Can attention selectively bias bistable perception? Differences between binocular rivalry and ambiguous figures

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It is debated whether different forms of bistable perception result from common or separate neural mechanisms. Binocular rivalry involves perceptual alternations between competing monocular images, whereas ambiguous figures such as the Necker cube lead to alternations between two possible pictorial interpretations. Previous studies have shown that observers can voluntarily control the alternation rate of both rivalry and Necker cube reversal, perhaps suggesting that bistable perception results from a common mechanism of top-down selection. However, according to the biased competition model of selective attention, attention should be able to enhance the attended percept and suppress the unattended percept. Here, we investigated selective attentional modulation of dominance durations in bistable perception. Observers consistently showed much weaker selective attentional control for rivalry than for Necker cube reversal, even for rivalry displays that maximized the opportunities for feature-, object-, or space-based attentional selection. In contrast, nonselective control of alternation rate was comparably strong for both forms of bistable perception and corresponded poorly with estimates of selective attentional control. Our results support the notion that binocular rivalry involves a more automatic, stimulus-driven form of visual competition than Necker cube reversal, and as a consequence, is less easily biased by selective attention.

Keywords: vision, visual perception, visual attention, binocular rivalry, bistable perception, ambiguous figures, Necker cube, cognitive control

Introduction

The visual system interprets most visual scenes according to a single best interpretation; however, certain types of stimuli lead to spontaneous perceptual alternations between two equally compelling interpretations. For example, in binocular rivalry, incompatible monocular images presented to the two eyes lead to spontaneous alternations between one monocular image and the other. Similarly, ambiguous figures such as the Necker cube, Rubin's face/vase, or the duck/rabbit involve pictorial depictions that can be perceptually organized in more than one way. These forms of bistable perception exemplify the interpretive nature of vision, and may serve as useful tools to investigate how the visual system selects a particular interpretation to be represented in awareness. A growing number of psychophysical, physiological, and neuroimaging studies have relied on bistable phenomena to investigate perceptual selection and the neural correlates of visual awareness (for reviews, see Blake & Logothetis, 2002; Tong, 2003). However, an important question that remains to be addressed is whether different forms of bistable perception result from common or separate neural mechanisms.

It is generally thought that bistable perception results from lateral competition between visual representations at some level of the visual pathway. Some evidence suggests that binocular rivalry results from an earlier form of visual competition than ambiguous figure reversal. Binocular rivalry involves fluctuations in the phenomenal visibility of low-level features, whereas in ambiguous figure reversal, the low-level features remain intact while the high-level organization of those features changes over time (Tong, 2001). Binocular rivalry also seems to be more automatic than ambiguous figure reversal. Rock and Mitchener (1992) found that only one third of naïve observers reported spontaneous reversals for ambiguous figures, and that knowledge of reversibility helped naïve observers to perceive ambiguous figure reversals (see also Girgus, Rock, & Egatz, 1977). In contrast, binocular rivalry occurs automatically for most observers with normal binocular vision (Blake, 2001). There is also considerable psychophysical and neuroimaging evidence to suggest that binocular rivalry results from low-level interocular competition between monocular channels (Blake, 1989; Blake, Westendorf, & Overton, 1980; Nguyen, Freeman, & Wenderoth, 2001; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001).

However, other psychophysical and neurophysiological evidence suggests that binocular rivalry also involves competition between high-level pattern representations, similar to what is presumed to occur in ambiguous figure reversal

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(Kovacs, Papathomas, Yang, & Feher, 1996; Logothetis, Leopold, & Sheinberg, 1996; Sheinberg & Logothetis, 1997). According to pattern competition theory, binocular rivalry and ambiguous figure reversal may reflect a common form of neural competition between high-level form representations.

An alternative to both interocular and pattern competition theories is the proposal that all forms of bistable perception result from a common mechanism of attentional selection (Helmholtz, 1866/1924). Top-down selection theory forwards that attention-related frontal-parietal areas are responsible for initiating perceptual alternations by sending top-down signals to guide activity in visual cortex toward one representation or another (Leopold & Logothetis, 1999). One functional imaging study found that frontal and parietal brain regions are more active when observers report binocular rivalry alternations than when they report steady-state periods in which one stimulus maintains dominance (Lumer, Friston, & Rees, 1998). Tong, Wong, Meng, and McKeeff (2002) also found greater prefrontal activity during voluntary control than passive viewing of the Necker cube. These neuroimaging results indicate that frontal-parietal activity is correlated with bistable alternations, but do not necessarily indicate a causal role for these regions in mediating these alternations.

To evaluate these different theories, we investigated whether selective attention can bias different forms of bistable perception, focusing on binocular rivalry and Necker cube reversal. By selective attention, we refer to the ability to enhance the desired perceptual interpretation and to suppress the unwanted perceptual interpretation during bistable perception. Previous studies have shown evidence of selective attentional control over ambiguous figure reversal (Gomez, Argandona, Solier, Angulo, & Vazquez, 1995; Horlitz & O'Leary, 1993; Liebert & Burk, 1985; Peterson, 1986; Toppino, 2003). However, it is not known whether selective attention can bias binocular rivalry.

According to top-down selection theory, selective attention should have an equally powerful influence on both rivalry and ambiguous figure reversal. Such attentional effects would also be consistent with the predictions of pattern competition theory. If one assumes that different forms of bistable perception are mediated by similar mechanisms of pattern-based competition, it follows that attention should be about equally effective at biasing different forms of bistable competition. However, if attention can bias ambiguous figure reversal but not binocular rivalry, this would support the notion that binocular rivalry differs from other forms of bistable perception, consistent with the predictions of interocular competition theory.

We investigated whether selective attention can bias dominance durations during bistable perception. According to the biased competition model of selective attention, concurrent visual inputs compete for representation across a network of visual areas, and attention serves to enhance the neural representation of attended stimuli and to suppress the neural representation of unattended stimuli (Desimone & Duncan, 1995). Here, we assessed selective attentional control of bistable perception by measuring observers' ability to increase the duration of the desired perceptual interpretation and to decrease the duration of the undesired perceptual interpretation. Previous studies have demonstrated that attention can strongly bias dominance durations during ambiguous figure reversal (Gomez et al., 1995; Horlitz & O'Leary, 1993; Liebert & Burk, 1985; Peterson, 1986; Toppino, 2003). If rivalry results from the same mechanisms as ambiguous figure reversal, then attention should be able to bias the dominance durations of binocular rivalry. However, if selective attention leads to much weaker bias effects for binocular rivalry, this would favor the notion that rivalry differs from ambiguous figure reversal and involves a more automatic, stimulus-driven form of visual competition.

Our measure of attention differs from previous studies, which focused on voluntary control over alternation rates during bistable perception (e.g., George, 1936; Lack, 1971, 1978; Meredith, 1962; Struber & Stadler, 1999). Such voluntary control over alternation rates may not necessarily reflect attentional selection. Just as increasing the signal strength of two rivaling stimuli leads to more rapid alternations, coarse physiological factors, such as increases in arousal, neural excitation, or the frequency of blinks and microsaccades, could easily increase the rate of alternation in a competitive network in a nonselective manner. Instead, attentional control should be reflected by the observer's ability to selectively enhance the desired percept while suppressing the unwanted percept.

Experiments 1 and 2 measured the extent of selective attentional control over Necker cube reversal and binocular rivalry, respectively, in naïve observers. The rivalry stimulus consisted of a red house and a green face to maximize the possible opportunities for feature-based and object-based attentional selection. Experiment 3 tested the generality of these effects in experienced observers, and further investigated whether selective attentional control of bistable perception differed from nonselective control of alternation rate. Experiment 4 used a spatially biased rivalry display to evaluate the extent to which rivalry can be biased by bottom-up spatial factors of eye position as compared to top-down effects of spatial attention. All four experiments consistently revealed much greater selective attentional control of Necker cube reversal than binocular rivalry.

Experiment 1: Attentional modulation of the Necker cube

The Necker cube was chosen because it is one of the most commonly studied ambiguous figures (George, 1936; Gomez et al. 1995; Horlitz & O'Leary, 1993; Kawabata, Yamagami, & Noaki, 1978; Long & Toppino, 1981; Long, Toppino, & Mondin, 1992; Necker, 1832; Toppino, 2003). Moreover, people show less attentional control of alternation rates for the Necker cube than for reversible figures that have multiple object interpretations (e.g., duck/rabbit, chef/dog) (Struber & Stadler, 1999). Thus, if naïve observers can selectively bias Necker cube reversal, it seems reasonable to assume that attentional control should be at least as effective for other such reversible figures.

We also assessed whether bottom-up factors such as fixation position could bias perception of the Necker cube (Figure 1a). Previous studies have shown that fixation position can bias perception of the Necker cube to a small extent (Kawabata et al., 1978; Toppino, 2003). This manipulation allowed us to compare the magnitude of top-down control and bottom-up influences, and also to test for possible interactions between bottom-up and top-down factors.

Method

Observers

Observers consisted of 16 undergraduate or graduate students from Princeton University who received payment or course credit in an introductory psychology course for participation. All observers had normal or corrected-to-normal visual acuity, and were naïve to the purpose of the experiment.

Apparatus and procedure

The Necker cube (width = 8.2°) was presented on a white background in the center of an Apple 17" CRT monitor (Figure 1a). The fixation crosshair (size 0.3°) was presented either in the center, 2.2° to the lower left of the center or 2.2° to the upper right of the center, to test if eye position could bias perception. Observers were instructed to maintain fixation throughout each 90-s trial and to avoid making eye movements. A chin rest was used to maintain head stability at a viewing distance of 40 cm.

There were three experimental conditions: (1) "just look at the cube passively"; (2) "attempt to perceive the cube from the top view for as long as possible" (i.e., as if seen from above); and (3) "attempt to perceive the cube from the bottom view for as long as possible" (i.e., as if seen from below). In total, there were nine conditions (3 fixation positions × 3 instructions). After two practice trials of passive viewing, observers received the nine conditions in a mixed randomized order (3 trials/condition). Observers continuously monitored their perceptual state and reported perceptual switches by pressing one of three keys to indicate when they perceived the bottom view of the Necker cube (as if seen from below), the top view, or an indeterminate/flat interpretation of the Necker cube. Observers were allowed to rest between trials.

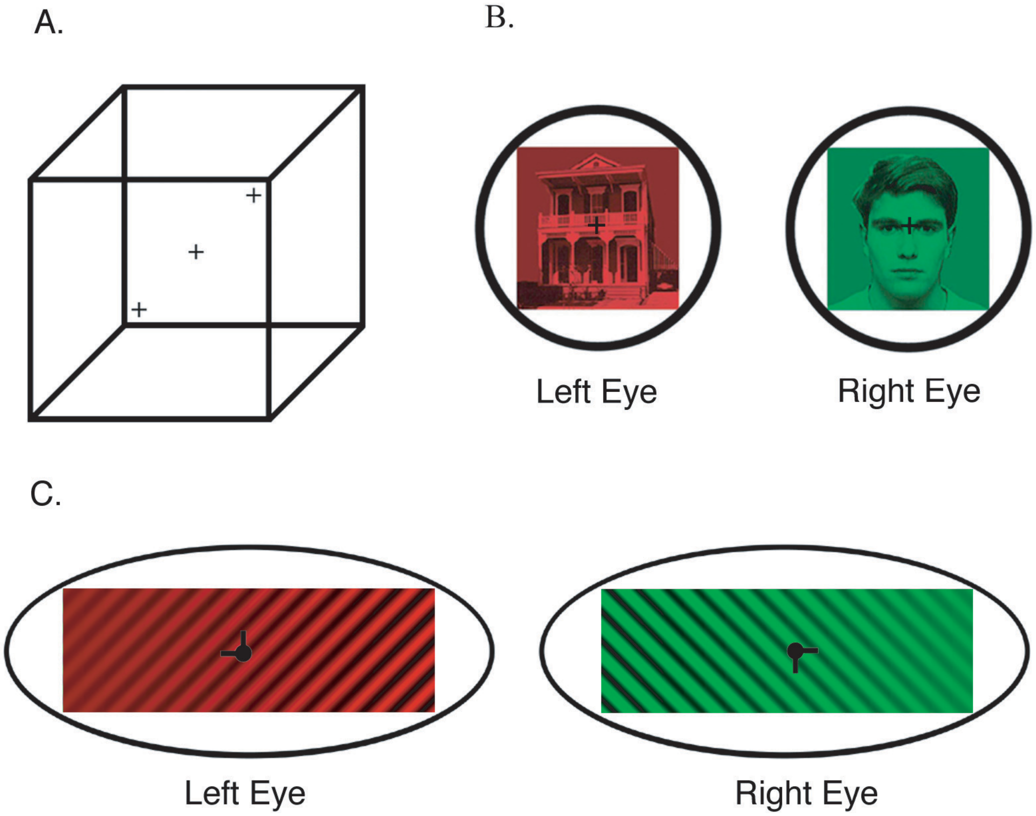

Figure 1. A. Necker cube stimuli in Experiment 1. Only one of the three crosshairs was presented in each trial as a fixation point. B. Binocular rivalry stimuli in Experiment 2. The contrast of the face was kept fixed at 30% while the contrast of the house was manipulated on each trial (15, 30, or 60%). C. Binocular rivalry stimuli in Experiment 4. The contrast of the left-tilted grating decreased linearly from left to right and the right-tilted grating increased from left to right (contrast range 10-90%).

Data analysis

Dominance durations were normalized to control for individual differences in alternation rate and to improve statistical sensitivity to possible differences between conditions. We first calculated the mean duration of the bottom view and top view percepts for each individual observer across all trials. Mean dominance durations ranged from 1.5 to 10.9 s for individual observers with a group average of 5.2 s. Normalized dominance durations were calculated by dividing the duration of each reported percept by the mean dominance duration for that observer. Although each individual's dominance durations followed a gamma-shaped distribution with some rightward skew, the use of normalized mean dominance durations provided a representative measure of the data by equally weighting all observations for all observers. Moreover, the distribution of normalized mean dominance durations across subjects appeared to be normally distributed as determined by tests of skewness and kurtosis. This was true for Experiments 1-4, and thus, all data analyses met the assumptions of analysis of variance. Within-subjects analysis of variance and planned contrasts were performed to compare the mean normalized dominance durations as a function of attentional condition and fixation position.

Results and discussion

On average, observers reported seeing the top, bottom, and indeterminate percepts of the Necker cube for 47.5%, 44.4%, and 8.1% of the time, respectively. Figure 2 shows the mean normalized dominance durations for bottom view (left) and top view (right) for all 16 observers. Note that all attentional control conditions are clearly separated.

The factor of attentional control was highly significant for both reported top views ($F(2, 30) = 30.36$, $p < 10^{-7}$) and reported bottom views ($F(2, 30) = 40.39$, $p < 10^{-8}$). Observers demonstrated a strong ability for both increasing the dominance duration of desired percept and decreasing the dominance duration of undesired percept for the Necker cube. When instructed to attempt to perceive the cube from the top view, observers were able to increase the dominance duration of top view ($F(1, 15) = 6.65$, $p < .03$), and to decrease the dominance duration of bottom view ($F(1, 15) = 19.80$, $p < .0005$), relative to passive viewing. Likewise, attending to the bottom view led to a significant increase in dominance durations for the bottom view ($F(1, 15) = 36.35$, $p < .0001$) and a significant decrease in dominance durations for the top view ($F(1, 15) = 32.47$, $p < .0001$), relative to passive viewing.

The factor of fixation position was significant when observers reported bottom view ($F(2, 30) = 10.12$, $p < .0005$), but failed to reach significance when observers reported top view ($F(2, 30) = 1.68$, $p = .203$). There was no significant interaction between attention and fixation position for both views ($F < 2$). Our results agree with another recent study of Necker cube perception, which also found that the effect of selective attention was much more powerful than, and independent of, the effect of fixation position (Toppino, 2003). However, these findings differ somewhat from Suzuki and Peterson's (2000) study of bistable apparent motion, in which they observed a significant interaction between top-down and bottom-up factors indicating a multiplicative effect of attention.

Our results demonstrate that naïve observers have strong selective attentional control over Necker cube reversal. Selective attentional control proved to be considerably more powerful than the bottom-up bias induced by shifts in fixation position. Observers can selectively enhance the attended percept while suppressing the unwanted percept of the Necker cube via top-down selection.

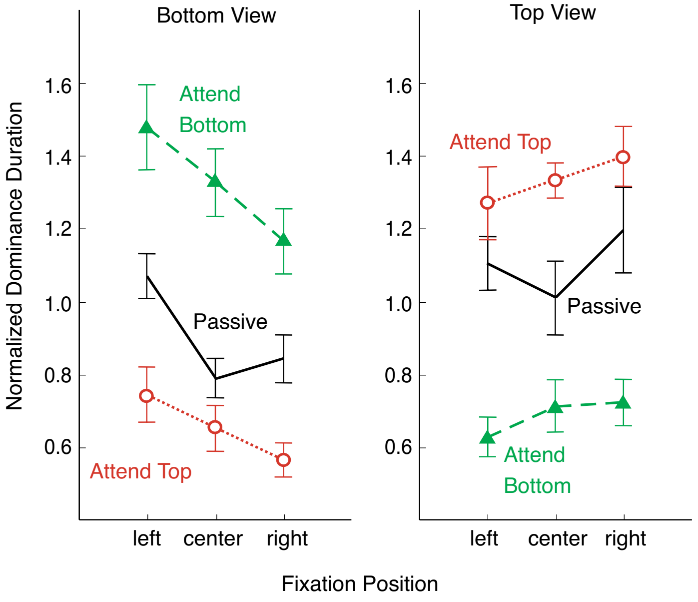

Figure 2. Mean normalized dominance durations for perceiving the bottom view (left) and top view (right) during selective attentional control of the Necker cube in Experiment 1 ($N = 16$). Observers were instructed either to passively view the Necker cube (black solid line), to try to attend to the bottom view interpretation (green dashed line), or to try to attend to the top view interpretation (red dotted line). Error bars represent ±1 *SEM*. Note that selective attention both facilitated the perception of the attended percept and inhibited perception of the unwanted percept, consistently across all fixation positions.

Experiment 2: Attentional modulation of binocular rivalry

To test for attentional control of binocular rivalry, we decided to use a red house and a green face as rivalry stimuli rather than conventional luminance gratings. The images were adopted from previous fMRI work from our lab, which demonstrated powerful awareness-related modulations during rivalry in high-level stimulus-selective regions of ventral extrastriate cortex (Tong, Nakayama, Vaughan, & Kanwisher, 1998). These stimuli were selected to maximize opportunities for attentional selection on the basis of differences in color, visual form, and object category. Feature and object-based attention can effectively bias perception under normal, dioptic viewing conditions (for a review see Kanwisher & Wojciulik, 2000), and could conceivably facilitate attentional selection during rivalrous dichoptic viewing. If selective attentional control is much weaker for binocular rivalry under such optimized conditions than for Necker cube reversal, then this would suggest a pervasive difference between these two forms of bistable perception.

On each trial, observers were instructed either to attend to the face, to attend to the house, or to view the stimuli passively, while reporting their online perception. Because attentional instructions might bias an observer's judgment of relative dominance during ambiguous periods of perceptual blending or piecemeal rivalry, we instructed observers to adopt a strict criterion for reporting exclusive dominance, and excluded all blend percepts from the analysis. The luminance contrast of the house was manipulated to bias perceptual dominance in a bottom-up fashion. This allowed us to compare the magnitude of top-down control and bottom-up influences, and also to test for possible interactions between bottom-up and top-down factors.

Method

Observers

Observers consisted of 16 undergraduate or graduate students from Princeton University who received payment or course credit in an introductory psychology course for participation. All observers had normal or corrected-to-normal visual acuity, and exhibited normal binocular perception of random-dot stereograms (see procedure below). All observers were naïve to the purpose of the experiment.

Apparatus and procedure

A mirror stereoscope was used to present rivalry stimuli to corresponding retinal locations. Random-dot stereograms of depth-defined letters were used to test if observers had normal binocular vision and to ensure that the stereoscope was properly aligned. Only observers who could correctly identify the depth-defined letters were allowed to continue (two observers were excluded by these criteria). A chin rest was used to maintain head stability at a viewing distance of 60 cm. Rivalry stimuli consisted of a red image of a house presented to the observer's left eye and a green image of a face presented to the observer's right eye (size = 4.2° × 4.2°, see Figure 1b). The two monocular images were set to the same mean luminance and presented on a mean yellow background (3.3 cd/m^2). A fixation crosshair (0.14° × 0.14°) was placed in the center of each image. Black circles (5.3° wide) and black square frames (11.1° wide) surrounded each monocular image to aid binocular fusion. The face was kept at 30% contrast while the contrast of the house was varied from trial to trial to bias perceptual dominance (15%, 30%, or 60%). Observers were instructed to maintain fixation and to (1) "just look at the stimuli passively"; (2) "try to maintain the percept of the house for as long as possible"; and (3) "try to maintain the percept of the face for as long as possible." There were three contrasts of the house and three attentional conditions for a total of nine condition types. After two practice trials, each of the nine condition types was presented 4 times each in a randomized mixed-trial design and each trial lasted 60 s. Observers continuously monitored their perceptual state and reported perceptual switches by pressing one of three keys to indicate when they saw the house, the face, or a blend/piecemeal rivalry.

Data analysis

Dominance durations were normalized using the same method as described in Experiment 1. ANOVAs were performed to analyze the mean normalized dominance durations for each condition.

Results and discussion

On average, the proportion of exclusive dominance for the house and face was 27.6% and 28.0%, respectively. Observers reported a fairly high incidence of blending or piecemeal rivalry (44.5% of total viewing time), presumably because they were instructed to adopt a strict criterion for exclusive dominance and especially because the rivalry stimuli were quite large.

Figure 3 shows the mean normalized dominance durations for perception of the face (left) and house (right). The factor of contrast was highly significant for both house perception, $F(2, 30) = 24.62$, $p < 10^{-6}$, and face perception, $F(2, 30) = 34.53$, $p < 10^{-7}$. This is consistent with previous studies, which showed that increasing the contrast of one rivalry stimulus can increase its predominance modestly while greatly decreasing the predominance of the competing stimulus (e.g., Bossink, Stalmeier, & De Weert, 1993).

The main effect of attentional control reached significance for perception of the house, $F(2, 30) = 7.20$, $p < .005$, and also the face, $F(2, 30) = 4.36$, $p < .05$. However, these attentional effects were much smaller than those found for the Necker cube. Planned comparisons indicated that when instructed to attend to the face, observers could only decrease the dominance duration of the house, $F(1, 15) = 8.60$, $p < .02$; they could not reliably increase the dominance duration of the face, $F(1, 15) = 1.89$, $p = .190$. Similarly, when instructed to attend to the house, observers could only decrease dominance durations of the face, $F(1, 15) = 5.45$, $p < .05$, and failed to increase dominance durations of the house, $F(1,15) = 2.24$, $p = .155$. There was no significant interaction between attention and stimulus contrast (all Fs < 2). These results indicate that

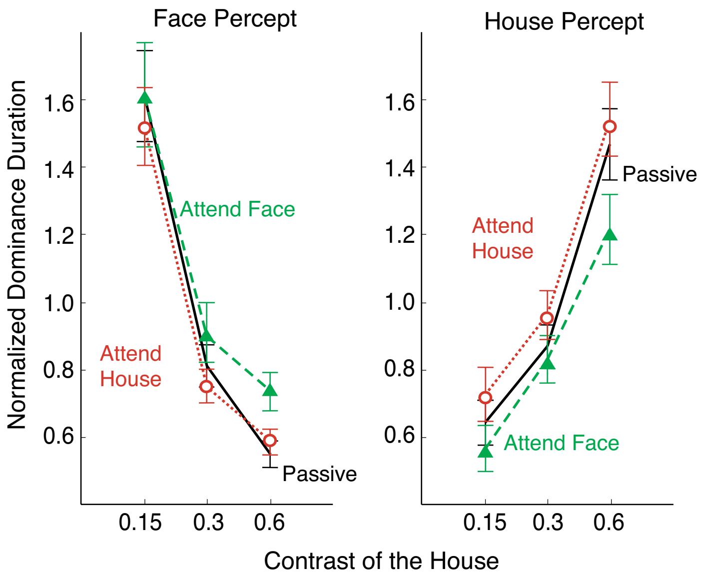

Figure 3. Mean normalized dominance durations for perceiving face (left) and house (right) during selective attentional control of binocular rivalry in Experiment 2 (*N* = 16). Observers were instructed to attend to the face (green dashed line), attend to the house (red dotted line), or passively view the stimuli (black solid line). The contrast of the house was manipulated while the contrast of the face was set to 30%. Error bars represent ±1 *SEM*. Selective attention led to weak modulations in dominance duration, as compared to bottom-up manipulations of stimulus contrast.

perceptual dominance in binocular rivalry can be strongly biased by bottom-up factors such as stimulus contrast, but can only be weakly and unreliably biased by selective attentional control.

Observers appeared to show much greater selective attentional control of Necker cube reversal (Experiment 1) than binocular rivalry. Figure 6a shows a comparison of the overall attentional modulation for Necker cube reversal (Experiment 1) and binocular rivalry (Experiment 2), averaged across all fixation positions and stimulus contrasts, respectively. The proportion of attentional modulation was calculated by using the following formula:

$$\mathrm{AM} = \frac{\left(\begin{array}{l}\text{dominance duration}\\ \text{of attention condition}\end{array}\right) - \left(\begin{array}{l}\text{dominance duration}\\ \text{of passive condition}\end{array}\right)}{\left(\begin{array}{l}\text{dominance duration}\\ \text{of passive condition}\end{array}\right)}.$$

For the Necker cube, magnitudes of attentional modulation ranged from 26-49% (mean modulation = 37%) and were always highly significant. In contrast, attentional modulation magnitudes for binocular rivalry ranged from 5-13% (mean modulation = 10%), and often failed to differ significantly from passive viewing. A between-subjects ANOVA revealed significantly greater attentional modulation of Necker cube reversal than binocular rivalry, $F(1, 30) = 14.56$, $p < .001$. The fact that observers showed very limited attentional control over rivalry between meaningful, color-differentiated images suggests that binocular rivalry may involve a more automatic form of visual competition than Necker cube reversal, and as a consequence is less easily controlled by visual attention.

Experiment 3: Comparison of selective attentional control and control of alternation rate for Necker cube reversal and binocular rivalry

Experiment 3 investigated whether *selective* attentional control of bistable perception differs from *nonselective* control of alternation rate. The previous experiment revealed poor selective attentional control over rivalry; observers could only enhance or suppress the dominance duration of a particular image by about 10% on average. In contrast, previous studies have shown that observers can voluntarily control the alternation rate of binocular rivalry to a considerable degree, and can as much as double their rate of fast alternations as compared to slow alternations (e.g., Lack, 1978). Unlike selective attentional control of rivalry, control of alternation rate might be realized by relying on nonselective or nonattentional strategies. For example, it has previously been reported that paralysis of the muscles of the eye leads to greatly diminished voluntary control over alternation rates for binocular rivalry, but has less of an effect on Necker cube reversal (George, 1936).

Here, we directly compared selective attentional control of perception and non-selective control of alternation rate for both Necker cube reversal and binocular rivalry in the same observers. We predicted that observers would show greater control of alternation rate than selective attentional control, and that this difference should be more salient in the case of rivalry. Because multiple psychophysical sessions were required, we chose to test experienced psychophysical observers who were more experienced at viewing rivalry stimuli, maintaining fixation for sustained periods, and reporting their perception under conditions of ambiguity.

Method

Observers

Six observers participated in this study; all had several previous sessions of training in other binocular rivalry experiments. One observer was an author, and the remaining five observers were naïve to the purpose of the experiment. All observers had normal or corrected-to-normal visual acuity, and good binocular perception of random-dot stereograms.

Selective attentional control experiment

Selective attentional control of Necker cube reversal and binocular rivalry was measured using the same methods and stimuli as those in Experiments 1 and 2. Observers performed three sessions each of Necker cube reversal and rivalry, in alternation, over a two-week period. Each session consisted of a mixed-trial design of thirty-six 60-s trials (4 trials per condition × 9 conditions = 36 trials). In total, each experimental condition was presented for 12 trials.

Control of alternation rate experiment

Control of alternation rate was measured in separate blocks for Necker cube reversal and rivalry. Alternation rate was calculated based on the number of switches between the two dominant percepts, irrespective of whether an intervening blend percept occurred or not. Reported changes from a dominant percept to the blend percept and then back to the original dominant percept were not considered as valid switches. On each trial, observers were instructed to (1) "just passively watch"; (2) "try to speed up the alternation rate"; or (3) "try to slow down the alternation rate." Unlike Experiment 1, only a single, central fixation position was used in this Necker cube experiment to reduce the number of sessions required. For the binocular rivalry experiment, the contrast of the house and face were both set at 15%, 30%, or 60% to bias the alternation rate in a bottom-up fashion. Observers received each condition in a randomized mixed-trial design with thirty-six 60-s trials per session. In total, each experimental condition was presented for 12 trials.

Results and discussion

Selective attentional control experiment

The experienced observers in Experiment 3 showed remarkably similar effects of attentional control as the naïve observers in Experiments 1 and 2. Figure 4 shows the Necker cube data. Observers showed highly significant effects of selective attentional control for both the bottom view ($F(2, 5) = 51.15$, $p < .0005$), and the top view of the Necker cube ($F(2, 5) = 37.98$, $p < .001$). Planned comparisons revealed that observers were able to reliably increase the dominance durations of the attended percept while decreasing the dominance of the unwanted percept in all conditions ($p < .05$).

The factor of fixation position was also significant for both bottom view ($F(2, 5) = 4.76$, $p < .05$) and top view ($F(2, 5) = 7.85$, $p < .01$), indicating that fixating above or below the center of the Necker cube increased the likelihood of perceiving it from above or below, respectively. Although shifts in eye position could bias perception of the Necker cube in a bottom-up fashion, top-down selective attention led to stronger bias effects on perception, over and above the effect of fixation position. There was no significant interaction effect between selective attention and fixation position for the bottom view ($F(4, 20) = 1.64$, $p = .204$). However, a significant interaction was found for the top view ($F(4, 20) = 4.99$, $p < .01$), similar to what a previous study found in bistable apparent motion (Suzuki & Peterson, 2000).

Figure 5 reveals poor selective attentional control of binocular rivalry. In contrast to the powerful ability to

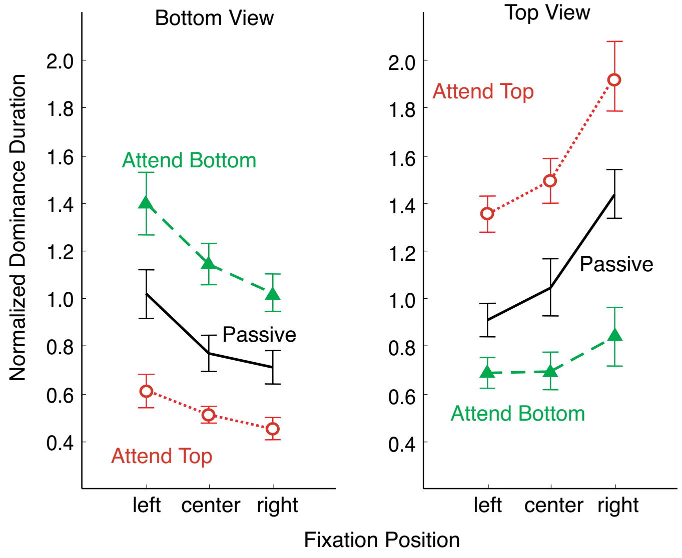

Figure 4. Mean normalized dominance durations for perceiving the bottom view (left) and top view (right) during selective attentional control of the Necker cube in Experiment 3 ($N = 6$). Observers were instructed to attend to the bottom view (green dashed line), attend to the top view (red dotted line), or passively view the Necker cube (black solid line). Error bars represent ±1 *SEM*.

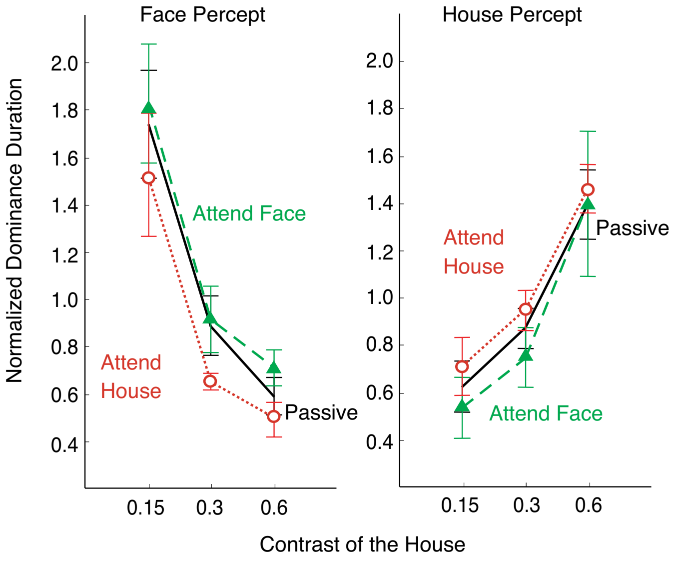

Figure 5. Mean normalized dominance durations for perceiving face (left) and house (right) during selective attentional control of rivalry in Experiment 3 ($N = 6$). Observers were instructed to attend to the face (green dashed line), attend to the house (red dotted line), or passively view the stimuli (black solid line). The contrast of the house was manipulated while the contrast of the face was set to 30%. Error bars represent ±1 *SEM*.

modulate perception of the Necker cube, observers were unable to modulate rivalry dominance durations of the house percept ($F(2, 5) = 1.25$, $p = .327$) or the face percept ($F(2, 5) = 2.30$, $p = .150$) in a statistically reliable fashion. All planned comparisons between attention conditions and passive viewing were also nonsignificant. Dominance durations, however, remained highly sensitive to bottom-up factors. The contrast of the house had a highly significantly effect on both face perception, $F(2, 5) = 19.80$, $p < .0005$, and house perception, $F(2, 5) = 10.67$, $p < .005$.

Figure 6b compares the proportion of selective attentional modulation for the Necker cube and binocular rivalry in Experiment 3. Observers showed significantly greater selective attentional control of the Necker cube than binocular rivalry ($F(1, 5) = 36.03$, $p < .002$), with an average proportion of modulation of 40% versus 13%, respectively. These magnitudes of attentional modulation for Necker cube and rivalry closely match those found in naïve observers in Experiments 1 and 2 (Figure 6a). All three experiments converge towards the suggestion that the neural mechanisms underlying Necker cube reversal and binocular rivalry are different. Binocular rivalry may involve an earlier stage of visual competition that cannot be readily biased by selective attention as compared to Necker cube reversal.

Control of alternation rate experiment

Figure 7a shows that the proportion of nonselective control over alternation rate for Necker cube reversal and binocular rivalry appeared to be quite comparable. Control of alternation rate was statistically significant for both Necker cube reversal, $F(2, 5) = 28.06$, $p < .005$, and binocular rivalry, $F(2, 5) = 6.45$, $p < .05$. Observers were able to reliably speed-up ($t(5) = 5.80$, $p < .005$), and slow-down ($t(5) = 2.07$, $p < .05$) their alternation rates for the Necker cube, relative to passive viewing. Figure 7b shows that ob-

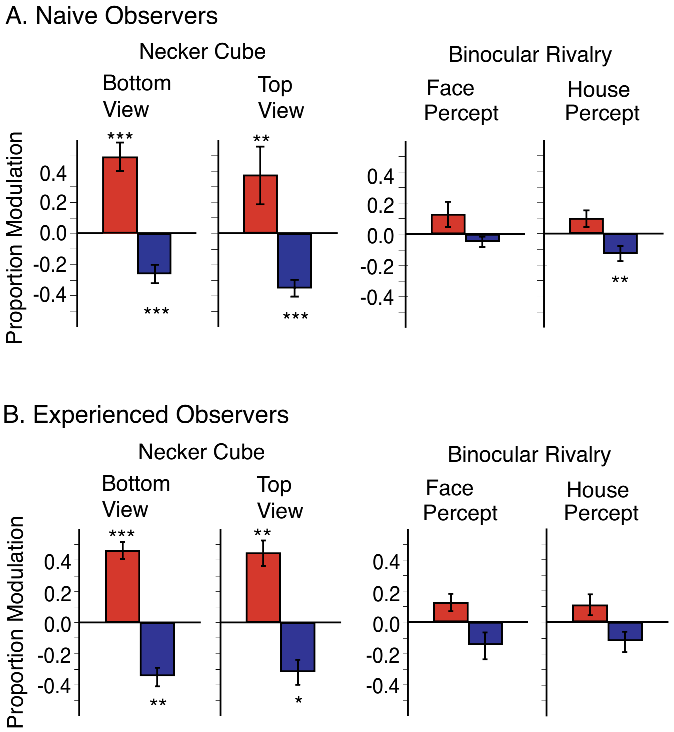

Figure 6. Comparison of the proportion of selective attentional modulation for Necker cube reversal and binocular rivalry (Experiments 1-3). Bar graphs indicate the proportion of modulation in mean dominance duration for each attentional condition relative to passive viewing. A. Data of naïve observers in Experiments 1 and 2. B. Data of experienced observers in Experiment 3. Asterisks indicate statistically significant modulations relative to passive viewing (*$p < .05$; **$p < .01$; ***$p < .001$). Error bars represent ±1 *SEM*. For Necker cube reversal, selective attention significantly increased the attended percept and decreased the unattended percept, whereas attentional modulation of binocular rivalry was weak and unreliable.

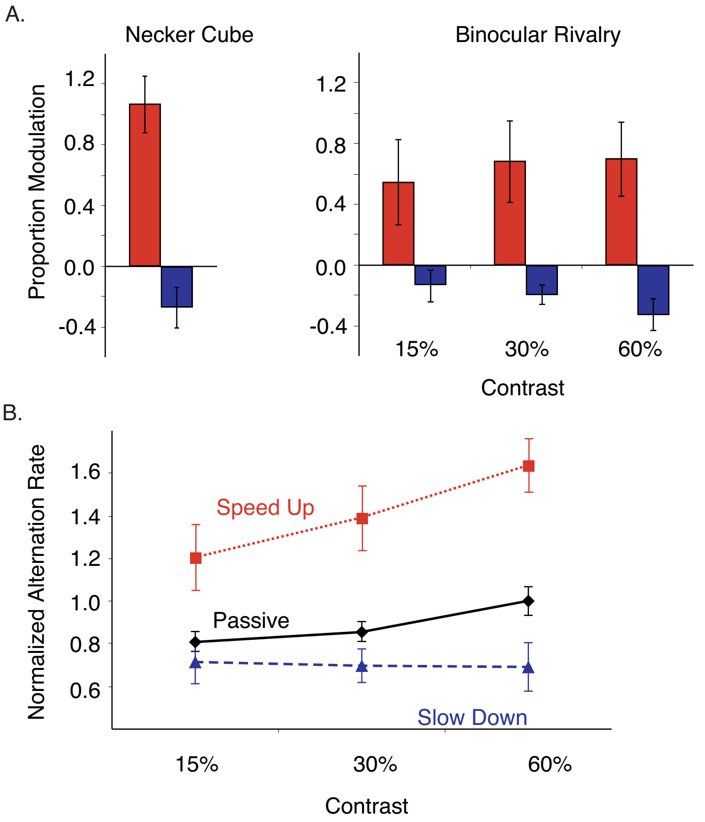

Figure 7. A. Comparison of the proportion of voluntary control over alternation rates for Necker cube reversal and binocular rivalry in Experiment 3. Bar graphs indicate the proportion of modulation in alternation rate for each voluntary control condition relative to passive viewing. Error bars represent ±1 *SEM*. Observers showed a strong ability to modulate the alternation rates of both Necker cube reversal and binocular rivalry. B. Normalized rates of alternation across contrast levels for binocular rivalry. Observers showed substantial control of rivalry alternation rates, and could roughly double the rate of fast alternations as compared to slow alternations. Moreover, the amount of control over rivalry alternations significantly increased as a function of stimulus contrast.

servers could significantly increase ($F(1, 5) = 8.76$, $p < .05$) and decrease ($F(1, 5) = 10.73$, $p < .05$) alternation rates during rivalry across all contrast levels. The amount of control over rivalry alternations increased as a function of stimulus contrast ($F(4, 20) = 4.49$, $p < .01$), such that at the highest contrast level, alternation rates in the speed-up condition were more than twice as fast as the slow-down condition.

The magnitude of voluntary control over alternation rates did not significantly differ for Necker cube reversal and binocular rivalry ($F(1, 5) = 3.56$, $p = .12$), and the proportion of modulation appeared quite comparable for Necker cube reversal and binocular rivalry, especially at the highest contrast level for rivalry. The amount of control over rivalry alternation rates found here matches that of previous rivalry studies (Lack, 1978; Meredith, 1962). Our results indicate that control of alternation rate is a poor predictor of selective attentional control, and poor at differentiating between different forms of bistable perception. It appears that observers can rely on certain nonselective strategies to control rivalry alternation rates, but are unable to use these strategies to modulate rivalry perception in a selective manner. In summary, observers can control the alternation rates of rivalry and Necker cube reversal to a comparable extent, but have much weaker selective attentional control over binocular rivalry than Necker cube reversal.

Experiment 4: Attentional modulation of spatially biased rivalry displays

In Experiments 1-3, observers consistently showed much weaker selective attentional control of binocular rivalry than Necker cube reversal. One interpretation is that binocular rivalry involves a more automatic, stimulus-driven form of visual competition than ambiguous figure reversal, and consequently, is less easily biased by selective attention. Alternatively, one might argue that attentional control of rivalry is weak because there is no opportunity for spatial attention to selectively bias overlapping rivalry stimuli. Although Experiments 1-3 maximized the opportunities for feature- and object-based attentional selection during rivalry, the lack of opportunity for spatial selection may account for the weak selective attentional control found for rivalry.

To evaluate this possibility, we devised a novel rivalry display that was spatially biased, in which one monocular grating increased linearly in contrast from left to right while the opposing grating decreased in contrast (see Figure 1c). Thus, the relative stimulus strength of the two monocular gratings varied locally from left to right. Our preliminary observations indicated that changes in dominance were more likely to originate from the high-contrast portion of the emerging grating and spread to the low-contrast region in a traveling wave (cf., Wilson, Blake, & Lee, 2001), indicating that the two rivaling stimuli had a local competitive advantage on opposite sides of the display. We predicted that shifts in fixation position from left to right should have a strong impact on the relative dominance of the two gratings, given that information near the fovea would be more strongly weighted in determining the outcome of rivalry.

This rivalry display allowed us to compare the strength of bottom-up spatial-bias effects induced by changes in fixation position and top-down spatial-bias effects induced by shifts in spatial attention. If spatial attention can strongly bias binocular rivalry, then observers should be able to selectively control their perception by shifting their attention from one side of the display to the other, analogous to physical shifts in eye position. However, if observers show weak or negligible effects of spatial attention on binocular rivalry, then this would suggest that differences between spatial attention and featural attention are unlikely to account for the consistently weaker attentional modulation found across rivalry experiments. Instead, rivalry would appear to involve a more automatic, stimulus-driven form of visual competition than ambiguous figure reversal.

Method

Observers

Six observers participated in this study; all had several previous sessions of training in other binocular rivalry experiments. One observer was an author, and the other five observers were naïve to the purpose of the experiment. All observers had normal or corrected-to-normal visual acuity, and good binocular perception of random-dot stereograms.

Apparatus and procedure

The experimental set-up and procedure were similar to Experiment 2, with modifications of the stimuli and the task instructions. Stimuli consisted of a green left-tilted grating and a red right-tilted grating presented to different eyes (size = 6° × 2°) (see Figure 1c). The gratings were set to the same mean luminance and presented on a mean yellow background (3.3 cd/m^2). The contrast of the left-tilted grating decreased linearly from left to right while the right-tilted grating increased from left to right (contrast range 10-90%). To test if this spatial asymmetry could bias binocular rivalry, the fixation crosshair (size 0.47°) was presented either in the center, 2.5° to the left or 2.5° to the right of each image. Black ovals (7.6° × 3.6°) surrounded each monocular image to aid binocular fusion. Observers were instructed to maintain fixation and to (1) “just look at the stimuli passively”; (2) “try to maintain the percept of the left-tilted grating for as long as possible”; and (3) “try to maintain the percept of the right-tilted grating for as long as possible.” For the attention conditions, observers were told to attend covertly to the high-contrast portion of the relevant grating, as this might enhance its predominance (e.g., attend to the left side to enhance the left-tilted grating).

There were three fixation positions and three attentional conditions for a total of nine condition types. Observers received each condition in a randomized mixed-trial design with thirty-six 60-s trials per session, for a total of three sessions. Observers continuously monitored their perceptual state and reported perceptual switches by pressing one of three keys to indicate when they saw the left-tilted grating, the right-tilted grating, or a blend/piecemeal rivalry.

Data analysis

Dominance durations were normalized using the same method as described in Experiment 1. ANOVAs were performed to analyze the mean normalized dominance durations for each condition.

Results and discussion

Figure 8 shows the mean normalized dominance durations for perception of the left-tilted grating and right-tilted grating. Changes in fixation position led to significant modulations in dominance duration for both the right-tilted grating, *F*(2, 10) = 10.67, $p < .005$, and the left-tilted grating, *F*(2, 10) = 7.53, $p < .05$.[1] Overall, the results demonstrate that the display induced a strong asymmetric spatial bias in rivalry predominance, and that when viewing such displays, binocular rivalry can be strongly biased by bottom-up spatial factors such as shifts in fixation position.

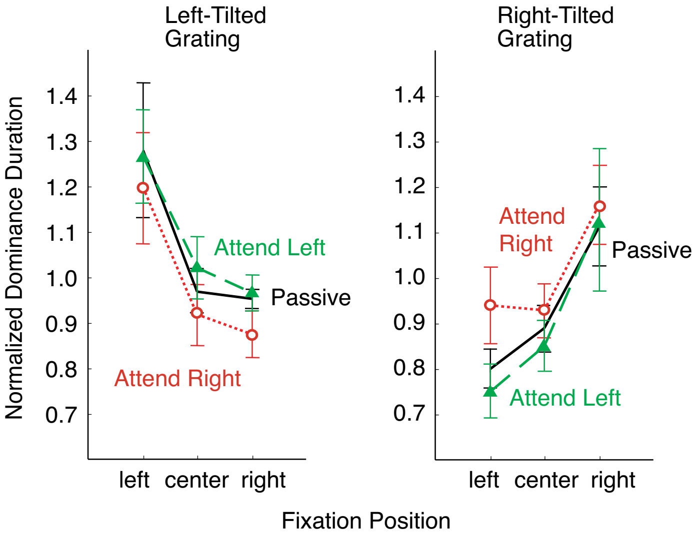

Figure 8. Mean normalized dominance durations for perceiving the left-tilted grating and right-tilted grating during selective attentional control of a spatially biased rivalry display in Experiment 4 (*N* = 6). Rivalry stimuli varied in contrast from left to right, to induce a physical spatial bias (see Figure 1c). Observers were instructed either to passively view the display (black solid line), to attend to the left side corresponding to the high-contrast portion of the left-tilted grating (green dashed line), or to attend to the right side corresponding to the high-contrast portion of the right-tilted grating (red dotted line). Error bars represent ±1 *SEM*. Shifts in fixation position strongly biased percept durations, whereas shifts in spatial attention led to poor selective control of rivalry.

In comparison, top-down shifts in spatial attention appeared to have a much weaker effect on rivalry. The main effect of attentional control was marginally significant for perception of the right-tilted grating, *F*(2, 10) = 3.51, $p = .07$, and significant for perception of the left-tilted grating, *F*(2, 10) = 9.81, $p < .005$. Planned comparisons indicated that when instructed to attend to the left-tilted grating, observers were unable to reliably decrease the dominance duration of the right-tilted grating, *F*(1, 5) = .402, $p = .540$, or increase the dominance duration of the left-tilted grating, *F*(1, 5) = .716, $p = .417$. When instructed to attend to the right-tilted grating, observers could only decrease the dominance duration of the left-tilted grating, *F*(1, 5) = 11.18, $p < .01$, and failed to significantly increase the dominance duration of the right-tilted grating, *F*(1,5) = 3.65, $p = .088$. There was no significant interaction between attention and fixation position (*F*(4, 20) < 1).

Figure 9 shows a comparison of the bottom-up effect of fixation position and the top-down effect of spatial attention in biasing binocular rivalry. Proportion modulation was measured based on mean dominance durations relative to central fixation and passive viewing, respectively. Shifts in eye position from one side of the display to the other led to overall modulations of 32%, whereas shifts in spatial attention led to much weaker modulations of only 10%, a difference of more than three-fold. These results indicate that perceptual dominance in binocular rivalry can be strongly biased by bottom-up spatial factors such as local stimulus contrast, but only weakly biased by spatial attention. Although our display tried to maximize opportunities for spatial attentional selection, observers showed no greater attentional modulation of rivalry in this experiment than in Experiments 2 and 3, which required feature-based attention to bias overlapping face/house stimuli.

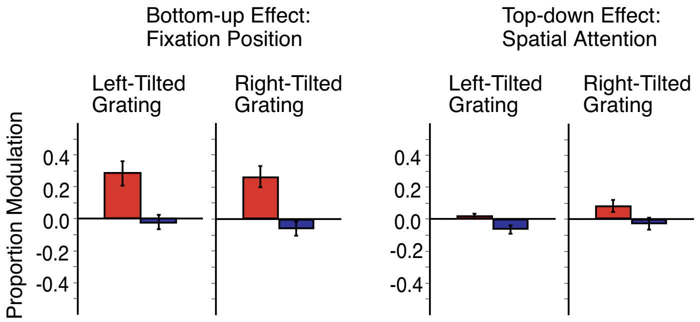

Figure 9. Proportion of modulation for the bottom-up effect of fixation position (left) and the top-down effect of spatial attention (right) in biasing binocular rivalry in Experiment 4. Error bars represent ±1 *SEM*. Note that shifts of fixation position led to overall modulations of about 30%, whereas shifts of spatial attention led to much weaker modulations of only about 10%.

A final point worth addressing is whether attentional control of rivalry is affected by the frequency of blending or piecemeal rivalry. Because observers were instructed to adopt a strict criterion for exclusive dominance, we expected that the frequency of piecemeal rivalry should have little effect on our estimates of attentional control over exclusive dominance durations. In Experiment 4, piecemeal rivalry was reported 32% of the time, and observers showed weak attentional modulation of rivalry relative to passive viewing (average attentional modulation= 5%). In a separate experiment using much smaller rivalry gratings of only 1-deg diameter, three trained observers reported piecemeal rivalry only 6.5% of the time and showed a similarly weak level of attentional control (average attentional modulation= 4.5%). In summary, we found consistently weak effects of selective attention for binocular rivalry, irrespective of frequency of piecemeal rivalry, stimulus type (grating or meaningful object), or attentional selection strategy (featural or spatial attention).

General discussion

The present study was the first to compare selective attentional control over different forms of bistable perception. Binocular rivalry was strongly influenced by bottom-up factors such as changes in contrast or fixation position, but only weakly modulated by top-down selective attention. In contrast, perception of the Necker cube was much more strongly modulated by selective attention than by shifts in fixation position. For Necker cube reversal, both naïve and experienced observers could selectively enhance the dominance duration of the attended percept and simultaneously decrease the dominance of the unattended percept to a considerable extent (mean modulation 37-40%). In comparison, selective attentional control of binocular rivalry was much weaker (average modulation 5–13%) and often failed to reach significance in the sample sizes tested here. Even the use of rivaling face and house images that differed in color, form, and object category did not seem to facilitate attentional selection (Experiments 2 and 3). Likewise, the use of spatially asymmetric rivalry stimuli, which led to strong biases in rivalry predominance during physical shifts in eye position, still led to weak attentional control (Experiment 4). Thus, rivalry displays that maximized the opportunities for featural and object-based attentional selection, or featural and spatial attentional selection, still led to a poor ability to select the desired percept.

The fact that selective attentional control was always much weaker for rivalry than Necker cube reversal cannot be readily explained by top-down selection theory. It seems implausible that a single top-down selection mechanism might mediate all forms of bistable perception yet still lead to such poor attentional control of rivalry. Our results are also inconsistent with the predictions of pattern competition theory. If rivalry and ambiguous figure reversal are mediated by common/similar mechanisms of pattern-based competition, then one would predict that attention should be about equally effective at biasing these different forms of bistable perception. Instead, our results most closely agree with the predictions of interocular competition theory, which forwards that rivalry involves competition at an earlier stage of processing than other forms of bistable perception. It seems reasonable to assume that earlier stages of visual competition should be more strongly influenced by bottom-up factors and more weakly influenced by top-down attention, as was found here for binocular rivalry. Our results support the notion that rivalry involves a more automatic, stimulus-driven form of visual competition than Necker cube reversal, and as a consequence, is less easily biased by selective attention.

Unlike selective attentional control, non-selective control of alternation rates proved to be about equally strong for both types of bistable perception (Experiment 3). Our observers could more than double their rate of fast alternations as compared to slow alternations when viewing high-contrast rivalry stimuli, matching the level of control found in previous studies (Lack, 1971; Lack, 1978; Meredith, 1962). Nonetheless, these same observers still showed weak selective attentional control over rivalry. Therefore, voluntary control of alternation rate appears to be a poor indicator of selective attentional control.

What strategies are observers relying on to control rivalry alternation rates in a non-selective fashion? Although this question was not the main focus of the present study, we suspect that observers can rely on strategies other than selective attention to modulate the overall alternation rate. Consistent with this notion, an early study found that paralysis of the intrinsic muscles of the eye led to decreased voluntary control of alternation rates for binocular rivalry between both real images and afterimages (George, 1936). Unlike rivalry, control of ambiguous figure reversal was hardly affected by such paralysis. This suggests that voluntary control of rivalry alternation rates may depend on eye movements or microsaccades. Future investigations of these issues may help reveal other important differences between non-selective control of alternation rate and selective attentional control in binocular rivalry.

Our results suggest that future studies should instead rely on measures of selective attentional control to assess top-down effects in bistable perception (see also Suzuki & Peterson, 2000). Along these lines, more recent studies have found evidence of selective attentional control over ambiguous figure reversal (Gomez et al., 1995; Horlitz & O'Leary, 1993; Liebert & Burk, 1985; Peterson, 1986; Toppino, 2003), consistent with the present findings. There have been some reports that voluntary attention can modulate perception during dichoptic masking or flash suppression, but reports are conflicting as to whether attention to an item facilitates or inhibits perception under such conditions (Ooi & He, 1999; Sasaki & Gyoba, 2002). In these dichoptic masking studies, the observer's attention was directed to an initially visible target, which may have enhanced the effects of attention. The weaker effect of attention found here during binocular rivalry may be due to the fact that rivalry involves the suppression of basic visual features, and that it may be more difficult for attention to modulate suppressed features than to modulate suppressed interpretations of figural organization for ambiguous figures. Alternatively, suppression during steady rivalry viewing may differ from suppression induced by transient dichoptic masking. Future studies should investigate if selective attention leads to similar or different effects for binocular rivalry and dichoptic masking.

According to attentional theories of bistable perception, both binocular rivalry and ambiguous figure reversal are believed to result from frontal-parietal bias signals that activate specific representations in visual cortex (e.g., Leopold & Logothetis, 1999; Lumer et al., 1998). However, recent neuroimaging data suggest that binocular rivalry involves early interocular competition in V1 (Tong & Engel, 2001; but see also Leopold & Logothetis, 1996). Moreover, rivalry suppression has been found to lead to concomitant suppression of V1 activity, irrespective of whether the observer is attending to the peripheral rivalry stimulus or to a difficult letter detection task at central fixation (Lee, Blake, & Heeger, 2003). In contrast, ambiguous figure reversal is associated with the activation of high-level ventral extrastriate areas (Kleinschmidt, Buchel, Zeki, & Frackowiak, 1998). Consistent with these neuroimaging studies, the present psychophysical data suggest that binocular rivalry and ambiguous figure reversal likely reflect separate mechanisms. Binocular rivalry appears to occur at an earlier stage of visual processing that is more automatic, stimulus-driven, and less accessible to selective attention.

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Footnotes

[1] Compared to central fixation, shifts to the left (or right) fixation position led to a significant increase in dominance durations for the left (or right) tilted grating ($p < .01$), but did not lead to a significant decrease in dominance duration for the opposing grating ($F < 1$). This asymmetry, though not of central interest here, may reflect the fact that we used a linear contrast ramp (10-90%) rather than a log contrast ramp, such that the decrease in contrast at the stimulus ends, relative to the stimulus center (10% vs. 45%), was proportionally greater than the increase in contrast (90% vs. 45%) at the stimulus ends. A dramatic decrease in the contrast of one grating would be expected to lead to a large increase in dominance duration for the opposing grating (cf., Levelt, 1968).

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