

Attention modulation of stimulus rivalry under swapping paradigm

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Abstract. Stimulus rivalry refers to the sustained periods of perceptual dominance that occur when different visual stimuli are swapped at a regular rate between eyes. This phenomenon is thought to involve mainly eye-independent mechanisms. Although several studies have reported that attention can increase image predominance in conventional binocular rivalry, it is unknown whether attention can specifically modulate stimulus rivalry. We addressed this question and manipulated the spatial characteristic of the stimuli to assess whether such an attention modulation could depend on visual processing hierarchy. The results showed that selective attention of stimulus rivalry significantly increased the predominance of the attended stimulus, regardless of the stimulus' spatial characteristics. No effect was observed on the swapping percept. The findings are discussed in the context of recent models attempting to characterize stimulus rivalry between eye-dependent and eye-independent levels.

Keywords: attention, binocular rivalry, stimulus rivalry, eye-dependent mechanisms, eye-independent mechanisms.

1 Introduction

Conventional binocular rivalry occurs when different stimuli filling corresponding retinal regions in each eye promote perceptual alternations of images, in which dominance durations typically follow a gamma density function. Several lines of evidence point toward multiple competition stages through the visual pathway involving eye-dependent and eye-independent mechanisms (Blake & Logothetis, 2002; Tong, Meng, & Blake, 2006; Wilson, 2003), although the relative contribution of both mechanisms is still debated.

Attention modulates rivalry dynamics (e.g., Dieter & Tadin, 2011; Paffen & Alais, 2011), and recent evidence suggests that it might play an important role in allowing competition to take place (Brascamp & Blake, 2012). The effect of selective attention on binocular rivalry is commonly evidenced by enhancing the relative predominance of the attended stimulus (Chong, Tadin, & Blake, 2005; Meng & Tong, 2004), although some studies have also reported a decrease in predominance of the unattended stimulus (e.g., Hancock & Andrews, 2007). Attention modulation is likely to depend on stimulus complexity (Alais, van Boxtel, Parker, & van Ee, 2010) and to increase with ascending visual hierarchy (Lee, Blake, & Heeger, 2007).

In 1996, Logothetis and coworkers reported an influential study in which observers were presented rival visual stimuli that switched between eyes at a regular and fast rate of 3 Hz (i.e., every 333 ms). Under this “swapping” paradigm, the observers experienced either perceptual periods of swapping, aligned with the effective stimulation of each eye, or, more surprisingly, perceptual stability or dominance with durations extending beyond 333 ms (Logothetis, Leopold, & Sheinberg, 1996). The remarkably slow changes in image dominance, occurring when rival flickering stimuli are swapped between each eye, refer to the so-called stimulus rivalry. Although restricted to some spatial

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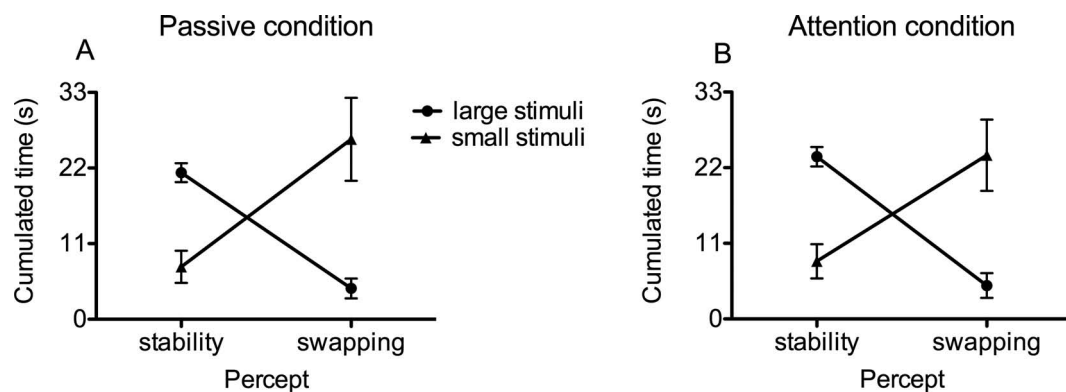


Figure 1. Cumulative duration of stability (leftward/rightward orientation) and swapping in both passive (A) and attention (B) conditions. Error bars represent ± 1 SEM.

and temporal frequencies (Lee & Blake, 1999), these slow changes show similar characteristics with exclusive image alternations, as found in conventional binocular rivalry (Logothetis et al., 1996). More specifically, they exhibit similar unimodal, asymmetric distribution of relative phase durations with a fast growth and long tail gamma distribution fitting. Furthermore, similar changes in mean duration dominance are observed when the strength of one of the rival stimuli is manipulated. Stimulus rivalry is thought to be solved at eye-independent levels (Freeman, 2005; Leopold, & Logothetis, 1999; Logothetis et al., 1996; Wilson, 2003).

In the current study, we tested the hypothesis that attention increases image predominance during stimulus rivalry under a swapping paradigm, and that attention modulation varies as a function of the spatial characteristics of the stimuli. To this end, we used, similarly to Bonnef, Sagi, and Karni (2001), two different sizes of stimuli that may determine the level of processing at which rivalry occurs: Large orthogonal gratings designed to elicit the receptive fields of extrastriate areas, and small orthogonal gratings to preferentially involve early visual processing (see Methods for details).

2 Results

Catch trials in attention conditions were first analyzed to detect subjects with potential response bias. Significant differences ($p < .05$) between leftward and rightward ratios (perceived-time divided by displayed-time, see Methods for details) were found for three participants, which were therefore excluded from the analysis. In accordance with Bonnef et al. (2001), stimulus size resulted in distinct patterns of perception: Large stimuli generated significantly longer periods of stability (leftward and rightward dominances together) than swapping, whereas the opposite pattern was found for small stimuli (Figure 1).

Very similar patterns were found between passive and attention conditions. The following repeated-measure ANOVA was conducted: Session (passive or attention) \times Size (1.4° or 10°) \times Percept (stability or swapping). Results revealed a significant Size \times Percept interaction, $F(1,8) = 37.71$, $p < .001$, but no other interaction (Session \times Size \times Percept: $F(1,8) = .023$, $p = .88$; Session \times Size: $F(1,8) = .29$, $p = .60$; Session \times Percept: $F(1,8) = .159$, $p = .70$) or main effect (Session: $F(1,8) = .01$, $p = .91$; Size: $F(1,8) = 3.87$, $p = .09$; Percept: $F(1,8) = .02$, $p = .89$). Of note, ambiguity periods, which corresponded to about half of the total cumulative time, did not differ between the passive and attention conditions. Although no significant interaction between attention and stimulus size was not found, it is noteworthy that the attention effect tended to be higher for large stimuli (Figure 2B). Indeed, the cumulative time between leftward and rightward percepts was larger for large ($M = 8.9$, $SD = 4.6$) than small stimuli ($M = 3.3$, $SD = 6.7$). The lack of significant difference ($t(8) = 1.98$, $p = .08$) was likely due to the more unstable and variable percepts evoked by the small stimuli.

To assess the effect of attention on the stimulus-cumulated dominance time, the following repeated-measure ANOVA was conducted: Session (passive or attention) \times Size (1.4° or 10°) \times Percept (leftward or rightward) (Figure 2). A significant Session \times Percept interaction was found ($F(1,8) = 20.02$, $p < .01$), as well as a significant main effect of Size ($F(1,8) = 42.39$, $p < .001$) and a significant main effect of Percept ($F(1,8) = 8.51$, $p < .05$). No other significant interaction (Session \times Size: $F(1,8) = .69$, $p = .43$; Size \times Percept: $F(1,8) = 3.29$, $p = .11$; Session \times Size \times Percept: $F(1,8) = 1.25$

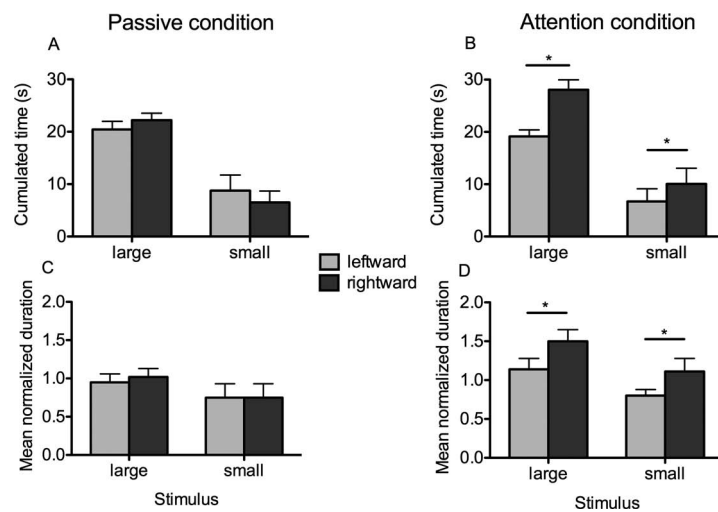


Figure 2. Cumulative time (s) of rightward (attended) and leftward stimuli in the passive and attention conditions per stimulus size (A–B). Mean normalized duration of rightward (attended) and leftward stimuli in the passive and attention conditions per stimulus size (C–D). Error bars represent ± 1 SEM.

$p = .30$) or main effect (Session: $F(1,8) = 1.48$, $p = .26$) was found (Figure 2). Post hoc analysis indicated higher rightward percept compared to leftward in the attention ($t(8) = -4.7$, $p < .01$), but not in the passive condition ($t(8) = .19$, $p = .86$).

A further repeated-measure ANOVA was conducted on the mean normalized duration, which allowed us to better determine whether attention also influences the unattended stimulus (Figure 2). As observed for the cumulated dominance time, a significant Session \times Percept interaction ($F(1,8) = 15.37$, $p < .01$), as well as a significant main effect of Percept ($F(1,8) = 9.51$, $p < .05$), was found. When both passive and attention sessions were compared, attention significantly increased the mean duration of the attended stimulus ($t(8) = -2.51$, $p < .05$), but did not change the unattended one ($t(8) = -.81$, $p = .44$). This pattern was the same regardless of the stimulus size.

Figure 3 illustrates the distribution of the mean normalized duration in the passive and attention conditions. The gamma function fittings in the attention conditions have a lower peak and broader upper tail than those in the passive condition. The Kolmogorov–Smirnov Test revealed that the distributions of the attended stimulus differed significantly between the passive and the attention conditions, for both the large ($d = .40$, $p < .001$) and the small ($d = .37$, $p < .01$) stimuli. No significant difference was found for the unattended stimulus between the passive and the attention conditions, either for the large ($d = .18$, $p = .30$) or the small ($d = .20$, $p = .46$) stimuli.

3 Discussion

In agreement with the results of Bonnef et al. (2001), we found different patterns of percept as a function of the stimulus size in the passive viewing condition. The same pattern was present under the endogenous attention condition, so that attending to one stimulus did not change the swapping duration or the stability as a whole. However, attention modulated the slow changes (stability periods) during stimulus rivalry by increasing the cumulated perceived time and mean dominance duration of the attended stimulus compared to the unattended one. This attention effect was not dependent on the size of the stimulus.

Changes in effective stimulus contrast have been suggested to account for attention control of rivalry (see Paffen & Alais, 2011 for review). In accordance with Levelt's (1968) second law, increasing the contrast of one rival stimulus decreases dominance durations of the other stimulus. While Hancock and Andrews (2007) reported a decrease in the dominance duration of the unattended stimulus, other reports (e.g., Chong, Tadin, & Blake, 2005) found the opposite effect, i.e., an increase in the predominance of the attended stimulus with no significant change to the unattended stimulus. The latter type of effect was found in the current study.

Wilson (2003) proposed that eye-independent competitive mechanisms are recruited during stimulus rivalry because the stimulus flickering used in the swapping paradigm defeats the eye-dependent

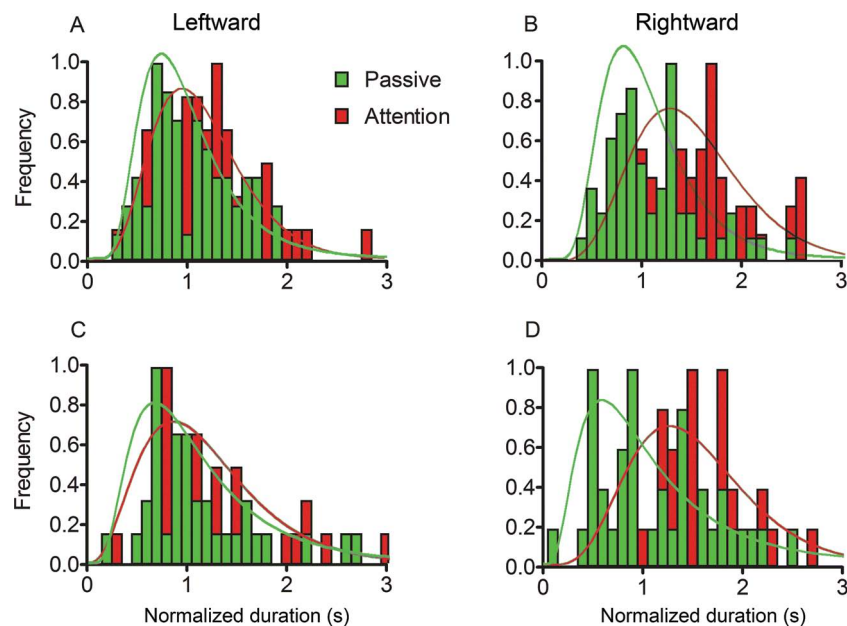


Figure 3. Gamma distributions ($f(x) = 1/(\lambda^k \Gamma(k)) x^{k-1} e^{-x/\lambda}$) of normalized duration in the passive vs. attention conditions for large (A–B) and small (C–D) stimuli. Data on the left and right sides refer to the leftward and rightward orientation stimuli, respectively. Parameters of gamma distribution for large stimuli (A–B): $k = 5.39$, $\lambda = 0.18$ for leftward and $k = 5.73$, $\lambda = 0.18$ for rightward in the passive condition; $k = 5.51$, $\lambda = 0.21$ for leftward and $k = 6.97$, $\lambda = 0.22$ for rightward in the attention condition. Parameters of gamma distribution for small stimuli (C–D): $k = 3.30$, $\lambda = 0.35$ for leftward and $k = 3.02$, $\lambda = 0.36$ for rightward in the passive condition; $k = 3.73$, $\lambda = 0.32$ for leftward and $k = 6.09$, $\lambda = 0.25$ for rightward in the attention condition.

competitive stage. Such an eye-independent feature of stimulus rivalry is thought to rely on high-level processing involving extrastriate areas (e.g., Bonneh et al., 2001; Freeman, 2005), in which the strength of the visual competition processing is likely to be higher (Desimone & Duncan, 1995; Dieter & Tadin, 2011). Interestingly, previous reports have shown an increase of attention modulation in disentangling and prioritizing alternative percepts while ascending the hierarchy of visual processing (Alais et al., 2010; Lee et al., 2007). Although no significant interaction between attention and stimulus size was found in the current study, it is noteworthy that the attention effect tended to be higher for large stimuli (Figure 2B), which preferentially solicit extrastriate processing.

Recently, Brascamp, Sohn, Lee, and Blake (2013) challenged the notion that stimulus rivalry resides at an eye-independent level. Without totally precluding binocular contribution, they proposed a model in which the slow changes in image dominance during stimulus rivalry could be explained by competition at eye-dependent (monocular) level. The model proposes two main types of orientation-tuned inhibition: Inhibition between pools of neurons coding for different eyes but the same orientation, and inhibition between pools of neurons coding for the same eyes but the opposite orientation. Both are characterized by different strengths and scale decays that can be unbalanced by stimuli flickering. Such a stimulus-flickering imbalance tends to favor changes in ocular dominance, resulting in perception of stability periods. In this framework, stimulus rivalry and swapping rely on the same underlying mechanisms in early visual cortex, but with varying strength.

If attention can affect stimulus rivalry, one could predict, according to Brascamp et al. model (2013), an attention modulation on the swapping percept as well, either directly or indirectly through changes of ambiguity; this was not observed here. One may argue, however, that swapping periods cannot be influenced by attention since there is no stable stimulus to attend to when the images alternate at 3 Hz. Although this is indeed a major challenge for attention modulation, it has been reported that even an unaware stimulus can be influenced by attention (e.g., Hancock and Andrews, 2007; Kaunitz, Fracasso, & Melcher, 2011). Therefore, our findings invite future research with other designs to better assess attention modulation in stimulus rivalry as a function of eye-independent and eye-dependent processing.

4 Method

Twelve adults were presented with different images to corresponding regions of the two eyes and were asked to indicate their perception by pressing the corresponding keys on a computer keyboard (leftward dominance, rightward dominance, or swapping), or by not pressing any key during ambiguity.

Similarly to Logothetis et al. (1996), circular orthogonal gratings ($\pm 45^\circ$), flickering at 15 Hz, were swapped between eyes at 3 Hz. To favor the occurrence of exclusive stimulus rivalry, stimuli, displayed on a grey background (60 cd/m^2), were colored in red in one eye and in green in the other. Equiluminance was ensured by heterochromatic flicker photometry. Color and orientation were counterbalanced between eyes. Stimulus size was either 1.4° or 10° in diameter with spatial frequencies of 5.7 or 0.8 cycles/degree, respectively, to keep the duty cycle constant. Stimuli were created with Psykinematix™ and presented through OLED stereoscopic goggles (eMagin Z800, Bellevue, WA).

Dioptic catch trials mimicking the time course of binocular rivalry were used in order to control/correct understanding of the task and potential response bias induced by attention instructions. They were randomized with experimental rivalry trials. On average, perceptual-dominance durations varied according to the stimulus size from 1.6 to 3 s, whereas swapping periods ranged from 10 to 35 s for large and small stimuli, respectively. There were two catch trials in the passive viewing condition (one per type of stimulus) and four catch trials in the attention condition (two per type of stimulus). To assess the performance for each participant in the catch trials, we calculated the ratios between the perceived time and the physically displayed time for both leftward and rightward stability periods. A paired *t*-test between leftward and rightward duration in the attention condition was conducted for each participant.

After 3 min of training, participants started the experiment, consisting of 30 trials of 60 s each split in two sessions. The first session was a passive viewing condition followed by a pause of 10 min. In the second session, observers were instructed to pay attention to the rightward stimulus ($+45^\circ$) and, once perceived, to try to maintain the percept as long as possible. The cumulative time and the mean normalized duration (in s) were used as dependent variables in the ANOVA analyses. For each observer, normalized dominance durations were calculated by dividing the duration of each reported percept (leftward or rightward) by the mean dominance duration (all stability percepts in all viewing conditions) for that observer. Gamma distribution fitting was applied to the data using mean-normalized dominance durations in accordance with the literature. All the statistical analyses were performed using SPSS 20 (SPSS Inc., Chicago, Illinois).

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