain the mechanism of the effect of both moderate and full attention withdrawal on BR.

2.3 A new attention model of BR based on the proposed hypothesis

A new mathematical model based on our hypothesis was constructed and examined in the consistency with empirical evidence and the model by Li et al. (2017). Previous models usually relied on neuron population competition between two opposing features (e.g. left tilted and right tilted gratings) to describe the wax and wane of the two mutually exclusive percepts (J. Brascamp et al., 2013; H.-H. Li et al., 2017; Said & Heeger, 2013; Seely & Chow, 2011; Shpiro et al., 2007; Wilson, 2003). Typically, the two units, representing two populations of neurons, show counter-phase fluctuations, in which the corresponding feature of the unit with a higher amplitude will be taken as the dominant feature, thus deciding the dominant percept. Such structure can represent the alternations of the exclusive percepts but offered no explicit representation of the mixture percept. This basic idea of a pair of competing units will be kept in the new model, but the present model will include multiple such pairs, each covering a certain region of visual space, to account for the spatial dimension of BR. This is similar to what has been done in previous models (Stollenwerk & Bode, 2003; Wilson, Blake, & Lee, 2001). In addition, each unit within a given pair will enjoy facilitation by units in an adjacent pair with the same feature preference; that unit will also experience suppression from adjacent units with different feature preference. The facilitation and suppression both depend on the distance between the receptive fields. Such facilitation and suppression are modulated by attention allocated to the stimuli. As a result, the multi-unit competition setup with attention modulating the perceptual grouping should lead to variations of mixture percepts observed in our experiments.

The model simulation was based on differential equations from Wilson et al. (2001), which is one of few models that considered the interaction between adjacent units of BR. Their model was designed to understand the transition between two exclusive percepts in the form of a traveling wave. Here, we adapted this model for further understanding of the dynamics of the switch frequency in BR.

2.3.1 Methods

The model is fundamentally constructed with several pairs of opposite-feature-selective units responsive to adjacent receptive fields. Each unit receive inhibition from units of opposite feature and the strength of this inhibition is a function of the response level of the inhibiting unit and the distance between the two units' receptive fields. Similarly, units sharing feature selection also facilitates each other as a function of the response level and the distance. Both the inhibition and facilitation terms work jointly in maintaining the status of the perception and facilitating exclusive percepts. To obtain the oscillation dynamics, adaptation was implemented in all units as a suppressive mechanism to allow the suppressed unit to gain dominance.

Model simulations were conducted in Matlab software on an iMac computer using a Runge-Kutta routine with constant step size (0.25 ms). The equations are:

$$\tau \frac{\mathrm{d}R_{ln}}{\mathrm{d}t} = -R_{ln} + \frac{100P_{+}^{2}}{(10 + H_{ln})^{2} + P_{+}^{2}} \quad where\ \tau = 20\ ms \tag{2}$$

$$P = E_l - 0.27 \sum_{k} I_{rk} \exp\left(-\frac{x_{nk}^5}{\sigma^5}\right) + g \sum_{n \neq k} R_{lk} \exp\left(-\frac{x_{nk}^5}{(2\sigma)^5}\right) \tag{3}$$

$$\tau_I \frac{\mathrm{d}I_{ln}}{\mathrm{d}t} = -I_{ln} + R_{ln} \quad where\ \tau_I = 11\ ms \tag{4}$$

$$\tau_H \frac{\mathrm{d}H_{ln}}{\mathrm{d}t} = -H_{ln} + 2R_{ln} \quad where\ \tau_H = 900\ ms \tag{5}$$

R_{ln} is the firing rate of one of the excitatory units driven by the left eye stimulus, I_{rk} and I_{ln} are firing rates of inhibitory units driven by the receptive excitatory units, and H_{ln} is the spike frequency adaptation variable for R_{ln}. The input P to each left eye unit includes a constant E_l representing the stimulus strength, subtractive inhibition from a spatially weighted sum of I_{rk} cells (σ = 1.0 mm), and a term embodying lateral facilitation. The 900-ms time constant for the d*H*/d*t* equation is based on slow after-hyperpolarizing potentials in human excitatory units. The units corresponding to the right eye stimuli were the same with the equations above once denotations for left and right are switched. For simplicity, the units were organized as a ring so that all the units are equivalent with each other in terms of connectivity. If the units are organized as a connected string, the units at two ends will receive different amount of inhibition and facilitation.

The lateral facilitation factor was set as g = 0.02 and 0.04 in Wilson et al.'s model and was adapted here. The first attempt to incorporate attention in Wilson et al.'s model is to directly equate attention as the gain of lateral facilitation. Specifically, we used g = 0.02 and g = 0.04 as the attention modulation implementation. In equation (2), $P_+ =$

$\max(P, 0)$ so that negative input strengths would drive the firing rate to 0. The maximum firing rate of the R_{ln} and R_{rk}were defined to be 100 by convention. Given that Wilson et al. chose 24 for the strength of a weak low contrast stimulus and 30 to be a high contrast stimulus, the effective stimuli strength of the rivaling monocular patterns were set to be $E_l = E_r = 27$, representing a medium contrast stimulus.

The model of the current settings and a model with noise modulation were both simulated. The lack of noise terms made the model deterministic. If the starting level of response for all the same-eye units were the same, no mixture percept will be expected. The model without noise was designed to understand the switch frequency dynamics before the application of noise, and the model with noise was examined on the mixture percept proportion, specifically, the consistency between the experiment above and this model. The noise term was implemented as a random factor in the response units.

2.3.2 Results

The time series of the response functions were simulated first without noise (see Figure 8b & 8c). The lower lateral facilitation gain (g = 0.02) gave rise to a switch frequency of 1.08 times per second, while the higher lateral facilitation gain (g = 0.04) turned out to be 0.88 times per second. After the implementation of the noise, this trend changed (low lateral facilitation gain: 1.56 times per second; high lateral facilitation gain: 1.72 times per second). The proportion of exclusive percepts was lower when the facilitation gain is low than when it is high (low lateral facilitation gain: 98.32%; high lateral facilitation gain: 99.02%).

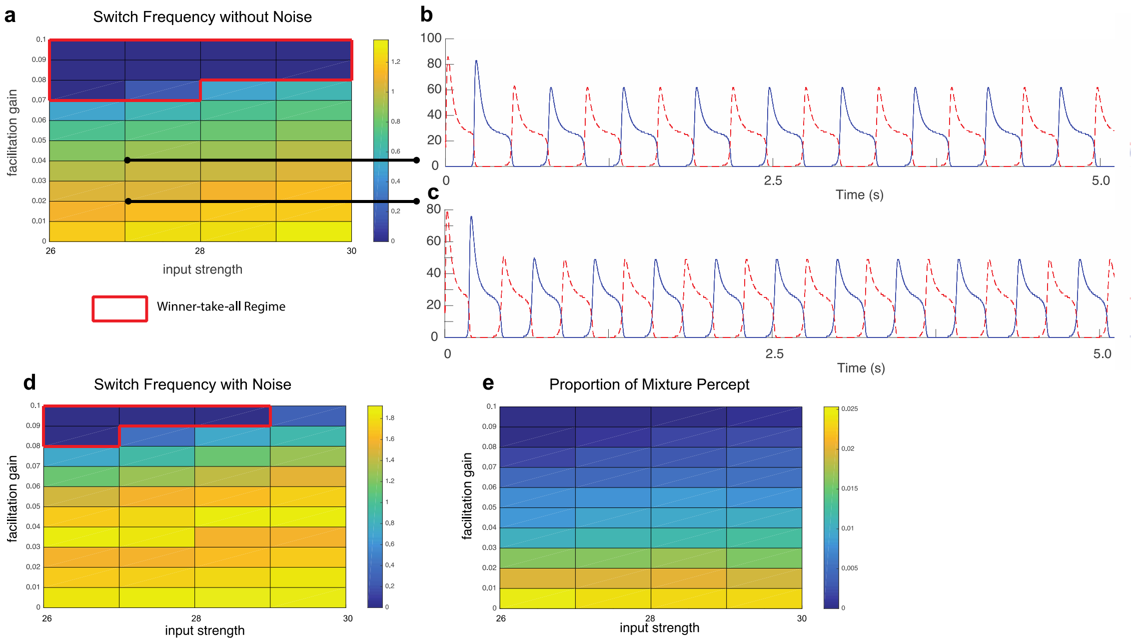

Figure 8. Results of the simulation implementing attention as a modulatory gain of the lateral facilitation.

(a) Perceptual switch frequency as a function of input strength and attentional facilitation gain in the simulation. (b & c) Examples of R_{ln} and R_{rk} as a function of time. (d) The same figure with (a) after implementation of the noise. (e) Simulated proportion of mixture percept as a function of input strength and attention facilitation gain.

The switch frequency trend of this model simulation still shared the same topology of the parameter space with Li et al. that the prediction of the switch frequency is wired the opposite direction from the empirical evidence (see Figure 8a & 8d). Specifically, increased attentional modulation produced decreased in switch frequency.

Simulation over a wide range of parameter values allowed the examination of the overall trend of the switch frequency change. Regardless of noise, the simulated switch frequency increased with the increase of input strength as well as the decrease of the attentional facilitation gain (see Figure 8a & 8d). Even though the pattern seems to be non-monotonic in the condition where noise was implemented (see Figure 8d), the overall trend of this parameter space still remained the same. Also, the oscillation regime with a slower switch frequency was connected with the winner-take-all regime rather than the equal activity regime (see Figure 8d). As a result, this model did not change in the pattern of switch frequency. Meanwhile, the proportion of exclusive percepts increased with the increase of attentional facilitation gain (see Figure 8e). This model can predict the proportion of exclusive percepts decrease with higher attentional modulation, which is consistent with the earlier analysis of the eye tracking data.

2.3.3 Discussion

Adding a spatial dimension to the basic structure of a neuronal competition model, even though it does not result in an accurate prediction regarding the switch frequency pattern, at least results in an accurate prediction regarding the proportion of exclusive percepts. Higher attentional modulation can facilitate the lateral connection between units and result in higher proportion of exclusive percepts. The spatial aspect of BR should be considered in future attention models on BR.

Equating attention with a gain factor of lateral facilitation resulted in increased switch frequency with less attention resources, which is the same erroneous prediction shared by non-spatial neuronal competition models of binocular rivalry. A plausible reason for this erroneous precition here is that the increased strength of lateral facilitation made the maximum response of units higher, resulting in a longer duration for adaptation to wear down the dominant unit. The next simulation explored another possibility of the implementation of attention.

2.4 Attention oscillation model of BR

The literature of voluntary attention has been inspiring on the possibilities of how such a high-level function comes into play in low-level perception. Recent studies revealed visual attention as a rhythmic environmental sampling (Fiebelkorn & Kastner, 2019). Specifically, the sensitivity during covert spatial attention fluctuated in the theta-band activity (3-8Hz) in both the behavioral patterns (Song, Meng, Chen, Zhou, & Luo, 2014) and the attention neural network (Fiebelkorn, Pinsk, & Kastner, 2018; Fiebelkorn, Saalmann, & Kastner, 2013; Helfrich et al., 2018). One recent study found that attention resources allocated to the dominant percept in BR gave rise to a higher sampling rate of that percept (8 Hz) than the sampling rate when attention was distracted (3.5 Hz) (Davidson, Alais, van Boxtel, & Tsuchiya, 2018). Both sampling frequencies happen to fall in the theta band range, thus offering a new approach to the implementation of the attention factor in the model of BR.

The implementation of attention on BR not only concerns which factor attention directly modulates, but also how the amount of attention is defined. This model simulation explores the possibility of attention implemented as a theta band oscillator in the BR model.

2.4.1 Methods

The simulated model was the same as the previous one except adding an oscillation term at the lateral facilitation term and modified the gain factor of mutual inhibition (equation 3 to equation 5).

$$P = E_l - 0.16 \sum_k I_{rk} \exp\left(-\frac{x_{nk}^5}{\sigma^5}\right) + g \sum_{n \neq k} R_{lk} \exp\left(-\frac{x_{nk}^5}{(2\sigma)^5}\right) (1 + \sin(2\pi f t)) \tag{6}$$

2.4.2 Results

The time series of the response functions were simulated first without noise (see Figure 9). The lower frequency oscillation (f = 3.5 Hz) gave rise to a switch frequency of 1.20 times per second, while the higher frequency oscillation (f = 8 Hz) turned out to be 1.36 times per second (see Figure 9b & 9c). After the implementation of the noise, this trend stayed the same (low frequency oscillation: 1.52 times per second; high frequency oscillation: 1.76 times per second; see Figure 9g & 9h). The proportion of exclusive percepts was lower when the facilitation gain is low than when it is high (low frequency oscillation: 80.24%; high frequency oscillation: 88.24%; see Figure 9i).

The parameter space was simulated to examine the overall trend of the switch frequency change. Despite some non-monotonic fluctuations, the switch frequency increased with the increase of attention oscillation frequency (see Figure 9a). When noise is implemented, such trend seems more obvious (see Figure 9f). To further understand the switch frequency dynamic, the average durations of exclusive percepts were also simulated, showing that the increase of attention oscillation frequency resulted in shorter durations of exclusive percepts (see Figure 9e & 9j). Meanwhile, the proportion of mixture percepts decreased with the increase of attentional oscillation frequency (see Figure 9i). This model can predict both the switch frequency dynamics and the proportion of exclusive percepts trend with attentional modulation, which is consistent with the earlier analysis of the eye tracking data.

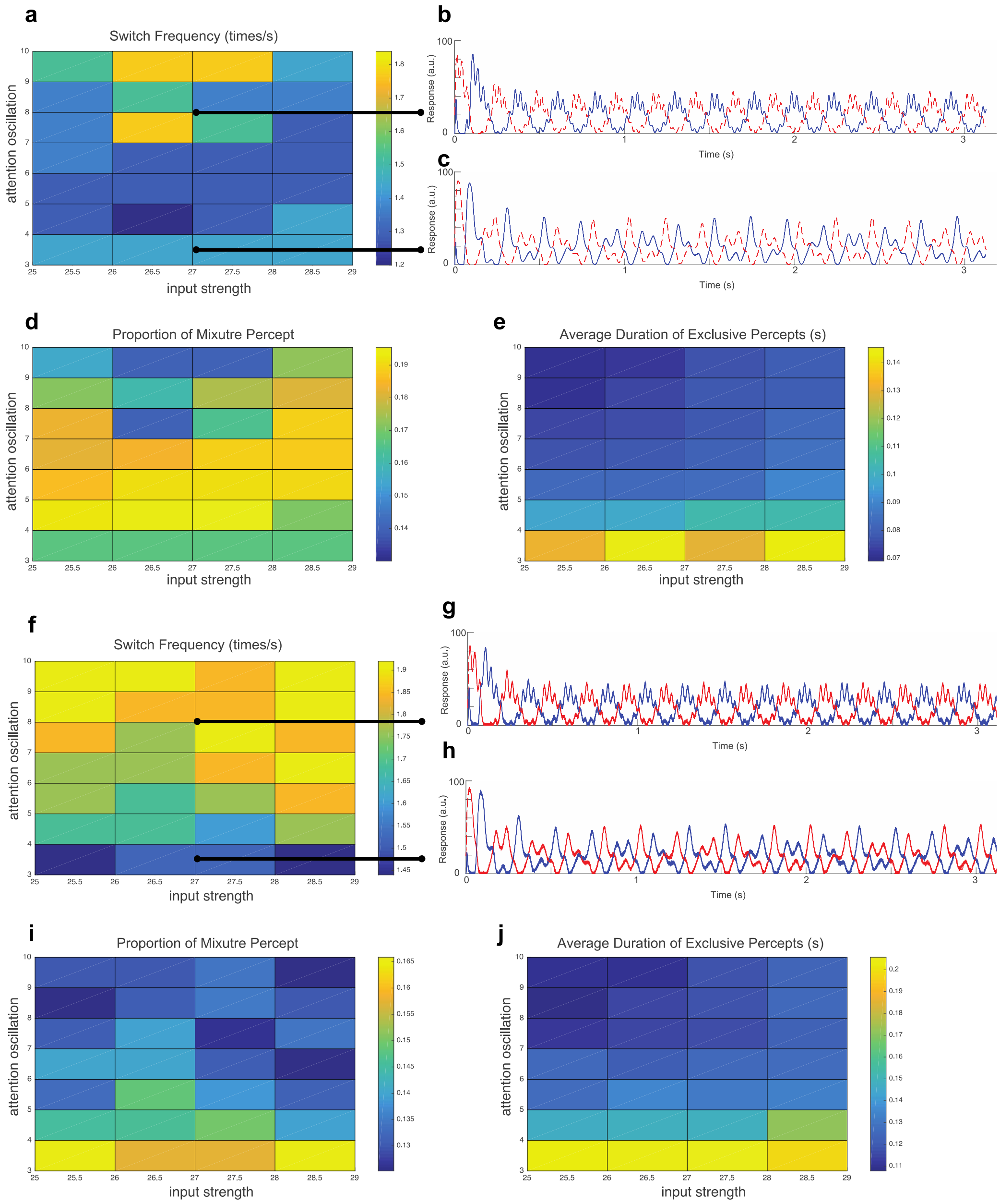

Figure 9. Results of the simulation implementing attention as a modulatory gain of the lateral facilitation without the implementation of noise (a-e) and with noise (f-j).

(a) Perceptual switch frequency as a function of input strength and attentional oscillation frequency in the simulation. (b & c) Examples of R_{ln} *and* R_{rk} as a function of time. (d) Simulated proportion of mixture percept as a function of input strength and attention facilitation gain. (e) Simulated average duration of exclusive percepts. (f) The same figure with (a) after implementation of the noise.

2.4.3 Discussion

The switch frequency dynamics were found to be consistent with the empirical evidence in the topology of the dynamics of switch frequency as well as the proportion of mixture percept, when attention was implemented as an oscillator with the frequency of 3.5 Hz and 8 Hz. The simulated parameter space further demonstrated that such effects were not due to random fluctuations in the parameter space but a generalizable effect. This simulation used attentional oscillator to allow the suppressed units to gain dominance at the trough of the activity of the dominant unit. Higher frequency oscillator thus offered more such opportunities than those of the lower frequency oscillator. Even though this model exerted consistent results with the experiments with moderate attentional withdrawal, the effect of full attention withdrawal cannot be reached by turning attentional oscillation to 0 Hz.

These models only considered the attentional involvement on the lateral facilitation term but not the mutual inhibition term. Both the mutual inhibition and the lateral facilitation facilitate the polarization of the response levels of two units with opposite features, so that the attentional oscillation can also be implemented on the mutual inhibition term without changing the general results.

The method of this simulation is only one of many ways to modify the model to fit the empirical data. As discussed in the previous simulation (2.3), the major reason previous models predicted the switch frequency in the opposite direction under moderate attentional withdrawal, is that the strong suppression and facilitation enable the dominant percept to achieve higher level of response in the dominant units, which takes longer duration for adaptation to flip the dominance. If attention can be applied onto the adaptation that more attention facilitates the accumulation speed of adaptation, the switch frequency pattern observed in empirical work can also be simulated.

3 General Discussion

How does attention modulate binocular rivalry? The current work offered several perspectives of this question. As indicated by the empirical work, the switch frequency of rivalry increases when more attention is applied to the rivalry stimuli, via either feature-based attention manipulation (2.1) or attentional load manipulation in the auditory domain (2.2). The reason why the switch frequency is decreased by moderate attention withdrawal was the decreased proportion of exclusive percepts (2.2). A hypothesis based on the findings above was then raised: attention modulates binocular rivalry by binding the same stimuli across the space. Then mathematical models were deployed to examine whether implementing the spatial domain in the binocular rivalry models can account for both the pattern of switch frequency and the proportion of exclusive percepts. Attention, if modeled as a gain factor of lateral facilitation, can only explain the decreased proportions of exclusive percepts under moderate attention withdrawal but predicted increased switch frequency with attentional withdrawal (2.3). The spatial aspect of BR should be an important building block of any attention model of BR, but it is clearly not the only factor that attention can modulate, and the mechanism of the modulation probably needs further empirical work to determine.

3.1 New mechanism of the effect of attention on BR

We hypothesized that attention facilitates the grouping of adjacent units of BR; thus, it is more likely to observe exclusive percepts with more attention attributed to the rivalry stimuli, as observed in the results. Meanwhile, more attention allocated to the rivalry stimuli can increase the proportion of exclusive percepts and reduce the proportion of mixture percept. The decreased switch frequency with more attention load might be a result of the increased duration of mixture percept. In the full attention withdrawal scenario, the rivalry percept, in this hypothesis, becomes an overall mixture percept. Those abolished rivalry in the previous literature, that Zhang et al. (2011) and Brascamp et al. (2012) have reported, might be a result of abolished grouping rather than abolished rivalry. Rivalry might still proceed in the absence of attention in the local spatial units. When attention is applied to the already rivaling stimuli, the percepts of adjacent spatial units are often grouped together, forming exclusive percepts most of the time.

Among all forms of bistabilities, BR has this distinct perceptual state, mixture percept, which was afforded by the spatial attribute of BR. This distinct characteristic of BR compared to other forms of bistabilities coincides with the distinct attentional modulation effect of BR compared to the effect of attention on other forms of bistabilities: only BR, but not other forms of bistabilities, is abolished by inattention (Dieter et al., 2016). This pattern in the literature and our experimental results accentuated the hypothesis that attention contribute majorly to spatial grouping, considering that other forms of bistabilities do not have a spatially ambiguous stage between two percepts. The mixture percept, working as the measurement of spatial grouping, appears to be a mosaic mixture of the two eyes' images and is often observed during the transitions between exclusive percepts. Previous modeling work usually simplify BR so that the spatial dimension has no explicit representation (Laing & Chow, 2001; Seely & Chow, 2011; Shpiro et al., 2007; Wilson, 2003, 2007), so the mixture percepts were ignored or viewed as an unimportant period of BR. Similarly, relevant empirical studies often only collected the data for exclusive percept switches, ignoring mixture percepts (Alais et al., 2010; Paffen et al., 2006). The mixture percept is often a phenomenon that researchers would design the experiments to avoid (Carmel, Arcaro, Kastner, & Hasson, 2010). Here, the characteristics of mixture percept is reviewed for further specifications of our hypothesis.

In empirical studies, a mixture percept is often observed when the rivalry stimuli subtend over a certain size (> 2 degrees; Carmel et al., 2010). Wilson et al. (2001) devised a paradigm to use the mixture percept to measure the propagation speed of one percept gaining dominance and found that the speed of the propagation depends on the cortical distance of V1, indicating that the spatial units of BR are related to the receptive fields in the cortex. The proportion of the mixture percept was found to be positively correlated with the stimulus size and negatively correlated with the retinal eccentricity (Blake, O'Shea, & Mueller, 1992). Considering that the size of receptive fields in the early visual cortex has a consistent property that the peripheral receptive fields are larger than the foveal ones (Dumoulin & Wandell, 2008), it is possible that the size variations of the receptive fields contribute to the resolution of the local visual field, thus higher resolution locus (i.e. the foveal area) can afford more mixture percept. In both Zhang et al. (2011) and Brascamp et al. (2012)'s studies, the rivalry stimuli are larger than the size of the receptive field (Dumoulin & Wandell, 2008) at the corresponding eccentricity (Zhang et al. 15° positioned at fixation, receptive field size: 0.3° at 1° of eccentricity; Brascamp et al. eccentricity: 2.5°, $\sigma = 0.39°$, receptive field size: 0.5° at 2.5° of eccentricity). It is a possibility that the classical rivalry alternation was not abolished but only continued in the unit of the size of the receptive fields.

Inattention, on the other hand, abolished the perceptual grouping of the dominant rivalry percept across space, leaving a mixture percept, which gave rise to the neural and behavioral response pattern as if no rivalry is occurring. Coincidentally, the only experiment that found neural signature of BR in the absence of attention used stimuli shaped as annulus whose width can fit into the size of a single receptive field (eccentricity: 2.1°, width: 1°; eccentricity: 4°, width: 0.8°; Lee et al., 2007).

3.2 Empirical support of the new mechanism

The BR literature provides substantial support for an important role of grouping in BR. Short presentation of the contextual stimuli can prolong the duration of dominance of the BR stimulus that is consistent in feature with the contextual stimuli as well as suppress the duration of dominance of the other stimulus of BR (Dieter, Melnick, & Tadin, 2015; van Lier & de Weert, 2003). The prolonged duration can be further enhanced by collinear contextual stimuli (Dieter et al., 2015).

Our hypothesis is also supported by a study on the attentional modulation of a different form of bistability, structure from motion (SFM), appearing as two dot fields moving to opposite directions around a cylinder ambiguous in the rotation direction. Although SFM does not have a mixture percept, researchers measured the probability two patches of SFM have the same percept with the manipulation of attention (Mareschal & Clifford, 2012). Under the attentional load, the degree of synchronization is significantly lower. Attention facilitates the grouping of the rotation directions of two patches of SFM.

Can attention access the spatial synchronization for BR? Attention needs to obtain the access to the representations of the two eyes' stimuli in order to facilitate the grouping in BR. In other words, our hypothesis requires attention to modulate the neural activities of V1, where there are monocular neurons representing each eye's input. Research showed that spatial attention can affect V1 (Brefczynski & DeYoe, 1999; Gandhi, Heeger, & Boynton, 1999; Hopf, Heinze, Schoenfeld, & Hillyard, 2009; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). More importantly, attention can also modulate the V1 response differently depending on the contextual receptive fields, such as linear facilitation (W. Li, Piëch, & Gilbert, 2004). Some evidence is from the studies of perceptual filling-in. This is a perceptual phenomenon in which one attribute of visual information (i.e. color, brightness, texture) is perceived in a region of the visual field, even though such visual information is only present in the surround (Komatsu, 2006). Filling-in process is by nature a faciliatory interaction across space and the visual material is filled in via the binding across space of the surrounding receptive fields. Empirical evidence showed that attention can facilitate the speed of perceptual filling-in (De Weerd, Smith, & Greenberg, 2006) and also the signals of V1 during the phantom filling-in (Meng, Remus, & Tong, 2005).

The grouping process in the current hypothesis may be related to with the figure filling in process after the figure ground segregation. Previous research on the time course of figure ground segregation showed that the boundary detection occurred before the figure filling-in process. Specifically, the edge detection process occurs earlier in a feedforward fashion receiving input from LGN and sending output to other layers of V1, while, more importantly, the region filling process is a feedback process from higher visual areas (Self, van Kerkoerle, Supèr, & Roelfsema, 2013). This feedback process is modulated by attention (Poort et al., 2012) and is absent when a monkey fails to detect the figure (Supèr, Spekreijse, & Lamme, 2001) or is anesthetized (Lamme, Zipser, & Spekreijse, 1998). This piece of evidence is consistent with our hypothesis that the perceptual grouping is modulated by attention.

The idea that attention facilitates grouping may seem to be contradictory to the other well-known attention effect: center-surround modulation in striate cortex (Carrasco, 2011; Müller & Kleinschmidt, 2004). Here, the attentional effect is particularly proposed to describe the grouping of percept in rivalry, where there are options of percepts to choose. If one receptive field had a dominant percept different from all the surrounding receptive fields, this receptive field is very likely to switch to become the same with the surrounding receptive fields.

3.3 Limitations and Future Directions

The current study, even though intriguing, can still be further analyzed and reexamined. As the modeling work suggested, a simple implementation of attention on the spatial binding cannot fully account for the empirical patterns found in previous literature and the current study. Possible future research is discussed here beyond the current work.

The reliability of the inference of perceptual switching gave rise to one concern. The inferred active rivalry condition had a significant higher switch frequency than that of the inferred active replay cognition, although neither of them was different from the corresponding key press switch frequency. This pattern was found in both previous research (Naber et al., 2011) and the pilot experiment. It is possible that observers' key press report cannot keep up with their perceptual switches, especially for those who have a faster switch frequency. Since the replay conditions were based on the key press report of the active rivalry condition, the switch frequency of all the replay conditions, irrespective of the measurements, tend to be lower than the inferred switch frequency of the active rivalry condition. However, it is also possible that the processing algorithm misclassified some of the nuances in the eye movement as perceptual switches in the active rivalry condition. A new algorithm that interpolated the saccades and blinks with a cumulative smooth pursuit estimation, rather than concatenating the time points without estimation, was found to be more accurate in switch identification than the current method (Aleshin et al., 2018).

A correct account of attentional effects on BR could not simply be achieved by identifying attention with a gain factor on lateral facilitation; however, the spatial domain should be incorporated in future models. Future models should explore how the perceptual grouping is implemented via attention. The wealth of attention literature offers many possibilities: attention can be applied to a spatial location or a feature in the stimuli, the specific allocation criteria of which can be examined in future empirical studies and simulated in future modeling work. Also, other variables in the BR model can be modulated by attention, namely, visual adaptation (Chaudhuri, 1990; Spivey & Spirn, 2000) and the effective stimuli strength (Carrasco, Ling, & Read, 2004). It is also possible to explore the relative contribution of the mechanism of attention on the interaction of these effects. Specifically, the modulatory strength of attention on adaptation, stimuli strength, or perceptual grouping can be simulated to compare to the empirical evidence of rivalry dynamics.

This attention model of BR proposed here can also become a new method in understanding the noise in BR. Modeling of BR typically add stochastic noise after the prediction of visual percepts, but it has been noted that such method can hardly capture the variation of the percept duration in real data (Dieter et al., 2016; Wilson, 2003). In the proposed mechanism, the noise of percept durations can originate from the fluctuations of each group of neurons for the same receptive field. The perceptual grouping then facilitates exclusive percepts, which induced interaction between adjacent populations of neurons and thus more variability in the duration of each exclusive percept.

The perceptual grouping process driven by attention could be the factor accounting for the large individual difference in BR switches. The individual difference in BR switch rate has been a major challenge in understanding BR (Dieter, Sy, & Blake, 2017; Patel, Stuit, & Blake, 2015). Previous modeling work had suggested that adaptation could contribute to the individual difference (Lankheet, 2006; Lehky, 1988; Noest, Ee, Nijs, & Wezel, 2007; Seely & Chow, 2011; Wilson, 2007). However, a recent meta-analysis showed that adaptation strength cannot account for the variability of BR (J. W. Brascamp, Becker, & Hambrick, 2018). Attention could be another candidate factor in explaining the individual difference in BR switch frequency. In the context of the proposed model, the perceptual grouping in BR varies across observers due to the individual differences in visual attention. Indeed, evidence suggested that the structure of the parietal cortex can account for some variance in individual differences in perceptual rivalry (Kanai, Bahrami, & Rees, 2010). The parietal cortex shows transient activations during attention shifts between locations (Corbetta, Shulman, Miezin, & Petersen, 1995; Yantis et al., 2002) or between overlapping objects (Serences, Schwarzbach, Courtney, Golay, & Yantis, 2004). Perceptual switches in various types of perceptual rivalry were also found to coincide with the parietal cortex (Kleinschmidt, Büchel, Zeki, & Frackowiak, 1998; Lumer, Friston, & Rees, 1998). The perceptual grouping mechanism offers another way to test whether attention contributes to the individual difference in BR.

Most of the previous BR models had a simplified BR input: two orthogonal gratings. However, BR should occur between any incompatible images including one simple grating and one natural scene. If attention does contribute to the perceptual grouping of BR, the grouping procedure should occur irrespective of the complexity of stimuli. However, the mutual inhibition structure requires opposing features, which might not operate as well where the rivalry stimuli are not at the same level of processing.

This study interrogated the temporal dynamics of binocular rivalry under various amounts of attention resources available for processing the rivalry stimulus. As an explanation of the observed influence of attention on rivalry's temporal dynamics, this study forwarded the idea that these are an indirect consequence of its influence in the spatial domain. Specifically, attention facilitates the spatial coherence of binocular rivalry, and more importantly, simplifies and unifies the content of visual awareness. One can speculate that this unifying role of attention allows the mind to effectively make sense of the visual input.

REFERENCES

REFERENCES

Alais, D., van Boxtel, J. J., Parker, A., & van Ee, R. (2010). Attending to auditory signals slows visual alternations in binocular rivalry. *Vision Research*, *50*(10), 929–935. https://doi.org/10.1016/j.visres.2010.03.010

Aleshin, S., Jochen-Braun, Kovács, I., & Gergő Ziman. (2018). *Automated analysis of BR-OKN facilitates large cohort studies*. https://doi.org/10.13140/rg.2.2.30856.88323

Bayne, T. (2012). *The Unity of Consciousness* (1 edition). Oxford: Oxford University Press.

Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review*, *96*(1), 145–167. https://doi.org/10.1037/0033-295X.96.1.145

Blake, R., Brascamp, J., & Heeger, D. J. (2014). Can binocular rivalry reveal neural correlates of consciousness? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1641), 20130211.

Blake, R., & Logothetis, N. K. (2002). VISUAL COMPETITION. *Nature Reviews Neuroscience*, *3*(1), 13–21. https://doi.org/10.1038/nrn701

Blake, R., O'Shea, R. P., & Mueller, T. J. (1992). Spatial zones of binocular rivalry in central and peripheral vision. *Visual Neuroscience*, *8*(05), 469–478. https://doi.org/10.1017/S0952523800004971

Boxtel, J. J. A. van, Tsuchiya, N., & Koch, C. (2010). Opposing effects of attention and consciousness on afterimages. *Proceedings of the National Academy of Sciences*, *107*(19), 8883–8888. https://doi.org/10.1073/pnas.0913292107

Brascamp, J., Sohn, H., Lee, S.-H., & Blake, R. (2013). A monocular contribution to stimulus rivalry. *Proceedings of the National Academy of Sciences*, *110*(21), 8337–8344. https://doi.org/10.1073/pnas.1305393110

Brascamp, J. W., Becker, M. W., & Hambrick, D. Z. (2018). Revisiting individual differences in the time course of binocular rivalry. *Journal of Vision*, 20.

Brascamp, J. W., & Blake, R. (2012). Inattention Abolishes Binocular Rivalry Perceptual Evidence. *Psychological Science*, *23*(10), 1159–1167. https://doi.org/10.1177/0956797612440100

Brascamp, J. W., & Naber, M. (2016). Eye tracking under dichoptic viewing conditions: a practical solution. *Behavior Research Methods*, 1–7. https://doi.org/10.3758/s13428-016-0805-2

Brefczynski, J. A., & DeYoe, E. A. (1999). A physiological correlate of the "spotlight" of visual attention. *Nature Neuroscience*, *2*(4), 370–374. https://doi.org/10.1038/7280

Carmel, D., Arcaro, M., Kastner, S., & Hasson, U. (2010). How to Create and Use Binocular Rivalry. *Journal of Visualized Experiments*, (45). https://doi.org/10.3791/2030

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*(13), 1484–1525. https://doi.org/10.1016/j.visres.2011.04.012

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience*, *7*(3), 308–313. https://doi.org/10.1038/nn1194

Chaudhuri, A. (1990). Modulation of the motion aftereffect by selective attention. *Nature*, *344*(6261), 60. https://doi.org/10.1038/344060a0

Cohen, M. A., Cavanagh, P., Chun, M. M., & Nakayama, K. (2012). The attentional requirements of consciousness. *Trends in Cognitive Sciences*, *16*(8), 411–417.

Corbetta, M., Shulman, G. L., Miezin, F. M., & Petersen, S. E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science; Washington*, *270*(5237), 802.

Crick, F., & Koch, C. (1998). Consciousness and neuroscience. *Cerebral Cortex*, *8*(2), 97–107.

Crick, F., & Koch, C. (2003). A framework for consciousness. *Nature Neuroscience*, *6*(2), 119–126. https://doi.org/10.1038/nn0203-119

Davidson, M. J., Alais, D., van Boxtel, J. J., & Tsuchiya, N. (2018). *Attention periodically samples competing stimuli during binocular rivalry*. 25.

Dayan, P. (1998). A Hierarchical Model of Binocular Rivalry. *Neural Computation*, *10*(5), 1119–1135. https://doi.org/10.1162/089976698300017377

De Weerd, P., Smith, E., & Greenberg, P. (2006). Effects of Selective Attention on Perceptual Filling-in. *Journal of Cognitive Neuroscience*, *18*(3), 335–347. https://doi.org/10.1162/jocn.2006.18.3.335

Dieter, K. C., Brascamp, J., Tadin, D., & Blake, R. (2016). Does visual attention drive the dynamics of bistable perception? *Attention, Perception, & Psychophysics*, *78*(7), 1861–1873. https://doi.org/10.3758/s13414-016-1143-2

Dieter, K. C., Melnick, M. D., & Tadin, D. (2015). When can attention influence binocular rivalry? *Attention, Perception, & Psychophysics*, *77*(6), 1908–1918. https://doi.org/10.3758/s13414-015-0905-6

Dieter, K. C., Sy, J. L., & Blake, R. (2017). Individual differences in sensory eye dominance reflected in the dynamics of binocular rivalry. *Vision Research*, *141*, 40–50. https://doi.org/10.1016/j.visres.2016.09.014

Dumoulin, S. O., & Wandell, B. A. (2008). Population receptive field estimates in human visual cortex. *NeuroImage*, *39*(2), 647–660. https://doi.org/10.1016/j.neuroimage.2007.09.034

Engel, S. A., & Tong, F. (2001). Interocular rivalry revealed in the human cortical blind-spot representation. *Nature*, *411*(6834), 195+. Retrieved from Health Reference Center Academic.

Eo, K., Cha, O., Chong, S. C., & Kang, M.-S. (2016). Less Is More: Semantic Information Survives Interocular Suppression When Attention Is Diverted. *Journal of Neuroscience*, *36*(20), 5489–5497. https://doi.org/10.1523/JNEUROSCI.3018-15.2016

Fiebelkorn, I. C., & Kastner, S. (2019). A Rhythmic Theory of Attention. *Trends in Cognitive Sciences*, *23*(2), 87–101. https://doi.org/10.1016/j.tics.2018.11.009

Fiebelkorn, I. C., Pinsk, M. A., & Kastner, S. (2018). A Dynamic Interplay within the Frontoparietal Network Underlies Rhythmic Spatial Attention. *Neuron*, *99*(4), 842-853.e8. https://doi.org/10.1016/j.neuron.2018.07.038

Fiebelkorn, I. C., Saalmann, Y. B., & Kastner, S. (2013). Rhythmic Sampling within and between Objects despite Sustained Attention at a Cued Location. *Current Biology*, *23*(24), 2553–2558. https://doi.org/10.1016/j.cub.2013.10.063

Fox, R., Todd, S., & Bettinger, L. A. (1975). Optokinetic nystagmus as an objective indicator of binocular rivalry. *Vision Research*, *15*(7), 849–853. https://doi.org/10.1016/0042-6989(75)90265-5

Frässle, S., Sommer, J., Jansen, A., Naber, M., & Einhäuser, W. (2014). Binocular rivalry: frontal activity relates to introspection and action but not to perception. *The Journal of Neuroscience*, *34*(5), 1738–1747. https://doi.org/10.1523/JNEUROSCI.4403-13.2014

Fujiwara, M., Ding, C., Kaunitz, L., Stout, J. C., Thyagarajan, D., & Tsuchiya, N. (2017). Optokinetic nystagmus reflects perceptual directions in the onset binocular rivalry in Parkinson’s disease. *PLOS ONE*, *12*(3), e0173707. https://doi.org/10.1371/journal.pone.0173707

Gandhi, S. P., Heeger, D. J., & Boynton, G. M. (1999). Spatial attention affects brain activity in human primary visual cortex. *Proceedings of the National Academy of Sciences*, *96*(6), 3314–3319. https://doi.org/10.1073/pnas.96.6.3314

Giles, N., Lau, H., & Odegaard, B. (2016). What Type of Awareness Does Binocular Rivalry Assess? *Trends in Cognitive Sciences*, *20*(10), 719–720. https://doi.org/10.1016/j.tics.2016.08.010

Helfrich, R. F., Fiebelkorn, I. C., Szczepanski, S. M., Lin, J. J., Parvizi, J., Knight, R. T., & Kastner, S. (2018). Neural Mechanisms of Sustained Attention Are Rhythmic. *Neuron*, *99*(4), 854-865.e5. https://doi.org/10.1016/j.neuron.2018.07.032

Hering, E. (1879). 1942 Spatial Sense and Movements of the Eye English translation by CA Radde (Baltimore, MD: American Academy of Optometry). *Google Scholar*.

Hopf, J.-M., Heinze, H.-J., Schoenfeld, M. A., & Hillyard, S. A. (2009). Spatiotemporal analysis of visual attention. In *The cognitive neurosciences, 4th ed* (pp. 235–250). Cambridge, MA, US: Massachusetts Institute of Technology.

Jusyte, A., Zaretskaya, N., Höhnle, N. M., Bartels, A., & Schönenberg, M. (2018). Binocular rivalry transitions predict inattention symptom severity in adult ADHD. *European Archives of Psychiatry and Clinical Neuroscience*, *268*(4), 373–382. https://doi.org/10.1007/s00406-017-0790-1

Kanai, R., Bahrami, B., & Rees, G. (2010). Human Parietal Cortex Structure Predicts Individual Differences in Perceptual Rivalry. *Current Biology*, *20*(18), 1626–1630. https://doi.org/10.1016/j.cub.2010.07.027

Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, *22*(4), 751–761.

Kleinschmidt, A., Büchel, C., Zeki, S., & Frackowiak, R. S. J. (1998). Human brain activity during spontaneously reversing perception of ambiguous figures. *Proceedings of the Royal Society of London B: Biological Sciences*, *265*(1413), 2427–2433. https://doi.org/10.1098/rspb.1998.0594

Komatsu, H. (2006). The neural mechanisms of perceptual filling-in. *Nature Reviews Neuroscience*, *7*(3), 220–231. https://doi.org/10.1038/nrn1869

Kovács, I., Papathomas, T. V., Yang, M., & Fehér, Á. (1996). When the brain changes its mind: Interocular grouping during binocular rivalry. *Proceedings of the National Academy of Sciences*, *93*(26), 15508–15511.

Laing, C. R., & Chow, C. C. (2001). Stationary Bumps in Networks of Spiking Neurons. *Neural Computation*, *13*(7), 1473–1494. https://doi.org/10.1162/089976601750264974

Lamme, V. A. F., Zipser, K., & Spekreijse, H. (1998). Figure-ground activity in primary visual cortex is suppressed by anesthesia. *Proceedings of the National Academy of Sciences*, *95*(6), 3263–3268. https://doi.org/10.1073/pnas.95.6.3263

Lankheet, M. J. M. (2006). Unraveling adaptation and mutual inhibition in perceptual rivalry. *Journal of Vision*, *6*(4), 1–1. https://doi.org/10.1167/6.4.1

Lee, S.-H., Blake, R., & Heeger, D. J. (2007). Hierarchy of cortical responses underlying binocular rivalry. *Nature Neuroscience*, *10*(8), 1048–1054. https://doi.org/10.1038/nn1939

Lehky, S. R. (1988). An Astable Multivibrator Model of Binocular Rivalry. *Perception*, *17*(2), 215–228. https://doi.org/10.1068/p170215

Li, H.-H., Rankin, J., Rinzel, J., Carrasco, M., & Heeger, D. J. (2017). Attention model of binocular rivalry. *Proceedings of the National Academy of Sciences*, 201620475. https://doi.org/10.1073/pnas.1620475114

Li, W., Piëch, V., & Gilbert, C. D. (2004). Perceptual learning and top-down influences in primary visual cortex. *Nature Neuroscience*, *7*(6), 651–657. https://doi.org/10.1038/nn1255

Lumer, E. D., Friston, K. J., & Rees, G. (1998). Neural Correlates of Perceptual Rivalry in the Human Brain. *Science*, *280*(5371), 1930–1934. https://doi.org/10.1126/science.280.5371.1930

Mareschal, I., & Clifford, C. W. G. (2012). Perceptual entrainment of individually unambiguous motions. *Journal of Vision*, *12*(1), 24–24. https://doi.org/10.1167/12.1.24

Meng, M., Remus, D. A., & Tong, F. (2005). Filling-in of visual phantoms in the human brain. *Nature Neuroscience*, *8*(9), 1248–1254. https://doi.org/10.1038/nn1518

Moradi, F., & Heeger, D. J. (2009). Inter-ocular contrast normalization in human visual cortex. *Journal of Vision*, *9*(3), 13–13. https://doi.org/10.1167/9.3.13

Müller, N. G., & Kleinschmidt, A. (2004). The attentional ‘spotlight’s’ penumbra: center-surround modulation in striate cortex: *NeuroReport*, *15*(6), 977–980. https://doi.org/10.1097/00001756-200404290-00009

Naber, M., Frässle, S., & Einhäuser, W. (2011). Perceptual Rivalry: Reflexes Reveal the Gradual Nature of Visual Awareness. *PLOS ONE*, *6*(6), e20910. https://doi.org/10.1371/journal.pone.0020910

Noest, A. J., Ee, R. van, Nijs, M. M., & Wezel, R. J. A. van. (2007). Percept-choice sequences driven by interrupted ambiguous stimuli: A low-level neural model. *Journal of Vision*, *7*(8), 10–10. https://doi.org/10.1167/7.8.10

Ooi, T. L., & He, Z. J. (1999). Binocular Rivalry and Visual Awareness: The Role of Attention. *Perception*, *28*(5), 551–574. https://doi.org/10.1068/p2923

Paffen, C., & Alais, D. (2011). Attentional Modulation of Binocular Rivalry. *Frontiers in Human Neuroscience*, *5*. https://doi.org/10.3389/fnhum.2011.00105

Paffen, C., Alais, D., & Verstraten, F. A. J. (2006). Attention Speeds Binocular Rivalry. *Psychological Science*, *17*(9), 752–756. https://doi.org/10.1111/j.1467-9280.2006.01777.x

Patel, V., Stuit, S., & Blake, R. (2015). Individual Differences in Temporal Dynamics of Binocular Rivalry and of Stimulus Rivalry. *Psychonomic Bulletin & Review*, *22*(2), 476–482. https://doi.org/10.3758/s13423-014-0695-1

Peirce, J. W. (2007). PsychoPy—Psychophysics software in Python. *Journal of Neuroscience Methods*, *162*(1), 8–13. https://doi.org/10.1016/j.jneumeth.2006.11.017

Peirce, J. W. (2009). Generating stimuli for neuroscience using PsychoPy. *Frontiers in Neuroinformatics*, *2*. https://doi.org/10.3389/neuro.11.010.2008

Poort, J., Raudies, F., Wannig, A., Lamme, V. A. F., Neumann, H., & Roelfsema, P. R. (2012). The Role of Attention in Figure-Ground Segregation in Areas V1 and V4 of the Visual Cortex. *Neuron*, *75*(1), 143–156. https://doi.org/10.1016/j.neuron.2012.04.032

Qian, C. S., & Brascamp, J. W. (2017). How to Build a Dichoptic Presentation System That Includes an Eye Tracker. *JoVE (Journal of Visualized Experiments)*, (127), e56033–e56033. https://doi.org/10.3791/56033

Revonsuo, A. (1999). Binding and the Phenomenal Unity of Consciousness. *Consciousness and Cognition*, *8*(2), 173–185. https://doi.org/10.1006/ccog.1999.0384

Said, C. P., & Heeger, D. J. (2013). A Model of Binocular Rivalry and Cross-orientation Suppression. *PLOS Computational Biology*, *9*(3), e1002991. https://doi.org/10.1371/journal.pcbi.1002991

Seely, J., & Chow, C. C. (2011). Role of mutual inhibition in binocular rivalry. *Journal of Neurophysiology*, *106*(5), 2136–2150. https://doi.org/10.1152/jn.00228.2011

Self, M. W., van Kerkoerle, T., Supèr, H., & Roelfsema, P. R. (2013). Distinct Roles of the Cortical Layers of Area V1 in Figure-Ground Segregation. *Current Biology*, *23*(21), 2121–2129. https://doi.org/10.1016/j.cub.2013.09.013

Serences, J. T., Schwarzbach, J., Courtney, S. M., Golay, X., & Yantis, S. (2004). Control of Object-based Attention in Human Cortex. *Cerebral Cortex*, *14*(12), 1346–1357.

Shpiro, A., Curtu, R., Rinzel, J., & Rubin, N. (2007). Dynamical Characteristics Common to Neuronal Competition Models. *Journal of Neurophysiology*, *97*(1), 462–473. https://doi.org/10.1152/jn.00604.2006

Song, K., Meng, M., Chen, L., Zhou, K., & Luo, H. (2014). Behavioral Oscillations in Attention: Rhythmic α Pulses Mediated through θ Band. *Journal of Neuroscience*, *34*(14), 4837–4844. https://doi.org/10.1523/JNEUROSCI.4856-13.2014

Spering, M., Pomplun, M., & Carrasco, M. (2011). Tracking Without Perceiving A Dissociation Between Eye Movements and Motion Perception. *Psychological Science*, *22*(2), 216–225. https://doi.org/10.1177/0956797610394659

Spivey, M. J., & Spirn, M. J. (2000). Selective visual attention modulates the direct tilt aftereffect. *Perception & Psychophysics*, *62*(8), 1525–1533. https://doi.org/10.3758/BF03212153

Stollenwerk, L., & Bode, M. (2003). Lateral Neural Model of Binocular Rivalry. *Neural Computation*, *15*(12), 2863–2882. https://doi.org/10.1162/089976603322518777

Sun, F., Tong, J., Yang, Q., Tian, J., & Hung, G. K. (2002). Multi-directional shifts of optokinetic responses to binocular-rivalrous motion stimuli. *Brain Research*, *944*(1–2), 56–64.

Supèr, H., Spekreijse, H., & Lamme, V. A. F. (2001). Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nature Neuroscience*, *4*(3), 304. https://doi.org/10.1038/85170

Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron*, *21*(4), 753–759.

van Lier, R., & de Weert, C. M. M. (2003). Intra- and interocular colour-specific activation during dichoptic suppression. *Vision Research*, *43*(10), 1111–1116. https://doi.org/10.1016/S0042-6989(03)00075-0

von Helmholtz, H. N. (1859). On air vibrations in pipes with open ends. *Crelle's J*, *57*, 1132.

von Helmholtz, H. N. (1910). *Physiological optics. Volume III. The theory of the perception of vision*. Dover.(Translated from 3rd German edition, 1910).[rMO].

Wheatstone, C. (1838). Contributions to the Physiology of Vision.--Part the First. On Some Remarkable, and Hitherto Unobserved, Phenomena of Binocular Vision. *Philosophical Transactions of the Royal Society of London*, *128*, 371–394.

Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academy of Sciences*, *100*(24), 14499–14503. https://doi.org/10.1073/pnas.2333622100

Wilson, H. R. (2007). Minimal physiological conditions for binocular rivalry and rivalry memory. *Vision Research*, *47*(21), 2741–2750. https://doi.org/10.1016/j.visres.2007.07.007

Wilson, H. R., Blake, R., & Lee, S.-H. (2001). Dynamics of travelling waves in visual perception. *Nature*, *412*(6850), 907–910. https://doi.org/10.1038/35091066

Wolfe, J. M. (1984). Reversing ocular dominance and suppression in a single flash. *Vision Research*, *24*(5), 471–478. https://doi.org/10.1016/0042-6989(84)90044-0

Xu, H., Han, C., Chen, M., Li, P., Zhu, S., Fang, Y., … Lu, H. D. (2016). Rivalry-Like Neural Activity in Primary Visual Cortex in Anesthetized Monkeys. *Journal of Neuroscience*, *36*(11), 3231–3242. https://doi.org/10.1523/JNEUROSCI.3660-15.2016

Yantis, S., Schwarzbach, J., Serences, J. T., Carlson, R. L., Steinmetz, M. A., Pekar, J. J., & Courtney, S. M. (2002). Transient neural activity in human parietal cortex during spatial attention shifts. *Nature Neuroscience*, *5*(10), 995–1002. https://doi.org/10.1038/nn921

Zhang, P., Jamison, K., Engel, S., He, B., & He, S. (2011). Binocular Rivalry Requires Visual Attention. *Neuron*, *71*(2), 362–369. https://doi.org/10.1016/j.neuron.2011.05.035

Zhang, R., Engel, S. A., & Kay, K. (2017). Binocular Rivalry: A Window into Cortical Competition and Suppression. *Journal of the Indian Institute of Science*, *97*(4), 477–485. https://doi.org/10.1007/s41745-017-0048-y

Zou, J., He, S., & Zhang, P. (2016). Binocular rivalry from invisible patterns. *Proceedings of the National Academy of Sciences*, *113*(30), 8408–8413. https://doi.org/10.1073/pnas.1604816113