Shifting eye balance using monocularly directed attention in normal vision

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In binocular vision, even without conscious awareness of eye of origin, attention can be selectively biased toward one eye by presenting a visual stimulus uniquely to that eye. Monocularly directed visual cues can bias perceptual dominance, as shown by studies using discrete measures of percept changes in continuous-flash suppression. Here, we use binocular rivalry to determine whether eye-based visual cues can modulate eye balance using continuous percept reporting. Using a dual-task versus single-task paradigm, we investigated whether the attentional load of these cues differentially modulates eye balance. Furthermore, both color-based and motion-based cue stimuli, non-overlaid and peripheral to the rivalry grating stimuli, were used to determine whether shifts in eye balance were stimulus specific. Aligned to cue stimulus onset, time series of percept reports were constructed and averaged across trials and participants. Specifically, for the monocular attention conditions, we found a significant shift in eye balance toward the cued eye and a significant difference in the time taken to switch from the dominating percept, regardless of whether the attention stimuli is color based or motion based. Although we did not find a significant main effect of attentional load, we found a significant interaction effect between the attentionally cued eye and attentional load on the shift in eye balance, indicating an influence of monocular attention on the shift in eye balance.

Introduction

In binocular rivalry, two different images are exclusively presented to the two eyes, and the resulting percept alternates between the two images. At times, one will dominate with the other suppressed and at other times a mixture of the two images is perceived (Blake, 1989). By having participants indicate the percept over time, it is possible to measure the weight of the contribution made by each eye. Furthermore, the strength of one eye's contribution to a percept can be modified, such as by adaptation of one eye (Blake, Westendorf, & Overton, 1980), by increasing the stimulus strength in one eye (Blake & Camisa, 1979) or by monocular attention tasks (Lack, 1974; Ooi & He, 1999). Because the presence of an attention-based cue may also effectively increase stimulus strength in one eye, these two effects may sometimes be confounded. Taking care to avoid such confounds, studies have shown that top-down, goal-based attention toward features of one eye's stimulus during binocular rivalry both prolongs its dominance (Chong, Tadin, & Blake, 2005; Ooi & He, 1999) and favors it during initial dominance (Chong & Blake, 2006). Similar feature-based effects are found for bottom-up attention. A monocular cue attracting involuntary attention to one eye can enhance that eye's dominance (Ooi & He, 1999). In addition, binocular attentional cues that are transiently flashed in a location peripheral to the

rivalry stimuli can prolong dominance durations when attentional cue features are congruent to the dominant stimulus, whereas a shift in dominance is promoted when attentional cue features are congruent with the suppressed stimulus (Dieter, Melnick, & Tadin, 2015).

Attention can also be directed monocularly by presenting a visual stimulus to one eye only (Zhang, Jiang, & He, 2012; Zhaoping, 2008). Zhang et al. (2012) used continuous flash suppression to investigate whether directing voluntary attention to one eye produces a monocular attentional effect. A target stimulus (rotating grating increasing in contrast) was presented to one eye and a noise stimulus (flashing Mondrian pattern) to the other. Attention was directed to one eye by presenting a separate visual stimulus, and subjects remained unaware of the eye of origin information. The latency to perceiving the target was reduced when attention was directed to the eye with the target stimulus, whereas it was increased when attention was directed to the eye with the noise stimulus. Moreover, this study reported that attention facilitated by a task related to the attention cues produced a significantly greater effect than attention elicited by stimulus presentation with no task, indicating a role specific to attention rather than simply the stimulus presence incrementing the overall stimulus strength in one eye.

In this study, we aimed to determine whether monocular cues designed to direct attention can shift the balance of contributions between the two eyes, specifically toward the attending eye, using a continuous binocular rivalry paradigm. We aimed to quantify the timeline of these effects, revealing whether they are brief or more extended and whether attention can shift perceptual dominance toward the cued eye. We used a method with a high temporal sampling of percept reports, achieved by using a joystick, in order to capture richer data on the timeline of any changes in percepts over time. Eye dominance measurements during binocular rivalry have been found to be a significant predictor of eye dominance in continuous flash suppression (Wang, McGraw, & Ledgeway, 2019). We anticipated that monocularly directed attention shifts eye balance toward the attentionally cued eye. That is, if the dominant eye is attentionally cued, eye balance shifts toward the dominant eye, and, similarly, if the non-dominant eye is attentionally cued, eye balance shifts toward the non-dominant eye. If both or neither eyes are attentionally cued, we expect there to be no shift in eye balance. Moreover, when eye balance changes occur, we expect that a higher attentional load would lead to greater shifts if attention is the driver of these effects.

Confirming our hypotheses, we found that there was an eye balance shift only in the monocular and not the binocular conditions, with monocularly directed attention shifting eye balance toward the attentionally cued eye, and a greater shift when the attentional load was higher. These changes in dominance were transient and not sustained. Our results suggest that visual cues acting via attentional mechanisms can influence information from monocular channels. Attention may affect parallel monocular pathways that retain eye of origin information in the cortex (Georgeson, Wallis, Meese, & Baker, 2016) and/or affect vision at a subcortical/cortical level where eye-specific modulation can occur (Dougherty, Cox, Westerberg, & Maier, 2019; McAlonan, Cavanaugh, & Wurtz, 2008; O'Connor, Fukui, Pinsk, & Kastner, 2002).

Methods

Participants

Twenty-two healthy observers (10 males, 12 females; 21–66 years of age) participated in Experiment 1, and 17 completed Experiment 1. The remaining five did not complete the experiment due to a lack of availability. We report the data and statistical analyses for the 17 observers who completed all conditions. Five of these 17 observers then participated in and completed Experiment 2. Three of the authors (SPW, ASB, KTM) were observers, and the remaining participants were naïve to the aims of the study. All had normal or corrected-to-normal visual acuity. Participants provided written informed consent. The experiments were performed in accordance with the tenets of the Declaration of Helsinki and were approved by the Research Ethics Board of the McGill University Health Centre.

Apparatus

Stimuli were generated using MATLAB (MathWorks, Natick, MA) and Psychtoolbox (Brainard, 1997). All stimuli were displayed on an ASUS (Taipei, Taiwan) desktop PC with a gamma-corrected 23-inch display. NVIDIA 3D Vision 2 (Santa Clara, CA) was used for stimulus presentation. Stimuli were presented using frame interleaving with synchronized shutter glasses. Each eye was presented stimuli at 60 Hz, for a total refresh rate of 120 Hz. The monitor resolution was 1920×1080 pixels with a mean luminance of 64 cd/m^2. The room was dark during testing with the test screen as the only light source.

Visual stimuli

Eye balance throughout the experiment was measured using binocular rivalry. Stimuli are illustrated
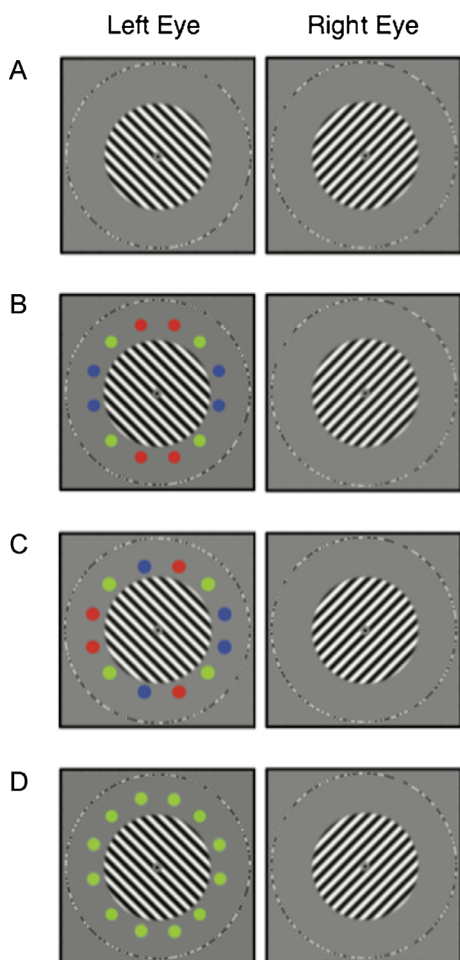
Figure 1. Stimuli presented to the left and right eye during one run in Experiment 1. In this example, attention is directed monocularly to the left eye using the chromatic attention stimuli. Binocular rivalry gratings are shown: (A) without attention stimuli, (B) with the target attention stimuli (colored circles with vertical and horizontal symmetry), (C) with the non-target attention stimuli (colored circles without symmetry), and (D) with the passive attention stimuli (circles of only one color).

in Figure 1. The two rivalry stimuli were gratings of orthogonal orientations, one presented to each eye (Figure 1A), oriented at +45° and –45°, with a diameter of 9.5 degrees of visual angle and spatial frequency of 1.26 cycles per degree at 50% contrast. The edges of the grating stimulus were softened with a raised cosine envelope (0.4° in diameter). The presentation of the two grating orientations was counterbalanced between the two eyes. Participants viewed the screen at a distance of 100 cm, giving a resolution of 60 pixels per degree of visual angle. A binocular fixation ring, 16° in diameter, was placed around all stimuli.

Attention was directed to one eye by presenting an additional visual stimulus to that eye, referred to as the attention cue stimulus. Two different types of

attentional cue stimuli were used: (a) a static ring of colored discs (Experiment 1), and (b) a ring including a global motion stimulus (Experiment 2), chosen to reflect ventral and dorsal stream biases, respectively. All cue stimuli appeared intermittently for 1 second. The delay between cueing stimuli was at least 5 seconds, with an additional delay of x seconds with probability $0.95^{(x/10)}$. The variable cue intervals helped prevent subjects from predicting the time at which the cue would appear.

Procedure

The experiment software sampled the behavioral responses of the subjects every 100 ms. At all times in every condition, participants were instructed to continuously report their grating percepts using a joystick, using only the left–right axis. Horizontal movement to the two extreme positions (left vs. right) represented exclusive grating percepts; for example, with the joystick in the center, the subject was indicating that their percept contained an equal amount of left-oblique and right-oblique content. Joystick positions in between the two extremes represented mixed percepts.

Experiment 1: Cueing with a color symmetry judgment task

In Experiment 1, to investigate the effects of differing attention loads, we included two different attentional cueing conditions: an active condition in which the subject had to perform a secondary task using the cue stimuli and a passive condition in which the cue stimuli were presented without asking the subject to respond to them. There was a further rivalry-only control condition with no cue stimuli, which measured a baseline of the expected rivalry behavior without attentional cues. With the cue stimuli, we would expect that the attention load in the active condition, a dual-task paradigm, would be higher than that in the passive condition, a single-task paradigm. The former should be more difficult than the latter, and the attention load should increase with task difficulty. In the condition without the cue stimuli, we would expect that the attention load would be lowest.

The attention stimuli in Experiment 1 were 12 chromatic discs (0.7° in diameter), presented in a ring surrounding the grating stimulus, 5.6° from the central fixation point (see Figure 1). In the active cueing condition, while maintaining central viewing, participants were asked to covertly monitor the screen during the rivalry task for a brief presentation of the surrounding cue stimulus. Upon presentation of the cue stimulus, the task was to press a button if the stimulus was a target (Figure 1B) and not press the button if it was a catch stimulus (Figure 1C). In target stimuli, the colored circles were arranged with
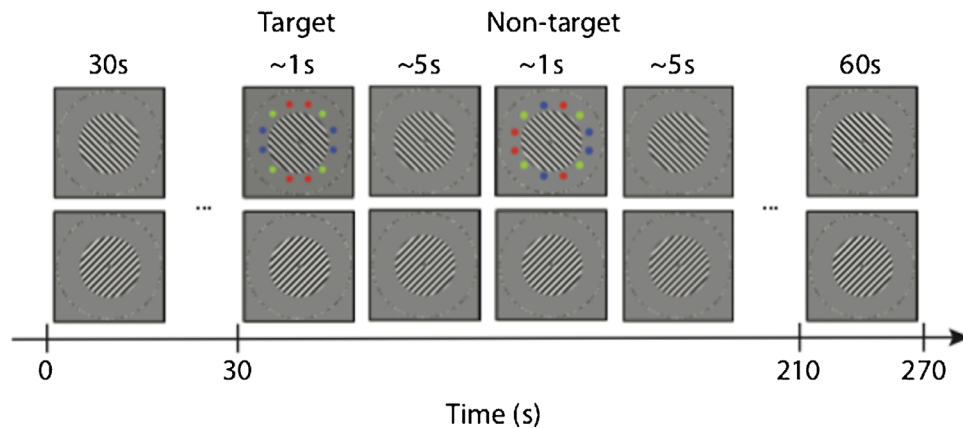
Figure 2. Timeline during one run of active attentional cueing in Experiment 1. The first 30 seconds consist of the rivalry stimuli only, followed by 180 seconds during which an attentional cue can appear. The cues appear for 1 second, with a minimum 5-second gap between each cue and an additional delay of *x* seconds with probability $0.95^{(x/10)}$. The last 60 seconds consists of rivalry stimuli only.

vertical and horizontal color symmetry, and stimuli without that color symmetry were the non-target "catch" stimuli. For each stimulus appearance, there was a 20% chance of being a target stimulus. Audio feedback occurred when a button was pressed during target presentation. Participants used one hand to press the button, located on top of the joystick. This did not impede simultaneous horizontal maneuvering of the joystick. The tone of the feedback indicated whether the subject had correctly identified a target. In the passive attention condition, participants were asked to ignore the cue stimuli. The same stimuli were used, but the circles were all the same color (Figure 1D). This was to prevent subjects from continuing to perform the task "in their head." In the condition of no attentional cueing, participants reported on the grating percept only (Figure 1A); hence, this control condition measured the behavior that occurred due simply to an extended period of binocular rivalry.

We measured behavior in four conditions. In separate blocks, the cue stimuli were presented (a) monocularly to the left eye only, (b) monocularly to the right eye only, (c) binocularly (to both eyes), or (d) monocularly to either the left or right eye, where in each presentation the cued eye was chosen randomly (with equal probability). The example in Figures 1B to 1D shows attention being directed to the left eye.

There were eight possible combinations of attention task condition (active vs. passive) and cued eye condition (left, right, binocular, and random). Each of these conditions and the rivalry-only control condition were tested five times. For each condition, the five repetitions were performed over 5 different days (these were not necessarily consecutive days). Figure 2 shows an example timeline of one repetition of the experiment. The grating stimuli were present continuously throughout the entire 270-second

duration. If the run included the cue stimuli (active or passive), then the time in which these could be presented spanned from 30 seconds until 210 seconds after the trial began. The no-attention (rivalry-only) condition was always the first condition tested in the day, and the order of the other conditions on each day was determined pseudorandomly.

Following is an example of one possible ordering of the nine conditions (one rivalry-only and eight cueing conditions) across 5 days: On the first day, the rivalry-only condition was tested first, followed by the passive random, left, right, and binocular conditions. The active left, binocular, random, and right conditions were then tested. On the second day, the rivalry condition was again tested first, followed by the passive right, left, binocular, and random conditions. The active binocular, right, random, and left conditions were then tested. This was repeated for 5 days, with a different order of conditions each day, with the rivalry condition always tested first, followed by the passive then active cueing conditions.

Experiment 2: Cueing with a motion coherence judgment task

The design of Experiment 2 was identical to that in Experiment 1 except that the attention cue was a motion coherence stimulus presented in an annulus surrounding the grating used for the binocular rivalry task. During the appearance of the attention stimuli, the dots moved within the annulus. The annulus had a width of 0.66°. It was centered 5.6° from the black central fixation point and consisted of 150 monochromatic dots (0.11° in diameter).

As in Experiment 1, participants completed a task in the active condition simultaneously with their binocular rivalry response. The task was to press a
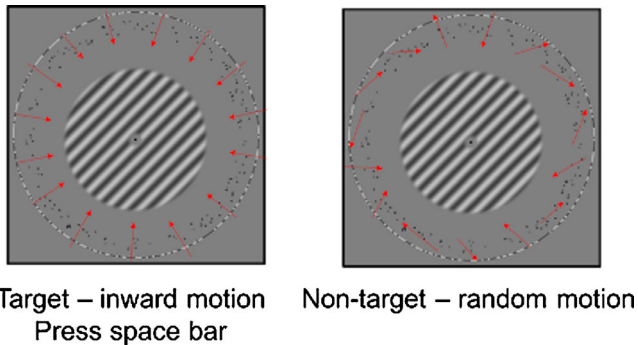
Figure 3. Stimuli with the motion coherence attention cue. The attention stimulus consists of small moving circles with varying grayscale values arranged within a ring peripheral to the grating stimuli. In the target attention stimuli, there is a small subset of circles that have motion toward the center of the screen, whereas the remaining circles have random motion. The non-target attention stimulus consists of circles that all have random motion. Note that red arrows indicate motion direction and do not appear in the stimulus.

button in response to the appearance of the target attention stimuli (Figure 3). For each attention stimuli appearance, there was a 50% chance that the stimuli would be either a target or a catch stimulus. The targets had some proportion of their dots moving in a coherent direction, toward the fixation point, and the remainder of the dots moved randomly. In the non-target catch stimuli, all dots moved randomly. For the target stimuli, the proportion of circles with coherent motion was determined individually for each subject. Before commencing the experiment, we determined each subject's motion coherence threshold. Motion coherence was defined as the proportion of dots that moved toward the center of the display, and threshold was the coherence level required to discriminate coherent from random motion at the 75% correct level. Motion coherence thresholds were obtained by fitting a logistic psychometric function from this two-interval, forced-choice task in Palamedes (Prins & Kingdom, 2018). Thresholds for each subject were measured five times and averaged. In the target, the proportion of circles with motion coherence was set to double the subject's threshold in order to standardize the task difficulty among subjects.

Five subjects, who had also completed Experiment 1, were tested in Experiment 2. As we were interested in whether we could modulate eye balance using a moving achromatic attention stimulus as opposed to a static chromatic attention stimulus, we used only an active and not a passive cueing condition. We also did not test the condition in which the cue was randomly assigned to appear monocularly in either eye, because, from Experiment 1, our analyses showed that results

from monocular eye cuing were similar whether the presentation was random or selected for one eye.

Bootstrapping

We used the same steps for each non-parametric bootstrapping analysis in this paper. For a given dataset, sampling with replacement was done 1000 times. The bootstrapped sample mean was calculated by taking the mean of the 1000 bootstrapped samples. The 95% CI was calculated by ordering the means of the 1000 bootstrapped samples and taking the values from the 2.5 to 97.5 percentile. Group averages for a given metric were found by bootstrapping with replacement from each subject's mean; for example, group averaged curves in the active cueing × dominant eye cueing condition were found by bootstrapping from each subject's average active cueing × dominant eye cueing curves. This means that for each bootstrap iteration we would randomly select N averaged data samples from our N subjects (sampling with replacement).

Analyses and interpretation of data

Determining baseline eye dominance

To characterize participants' baseline eye dominances, we use an ocular dominance index (ODI) metric, calculated from the recorded joystick movements made by subjects reporting their percept of the rivalry gratings. An example of one participant's joystick movement is shown in Figure 4. The ODI was calculated by taking the difference of the joystick curve area representing the left eye percept and the right eye percept over the sum of the areas. This simplifies to:

$$\mathrm{ODI} = \frac{\sum y}{\sum |y|}$$

where y is the joystick position between the two extreme values $-1 \leq y \leq 1$, representing exclusive percepts in the left or right eye, respectively.

Over a particular time period, a positive ODI value indicates right-eye dominance and a negative ODI indicates left-eye dominance (see Figure 4). For a given participant, baseline sensory eye dominance was calculated by averaging the ODIs of the first 30 seconds of all 45 trials (five repeats of nine conditions). Baseline ODIs can be seen in Figure 5 with error bars giving bootstrapped 95% confidence intervals (CIs). Consistent with the literature (Dieter, Sy, & Blake, 2017), right-eye dominance prevailed in our subjects. We used each participant's assigned eye dominance to determine whether the cue was presented to the dominant or non-dominant eye.
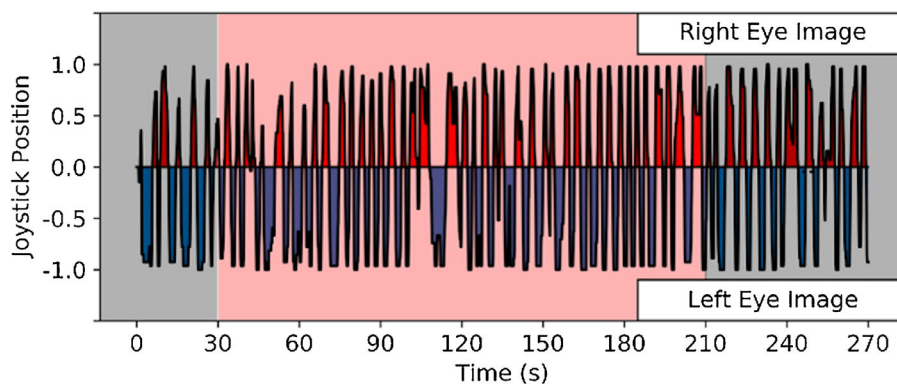
Figure 4. Example joystick positions from one run. Gray-shaded areas represent times when attentional cues are absent and only the grating stimuli are shown. Pink shaded areas represent times when the attentional cueing stimuli appear. Positive joystick positions indicate periods when more of the right eye's grating was dominant relative to the left eye's grating. Similarly, negative values indicate periods when more of the left eye's grating was dominant relative to the right eye's grating. Exclusive percepts are represented by −1 and 1; mixed percepts are represented by values in between.
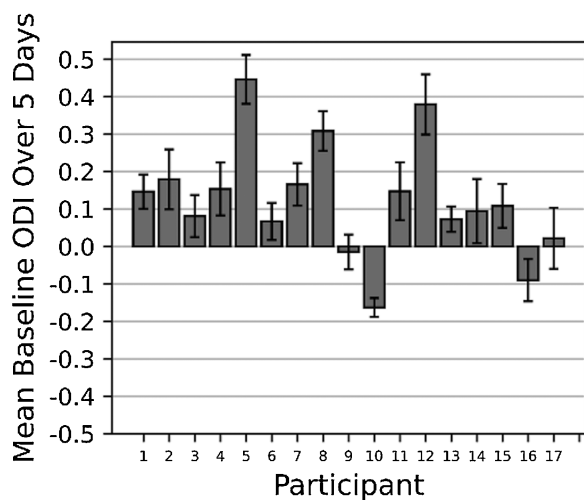

Figure 5. Mean baseline ocular dominance indices over 5 days for each participant from Experiments 1 and 2. Positive values represent right-eye dominance and negative values represent left-eye dominance. Balanced eye dominance is represented by 0. Error bars are the 95% CIs.

Determining eye balance: Time series analysis

We transformed the series of joystick positions (the percept reports) to calculate an eye balance time series representing the variation in eye balance over time. Derived from the eye balance time series, we used two different metrics to characterize changes in eye balance following cue onset: (a) eye balance shift (Figures 6 and 7), and (b) time to percept switch (Figures 8 and 9). For the first, within each eye-cueing condition and for each subject, we took the joystick time series from all days and divided them into epochs based on when the individual cue stimuli were presented.

We aligned these epochs to the attention stimulus onset and averaged across percept reports to obtain a mean eye balance time series for each subject. Because there was no attention stimulus in the rivalry-only condition, the timing of attention stimulus onset from a trial with attention stimuli was used to conduct the analysis. Each group-averaged time series was found by bootstrapping the set of subjects' mean eye balance time series 1000 times with replacement, as described above, and represented as a curve in Figures 6A and 6B and Figures 7A and 7B. Eye balance is shown relative to the subject's dominant eye with positive values and the non-dominant eye with negative values. The greater the magnitude, the greater the shift in balance toward one eye. The bootstrapped 95% CIs of the group-averaged time series were also found. The maximum change in eye balance after cue onset was found for each set of time series for each subject, and group statistical analyses were carried out on this dataset.

The second metric used was the time taken for the rivalry percept to switch after cue onset. The percept that was dominating at the time of cue onset is referred to as the perceiving eye's percept, and the percept that was suppressed is referred to as the non-perceiving eye's percept. To find the time to percept switch in the monocular cueing conditions, we again divided the time series into epochs based on when the individual cue stimuli were presented, but we labeled each epoch according to whether the perceiving or non-perceiving eye was cued. In the binocular condition, every epoch was labeled as binocularly cued because both perceiving and non-perceiving eyes were cued. Group-averaged time series were calculated as before and are shown in Figures 8A and 8B and Figures 9A and 9B. Eye balance is shown relative to the perceiving eye with positive values and the non-dominant eye with negative
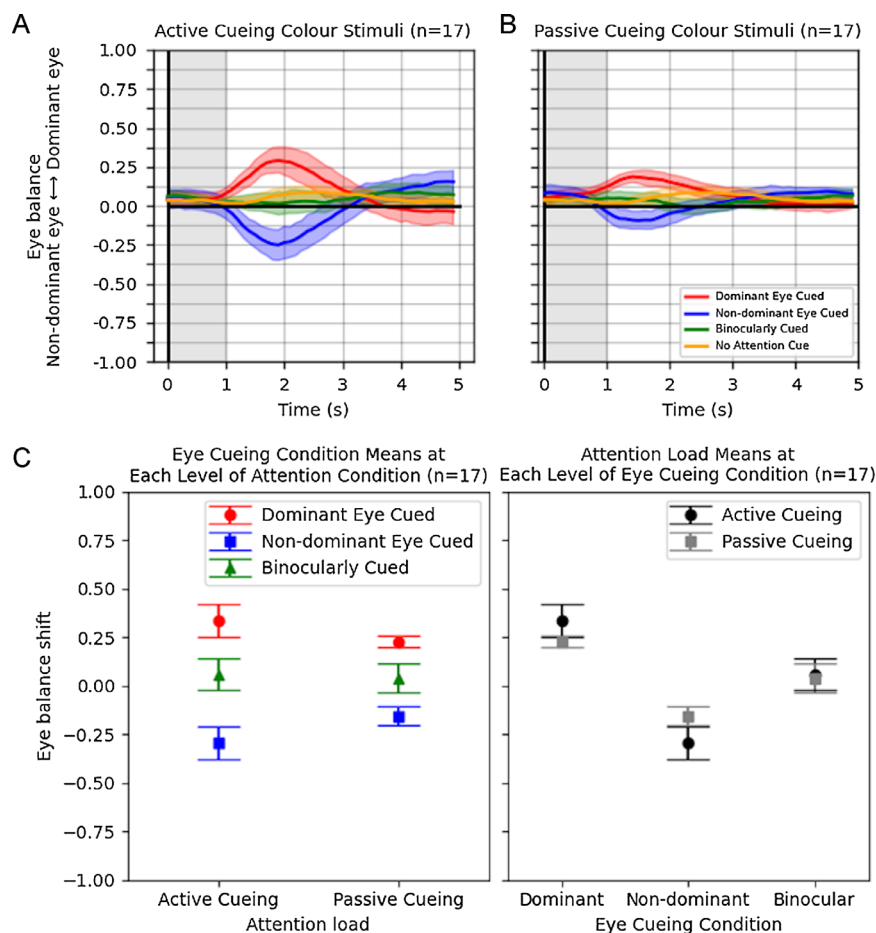
Figure 6. Time series of group averaged eye balances aligned to attention stimuli onset ($t = 0$) in the (A) active cueing condition with color stimuli and (B) passive cueing condition with color stimuli in Experiment 1 ($n = 17$). Within each plot, group-averaged curves are categorized by the eye cueing condition: dominant eye (red), non-dominant eye (blue), binocular (green), and no cueing/rivalry only (orange). The 95% CIs of the group-averaged curves are represented by the colored shaded regions. The gray-shaded region represents the presentation duration of the attention stimuli. Eye balance is shown relative to each participant's dominant eye (DE) with positive values and the non-dominant eye (NDE) with negative values. The greater the magnitude, the greater the shift in balance toward one eye. Non-overlapping shaded regions between conditions for any given time indicate a significant difference. (C) Group mean eye balance shifts by eye cueing and attention condition. Error bars are 95% CIs of the group means. A two-way repeated-measures ANOVA showed a statistically significant main effect for eye cueing condition on the size of the eye balance shifts, $F(2, 32) = 74.376$, $p < 0.01$, $\omega^2 = 0.747$; no statistically significant main effect of attention load on the size of the eye balance shifts, $F(1, 16) = 0.031$, $p = 0.862$, $\omega^2 = 0$; and a statistically significant interaction between attention load and eye cueing condition on the size of the eye balance shifts, $F(2, 32) = 7.077$, $p = 0.003$, $\omega^2 = 0.170$. Post hoc comparisons with Bonferroni correction on eye cueing condition showed significant differences between cueing the dominant eye and non-dominant eye ($p < 0.01$; 95% CI of the difference, 0.379–0.632), cueing binocularly and the dominant eye ($p < 0.01$; 95% CI of the difference, −0.340 to −0.124), and cueing binocularly and the non-dominant eye ($p < 0.01$; 95% CI of the difference, 0.177–0.370). Simple-effect analyses showed a significant difference in the size of eye balance shift between eye cueing conditions at both attention load levels, active cueing ($p < 0.01$) and passive cueing ($p < 0.01$), and a significant difference in size of eye balance shift between attention load levels when the dominant eye was cued ($p = 0.021$) and when the non-dominant eye was cued ($p = 0.012$) but not when cued binocularly ($p = 0.684$).

values, as categorized by the state at cue onset. The x-intercept represents the time of the switch between percepts. The bootstrapped 95% CIs of the group-averaged time series were also found. The time to percept switch after cue onset was found for each set of time series for each subject, and group statistical analyses were carried out on this dataset.

Results

Main results

Our main results for both experiments are analyzed in similar formats. We averaged the eye balance
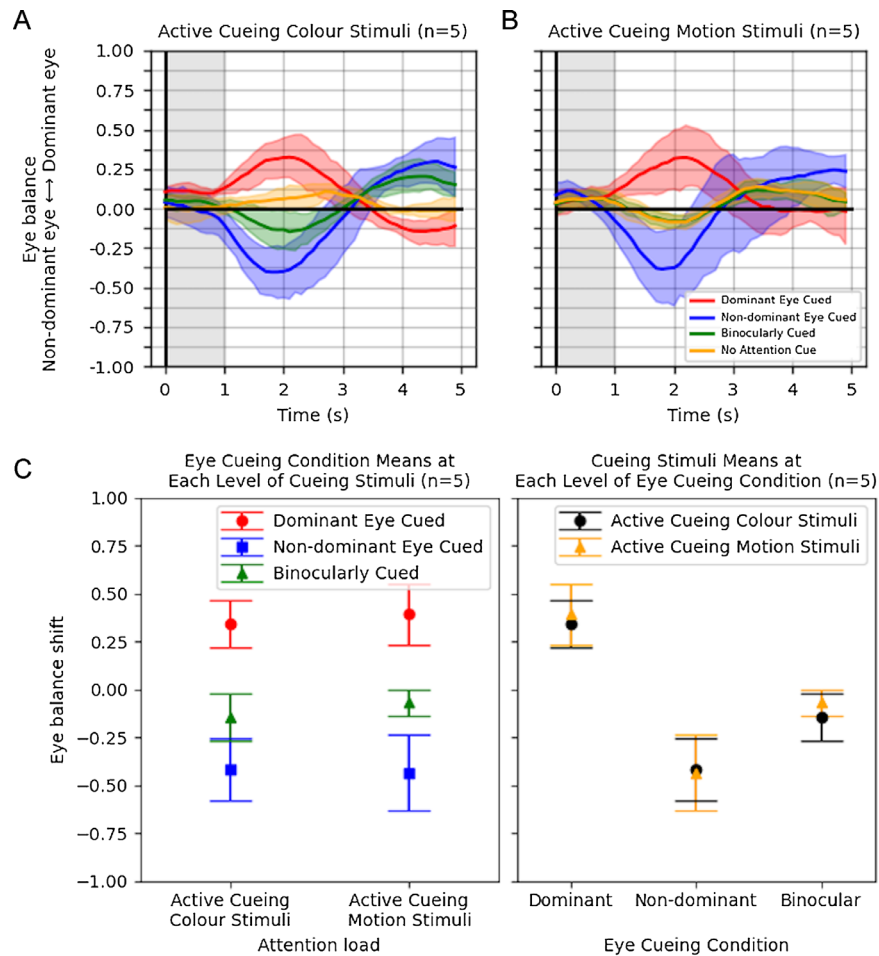
Figure 7. Time series of group-averaged eye balances aligned to attention stimuli onset ($t = 0$) in the (A) active cueing condition with color stimuli and (B) active cueing condition with motion stimuli for subjects who completed all conditions in Experiments 1 and 2 ($n = 5$), plotted as in Figure 6. (C) Group mean eye balance shifts by eye cueing and cueing stimuli conditions. Group means were found by taking the mean maximum eye balance shifts for each subject for each combination of conditions. Error bars are 95% CIs of the group means. A two-way repeated-measures ANOVA showed a significant main effect of eye cueing condition, $F(2, 8) = 20.573$, $p < 0.001$, $\omega^2 = 0.781$; no significant main effect of cueing stimuli condition, $F(1, 4) = 0.385$; $p = 0.569$, $\omega^2 = .000$; and no significant interaction effect, $F(2, 8) = 1.065$, $p = 0.389$, $\omega^2 = 0.005$.

time series, aligned to attention stimulus onset. We performed this analysis separately for each attention and eye cueing condition. In Figures 6 to 9, solid lines are the bootstrapped means across all instances of cue onsets for all participants in an attention condition. The shaded regions are the bootstrapped 95% CIs; if the 95% CIs do not overlap at a given time for two conditions, then there is a significant difference between eye balance at that time relative to cue onset. In Figures 6 and 7, positive and negative values on the *y*-axis represent the dominant and non-dominant eye, respectively. In Figures 8 and 9, positive and negative values on the *y*-axis represent the perceiving eye and non-perceiving eye, respectively, at cue onset. The shaded gray region represents the 1-second duration when the attention stimuli was presented onscreen.

Based on previous findings (Zhang et al., 2012), we hypothesized that the eye dominance would shift toward the eye in which the attention cues were presented. In the binocular condition in which attention was directed to both eyes, we predicted that this would cause no shift in eye dominance. Furthermore, we predicted that this shift would be greater when more attention was directed to one eye, with a greater shift in the active than passive attentional cueing condition. Because we are interested in whether a shift in dominance occurs when attention is directed monocularly versus binocularly, rather than relative to the left or right eye, we display the data relative to the dominant eye and non-dominant eye.

Participant performance on target versus catch stimuli trials was evaluated by calculating the hit rate,
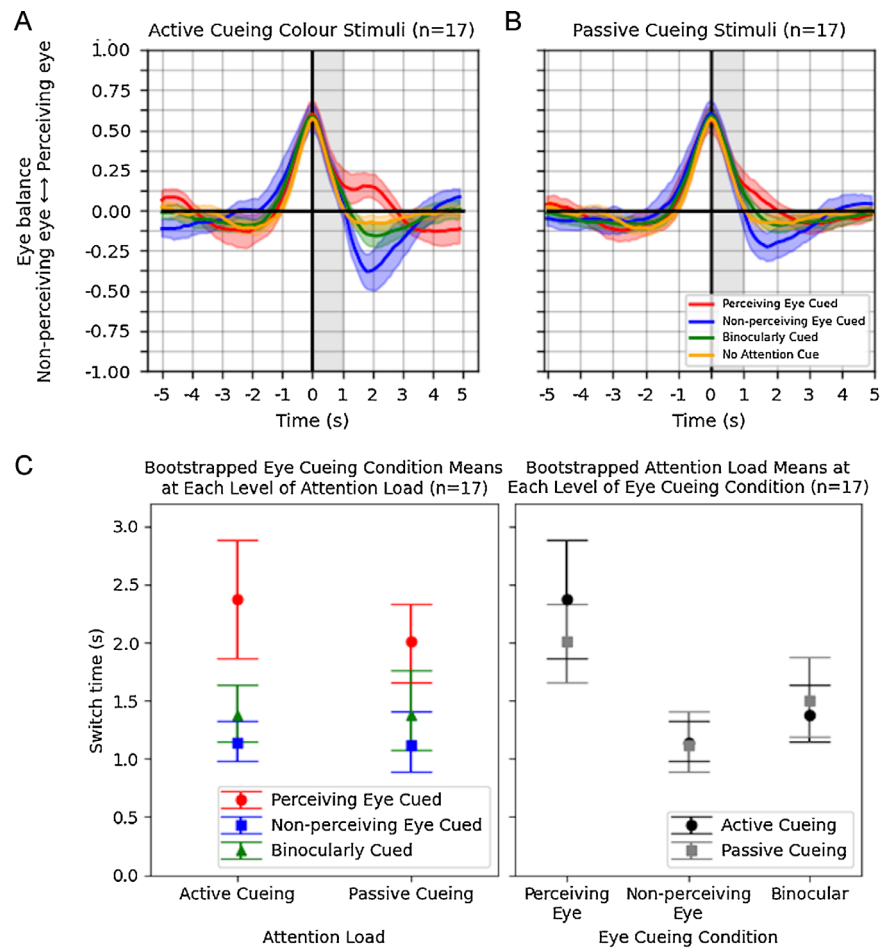
Figure 8. Time series of group-averaged eye balances aligned to attention stimuli onset ($t = 0$) in the (A) active cueing condition with color stimuli and (B) passive cueing condition with color stimuli for subjects who completed all conditions in Experiment 1 ($n = 17$). Time series of eye balances are shown relative to the eye that is dominating the percept (the perceiving eye) at the time of attention stimuli onset, plotted from 5 seconds before until 5 seconds after the attention stimuli onset to illustrate the asymmetry of the time series before and after the cue stimulus. (C) Bootstrapped group mean percept shift times by eye cueing and attention condition. Group means were found by bootstrapping the mean switch times 1000 times with replacement. Error bars are 95% CIs of the bootstrapped mean switch times. Friedman's test showed a significant main effect of eye cueing condition on time to percept switch, $\chi^2(2) = 32.576$, $p < 0.001$, and no significant main effect of attention load on time to percept switch, $\chi^2(1) = 0.346$, $p = 0.556$. Pairwise comparisons using Conover's post hoc test with Bonferroni correction showed that the mean time to change in percept was significantly different between eye cueing conditions when attention was directed to the perceiving or the non-perceiving eye ($p = 0.036$) and no significant difference in time to percept shift between cueing the non-perceiving eye and binocularly ($p = 0.565$) or cueing the perceiving eye and binocularly ($p = 0.649$). The non-parametric Wald-type statistic showed no significant interaction between attention load and eye cueing condition on percept switch times ($p = 0.326$).

taking account of false positives, using the following formula:

$$HR = TP/(TP+FN) - FP/(FP+TN)$$

where HR is hit rate, TP is true positive, FN is false negative, FP is false positive, and TN is true negative. In Experiment 1, 15 participants had hit rates that ranged from 74% to 96%, one participant had a hit rate of 67%, and one participant had a hit rate of 33%.

Although the wide ranges of hit rates indicate that task difficulty varied for each participant, most participants performed well above chance (a corrected hit rate of 0%). In Experiment 2, all five participants had hit rates that ranged from 52% to 76%. Participants could perform the task despite its difficulty.

Previous results have shown modulation of rivalry dynamics by binocularly presented transients to depend on their time of presentation. Specifically, modulatory effects disappear when cue presentations near the end of exclusive dominance periods are excluded
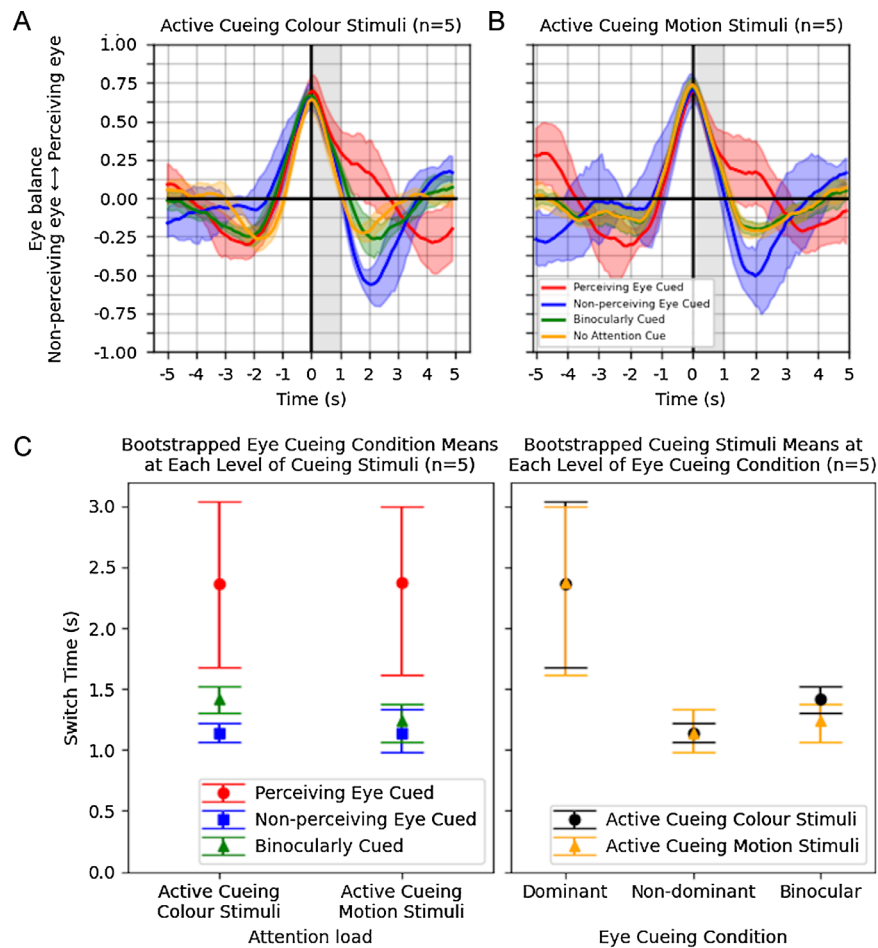
Figure 9. Time series of group-averaged eye balances aligned to attention stimuli onset ($t = 0$) in the (A) active cueing condition with color stimuli and (B) active cueing condition with motion stimuli for subjects who completed all conditions in Experiments 1 and 2 ($n = 5$), plotted as in Figure 8. (C) Bootstrapped group mean percept shift times by eye cueing and attention condition. Group means were found by bootstrapping 1000 times with replacement the mean switch times of the five subjects who completed the active cueing conditions in Experiments 1 and 2. Error bars are 95% CIs of the bootstrapped mean switch times. Friedman's test showed no significant main effect of attention load on time to percept switch, $\chi^2(1) = 0.867$, $p = 0.352$, and a significant main effect of eye cueing condition on time to percept switch, $\chi^2(2) = 12.482$, $p = 0.002$. The non-parametric Wald-type statistic showed a significant interaction between attention load and eye cueing condition on percept switch times ($p = 0.00686$).

(Dieter et al., 2015). However, this was not the case in our experiment. We performed an analysis for the binocular and monocular eye cueing conditions. Contrary to Dieter et al. (2015), excluding cue onsets that occurred near the end or near the beginning of a dominating period did not change our results.

Averaged eye balance time series relative to the dominant eye (Figures 6A, 6B and Figures 7A, 7B) and relative to the perceiving eye (Figures 8A, 8B and Figures 9A, 9B) are shown. Time series are plotted by eye cueing condition—attention directed to the dominant eye (red), non-dominant eye (blue), or both eyes (green)—and the different panels show the attentional cueing condition used (A, active; B, passive). The no-attention (rivalry-only) condition time series (orange) are included as a control comparison and are

identical in the plots for the active and passive cueing conditions (Figures 6A, 6B and Figures 8A, 8B). We opted to exclude the random condition from the figures because we found that, when the eye balance time series were grouped by the eye that was randomly cued within the trial, the results replicated those found in exclusive monocular cueing.

We defined the size of the eye balance shifts as the maximum shift in the curve after cue onset. Interestingly, the dominant eye curve in red and the non-dominant eye curve in blue clearly moved in opposite directions after attention stimuli onset (Figures 6A and 6B). Specifically, when attention was directed to the dominant eye, there was a shift in eye balance toward the dominant eye; similarly, when attention was directed to the non-dominant eye, there

was a shift in eye balance toward the non-dominant eye. In both attention conditions, the green and orange curves, representing binocularly directed attention and no directed attention, respectively, remained relatively flat (close to the $y = 0$ line) after attention stimulus onset.

Using a two-way repeated-measures analysis of variance (ANOVA), we test whether two factors, attention load and eye cueing condition, had significantly different effects on the size of the eye balance shifts. Within attention load there were two levels: active cueing and passive cueing. Within the eye cueing condition there were three levels: dominant eye cued, non-dominant eye cued, and binocularly cued. The mean maximum shift for each subject in each set of conditions was used. Group means of eye balance shift per condition are shown in Figure 6C. Group means were found by taking the mean maximum eye balance shifts for each subject for each combination of conditions.

We found a statistically significant main effect for eye cueing condition on the size of eye balance shift, $F(2, 32) = 74.376$, $p < 0.01$, $\omega^2 = 0.747$. We did not find a statistically significant main effect of attention load on the size of the eye balance shifts, $F(1, 16) = 0.031$, $p = 0.862$, $\omega^2 = 0$; however, we found a statistically significant interaction between attention load and eye cueing condition, $F(2, 32) = 7.077$, $p = 0.003$, $\omega^2 = 0.170$. This suggests that the effects of eye cueing on the size of the eye balance shifts are different depending on the attention load. Post hoc comparisons with Bonferroni correction on eye cueing condition showed significant differences ($p < 0.01$) between all pairs of eye cueing conditions (see legend for Figure 6).

We conducted simple-effects analyses to investigate the effect of attention load at each level of eye cueing condition and vice versa. We found a significant difference in size of eye balance shift between eye cueing conditions at both attention load levels ($p < 0.01$), as well as a significant difference in size of eye balance shift between attention load levels when the dominant eye was cued ($p = 0.021$) and when the non-dominant eye was cued ($p = 0.012$) but not when binocularly cued ($p = 0.684$). This indicates that the eye balance shifts arising from monocular eye cueing are dependent on attention load and appear to be greater in the active cueing condition compared to the passive cueing condition (Figure 6C).

We were interested in whether the size of eye balance shifts differed between the achromatic motion-based and static color-based cueing stimuli. To answer this question, we conducted a two-way repeated-measures ANOVA with two factors, cueing stimuli and eye cueing condition, on eye balance shifts from the five participants who participated in both active cueing conditions in Experiments 1 and 2. Here, cueing stimuli had two levels: color stimuli and motion stimuli. The

eye cueing condition had the same three levels as for the previous ANOVA. Figure 7A shows data from the five subjects who participated in the active cueing condition which are included for comparison with our main results for Experiment 2 in Figure 7B.

We found a significant effect of eye cueing condition, $F(2, 8) = 20.573$, $p < 0.001$, $\omega^2 = 0.781$, but no significant main effect of cueing stimuli, $F(1, 4) = 0.385$, $p = 0.569$, $\omega^2 = 0.000$, and no significant interaction effect, $F(2, 8) = 1.065$, $p = 0.389$, $\omega^2 = 0.005$.

Figure 8 uses the same datasets from Experiments 1 and 2, which are shown in Figures 6 and 7, but they are analyzed and presented differently to illustrate the differential effects of the attention cue when presented to the eye dominating the rivalry percept (perceiving eye) versus the suppressed eye (non-perceiving eye). The time series are taken from 5 seconds before until 5 seconds after attentional cue onset ($t = 0$). On the y-axis, eye balances are represented relative to the eye dominating the percept (perceiving eye) at the time of attentional cue onset. Eye cueing conditions are split by whether attention was directed to the perceiving eye (red), the non-perceiving eye (blue), or to both eyes (green). The no-attention (rivalry-only) condition (orange) is included as a control and represents the average shift in eye balance relative to the perceiving eye 5 seconds before and 5 seconds after some time point selected from the times of attention cueing in a condition with directed attention. In the no-attention (rivalry-only) condition, the tendency for the percept to shift first toward and then away from that of the perceiving eye is illustrated by the vertical symmetry about the y-axis in the no attention (rivalry-only) condition time series. The shape and symmetry are similar when attention is directed binocularly. Notably, however, when attention is directed to the perceiving and non-perceiving eyes, the time series are asymmetrical about the y-axis. Specifically, when the attention cue is directed to the perceiving eye, eye balance toward that eye is prolonged compared to when no cue is presented or if cues are presented to both eyes. When the attention cue is directed to the non-perceiving eye, there is a more rapid shift in eye balance toward the non-perceiving eye, compared to the no cue or binocular cue presentations. The average time series for the active and passive attentional cueing conditions in Experiment 1 are shown in Figures 8A and 8B, respectively. The x-intercept (zero crossing) in Figures 8A and 8B represents the average time at which the percept switched from that of the perceiving eye to that of the non-perceiving eye. Distributions of percept switch times between eyes are shown for the active (Figure 10A) and passive (Figure 10B) color cueing attention conditions in Experiment 1 and for the motion cueing condition in Experiment 2 (Figure 10C). These show how the switch between eyes is delayed if the cue appears in the perceiving eye but is
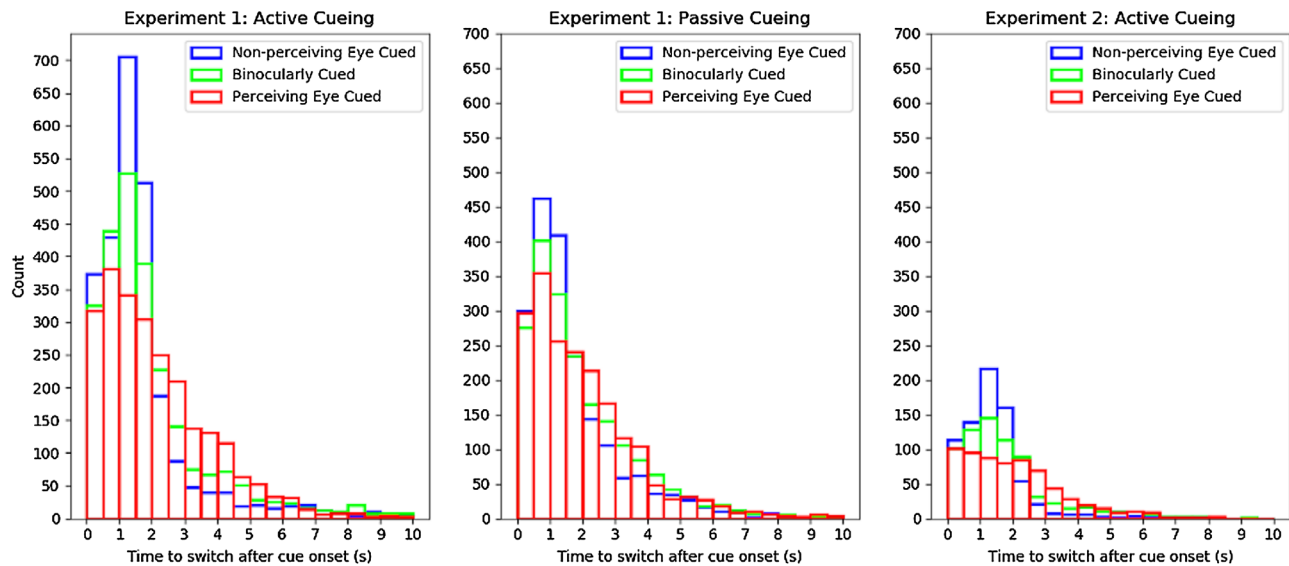
Figure 10. Histogram of switch times from Figure 7 for (A) Experiment 1 active condition, (B) Experiment 1 passive condition, and (C) Experiment 2. Eye cueing conditions are split by perceiving eye cued (red), non-perceiving eye cued (blue), and binocularly cued (green). Consistent with Figures 8 and 9, the distribution for when the perceiving eye was cued (red) includes more switch times that occurred later compared to when the non-perceiving eye was cued (blue). The binocular cue condition (green) does not have a distribution as spread out as when the perceiving eye was cued, nor does it have as great of an early peak in its distribution as when the non-perceiving eye was cued.

hastened if it appears in the suppressed, non-perceiving eye.

We investigated the effect of attention load (active or passive cueing) and attentionally cued eye (binocular, monocular perceiving eye, monocular non-perceiving eye, or no cueing) on the average time from attention stimulus onset to a change in percept (the *x*-intercept). Each data point was calculated from a subject's average time to percept switch for a given condition. From the Shapiro–Wilk's test, we found that some of the groups did not have a normal distribution, so we conducted the Friedman's test, the non-parametric form of a repeated-measures ANOVA. We found that there was a significant main effect of eye cueing condition on time to percept switch, $\chi^2(2) = 32.576$, $p < 0.001$, and no significant main effect of attention load (active or passive cueing) on time to percept switch, $\chi^2(1) = 0.346$, $p = 0.556$. Pairwise comparisons using Conover's post hoc test with the Bonferroni correction showed that the mean time to change in percept was significantly different between eye cueing conditions when attention was directed to the perceiving or non-perceiving eye ($p = 0.036$). However, there was no significant difference in time to percept shift between cueing the non-perceiving eye and binocularly ($p = 0.565$) or cueing the perceiving eye and binocularly ($p = 0.649$). The non-parametric Wald-type statistic showed no significant interaction between attention load and eye cueing condition on percept switch times ($p = 0.326$).

To illustrate group means, we found the bootstrapped mean of percept switch times for each combination of attention load and eye cueing condition, shown in Figure 8C. Mean switch times in Experiment 1 were resampled 1000 times with replacement. Error bars are 95% CIs of the bootstrapped mean switch times. Non-overlapping error bars indicate that there were significant differences between mean switch times when the perceiving eye and non-perceiving eye were cued regardless of attention load.

A graph for the active attentional cueing condition of Experiment 1 (Figure 9A) and data from the five subjects who also participated in Experiment 2 are included for comparison to results for Experiment 2 (Figure 9C). As in Experiment 1, we observed asymmetry in the time series in Experiment 2 when attention was directed to the perceiving eye or the non-perceiving eye (Figure 9C). The transient shift in eye balance toward the attentionally cued eye is present in both the monocular attention conditions. However, this shift was not present when directed binocularly, as it was not differentiable from the average time series of the no-attention (rivalry-only) condition, as indicated by their overlapping 95% CIs.

In Experiment 2, we compared the effect of eye cueing (perceiving eye cued, non-perceiving eye cued, and binocularly cued) on average time after attention stimuli appearance to a switch in the percept (the *x*-intercept). We used the non-parametric Friedman's

test and found a significant main effect of eye cueing condition on time to percept switch, $\chi^2(2) = 6.5$, $p = 0.039$. Pairwise comparisons using Conover's post hoc test with Bonferroni correction showed that the mean time to change in percept was not significantly different between specific eye cueing conditions (non-perceiving and perceiving eye, $p = 0.102$; binocular and perceiving eye $p = 0.316$; binocular and non-perceiving eye $p = 1.000$).

We also compared the effect of using the color or motion stimuli on the percept switch time within the five subjects who completed the active cueing conditions in Experiments 1 and 2. Eye cueing had three levels as before, whereas the cueing stimuli had two levels: color stimuli and motion stimuli. We used the non-parametric Friedman's test and found no significant main effect of cueing stimuli on time to percept switch, $\chi^2(1) = 0.867$, $p = 0.352$. We found a significant main effect of eye cueing condition on time to percept switch, $\chi^2(2) = 12.482$, $p = 0.002$. The non-parametric Wald-type statistic showed a significant interaction between cueing stimuli and eye cueing condition on percept switch times ($p = 0.00686$).

To illustrate group means, we found the bootstrapped mean of percept switch times for each combination of cueing stimuli and eye cueing condition, shown in Figure 9C. Mean switch times of the five subjects who completed all active cueing conditions in Experiments 1 and 2 were resampled 1000 times with replacement. Error bars are 95% CIs of the bootstrapped mean switch times. Non-overlapping error bars indicate that there were significant differences between mean switch times when the perceiving eye and non-perceiving eye were cued regardless of attention load.

Discussion

In this study, we found that monocularly cueing one eye during binocular rivalry briefly shifted perceptual dominance toward that eye. Similar results were obtained whether the attention-related task was static and color based or achromatic and motion based, reflecting ventral and dorsal stream biases, respectively. We found a significant interaction consistent with an influence of attentional load on the size of the shift in eye balance. In a continuous flash suppression experiment, Zhang et al. (2012) found that the time taken to perceive a suppressed target image was decreased when attention was directed to the suppressed eye and increased when attention was directed to the dominating eye, with a greater effect when attention was engaged in a task related to the attention stimuli compared to when there was no task. Here, we also found that monocularly directed attention shifted eye dominance toward the attending eye. Our approach,

rather than using a metric such as reaction time or contrast that captures the percept at a single time point, allowed us to demonstrate the dynamic time course of reported percept changes during binocular rivalry and to capture continuously over time the perceptual consequences of directing attention to one eye. Compared to continuous flash suppression, a tool that confers prolonged invisibility and is insensitive to repeated transient events, binocular rivalry is more useful for studying perceptual bistability and its underlying neural dynamics (Tsuchiya, Koch, Gilroy, & Blake, 2006).

In addition to playing a role in eye balance, attention has been shown to be necessary for binocular rivalry to occur (Brascamp & Blake, 2012; Zhang, Jamison, Engel, He, & He, 2011). An experiment in which the cortical representations of conflicting images were frequency tagged and tracked using electroencephalography showed that rivalry stopped when attention was diverted away from the rivalry stimuli (Zhang et al., 2011). Furthermore, after a period of diverted attention from rivalry stimuli, reported rivalry percepts were found to match those predicted from physical removal of the rivalry stimuli rather than if rivalry continued during inattention (Brascamp & Blake, 2012).

Moreover, attention can influence initial percept dominance, as well as rivalry dynamics. Voluntary and involuntary attention to an image prior to rivalry can prevent the attended image from being suppressed upon initial rivalry onset (Abe, Kimura, & Goryo, 2011; Chong & Blake, 2006; Kamphuisen, van Wezel, & van Ee, 2007; Mitchell, Stoner, & Reynolds, 2004; Ooi & He, 1999). During ongoing rivalry, studies have found that attending to relevant features of a rivalry stimulus can increase dominance durations of the attended stimulus (Chong et al., 2005) or decrease those of the unattended stimulus (Hancock & Andrews, 2007). Also, when attention is diverted to a concurrent task, rivalry alternation rates can be slowed (Paffen, Alais, & Verstraten, 2006). Remarkably, the predominance of an eye-specific stimulus can be increased significantly by training in a perceptual learning task in which features of a rivalry stimuli are attended (Dieter, Melnick, & Tadin, 2016). Indeed, studies have demonstrated that prolonged training on visual tasks can lead to significant changes in visual plasticity (Hess, Mansouri, & Thompson, 2010; Li, Thompson, Deng, Chan, Yu, & Hess, 2013; Tsirlin, Colpa, Goltz, & Wong, 2015). In contrast, control of rivalry dynamics during passive viewing of rivalry stimuli appears limited (Meng & Tong, 2004).

In addition to using tasks in which rivalry stimuli have task-relevant features to sustain attention, attention can be cued by transient and binocularly presented stimuli that are external to the rivalry stimuli. Specifically, rivalry stimuli that have feature congruence with binocularly presented transient stimuli

are promoted (Dieter et al., 2015). Binocular cueing can also promote perceptual alternations at the location of the cueing (Paffen & Van der Stigchel, 2010). In a novel addition to these findings of feature- and location-based modulatory effects of binocularly presented transient stimuli on rivalry dynamics, here we report a monocular, eye-based effect of transient cueing. Our monocularly presented transient cues external to the rivaling stimuli shifted eye balance toward the rivalrous stimulus in the cued eye, delaying the switch between eyes if the cue appeared in the perceiving eye or shortening it if it appeared in the suppressed eye. These effects are unlikely to be attributable to feature congruency, as our two different cue stimuli (a surrounding ring containing static, chromatic dots and an achromatic random dot kinematogram) were highly incongruous with our rivalry stimuli of oriented, achromatic gratings. Furthermore, the spatial factors mentioned above were unlikely to play a role, as our cue stimuli were well separated from and not co-extensive with the rivalry stimuli.

We have argued that the shift in eye balance toward the eye in which a monocular attentional cue is presented are mainly the results of attentional mechanisms (Figures 6 and 7). Instead, and as discussed by Ooi and He (1999), one might argue that these changes arise directly from interocular stimulus effects, in which the attentional stimulus itself modulates mechanisms of interocular suppression through the additional visual stimulation provided by the transient cue. If this were the case, the brief presence of the attentional stimulus in one eye (e.g., the ring of colored spots) would, in relative terms, facilitate the dominance of that eye and suppress the other eye, in a form of dichoptic masking. For example, Meese and Hess (2004), using sinewave gratings as test and mask, found that surround masking, using an annular mask presented dichoptically, tends to reduce contrast sensitivity and contrast perception in the unmasked eye. However, this effect was very small when a spatial frequency the same as ours (1 cycle per degree) was used. The presence of a monocularly presented ring surrounding the stimulus also had a similar masking effect, which was reduced as the ring became larger in diameter and farther away from the stimulus (Meese & Hess, 2005). Both effects were attributed to a mechanism of interocular suppression, and a role of attention was not investigated. Moreover, these were specifically contrast masking effects and did not involve binocular rivalry.

Although we cannot eliminate a contribution of interocular suppression to our results, we do not think that this is likely to be the main driving force for the eye dominance changes that we observed. If our effect was due directly to interocular effects and not attention, a similar modulatory influence should be seen across both attentional load conditions, as the only difference between the two stimuli was the color of the circles. There were clear differences between the two attentional load conditions on the shift in eye balance (see Figure 6 for active vs. passive cueing), with active cueing having a greater effect, and we found a significant interaction in which the size of the eye balance shifts depended on the attentional cueing (active vs. passive). Finally, it may be argued that there is an interocular stimulus effect that is susceptible to attentional modulation (Li, Carrasco, & Heeger, 2015; Li, Rankin, Rinzel, Carrasco, & Heeger, 2017). In this case, it is very difficult to separate between the effect of attention per se and an indirect effect of attention on interocular suppression.

It is also interesting to note that we did not find that the effect on percept modulation depended on the time of the transient cue presentation within a dominance period. Although this finding conflicts with the finding by Dieter et al. (2015) that percept modulation is most effective when transient cues are presented near the end of a dominance period, this may be explained by a key difference between our experiments, which were designed to answer different questions. Because we were interested in tracking changes in eye balance using rivalry reports, our rivalry stimuli were much larger in size. As such, rivalry reports consisted largely of mixed percepts, which was also when the attentional cues usually appeared. Because percepts with unresolved competition are the most susceptible to attentional modulation (McMains & Kastner, 2011), monocular attentional cues modulated rivalry percepts regardless of their presentation time, likely because they occurred during periods of mixed percepts. This is consistent with the interpretation by Dieter et al. (2015) of their own results: Rivalry percepts are more susceptible to modulation when transient stimuli are presented near the end of an exclusive dominance period, when percepts become unstable and lead to mixed percepts.

If monocular attention can shift the eye balance toward one eye, the question arises as to how attention has access to the monocular eye of origin information. As measured by both electroencephalography and functional magnetic resonance imaging, when one eye's image becomes dominant, its cortical signal becomes stronger, whereas that of the eye with the suppressed image becomes weaker (Brown & Norcia, 1997; Haynes, Deichmann, & Reese, 2005; Tong, Nakayama, Vaughan, & Kanwisher, 1998). One possibility is that attention has access to monocular information at a level at which the eye of origin information is still preserved, the lateral geniculate nucleus (LGN) and monocular neurons of V1, as there is no strong physiological evidence for monocular pathways at a higher cortical level than V1. Furthermore, there is evidence that neural competition underlying binocular rivalry is largely resolved before visual information reaches later stages of the visual pathway, such as the fusiform face area and parahippocampal place area (Tong et

al., 1998). There is functional magnetic resonance imaging evidence indicating that the suppression of eye-based signals occurs at an early stage of visual processing (Haynes et al., 2005; Wunderlich, Schneider, & Kastner, 2005). Blood oxygen level–dependent (BOLD) responses were found to vary during binocular rivalry (of cross-oriented gratings), correlating with the modulations in eye-based suppression in both the human LGN and V1. Such eye-specific modulations in the LGN may reflect a feedback signal from V1, where orientation-tuned neurons are found, as there are substantial corticothalamic feedback projections originating from cortical layer 6 (Sherman & Guillery, 2002). Moreover, it is known that the LGN BOLD response is modulated by attention (O'Connor et al., 2002), presumably from this same cortical feedback. Hence, it seems possible that attention has access to eye-of-origin information, although exactly how such top–down biases, such as attention, affect alternating global percepts in rivalry at the monocular level remains unknown. When the activity of the monocular neurons associated with the attentionally cued eye has been facilitated by attention, what happens perceptually could be something akin to an increased contrast gain in the attended eye compared to the other eye. Indeed, attention has been shown to boost apparent stimulus contrast (Carrasco, Ling, & Read, 2004).

Another possibility is that attention does not directly modulate the information in the monocular channels. Instead, attention might modulate binocular neurons in V1 which in turn modulate the activity of the monocular neurons in V1, as well as the LGN. From electrophysiological recordings, monocular neurons in V1 have been found to be suppressed by binocular stimulation compared to when they are monocularly stimulated; the more a neuron prefers one eye over the other, the more it is suppressed by binocular stimulation (Dougherty et al., 2019). Because the attention stimulus is shown monocularly, the overall binocular suppression of monocular neurons should be less in the attentionally cued eye compared to the non-attentionally cued eye. The shift in eye balance toward the attentionally cued eye could occur because fewer monocular neurons are binocularly suppressed, leading to transiently favoring that eye's image. This could be an explanation for why bottom–up attention shifts eye balance. Is there a role for top–down attention? Because monocular neurons have been shown to respond to binocular stimuli to varying degrees, top–down attention might act to modulate the binocular neurons in V1 such that activity in the attentionally cued eye is greater than that of the non-attentionally cued eye. It is also possible that attention facilitates all responses in V1, and, because there are more monocular neuron responses to the eye with the monocular attention stimuli than the eye without it, the overall activity is increased more in the attending eye than in the non-attending eye.

Conclusions

Here, we have demonstrated using binocular rivalry that eye balance can be transiently shifted by monocularly directed attention, regardless of whether a motion- or color-based stimulus is used. We also found that increased attention load affected the size of the eye balance shift but not the percept shift time. It remains to be seen whether eye balance can be permanently shifted after prolonged or repeated time periods of monocular attention. Results of such studies would provide greater knowledge of how attention interacts with the underlying mechanisms of binocular combination and interocular suppression in the visual system. Moreover, a greater understanding of how attention modulates eye balance would help to further develop treatments to balance the eyes for people with large eye imbalances, such as individuals with amblyopia.

Keywords: binocular rivalry, monocular attention, eye balance, binocular vision

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