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# Voluntary Attention Modulates Processing of Eye-Specific Visual Information

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## Abstract

Visual attention functions to select relevant information from a vast amount of visual input that is available for further processing. Information from the two eyes is processed separately in early stages before converging and giving rise to a coherent percept. Observers normally cannot access eye-of-origin information. In the research reported here, we demonstrated that voluntary attention can be eye-specific, modulating visual processing within a specific monocular channel. Using a modified binocular-rivalry paradigm, we found that attending to a monocular cue while remaining oblivious to its eye of origin significantly enhanced the competition strength of a stimulus presented to the cued eye, even when the stimulus was suppressed from consciousness. Furthermore, this eye-specific attentional effect was insensitive to low-level properties of the cue (e.g., size and contrast) but sensitive to the attentional load. Together, these findings suggest that top-down attention can have a significant modulation effect at the eye-specific stage of visual information processing.

## Keywords

visual attention, visual perception

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Visual attention allows for the selection of relevant information from a vast amount of visual input that is available for further processing. The mechanisms and properties of attentional selection have been a focus of psychological research for decades. Researchers have found that attentional selection can be location-specific (Posner, 1980), feature-specific (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990), or object-specific (Blaser, Pylyshyn, & Holcombe, 2000). In this study, we investigated whether top-down selective attention can also be based on visual input's eye of origin.

In the early stages of visual processing, information from the two eyes remains separate. Neurons in the lateral geniculate nucleus of the thalamus are segregated into ocular layers for the processing of eye-specific information. Neurons in the input layer of primary visual cortex (V1) are mostly monocular and are organized in periodic stripes alternating between the left and the right eye, known as ocular dominance columns (Horton, Dagi, McCrane, & de Monasterio, 1990; Menon, Ogawa, Strupp, & Ugurbil, 1997). However, most neurons in extrastriate visual areas are binocular, responding to visual stimulation to either one eye or both eyes. Although some previous studies have suggested that attentional modulation of neural responses can occur in V1 and even in the lateral geniculate nucleus (O'Connor, Fukui, Pinsk, & Kastner, 2002), such modulation could be achieved without differentiation between input signals from the two eyes and need not be specific to a particular monocular channel.

Recent studies using monocular-cuing paradigms have suggested that involuntary (exogenous) attentional capture is eye-specific. A stimulus is more likely to become dominant in binocular rivalry if it is accompanied by a pop-out cue presented in proximity to the same eye (Ooi & He, 1999). Other research has shown that an ocular singleton can capture attention even if it is not available to awareness (Zhaoping, 2008). Findings that exogenous attention can be summoned by implicit eye-specific visual information converge with findings that involuntary orienting of attention does not necessarily depend on conscious awareness of cuing information (Ivanoff & Klein, 2003; Jiang, Costello, Fang, Huang, & He, 2006; McCormick, 1997). However, the important question of whether voluntary goal-directed, top-down endogenous attention can modulate the neural response to a visual stimulus in a specific monocular channel has yet to be answered. Given that observers do not have explicit access to eye-of-origin information for a visual stimulus when nonvisual artifacts are well controlled (Wolfe & Franzel, 1988),

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one might expect that voluntary attentional modulation cannot operate at the level of eye-specific processing.

In the current study, we used a modified version of a binocular-rivalry paradigm (Jiang, Costello, & He, 2007) to investigate whether voluntary attention can indeed modulate visual processing specific to one eye.

## General Method

### Observers

Six healthy observers (3 males, 3 females) participated in all experiments. Their ages ranged from 20 to 29 years. All subjects gave written informed consent in a manner approved by the institutional review board of the University of Minnesota.

### Stimuli and procedure

Stimuli were generated in MATLAB (The MathWorks, Natick, MA) with Psychophysics Toolbox 3 (Brainard, 1997; Pelli, 1997) and were displayed on a 19-in. Sony Trinitron G420 monitor (1024 × 768 pixels; 60-Hz refresh rate). The images presented to the two eyes were displayed side by side on the monitor and were viewed through a mirror stereoscope mounted on a chin rest.

High-contrast binocular frames were used to facilitate convergence of the eyes. A radial grating (target) was presented to one eye at the fovea while a high-contrast dynamic noise patch was presented to the other eye in the corresponding retinal location (Fang & He, 2005; Tsuchiya & Koch, 2005). Both the target grating and the noise patch were 2° in diameter. The noise patch consisted of an array of randomly generated Mondrian-square patterns with random size and color, flashing at a rate of 10 Hz. Such randomly generated noise patterns are often referred to as continuous-flash-suppression (CFS) noise (Tsuchiya & Koch, 2005).

Over the course of each trial, the contrast of the target grating increased linearly (from 0% to 100% in 2 s) until subjects pressed a button. If no response was made within 2 s, the target grating remained at full contrast until the button press. This ramping-up procedure ensured that the target was suppressed by the CFS noise when it was initially presented. A trial ended when the subject pressed a button to indicate detection of the target grating; the suppression time (the time from the onset of the target to the button press) was recorded. Subjects were instructed to press the button as soon as any part of the target grating became visible. The suppression time of the initially invisible target served as an index of the signal strength of the suppressed grating in the early visual cortex (Jiang et al., 2007).

Attentional cues were presented at the parafoveal locations. The cues were either 1° (Experiments 1, 2, S1, S2, S4, and S5) or 2° (Experiments S1 and S3) in diameter. In all experiments but Experiment S2, the edge-to-edge distance between the rival stimuli and the cues was 0.8° (in Experiment S2, this distance varied from 0.8° to 4°). The cues randomly and

smoothly changed color (red, gray) and shape (fat, thin) over time. On each trial, subjects had to detect a prespecified conjunction state of the cues (e.g., when one cue was fat and red or when both cues were the same color) and count how many times the cues appeared in this conjunction state. They performed this attention task concurrently with the binocular-rivalry target-detection task described in the previous paragraph. After the binocular-rivalry and cuing display was terminated by the button press, a number appeared at fixation, and subjects pressed one of two keys to indicate whether or not the number matched the number of times the cues had appeared in the prespecified conjunction state. Incorrect answers were followed by auditory feedback. Mean accuracy in the attention task was 74.2% in Experiment 1a, 88.5% in Experiment 1b, 86.5% in the low-load condition in Experiment 2, 58.9% in the high-load condition in Experiment 2, 88% in Experiment S1, 92% in Experiment S2, 82% in Experiment S3, 87% in Experiment S4, and 84% in Experiment S5.

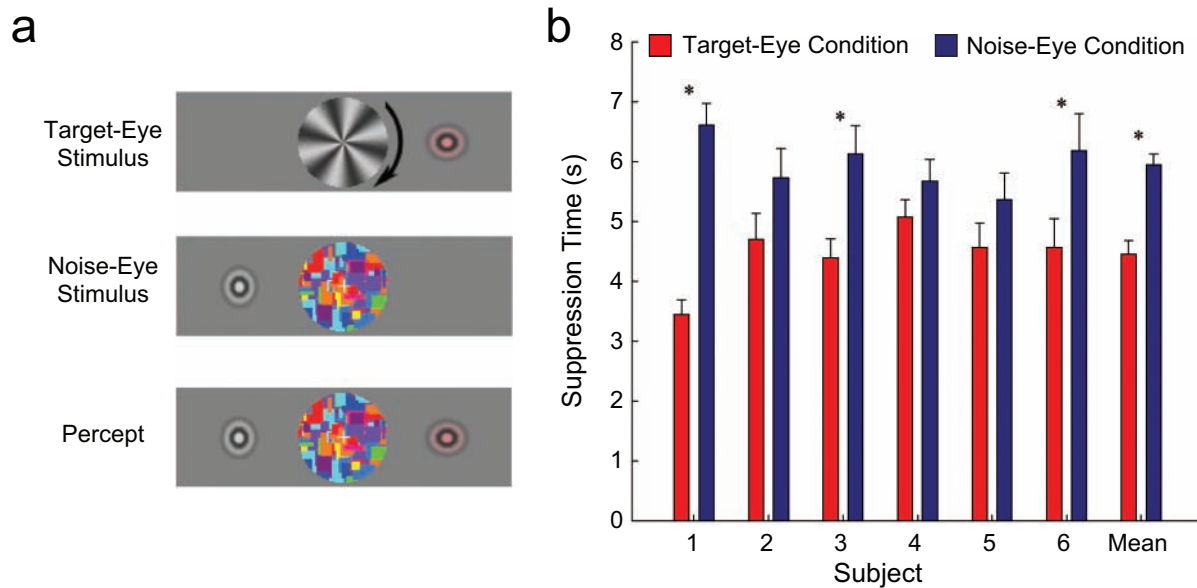
## Experiment 1: Modulation of Eye-Specific, Invisible Visual Information by Attention to Monocular Cues

In Experiment 1, we investigated whether top-down attention to a monocular cue could modulate the suppression time of an invisible target when observers paid attention to either the cue presented to the eye receiving target information (the *target eye*) or the cue presented to the eye receiving noise (the *noise eye*).

### Experiment 1a

In this experiment, a monocular target stimulus was presented to one eye (centered on fixation) while CFS noise was presented to the corresponding location in the other eye (Fig. 1a). Two monocular attentional cues, one for each eye, were presented, respectively, to the left and the right sides of the rival stimuli. Subjectively, none of the observers could tell whether a given monocular cue was being presented to the left or the right eye. Three of the observers completed a forced-choice task in which they indicated whether the two parafoveal cues were presented to the same eye or separately to the two eyes (the cues were presented to the same eye or the two eyes with equal probabilities; subjects were instructed to look for any perceptual differences between the cues). Mean accuracy in this forced-choice task was at chance level (52.8%,  $SE = 3.7\%$ ), which indicates that subjects had no explicit knowledge of the cues' eye of origin.

Observers were instructed to perform a feature-conjunction task on one of the cues (i.e., to count the number of occurrences of a conjunction state) while simultaneously monitoring the appearance of the central rivalrous stimuli and pressing a button as soon as the target emerged from suppression. Observers' mean accuracy in the feature-conjunction task



**Fig. 1.** Example stimuli and results from Experiment 1a. Two parafoveal monocular cues, one on each side of the central rivalry stimuli, were presented dichoptically (a); one cue was presented to the same eye as the suppressed central target (i.e., to the target eye; top row), and the other cue was presented to the same eye as the suppression noise (i.e., to the noise eye; middle row). Subjects were not aware of the monocular nature of the cues (bottom row) and were instructed to direct their attention to either the left or the right cue and to press a key when the suppressed target emerged from the suppression noise. In the target-eye condition, subjects attended to the cue presented to the target eye (the right eye in this example), and in the noise-eye condition, they attended to the cue presented to the noise eye (the left eye in this example). The graph (b) shows the mean suppression time of the target for the two conditions, as well as individual suppression times for the 6 subjects. Asterisks indicate significant differences between suppression times in the two conditions ( $*p < .05$ ). Error bars indicate standard errors of the mean.

was 74.2%, which indicates that the task was moderately difficult (as intended) and that observers had followed the instructions.

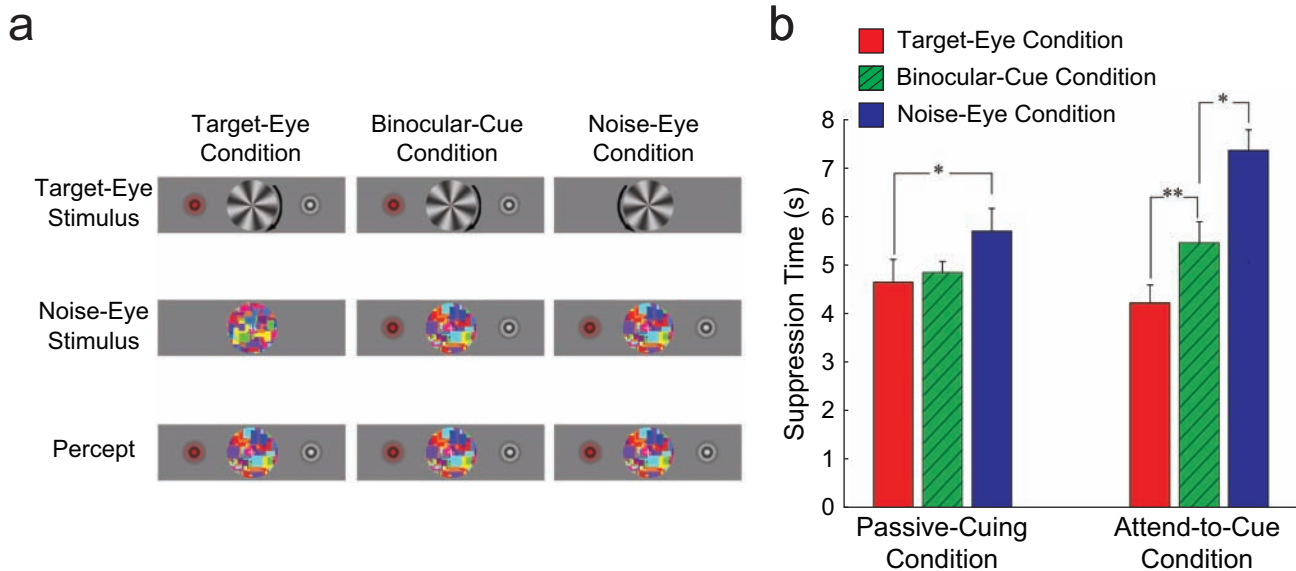
Previous studies have shown that the effects of attention are not restricted to attended stimuli but can extend to nearby zones (Downing & Pinker, 1985; Eimer, 1997; Mangun & Hillyard, 1988). In Experiment 1a, the target and the CFS noise were presented at the same spatial location and were equidistant from the cues. Therefore, we expected the target to have a shorter suppression time when attention was directed to the cue presented to the same eye as the target than when attention was directed to the cue presented to the same eye as the noise only if attention could selectively modulate information at the monocular-processing level and exert an eye-specific influence on the processing of information surrounding the attended cue.

Indeed, the suppression time of the target was significantly shorter when attention was directed to the cue presented to the same eye as the target than when attention was directed to the cue presented to the same eye as the noise,  $t(5) = 3.96$ ,  $p < .05$ , and results were highly consistent across subjects (Fig. 1b). This pattern of results suggests that top-down, voluntary attention can selectively modulate the visual processing associated with the attended monocular channel.

## Experiment 1b

Next, we investigated whether the eye-specific attentional modulation was due to enhanced competition strength of the suppressed target (shorter suppression time) when observers attended to the cue presented to the same eye as the target or due to enhanced competition strength of the dominant CFS noise (longer dominance time) when observers attended to the cue presented to the same eye as the noise.

In this experiment, both cues were presented to the same eye, either with the suppressed target (target-eye condition) or with the CFS noise (noise-eye condition); in addition, we included a binocular-cue, control condition in which both cues were presented to both eyes (see Fig. 2a). Because previous studies have suggested that bottom-up (stimulus-driven) factors might have an eye-specific influence on binocular rivalry (Fukuda & Blake, 1992; Ooi & He, 1999), we also manipulated whether or not subjects performed the attention task, to assess the magnitude of the eye-specific effect when attention was not voluntarily directed to the cues. In the attend-to-cue condition, subjects tracked the color changes of both cues and pressed a button when both cues were the same color while concurrently performing the binocular-rivalry task. In the passive-cuing condition, subjects were instructed to detect the



**Fig. 2.** Stimuli and results from Experiment 1b. As illustrated in (a), two parafoveal cues were presented either monocularly (target-eye and noise-eye conditions; left and right columns) or binocularly (binocular-cue condition; middle column). A radial grating (target) was presented to one eye at the fovea (top row) while a high-contrast dynamic noise patch was presented to the other eye in the corresponding retinal location (middle row); the eyes to which the noise and the target were presented were counterbalanced across trials. Subjects had the same percept in all three conditions (bottom row). The graph (b) shows suppression time as a function of attention condition and the cues' eye of origin. Asterisks indicate significant differences in suppression times (\* $p < .05$ , \*\* $p < .01$ ). Error bars indicate standard errors of the mean.

central target and to ignore the parafoveal cues. Therefore, this experiment had a 3 (cues' eye of origin: target eye, noise eye, both eyes)  $\times$  2 (attention: attention to cue, passive cuing) design.

An analysis of variance revealed a significant eye-specific effect of the cue,  $F(2, 8) = 15.1$ ,  $p < .005$ , and this eye-specific effect was significantly modulated by attention,  $F(2, 8) = 21.2$ ,  $p < .001$ : It was much stronger in the attend-to-cue condition than in the passive-cuing condition (see Fig. 2b). For the attend-to-cue condition, a paired  $t$  test showed that the suppression time of the central target was significantly shorter in the target-eye condition than in the noise-eye condition,  $t(4) = 5.91$ ,  $p < .01$ ; this result is consistent with the results from Experiment 1a. Furthermore, the suppression time for the central target grating was shorter in the target-eye condition,  $t(4) = -5.48$ ,  $p < .01$ , and longer in the noise-eye condition,  $t(4) = 3.85$ ,  $p < .05$ , than it was in the binocular-cue, control condition. These results suggest that eye-specific attention can modulate information processing in either monocular channel (dominant or suppressed), depending on which eye's cue is actually attended. In a supplemental experiment (Experiment S4), we ruled out the possibility that the eye-specific effect was due to differential fixational eye movements in the two eyes (for more details, see the Supplemental Material available online).

For the passive-cuing condition, a post hoc  $t$  test showed no significant reduction of suppression time in the target-eye condition compared with the binocular-cue condition (see Fig.

2b),  $t(4) = -0.56$ ,  $p > .5$ . Still, suppression time was slightly longer in the noise-eye condition than in the binocular-cue condition,  $t(4) = 1.68$ ,  $p < .1$ , and was significantly longer in the noise-eye condition than in the target-eye condition,  $t(4) = 3.21$ ,  $p < .05$ . Therefore, monocular cues induced a weak eye-specific effect even when they were not attended to. This eye-specific modulation effect in the passive-cuing condition was likely a bottom-up, stimulus-driven effect and appeared to be limited mainly to the dominant eye; this result is consistent with findings that involuntary attention can be summoned by monocular cues (Ooi & He, 1999; Zhaoping, 2008). Nevertheless, the eye-specific effect observed in the passive-cuing condition was much smaller than the effect observed in the attend-to-cue condition.

Could the observed effect of attending to the monocular cues simply have been due to enhanced interocular interactions between spatially nonoverlapping stimuli (i.e., the cues and the target or noise)? In other words, even though the monocular cues and the rival stimuli were separated, the cue presented to one eye could potentially have competed with the central stimulus (either the CFS noise or the target) presented to the other eye; the observed attentional modulation of suppression time could thus have been due to an attentional modulation of the cues' rivalry strength, rather than to direct eye-specific attentional modulation on eye-specific visual processing of the rival stimuli.

We investigated this issue in several supplementary experiments. In Experiment S1, we manipulated different stimulus



properties (i.e., size and contrast) of the attentional cues. In Experiment S2, we manipulated the distance between the cues and the rival stimuli. In Experiment S3, we manipulated the distance between the neural representations of a single cue and the rival stimuli in early visual cortex by manipulating whether the cue and rival stimuli were presented on different sides of the vertical meridian or on the same side.

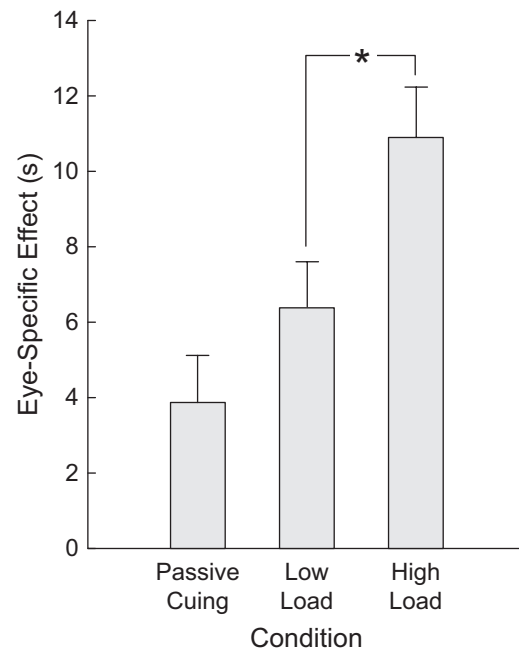
Results showed that varying the size and contrast of the attentional cue did not have a significant influence on the observed eye-specific attentional effect (Experiment S1), that the eye-specific attentional effect reached well beyond the zone of interocular competition (Experiment S2), and that even a dramatic increase in cortical distance between the cue and rival stimuli had no impact on the eye-specific attentional effect (Experiment S3). (See the Supplemental Material for more information about the procedures and results for Experiments S1, S2, and S3.)

## Experiment 2: Sensitivity of the Eye-Specific Attentional Effect to Attentional Load

Next, we examined whether and to what degree the eye-specific effect observed in Experiment 1 was influenced by attentional load. Experiment 2 included three conditions with varying levels of attentional load. In the low-load condition, the attentional task performed on the parafoveal cues was the same as in Experiment 1b: Subjects attended to the changing colors of the cues. In the high-load condition, subjects performed a feature-conjunction task in which they attended to changes in both the color and the shape of the cues; subjects pressed a button when both cues were either the same color but different shapes or the same shape but different colors. In the passive-cuing condition (no attentional load), subjects were asked only to detect the central target. Mean accuracy on the attentional task was 86.5% in the low-load condition and 58.9% in the high-load condition.

As Figure 3 shows, the eye-specific attentional effect was significantly modulated by attentional load,  $F(2, 10) = 10.17$ ,  $p < .01$ . Post hoc analyses showed that the eye-specific effect was much more robust in the high-load condition than in the low-load condition,  $t(5) = 3.49$ ,  $p < .05$ , and there was a marginally significant difference between the low-load condition and the passive-cuing condition,  $t(5) = 2.02$ ,  $p < .1$ . These findings clearly show that the eye-specific effect was indeed sensitive to the manipulation of attentional load. In an additional supplementary experiment (Experiment S5), we physically mimicked the emergence of the suppressed target from the CFS noise and found that the modulation of the eye-specific effect by attentional load was not due to longer reaction times under higher task load (for more information about procedures and results for Experiment S5, see the Supplemental Material).

Results from multiple conditions in which we directly manipulated the attentional load showed that higher attentional load significantly increased the eye-specific effect. Together



**Fig. 3.** Eye-specific effect (difference between suppression times in the noise-eye and target-eye conditions) as a function of attentional-load condition in Experiment 2. The asterisk indicates a significant difference between conditions ( $*p < .05$ ). Error bars indicate standard errors of the mean.

with results from our supplementary experiments showing that low-level image manipulations did not influence the eye-specific attentional effect, these results strongly suggest that this effect was due to direct, top-down attentional modulation rather than to a direct, low-level interocular interaction.

## Discussion

Results from these experiments show that top-down, voluntary attention can modulate visual processing specific to one eye. Interocular suppression time of an invisible stimulus (target) decreased when observers attended to a monocular cue presented to the same eye as the target and increased when the cue was presented to the same eye as the suppression noise. It is important to note that while observers attended to a monocular cue, they could not tell explicitly which eye the cue was presented to, and their accuracy on the forced-choice task in which they had to identify the cues' eye of origin was at chance level. These results constitute strong evidence that top-down, voluntary attention can modulate eye-specific visual processing without observers' explicit knowledge of eye-of-origin information.

Previous studies have found that endogenous attention can prolong the duration of the dominance of an attended target in binocular rivalry (Chong, Tadin, & Blake, 2005) or prevent an attended image from being suppressed (Ooi & He, 1999). However, these results are usually attributed to enhanced rivalry strength of an attended dominant (visible) stimulus.

Our findings from Experiment 1b clearly show that voluntary attention can also enhance the rivalry strength of a stimulus presented to the suppressed eye and reduce the suppression duration of an invisible stimulus.

We observed a significant eye-specific effect in the passive-cueing condition in Experiment 1b, which suggests that bottom-up, stimulus-driven factors contributed to the eye-specific effect. Activity in V1 monocular neurons could facilitate the receipt of input from the same eye through horizontal connections within a limited spatial range. Experiment S2 showed that the effective zone of the eye-specific effect in the passive-cueing condition ( $< 2.0^\circ$ ) was commensurate with the range of horizontal connection in primate V1, indicating that this effect was probably due to horizontal interactions in V1 (Angelucci et al., 2002). However, the results from our series of supplemental experiments suggest that the observed effect of eye-specific, voluntary attention cannot be completely accounted for by a simple attentional modulation of the lateral interaction between neurons responding to the cues and the rival stimuli.

If attention modulated the lateral excitatory interactions between the cues and rival stimuli, the eye-specific attentional effect should have increased as the stimulus strength of the cues increased, but we found in Experiment S1 that dramatically varying the size and contrast of the attentional cues had little influence on the eye-specific effect. In Experiment S2, the eye-specific effect was measurable when the distance between the cue and the rival stimuli was large (about  $4^\circ$  of visual angle). This distance is well beyond the spatial zones of interocular competition (Blake, O'Shea, & Mueller, 1992; Fukuda & Blake, 1992) and beyond the spatial scale of horizontal interaction in primate V1 (Angelucci et al., 2002). In Experiment S3, the eye-specific effect was essentially the same whether the cue and rival stimuli were projected to the same visual hemisphere or to different visual hemispheres; this pattern of results indicates that this effect was not purely the result of direct local interactions in early visual cortex. In contrast, we found in Experiment 2 that this eye-specific attentional effect was sensitive to top-down attention-related factors. The modulation of the eye-specific effect by varying attentional load suggests that top-down attentional modulation mediates this eye-specific effect. In Experiment S4, we ruled out the possibility that the effect was due to differential fixational eye movements in the two eyes.

Taken together, our findings suggest that top-down attention can selectively modulate the neural response in a specific monocular channel. Although observers can voluntarily direct attention only to information that has reached awareness, attending to a monocular stimulus preferentially enhances the corresponding neural response in that monocular channel and may weaken the response for neurons tuned to the opposite eye.

However, given that binocular rivalry is a relative measure, our results are consistent with either or both of two interpretations: (a) that the eye-specific effect was due to attention enhancing the neural response in the attended eye and (b) that the effect was due to attention suppressing the neural response

in the unattended eye. The observed eye-specific attentional effect on the processing of invisible stimuli is consistent with, yet distinct from, evidence from previous studies that attending to visible information modulates the response to neighboring invisible information. For example, it has been found that the tilt aftereffect from a suppressed Gabor patch increases when observers attend to a visible Gabor patch in the same orientation at a separate location (Kanai, Tsuchiya, & Verstraten, 2006) and decreases when perceptual load is increased at a nearby location (Bahrami, Carmel, Walsh, Rees, & Lavie, 2008). Our findings add to the growing evidence that distinct mechanisms are involved in visual awareness and attention (Koch & Tsuchiya, 2007). In the visual system, feedback connections abound at multiple stages (e.g., the stage at which massive feedback fibers from striate cortex reach the lateral geniculate nucleus). Apparently, the modulatory effect of voluntarily directed attention can take advantage of these feedback paths, reach back to monocular neurons, and selectively modulate visual information processing via eye-specific feedback mechanisms.

### Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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### Supplemental Material

Additional supporting information may be found at <http://pss.sagepub.com/content/by/supplemental-data>

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