Vision Research 83 (2013) 76–81

Contents lists available at SciVerse ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Effects of attention on visual experience during monocular rivalry

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ARTICLE INFO

Article history:
Received 20 November 2012
Received in revised form 4 February 2013
Available online 13 March 2013

Keywords:
Visual attention
Monocular rivalry
Consciousness
Afterimages

ABSTRACT

There is a long-running debate over the extent to which volitional attention can modulate the appearance of visual stimuli. Here we use monocular rivalry between afterimages to explore the effects of attention on the contents of visual experience. In three experiments, we demonstrate that attended afterimages are seen for longer periods, on average, than unattended afterimages. This occurs both when a feature of the afterimage is attended directly and when a frame surrounding the afterimage is attended. The results of these experiments show that volitional attention can dramatically influence the contents of visual experience.

1. Introduction

Can volitional attention alter the appearance of visual stimuli? Disagreement over this question has persisted for over a century, with, for example, Hermann von Helmholtz arguing in the affirmative and Gustav Fechner in the negative (Helmholtz, 1866/1924). In recent years, evidence has begun to accumulate in favor of the position that volitional attention can indeed alter the appearance of visual stimuli (Abrams, Barbot, & Carrasco, 2010; Liu, Abrams, & Carrasco, 2009; Tse, 2005). Volitional attention can also alter the contents of visual experience by biasing perception toward a particular percept in binocular rivalry and ambiguous figure perception, where visual experience alternates between several different percepts (Chong, Tadin, & Blake, 2005; Hancock & Andrews, 2007; Meng & Tong, 2004; Ooi & He, 1999; van Ee, van Dam, & Brouwer, 2005). Here we demonstrate for the first time an effect of volitional attention on another type of perceptual multistability: monocular rivalry.

In monocular rivalry, a single image of two spatially overlapping transparent surfaces can lead to the experience of perceptual alternations between the two surfaces (Breese, 1899). Qualitatively, monocular rivalry resembles binocular rivalry, where different images presented to the two eyes alternate in visibility. Indeed, there is evidence that the alternation dynamics and suppression effects which occur in monocular rivalry are similar to those of binocular rivalry (Maier, Logothetis, & Leopold, 2005; O'Shea et al., 2009).

Binocular rivalry has been characterized far more extensively than monocular rivalry (for reviews, see Blake, 2001; Blake & Logothetis, 2002; Leopold & Logothetis, 1999). It has been shown to exhibit a characteristic distribution of dominance durations and alternation rates that is similar to those observed in ambiguous figure perception (Brascamp et al., 2005; van Ee, 2005; Zhao et al., 2004). Based largely on the similar properties of binocular rivalry and ambiguous figure perception, some have proposed that a single, supra-modal mechanism for resolving perceptual ambiguity could drive the alternations in all forms of perceptual multistability (Leopold & Logothetis, 1999). If this is true, then it would follow that manipulations which affect the alternation process in one form of multistability would likely have similar effects on the alternation process in other forms of multistability.

Binocular rivalry and ambiguous figure perception can both be influenced by volitional attention (Chong, Tadin, & Blake, 2005; Hancock & Andrews, 2007; Meng & Tong, 2004; Ooi & He, 1999; van Ee, van Dam, & Brouwer, 2005). If shared mechanisms are responsible for the perceptual switching that occurs in monocular rivalry, binocular rivalry, and ambiguous figure perception, then attention might have a similar effect on perceptual switching in monocular rivalry as it does in other types of multistable perception. To our knowledge, it remains an open question whether attention influences monocular rivalry (although O'Shea (2006), published an abstract reporting possible effects of attention on monocular rivalry).

Here, we examine the influence of volitional attention on the visual experience of color afterimages engaged in monocular rivalry. Afterimages were induced by stimuli like those shown in Fig. 1. Color afterimages typically occur when opponent-coded retinal ganglion cells undergo a rebound in firing following prolonged exposure to an unchanging stimulus (Zaidi et al., 2012). To the viewer, the afterimages appear like a weak version of the color

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http://dx.doi.org/10.1016/j.visres.2013.03.002

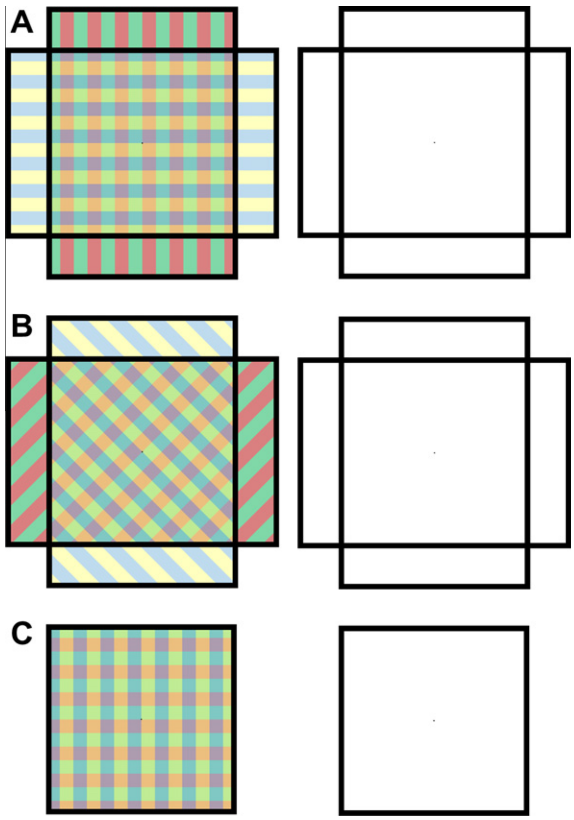

Fig. 1. Example stimuli. Please refer to the web version of the article for color stimuli. Panel A corresponds to a 'parallel stripes' trial in Experiment 1. Panel B shows an example from Experiment 2. Panel C illustrates a trial from Experiment 3. The reader can experience a demonstration of the effects by fixating in the center of one of the three colored stimuli for ten or more seconds, then shifting fixation to the empty frames at right, and attending to one of the two frames (or stripe orientations, in Panel C) The afterimage corresponding to the attended surface should tend to be seen for longer periods than the unattended surface.

inverse of the adapting stimulus, but the exact contents of the percept can be influenced by contextual cues presented during afterimage perception (Daw, 1962; van Lier, Vergeer, & Anstis, 2009). For post-retinal visual processes such as attention, afterimages are likely equivalent to direct retinal input. The main advantage of using afterimages to study monocular rivalry is that afterimage percepts are stabilized on the retina, and are therefore conveniently immune to the confounding effects of eye movements that can otherwise influence monocular rivalry alternations (Crassini & Broerse, 1982; Georgeson, 1984).

In three experiments, we show that the mean dominance duration of attended afterimage surfaces engaged in monocular rivalry is longer than that of unattended afterimage surfaces. In Experiment 1, we establish the basic effect of volitional attention on rivaling afterimages. Experiment 2 controls for a potential stimulus confound in Experiment 1 and replicates the effect. Experiment 3 demonstrates that the effect holds when attention is directed to a feature of the afterimage itself, rather than a static afterimage boundary as in Experiments 1 and 2.

2. Experiment 1

2.1. Methods

Twenty-one naïve observers (5 males, mean age 19.9 years, SEM = 0.60 years) participated for payment or course credit. One additional participant was tested but excluded from analysis as an outlier who, in several analyses, was more than three standard deviations from the group mean. Exclusion of the outlier did not change the direction or significance of any of the reported results. In this and subsequent experiments, all participants gave informed consent to participate, and all experimental procedures were approved by the Dartmouth Committee for the Protection of Human Subjects.

Participants viewed stimuli on a Mitsubishi Diamond Pro 2070SB CRT monitor from a distance of 57 cm, in a darkened room. Stimuli were generated and presented using the Psychophysics Toolbox, version 3, on a PC running MATLAB R2010a in Linux (Brainard, 1997; Pelli, 1997; MathWorks, Natick, MA).

Each participant completed 100 experimental trials. On each trial, participants fixated on a dot in the center of the screen and pressed a key to initiate the trial. While fixating, they passively viewed an adapting stimulus for 10 s (example in Fig. 1a). The adapting stimulus contained two overlapping rectangular frames forming a plus-sign (12×12 deg vis. ang., area of overlap 8×8 deg). Each frame was filled with a transparent texture of blue and yellow or red and green stripes. The background had a mean luminance of 102 cd/m^2, and the adapting stimuli had a mean luminance of 64 cd/m^2 in the overlapping region. The color of the texture within each frame was randomly assigned for each trial. The orientation of the stripes was counterbalanced: half of the trials contained stripes perpendicular to the rectangles, half parallel to the rectangles.

After the adapting period of each trial, all stimuli except the fixation point disappeared, and a tone sounded for 50 ms as a non-visual attentional cue. Participants were instructed to pay attention to the vertical frame on trials when they heard a high tone, and to the horizontal frame on trials when they heard a low tone.

Immediately after the tone, the rectangular frames reappeared for 10 s. Participants reported what they saw at each moment within the square region of overlap between the two rectangles. They held one key if they saw vertical stripes, another if they saw horizontal stripes, and a third if they saw a mixture of both orientations. They were instructed to hold the third key anytime the overlapping region was not exclusively filled by just one of the two afterimage patterns (i.e., if there was any amount of piecemeal rivalry). Participants switched keys as often as necessary to accurately reflect their visual experience, and released all the keys when they no longer saw an afterimage.

2.2. Results

The average probability of every possible response at each moment of the response period can be seen in Fig. 2a. Responses congruent with the attended stimulus are in green, those congruent with the unattended stimulus are in red, and mixed responses in black. Shading indicates 95% confidence intervals based on the *t*-statistic. Hence, non-overlapping regions have significantly different response probabilities. Responses congruent with the attended stimulus are significantly more probable than those congruent with the unattended stimulus between 820 and 1910 ms post-cue, and both types of single-percept response are significantly more probable than mixed percepts until very late in the reporting period when percepts of any kind were quite rare because afterimages had faded. Since mixed percepts accounted for only 10.7% of the total time participants reported any percept, they were excluded from later analyses.

On average, observers reported 3.25 dominance epochs per trial (SEM = 0.25). On average, for the first 3 dominance epochs of the alternation process, the attended stimulus tended to be seen for longer than the unattended stimulus. In a repeated-measures ANOVA with factors attention (attended, unattended) and dominance epoch (1, 2, 3), there was a significant main effect of attention

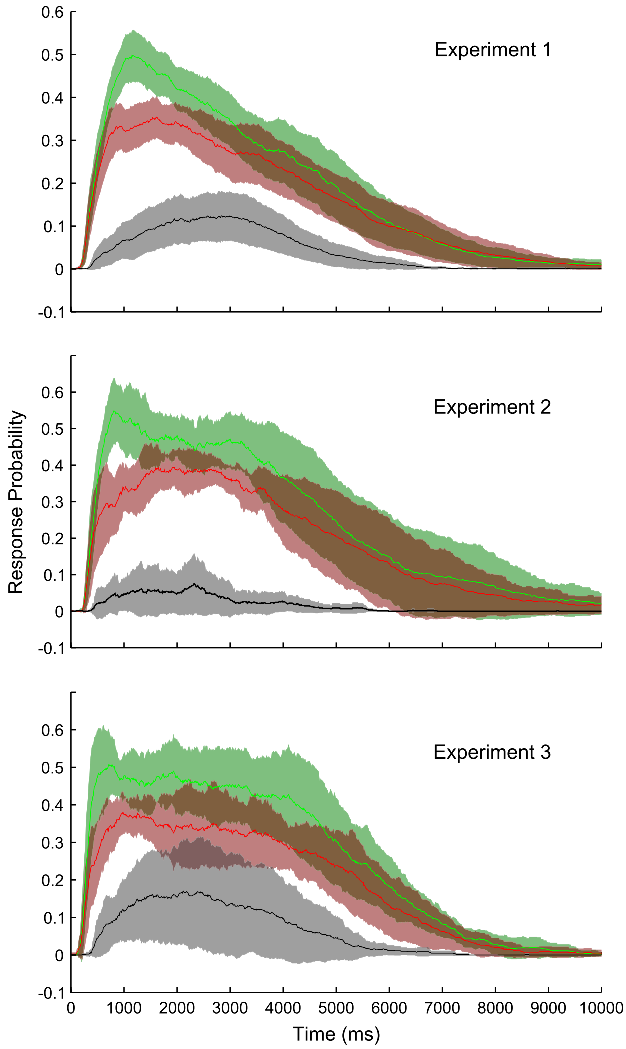

Fig. 2. Probability of each possible response, over time. Lines indicate the probability of every possible response at each moment of the 10-s response period. The green line indicates the probability that the surface congruent with the attentional cue was perceived. The red line indicates the probability that surface incongruent with the attentional cue was perceived. The black line indicates the probability that a mixed percept was perceived. Shading indicates 95% confidence intervals based on the *t*-statistic. Therefore, response probabilities in areas of non-overlap are significantly different. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

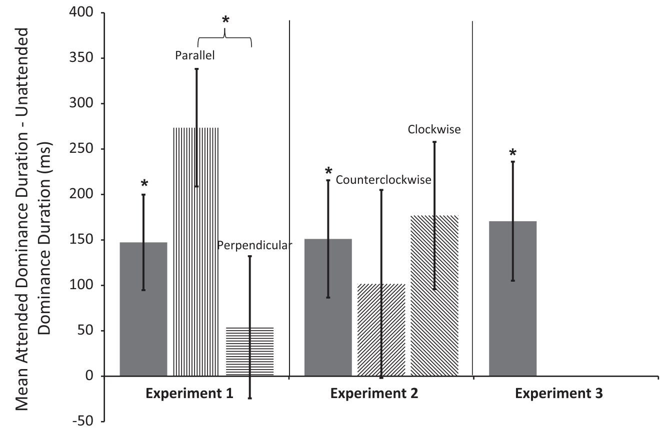

Fig. 3. Differences in dominance period length. In Experiment 1, the overall effect of attention is a significant increase in dominance duration for the attended stimulus (solid bar). This effect is driven by the trials where the two surfaces contain stripes parallel to the overlapping frames (vertical pattern), and greatly reduced in trials containing perpendicular stripes (horizontal pattern). Experiments 2 replicates this effect of attention with afterimages oriented obliquely to the frames. While the effect across all trials (solid bar) is similar to Experiment 1, there is no significant effect of stripe orientation in Experiment 2 (diagonally-striped bars). Experiment 3 replicates the difference between attended and unattended afterimages with completely overlapping afterimage patterns and attention cued to a feature of the afterimages themselves. All error bars represent SEM.

($F(1,20) = 11.67$, $p = 0.003$, $\eta_P^2 = .037$), but no main effect of dominance epoch ($F(2,19) = 1.61$, $p = 0.23$, $\eta_P^2 = 0.15$), and no interaction ($F(2,19) = 0.34$, $p = 0.72$, $\eta_P^2 = 0.03$).

Exploration of the data suggested that the effects of attention on afterimage perception were largely dependent upon trials where the stripes of the afterimage were parallel to the rectangular frames. To quantify this, we performed a 2×2 repeated measures ANOVA on all the data (i.e., including information from dominance epochs later than the third) with factors attention (attended, unattended) and stripe orientation (parallel, perpendicular). This analysis confirmed the significant main effect of attention found in the previous analysis with data from the first three dominance periods, such that the mean dominance duration for the attended stimuli was on average 147 ms longer than the unattended stimuli (see Fig. 3a) ($F(1,20) = 9.67$, $p = 0.006$, $\eta_P^2 = 0.33$). There was no significant effect of orientation ($F(1,20) = 0.927$, $p = 0.35$, $\eta_P^2 = 0.04$), but the analysis revealed a significant interaction between attention and orientation ($F(1,20) = 5.07$, $p = 0.036$, $\eta_P^2 = 0.20$). Specifically, as can be seen in Fig. 3a, the effect of attention on dominance duration was greater in the parallel conditions (mean difference = 273 ms, SEM: 64 ms) than in the perpendicular conditions (mean difference = 53 ms, SEM: 78 ms). The interaction was driven primarily by decreased dominance durations for the unattended parallel stimuli ($M = 1156$ ms), while the mean dominance durations for the other three conditions were similar (attended parallel $M = 1429$ ms, attended perpendicular $M = 1400$ ms, unattended perpendicular $M = 1346$ ms).

In perpendicular trials, attended stimuli were significantly less likely to be the first reported percept than unattended stimuli (35.91% of trials and 64.10% of trials, respectively) ($t(20) = -3.94$, $p < 0.001$). In parallel trials, the reverse was true: attended stimuli were significantly more likely to be the first reported percept (64.38% of trials) than unattended stimuli (35.62%) ($t(20) = 3.58$, $p = 0.002$).

2.3. Discussion

Experiment 1 demonstrates that volitional attention modulates the contents of visual experience during monocular rivalry. In the central overlapping region, observers perceived the afterimage consistent with the unattended rectangular frame for shorter durations than the one consistent with the attended frame. Percepts consistent with the attended frame were significantly more frequent early in the average perceptual timecourse, but this effect diminished over time. However, when the durations of the first three dominance epochs of each participant were computed for each trial, and the duration of attended versus unattended percepts were compared, attended percepts were perceived for longer regardless of when they occurred in time. Why are significant differences in the probability of perceiving the attended versus unattended surface not apparent later in the perceptual timecourse, averaged across subjects, if differences in attended versus unattended surfaces are apparent in the average durations of the first three perceptual dominance periods for each participant? This can be explained by inter-subject differences in the dominance durations: subject-wise differences in alternation rate would be expected to produce a compounding decline in the likelihood that different subjects would be in the same cycle of perceptual alternation as time progressed.

Surprisingly, the attentional effect in Experiment 1 was driven almost exclusively by trials in which the stripes of the adapting stimuli were parallel to the orientations of the rectangles. In parallel trials, attended stimuli were also more likely to be reported as the first percept, while the reverse was true for perpendicular trials. Is the effect of volitional attention on rivaling afterimages limited to stimulus configurations in which the orientations of the afterimage and the attended frame are congruent? Experiment 2 tests the generalizability of the effect by modifying the stimulus configuration to remove consistencies in orientation between the afterimage and attended frame. In Experiment 2, the afterimage stripes were rotated 45° within the frames, while all other factors were kept consistent. Though in principle the frames could have been rotated and the inducers kept in cardinal orientations, the frame orientations were maintained so that the attentional cues ('attend vertical' vs. 'attend horizontal') could be kept constant, eliminating the possible confound that participants might find it easier to attend to certain orientations than others.

Furthermore, reorientation of the afterimages controls for possible response bias in Experiment 1, wherein participants might simply be more likely to respond with the key corresponding to the attentional cue. Rotation of the afterimages makes the response criterion (afterimage tilted clockwise/counterclockwise) orthogonal to the attentional cue (attend to the vertical/horizontal frame).

3. Experiment 2

3.1. Methods

Nine observers (6 males, mean age 25.3 years, SEM = 1.09 years) naïve to the purpose of the experiment participated for payment or course credit.

The methods in Experiment 2 were identical to Experiment 1, except that the stripes in the adapting surfaces were rotated 45 degrees within the existing frames, so their orientations were different than either of the frames (see Fig. 1b). Observers responded that the afterimage perceived was tilted clockwise, counterclockwise, or both, from vertical. As before, they held a separate key anytime there was any amount of piecemeal rivalry or a mixture of the two stimuli perceived.

3.2. Results

The probability of each possible response at each moment of the 10-s response period can be observed in Fig. 2b. As in Experiment 1, percepts congruent with the attended afterimage were significantly more probable than percepts congruent with the unattended afterimage early in the response period, between 630 and 1270 ms post-cue, and these differences diminished over time. Again, mixed percepts were quite rare. In fact, the probability of a mixed percept was generally not significantly different from 0. Since subjects only reported mixed percepts for 3.8% of the total time in which they reported any percept, those responses were excluded from further analysis. Initial responses consistent with the cued condition were not significantly more frequent (55.89% of trials) than uncued responses (44.11%) ($t(8) = 1.54$, $p = 0.16$).

Subjects reported an average of 3.77 dominance epochs before the afterimage faded (SEM = 0.43). As in Experiment 1, a 2×3 repeated-measures ANOVA with factors attention and dominance epoch (1,2,3) indicates that attended stimuli were perceived for longer, on average, than unattended (attention main effect $F(1,8) = 5.77$, $p = 0.04$, $\eta_P^2 = 0.42$). There was also a trend toward later dominance periods being longer than early ones (dominance epoch main effect $F(2,7) = 4.12$, $p = 0.07$, $\eta_P^2 = 0.54$). However, there was no interaction between attention and epoch ($F(2,7) = 0.58$, $p = 0.58$, $\eta_P^2 = 0.14$).

Attention also significantly influenced mean dominance durations when the mean dominance duration of all dominance epochs (including those beyond three) was analyzed. Across all dominances, afterimages consistent with the attended frame were perceived for 151 ms longer, on average, than those consistent with the unattended frame (SEM = 64 ms, $t(8) = 2.34$, $p = 0.047$, two-tailed) (see Fig. 3b).

In order to ensure that the change in afterimage stripe orientation did indeed abolish the interaction between orientation and attention seen in Experiment 1, we conducted a 2×2 repeated measures ANOVA on the full dataset in exactly the same fashion as in Experiment 1 (with factors orientation and attention). In contrast to Experiment 1, there was no significant interaction between orientation and attention ($F(1,8) = 0.32$, $p = 0.59$, $\eta_P^2 = 0.04$) (see Fig. 3b).

3.3. Discussion

The results of Experiment 2 confirm and extend the results of Experiment 1: volitional attention alters the experience of rivaling afterimages, even when the orientations of the afterimage textures are neither parallel nor perpendicular to the attended frames. Furthermore, as expected, the interaction between frame and afterimage orientations seen in Experiment 1 are not observed when these parallels are removed in Experiment 2. These differences allow us to conclude that although the attentional effects on the visibility of an afterimage can be influenced by stimulus configuration, these effects do not depend upon a specific configuration.

In the following experiment we further investigate the effects of stimulus configuration on attentional modulation of monocular rivalry. In both Experiments 1 and 2, the adapting surfaces had regions of non-overlap. It could be that these non-overlapping regions are critical for the effect, allowing an unambiguous region to be attended and filling-in of the ambiguous central region to proceed from there. Thus, the question remains: is the ability of attention to influence the perceived afterimage dependent upon these non-overlapping regions? This question is addressed by Experiment 3, wherein the sections of non-overlap are eliminated and attention is directed directly to a feature of one of the competing afterimages (orientation).

4. Experiment 3

4.1. Methods

Eight observers (3 males, mean age 26.6 years, SEM = 1.02 years) participated for payment or course credit. All observers were naïve to the purpose of the experiment, but four had participated in Experiment 2, and one had participated in Experiment 1.

The methods were again nearly identical to those employed in Experiments 1 and 2. However, the adapting stimulus consisted of a single square (8×8 deg. vis. ang.) corresponding to just the overlapping region of the stimuli used in the previous experiments, as shown in Fig. 1c. Thus, the two surfaces – cropped versions of those used in Experiment 1 – were completely overlapping. The same auditory tones were used to cue attention as in the previous two experiments, but participants were instructed to attend to the vertical or horizontal *stripes* following the cue, rather than the vertical or horizontal frames, as in the two previous experiments. Observers held a separate key when any amount of piecemeal rivalry or a mixed percept was perceived.

4.2. Results

The probability of each of the three possible percepts, over time, is shown in Fig. 2c. The general pattern of results is similar to that of Experiments 1 and 2. Percepts congruent with the attended surface were significantly more probable than incongruent percepts early in the response period (520–910 ms post-cue), and mixed percepts were significantly less probable than either single-surface percept for the majority of the response period (although the difference between mixed and unattended responses was not significant between 1620 and 3820 ms post-cue). Again, due to the relative rarity of mixed percepts (only 11.5% of all reported percepts), those responses were excluded from further analysis. As in the previous experiments, afterimages generally faded from view well before the end of the response period. Initial responses consistent with the cued condition were marginally more frequent (56.88% of trials) than uncued responses (43.13%) ($t(7) = 2.11$, $p = 0.07$).

Participants reported an average of 4.03 dominance periods before the afterimage faded (SEM = 0.67). As in the previous two experiments, we performed a 2×3 repeated-measures ANOVA with factors attention (attended, unattended) and dominance epoch (1–3). There was a marginally significant main effect of attention ($F(1,6) = 4.80$, $p = 0.07$, $\eta_P^2 = 0.44$), but no main effect of dominance epoch ($F(2,5) = 2.43$, $p = 0.18$, $\eta_P^2 = 0.49$), and no interaction ($F(2,5) = 0.16$, $p = 0.86$, $\eta_P^2 = 0.06$).

The effect of attention was evident when the data from all dominance epochs (not just the first three) were analyzed. Afterimages of the stripes matching the attended orientation were seen for 170 ms longer, on average, than afterimages of the stripes matching the unattended orientation ($t(7) = 2.61$, $p = 0.04$, two-tailed, SEM = 65 ms) (see Fig. 3c).

4.3. Discussion

Experiment 3 replicates and extends the findings of the previous two experiments. Again, attended afterimages are significantly more likely to be perceived than unattended ones. Experiment 3 demonstrates that this continues to hold true when a feature of the afterimage itself (orientation) is attended, rather than the bordering outline attended in the previous two experiments. Furthermore, Experiment 3 demonstrates that attention influences rivalry dominance durations even when the competing stimuli are completely overlapping. This refutes the hypothesis that areas of non-overlap are necessary to provide an unambiguous ‘handle’ to which attention can be directed that might enable filling-in to ambiguous overlapping regions.

5. General discussion

The results of the three experiments reported here demonstrate that volitional attention can alter the contents of experience. Specifically, volitional attention can alter the appearance of overlapping transparent surfaces engaged in monocular rivalry. Attended surfaces are perceived for longer durations than unattended surfaces across a variety of stimulus configurations. The effect is demonstrable within a single trial, yet quantifiable by averaging the influence of attention on rivalry dominance period length over many trials. Attention modulates visual experience whether it is allocated to surrounding frames or to the orientation of the afterimages. Thus, the results speak strongly in favor of the view that volitional attention influences the subjective appearance of visual stimuli engaged in monocular rivalry.

The interaction between afterimage and frame orientation in Experiment 1 demonstrates that the effects of attention on appearance in monocular rivalry can be modulated by the properties of the stimulus. Certain configurations (e.g., parallel afterimage and frame orientations) appear to facilitate the effects of attention while others diminish it (e.g., perpendicular afterimage and frame orientations). A fuller exploration of what types of stimuli facilitate attentional influences on rivalry and why is an important area for future study.

Intriguingly, the significant interaction between stripe orientation and attention in Experiment 1 is consistent with the possibility that spatial and feature-based volitional attention could have independent influences on dominance duration. It is possible that allocation of attention to an oriented frame involves both spatial attention to the region and feature-based attention to the orientation itself. Were that the case, in Experiment 1, parallel trials would have elicited the allocation of spatial and feature-based attention to the same surface, while perpendicular trials would elicit spatial attention to one surface and feature-based attention to its rival. In other words, the results of Experiment 1 could have been caused by independent, additive effects of spatial and feature-based attention on dominance duration, which cancelled each other out in the perpendicular condition. This would be consistent with existing physiological data showing that spatial and feature-based attention have additive effects on neural activity (e.g., Andersen, Fuchs, & Müller, 2011; Hayden & Gallant, 2005, 2009; Treue & Martinez-Trujillo, 1999).

Our results also have implications for present theories of perceptual multistability. We demonstrate that dominance durations in monocular rivalry can be influenced by attention. This parallels findings from studies of binocular rivalry and ambiguous figure perception (Chong, Tadin, & Blake, 2005; Meng & Tong, 2004; Ooi & He, 1999). Indeed, the dominance durations and attentional effects we report are of similar order of magnitude to those reported in the binocular rivalry literature (e.g., van Ee, van Dam, & Brouwer, 2005), though this similarity must be interpreted with caution because of the known dependence of such durations on size, contrast, and other basic stimulus characteristics that differ across experiments. Our results are consistent with the theory that various forms of perceptual multistability are driven by a common mechanism of alternation. We show that monocular rivalry is affected by volitional attention in much the same way as binocular rivalry and ambiguous figure perception, which could mean that attention is influencing a common mechanism of alternation in all three instances.

Because our experiments did not include a ‘no attention’ condition, it is not possible to determine from our results whether the effects of attention resulted from an enhancement of processing of the attended stimulus, or from inhibition of processing of the suppressed stimulus. The attentional effects observed in binocular rivalry appear to result from enhancement of processing of the attended stimulus, equivalent to an increase in contrast for that stimulus during periods of dominance (Chong, Tadin, & Blake, 2005). Attention might have a similar effect of increasing the effective contrast of the attended stimulus during dominance periods in monocular rivalry, but additional experiments must be performed to test this empirically.

In summary, we identify a new domain in which volitional attention modulates the contents of visual experience. Our results demonstrate that endogenous, volitional factors such as attention can dramatically influence the perception of stimuli undergoing monocular rivalry. Thus, we provide new support for the theory that visual experience can be influenced by volitional attention.

Acknowledgments

This work was supported by a grant from the Templeton Foundation (to P.U.T.), and a National Science Foundation Graduate Research Program fellowship (to E.A.R.). G.P.C. was supported by an Institutional Development Award (IDeA) from the National Institute of General Medical Sciences of the National Institutes of Health under grant number 1P20GM103650-01, and a grant from the National Eye Institute: 1R15EY022775.

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