

Binocular rivalry and visual awareness: the role of attention

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Abstract. When the right eye and the left eye view dissimilar scenes, the observer does not experience a stable superimposed percept of the images presented to the two eyes, but instead perceives an alternation between the images seen by each eye. A critical question confronting this robust and intriguing phenomenon of binocular rivalry is how the visual system selects the image to be perceived (dominant). The current main-stream literature emphasizes a bottom-up explanation in which the rivalry stimulus with the higher contour strength has the advantage, and becomes dominant in rivalry. Nevertheless, some workers in the past have favored an attention-selection explanation for binocular rivalry. We investigated the role of attention in binocular rivalry by employing novel psychophysical paradigms which capitalized on several established phenomena (eg the Cheshire Cat effect, attention cueing, pop-out effect). Our results revealed two major aspects of attention modulation in binocular rivalry. We found that a dominant image is less likely to be suppressed when voluntary attention is directed to it. This suggests the role of voluntary attention in retaining the dominant image in visual awareness. Second, a rivalry stimulus is more likely to become dominant if accompanied by a pop-out cue (in the same eye and proximity). Since a pop-out cue attracts involuntary attention to its location/eye, this result suggests that cue-mediated involuntary attention can promote the ability of a rivalry stimulus to reach visual awareness.

1 Introduction

Binocular rivalry occurs when the two eyes are presented with nonidentical visual stimuli. Perception during binocular rivalry alternates incessantly between the images viewed by the right eye (RE) and the left eye (LE), with seemingly little regard to the observer's whim to control which eye's image to perceive. The eye whose image is momentarily perceived is referred to as the dominant eye and the fellow eye, the suppressed eye.

The phenomenon of binocular rivalry has continued to attract the curiosity of scientists ever since it was first demonstrated two centuries ago. This is evident from the volumes of literature it has generated. With regard to its stimulus attributes, we now know, for example, that an eye viewing a stimulus having a higher stimulus strength (contrast energy) during binocular rivalry predominates, ie its stimulus is perceived for a larger percentage of time compared to the fellow eye's stimulus for a given observation period. When both dichoptic rivalry stimuli have equal stimulus strength, the rivalry between them becomes more robust as their stimulus strength is increased (Breese 1899, 1909; Levelt 1965; Liu et al 1992; see also excellent reviews by Blake 1989; Fox 1991).

Meanwhile other studies of binocular rivalry have concentrated on developing various manipulations to force the suppressed eye to dominance. For example, Walker and Powell (1979) and Blake et al (1990) induced eye dominance by perturbing the suppressed eye with an abrupt reversing contrast stimulus. Wolfe (1984) and Ooi and Loop (1994) induced eye dominance by allowing the eye to be suppressed to preview the rivalry stimulus.

Another method is the one referred to as the Cheshire Cat effect (Duensing and Miller 1979) or binocular motion masking (Grindley and Townsend 1965). To create this effect, an observer views an object (eg a face, grating, etc) with one eye while the fellow eye views a blank field. This results in the observer experiencing a rather stable percept of the object. Then the experimenter suddenly perturbs the eye viewing the blank field with a real-motion stimulus (eg by waving a hand or moving a rod). When this happens, the observer experiences the object's disappearance, and perceives the blank field instead. (Of interest, this effect is dubbed the Cheshire Cat effect because, when the object is a face, sometimes the entire face except the eyes and lips disappears, which reminds one of the Cheshire cat in *Alice in Wonderland*.)

This said, there is no doubt that binocular rivalry is both an intriguing and important 'tool' for us to understand how the brain selects the visual information that reaches our conscious perception (Crick and Koch 1995; Myerson et al 1981). This is because during binocular rivalry, even though both eyes are presented with visual stimuli, only one stimulus is perceived. Meanwhile, the stimulus viewed by the suppressed eye might as well not be present, since its image is prevented from reaching consciousness. Further, the alternating percept of rivalry is largely independent of the observer's will. Yet, in situations such as the Cheshire Cat effect, one can quite readily force a suppressed eye to dominance simply by perturbing it. In this regard, a fundamental question in binocular rivalry is: "*What mechanism determines whether the right or left eye's image reaches conscious perception during binocular rivalry?*" Although much effort has been expended in the past in searching for an answer, the solution still eludes us. Historically, workers in this field have been divided in their beliefs—beliefs that are best traced to the two often antagonistic figures in vision science, Hering and Helmholtz.

Hering (1879/1942) proposed that the eye receiving the stronger contour information (stimulus strength) becomes dominant during binocular rivalry, thus formulating the *predominance-of-contour hypothesis*. He recounted a demonstration where a contoured stimulus (parallel lines) was presented to one eye and a homogenous field (an empty square) to the corresponding retinal region in the fellow eye, which resulted in a stable perception of the parallel-line stimulus. Hering thought that this demonstration argued strongly for the predominance-of-contour hypothesis of binocular rivalry. Levelt (1965) employed the principles of a weighting function and the law of complementary share to provide a similar but more quantitative explanation. These principles assume that the right and left monocular channels (eyes) each contribute some weight to the binocular system, and the sum of these weights is unity. The weight of each monocular channel is determined by the strength of the target it receives. In binocular rivalry, each monocular channel attains a weight of unity, which violates the law of complementary share. To restore this law, an eye has to be suppressed so that its weight is reduced to zero. Thus binocular rivalry is explained as the visual system's attempt to restore the law of complementary share; and rivalry alternation is due to the visual system not having preference for either eye's image. To date, various related observations showing that a stronger stimulus in one eye leads to the predominance of that eye during binocular rivalry seem to be consistent with the contour hypothesis (eg Blake 1977; Blake and Camisa 1979; Fox and Rasche 1969; Hollins 1980; Kaplan and Metlay 1964).

On the other hand, Helmholtz (1910/1962) emphasized the role of attention in controlling binocular rivalry, putting forward the *attention hypothesis* (also see James 1891). In stating the attention hypothesis, he was careful to make an important distinction between an immediate-attention and a mediate-attention process. Paraphrasing Helmholtz, an immediate attention is one which the observer can summon and maintain at will (ie voluntary, or endogenous attention). Conversely, a mediate attention has to be summoned by a novel stimulus and cannot be maintained at will (ie involuntary, exogenous attention). Helmholtz proposed that eye dominance during binocular rivalry

is controlled by these distinct aspects of the attention mechanism. To illustrate his proposal, Helmholtz recounted his experience when observing binocular rivalry between a pair of dichoptic stimuli comprised of parallel lines oriented at 45° and 135° , in which he made two important observations. First, he found that if he (voluntarily) 'concentrated' his attention on the momentarily dominant stimulus he was able to maintain the perception of that stimulus in the dominant phase for a longer duration. [In fact, Hering (1879/1942) concurred with this observation too, although he did not provide further elaboration on this subject.] Second, Helmholtz found that it was difficult to keep attention on a particular stimulus for a prolonged duration without having to concurrently have some definite purpose in mind to "stimulate attention incessantly and to keep it active, such as counting the lines of the stimulus or comparing the intervals between the parallel lines of the stimulus, etc". This insightful experience led Helmholtz to conclude that the attention mechanism controlling binocular rivalry is not entirely subservient to the conscious will of the observer (ie involuntary); its (voluntary) hold on a dominant object diminishes readily when the dominant stimulus ceases to be novel. However, owing to the lack of critical empirical evidence, this attention hypothesis has not gained wide acceptance, even though it has been favored by some workers in the past (see reviews by Fox 1991; Lack 1978; Walker 1978).

Over the last few years, neurophysiological findings from various laboratories have furnished us with new evidence pertaining to the neuronal correlates of binocular rivalry. For instance, Sengpiel and Blakemore (1994) showed that the firing rate of cortical cells of anesthetized cats in response to an optimal stimulus in one eye was reduced when a second (binocular rivalry) stimulus was presented to the contralateral eye. Working on alert behaving monkeys, Logothetis and his collaborators found selected neurons along the visual pathway, from areas V1 and V2 to V4, MT, and IT, whose modulations were correlated with the perceptual observations of the monkeys (Leopold and Logothetis 1996; Logothetis and Schall 1989; Sheinberg and Logothetis 1997). Further, they found that more neurons, predominantly binocular neurons, in the higher cortical levels than in the lower cortical levels were correlated to rivalry alternation. These findings, along with their psychophysical observation that an 18 Hz flickering binocular rivalry stimulus that was swapped between the eyes at 333 ms intervals resulted in a rivalry perception not unlike that of the conventional rivalry stimulus, led them to suggest that it is the stimulus and not the eye that competes for dominance during rivalry (Logothetis et al 1996; also see Kovács et al 1996).

Together, the neurophysiological findings of Logothetis and colleagues, plus the report from Sengpiel et al (in anesthetized cats; 1995) and Lehky and Maunsell (in alert monkeys; 1996) that the lateral geniculate nucleus (LGN) neurons did not demonstrate rivalry modulation, put to rest an earlier speculation that the LGN might be the site of binocular rivalry (Varela and Singer 1987; but see also Fries et al 1997). Overall, these studies suggest that the binocular rivalry process takes place over several visual cortical stages, including areas V4, MT, and IT. And, since other studies (eg Chelazzi et al 1993; Moran and Desimone 1985; Treue and Maunsell 1996; see also the review by Desimone and Duncan 1995) have shown that neurons in V4, MT, and IT exhibit attentional modulation, it seems fitting to us to ask if the attention hypothesis of binocular rivalry holds some truth.

Thus, the aim of this paper is to examine whether attention has a role in determining perceptual dominance during binocular rivalry. We will first demonstrate that voluntarily attending to a rivalry stimulus in the dominant state can sustain its dominance. Second, we will show that when involuntary attention is attracted by a cue to an eye with a rivalry stimulus, that stimulus is more likely to become dominant in rivalry. Preliminary reports of this work have been presented in abstract form elsewhere (Ooi and He 1995, 1996, 1997, 1998).

2 Background and prediction for experiments 1 and 2

The impetus for our study was motivated by Helmholtz's keen observations of the binocular rivalry phenomenon. As reviewed earlier, he noticed that a dominant stimulus could be sustained longer in the dominant state if he 'attended' to it (by way of counting or comparing the spacing between the lines of the dominant stimulus). But this strategy, Helmholtz noted, worked only if the dominant stimulus has not succumbed to the forces of suppression. This implies that voluntary attention may affect rivalry only in its dominant state. Admittedly, Helmholtz's observations were qualitative and more controlled experiments are required to substantiate his claim. Thus our goal in the first two experiments is to substantiate the voluntary-attention hypothesis.

To achieve this goal, we need to demonstrate that a dominant eye is less likely to be suppressed when the observer attends to the dominant stimulus. Obviously, this is by no means an easy task since the experiment requires the ability to both combine and coordinate the attention paradigm and binocular rivalry paradigm together. Further, both the attention and binocular rivalry paradigms must command high predictive powers, ie the former should be able to reliably deploy attention and the latter should be able to reliably ensure that the target is dominant when the observer is instructed to attend to it. A search of the literature reveals that a combination of the covert-attention-deployment paradigm (Posner 1980) and the Cheshire Cat effect paradigm (Duensing and Miller 1979; Grindley and Townsend 1965) meets this requirement.

The covert-attention paradigm is a method that allows one to successfully deploy attention to a stipulated location simply by obeying a command to attend to that location. On the other hand, the Cheshire Cat effect paradigm, as mentioned in section 1, allows an image to remain in the dominant state until the fellow eye is perturbed. Thus our strategy to test the attention hypothesis is this: the covert-attention paradigm will be used to direct the observer's attention to the dominant target. Then a perturbing stimulus will be introduced to the suppressed eye. If the attention hypothesis holds, this experiment should demonstrate that the perturbing stimulus is less effective in terminating the dominant state of the target when attention is directed to it. This hypothesis will be tested in experiment 2. But first, in experiment 1, we will develop a Cheshire Cat effect paradigm that is adaptable to our purpose.

3 Experiment 1. The apparent-motion (AM) perturbation effect

In the conventional Cheshire Cat effect paradigm, a real-motion stimulus is used as the perturbing stimulus (Duensing and Miller 1979; Grindley and Townsend 1965). The experimenter waves a hand or a rod over the blank field at a region approximately corresponding to the stimulus in the other eye to cause that stimulus to disappear (suppress it). While this perturbation technique is very effective in causing suppression of the dominant stimulus, we wondered if we could use a more subtle stimulation method to produce the Cheshire Cat effect. The reason being that we wanted to ensure that the perturbing stimulus used in our experiment never physically encroached on the visual field corresponding to the dominant stimulus. Consequently, we decided to test if a long-range apparent-motion (AM) stimulus can also produce the Cheshire Cat effect.

During the experiment (figure 1a: AM cueing condition), one eye (right eye in figure 1a) viewed four grating patches, while the fellow eye (left eye) viewed a blank field. A pair of AM tokens (black squares) was then alternately presented to the eye viewing the blank field in an area approximately corresponding to the location of one grating in the fellow eye. The observer was instructed to maintain steady fixation at the center of the display where the fixation cross was placed. Then, upon perceiving the AM, the observer reported whether the grating (ie the dominant target) traversed by the AM (in visual space) disappeared. Predictably, if the AM display is able to act as a

perturbing stimulus, the target traversed by the AM (in visual space) will disappear and the blank field will revert to dominance.

But, because the observer was instructed to maintain steady fixation at the fixation cross, one could argue that the desired disappearance of the target might not be due to the perturbing AM, but simply to the Troxler effect where a relatively stabilized retinal image fades. To discount this possibility, we designed a control condition (figure 1b) where the AM tokens were now presented to the eye viewing the four grating patches. Thus in this case a finding of equal percentage of target disappearance as in the AM cueing condition above will indicate an effect independent of the AM stimulus. On the other hand, if the percentage of target disappearance is reduced in the control condition, then we can conclude that the AM stimulus can successfully act as a perturbing stimulus.

3.1 General apparatus and condition

The stimuli for the entire study were controlled by a Commodore computer (A2000 or A3000) and presented on a computer monitor. For experiments 1 and 2, a haploscopic prism setup was used to achieve binocular fusion. For experiments 3, 4, and 5, the observers viewed the stimuli with a phase haploscopic device, which consists of shuttered glasses that synchronize transmission in each eye with the alternating computer monitor frames to ensure a dichoptic viewing condition. The viewing distance was 57 cm.

Informed consents were obtained from all observers before starting the experiments.

3.2 Stimulus and procedure

A trial began with the observer pushing a mouse button to display the fixation cross ($48 \text{ min} \times 43.2 \text{ min}$) on a 3.37 cd m^{-2} gray background (figure 1). One second later, four monocular grating patches ($3.5 \text{ cycles deg}^{-1}$; $76.8 \text{ min} \times 75.6 \text{ min}$; 30.7 cd m^{-2}) that were located about 3.3 deg diagonally from the fixation cross were added. Two hundred milliseconds after this, two AM tokens (black squares, $81.6 \text{ min} \times 86.4 \text{ min}$, with a frame duration of 117 ms and 0 ms ISI) were presented alternately ($3\times$) to the eye viewing the blank field at a location approximately corresponding to an area occupied by one of the gratings in the fellow eye, for the AM cueing condition (figure 1a). [The presentation sequence and duration were the same for the control condition (figure 1b), except that here the two AM tokens were presented to the eye viewing the grating patches.] The trial ended with the display of a mask (not shown).

During a trial, the observer was instructed to fixate steadily at the fixation cross while viewing the entire display. Then at the end of a trial he was to report, by pressing one of two keys on the keyboard, whether the grating (target) traversed by the perturbing AM stimulus disappeared.

During the experiment, both the AM cueing and control conditions were run in the same block. Further, the gap size (ie separation between the AM token and the corresponding grating) was varied. Five gap sizes (1.26, 1.71, 2.16, 2.61, 3.06 deg) were tested, with 112 trials in each gap size.

3.3 Observers

The two authors and two other observers, who were naive to the purposes of the study, participated in the experiment. All observers had normal color vision, stereoacuity of at least 40 s of arc with the Stereo Fly test, and normal or corrected-to-normal visual acuity.

3.4 Results and discussion

Our observers experienced a significant amount of target disappearance in the AM cueing condition (figure 1a), as shown by their average data in filled squares in figure 1c (t -test, $p < 0.05$). Noticeably, even though this perturbation effect decreases with the separation between the target and the AM tokens (gap size), it is still significant at the largest gap size tested (3.06 deg). This finding, that remotely placed AM tokens can revert a suppressed stimulus (blank field) to dominance is consistent with earlier

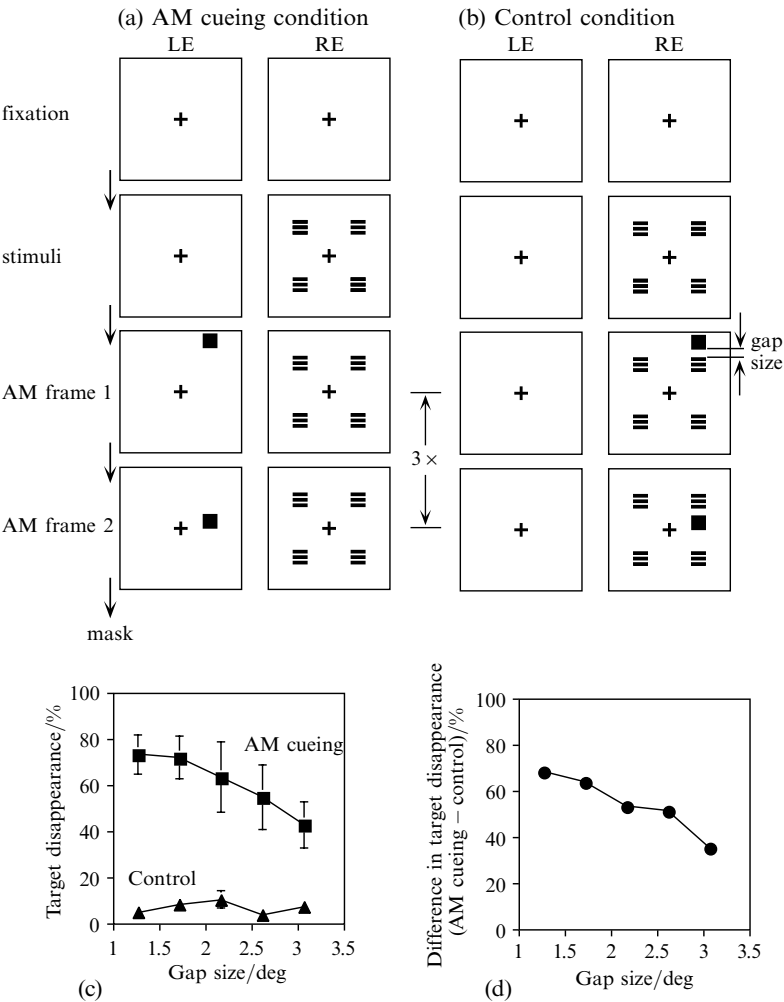


Figure 1. Apparent-motion (AM) perturbation paradigm. (a) AM cueing condition: a trial begins with the display of a fixation cross for 1 s, followed by four monocular patches of gratings. 200 ms later, two AM tokens (black squares, 117 ms per frame) are presented alternately ($3\times$) to the eye viewing the blank field at a location corresponding to an area occupied by one of the gratings in the fellow eye. The trial ends with the display of a mask (not shown). During the experiment the separation between the AM token and the corresponding grating (gap size) is varied. (b) Control condition: similar to (a) except that the AM tokens are displayed to the eye viewing the gratings. (c) The average percentage in target disappearance is plotted as a function of the gap size for the AM cueing (filled squares) and control (filled triangles) conditions. The higher percentage of target disappearance in the AM cueing condition indicates that apparent motion can be effectively utilized as a perturbing stimulus to create the Cheshire Cat effect. (d) To facilitate comparison, the percentage difference in target disappearance between the AM cueing and control conditions is computed. The difference curve shows that more target disappearance occurred in the AM cueing condition.

observations by others with different paradigms, that interocular suppression extends to some areas outside the location of the rivalry stimulus (see Blake et al 1992; Kaufman 1963). Together, they suggest that factors beyond local contours (eg long-range motion/attention tracking) can determine eye dominance (Blake et al 1998; Cavanagh 1992; Tyler and Kontsevich 1995).

The average data for the control condition (figure 1b) are plotted on the same graph (figure 1c) in filled triangles. Clearly, the percentage of target disappearance

in this condition is much smaller than that in the AM cueing condition (two-way repeated-measures ANOVA, $F = 26.17$, $p < 0.025$).

To facilitate comparison between the results of the two conditions in figure 1c, we decided to replot its data in figure 1d. Here, we calculated the percentage difference in target disappearance between the AM cueing condition and the control condition. As alluded to at the beginning of this experiment, had the target disappearance been due to the Troxler effect, the observers would experience equal numbers of target disappearance in the AM cueing and control conditions. Thus, the percentage difference in target disappearance will be zero. But had the target disappearance been due to the AM stimulus, the observers would experience more target disappearance in the AM cueing condition (ie the perturbation effect occurs). This will result in a positive difference between the two conditions, as currently found in our results (figure 1d). Clearly then, our finding indicates that the AM perturbing stimulus can effectively produce the Cheshire Cat effect.

4 Experiment 2. The role of voluntary attention in sustaining dominance

An important function of voluntary attention is to allow the observer to retain the object of interest in the state of awareness. In a similar vein, we wondered if a dominant target can, to some degree, be retained in the dominant state when the observer attends to it. To test this hypothesis, we now capitalized on the AM perturbation paradigm from experiment 1.

4.1 Prediction and procedure

Our experiment employed a covert-attention-cueing paradigm to demonstrate that willfully attending to a dominant stimulus can prevent it from being suppressed when an AM stimulus perturbs the fellow (suppressed) eye. During the experiment, the observer was instructed to selectively exert voluntary attention over a particular grating in the display by way of an attention cue (a gray square pointer) attached to the fixation cross (figure 2). Then the AM tokens were presented to the eye viewing the blank field, either corresponding to the region of the attended grating (cue-valid condition, figure 2a), or to an unattended region diagonally opposite the attended grating (cue-invalid condition, figure 2b). The observer's task was to report whether the grating (target) traversed by the AM in visual space disappeared. Predictably, if voluntarily attending to a dominant target in the cue-valid condition can help it to better resist the force of the perturbing AM stimulus to succumb to suppression, the percentage of target disappearance due to AM perturbation will be reduced. Conversely, when the target is unattended to, ie in the cue-invalid condition, the percentage of target disappearance due to AM perturbation will be relatively increased.

As in experiment 1, control cases where the perturbing AM stimulus was presented to the eye viewing the gratings were employed in both the cue-valid and cue-invalid test conditions to discount the Troxler effect (not shown in figure). For each condition, both the AM cueing and control trials were run in the same block, and the percentage target disappearance in the AM cueing trials and in the control trials was calculated. Eventually by taking the percentage difference in target disappearance between the AM cueing trials and control trials, for the cue-valid condition and cue-invalid condition, respectively, the AM perturbation effect for each condition can be derived (see figure 2c later). This method of data analysis also allows us to check against the possibility that our desired effect, ie a higher percentage of target disappearance in the cue-invalid case, is due to none other than the observer finding it difficult to judge the rate of target disappearance. If the observer had difficulty judging the target, then the difference between the AM cueing and control trials would not be significantly different from zero.

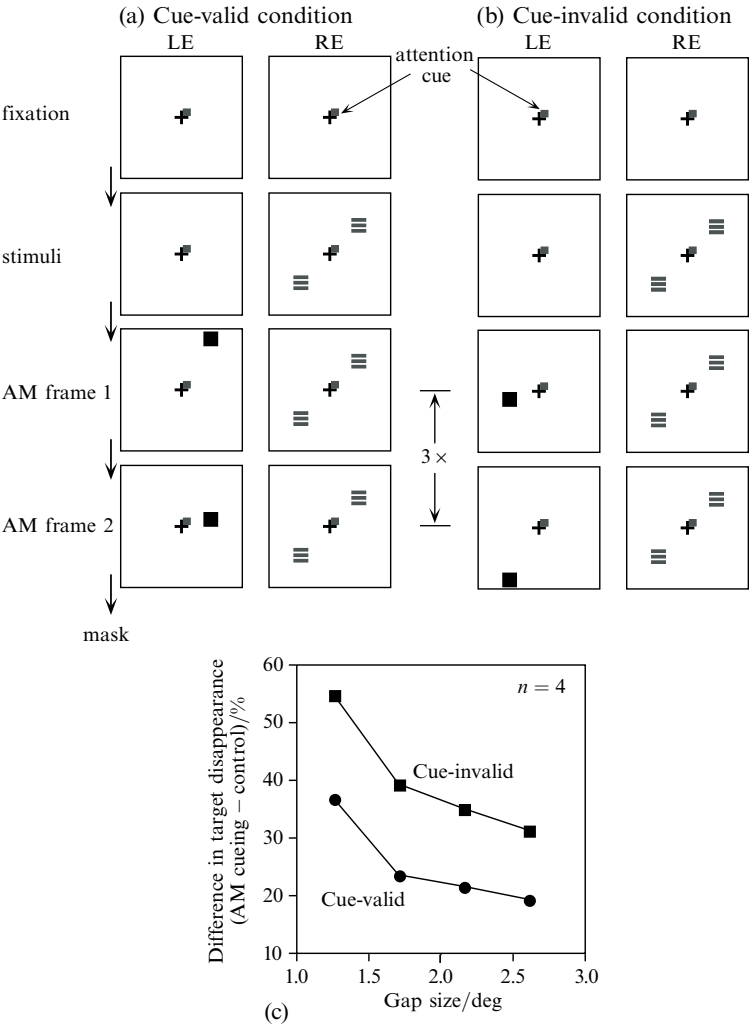


Figure 2. Maintaining the dominant state of a target by attending to it. The essential elements of the AM perturbation paradigm (ie dimension and sequence of the display) employed in this experiment are similar to those used in experiment 1, except for two minor changes. First, only two grating patches instead of four are used. Second, a gray square pointer is attached to the fixation cross and is used to instruct the observer to selectively attend to one of the two gratings. Two attention cueing conditions are tested. (a) Cue-valid condition: the AM traverses the attended grating (in visual space). (b) Cue-invalid condition: the AM traverses the unattended grating that is located diagonal to the attended grating (in visual space). As in experiment 1, the results obtained in each condition are analyzed in terms of the percentage difference in target disappearance, by comparing the observers' performance when the AM tokens are presented to the eye viewing the blank field (AM cueing case) and when the AM tokens are presented to the eye viewing the gratings (control case—not shown). (c) The average percentage difference in target disappearance for the cue-valid (filled circles) and cue-invalid (filled squares) conditions are plotted as a function of the gap size. The results show that observers experienced less target disappearance under the cue-valid condition, indicating that target dominance can be retained when attention is directed to it.

4.2 Observers

The same observers who participated in experiment 1 participated in the current experiment.

4.3 Results and discussion

The percentage difference in target disappearance between the AM cueing and control cases, ie the perturbation effect, was computed for each observer and their average results are shown in figure 2c. Clearly, the perturbation effect in the cue-valid condition (filled circles) is much smaller than that in the cue-invalid condition (filled squares) (two-way repeated-measures ANOVA, $F = 22.05$, $p < 0.025$). This difference indicates the influence of voluntary attention on the AM perturbation effect.

Arguably, voluntary attention could produce the results in figure 2c in two possible ways. The first, which we favor, is that voluntary attention operates directly to retain the dominant target in awareness by resisting extraneous influences to yield to suppression. The second possibility is via a more indirect route, through the primary impact of voluntary attention on the apparent-motion process. However, we believe that this second possibility is moot. This is because the AM frame duration used in our experiment (117 ms) was relatively short, which means that our AM stimulus would not be strongly subjected to top-down influences (Ramachandran and Anstis 1985). But even if attention had affected our AM stimulus, an opposite result to that found in figure 2c would be predicted. Namely, in the cue-valid condition, where the AM tokens were displayed in the vicinity of the cued target (grating) in visual space, an increased attentional influence on the AM tokens should facilitate its effectiveness in reverting the blank field to dominance (ie increase the percentage of target disappearance). In turn, a reduced attentional influence on the AM tokens in the cue-invalid condition should lower the impact of the suppressive effect of the AM (ie decrease the percentage of target disappearance). Clearly, such prediction of the second alternative explanation is not supported by our observers' data.

Thus, our finding above is consistent with Helmholtz's phenomenological observation that willfully attending to a dominant image helps retain it in the dominant state. This is because we are able to show that a dominant stimulus can more effectively resist suppression by an AM perturbing stimulus when attention is directed to it.

How might the visual system benefit from having such an attentional factor in binocular rivalry? According to Neisser and Becklen (1975), voluntary attention allows us to select and examine an image of interest in a dichoptic situation. In their experiment, they presented one eye with a scene of people playing a hand game and the other eye with a scene of people playing a ball game. They then instructed their observers to respond exclusively to events that occurred either in the hand game or the ball game scene. Their results showed that the observers were able to monitor and selectively track either of the dichoptic rivalry events easily, leading them to conclude that attention aids in selecting the scene of interest for perception. This intriguing finding suggests that their observers saw very little piecemeal rivalry, despite the size of the scene being no doubt greater than 1 deg (Blake et al 1992). In view of our current voluntary-attention finding, we speculate that their observers' ability to avoid perceiving piecemeal rivalry could be attributed to the function of attention of "picking up, retaining, and binding" an image of interest. That is, it is likely that an initially patchy dominant percept of the scene might be retained in the dominance phase by attention until neighboring parts of the suppressed scene alternate to dominance. When this is accomplished, attention can then extend or spread over the entire scene to enable the observer to perceive a coherent scene. It is possible that attention picks up and binds the pieces of an image on the basis of its 'meaningfulness' (ie whether the pieces form a 'good' figure or object). This speculation may also explain the intriguing report by Kovács et al (1996) that, when parts of an otherwise coherent scene were scrambled and presented to the two eyes in a rivalry situation, their observers were able to perceive a coherent scene.

Besides its ability to resist suppression, can voluntary attention revert a suppressed stimulus to dominance? Probably not, since we know that a momentarily suppressed

image cannot be willed to dominance simply by the whim of the observer, even when its physical pattern is known to the observer prior to the suppression. This limitation of voluntary attention may be related to the fact that the suppressed image does not reach visual awareness and thus cannot be affected by voluntary attention (Schall et al 1993).

Earlier in section 1, we suggested that the notion of voluntary attention in binocular rivalry may not be far-fetched. This is because recent neurophysiological findings have indicated that rivalry occurs over several cortical stages, including areas V4, MT, and IT, whose neural activities can be modulated by attention. Further, extrastriate cortical neurons in V2 and V4 are thought to be involved in mediating grouping, occlusion, perceptual organization, etc. Thus, neurons in these areas that are associated with rivalry are likely to act on the rivalry stimulus on the basis of its regularities and biological significance, in addition to its physical image properties (eg contrast energy). In fact, in a psychological study Engel (1956) found that during binocular rivalry observers tended to perceive an upright face in dominance more frequently when the other eye was stimulated by an inverted face. This led him to conclude that the (perceptual) content of the stimuli can influence binocular rivalry.

Blake (1988) induced rivalry by having his observers view semantically meaningful words in one eye and nonsense words in the other eye. But, in contrast to Engel's study, Blake found that his observers did not experience increased predominance in the eye stimulated by the semantically meaningful words. This led Blake to suggest the possibility that rivalry could be modulated by the visual content but not semantic content of the image. Indeed, we believe this is an important distinction.

5 Experiment 3. Reverting a suppressed image to dominance with attentional cueing

In the previous section, we discussed why the top-down, voluntary-attention mechanism is unable to revert a suppressed eye to dominance. A main reason for this might be attributed to the fact that a suppressed stimulus which does not reach visual consciousness is not accessible to voluntary attention. This opens up an interesting question: Can another form of attention, which is driven by a bottom-up stimulus and to a certain degree independent of the conscious will of the observer revert a suppressed eye to dominance? No doubt, an affirmative answer would provide additional support for Helmholtz's attention hypothesis of binocular rivalry.

The remainder of this paper is devoted to this question. To address it, we employed an attention-cueing paradigm in which a novel stimulus is used as a cue to attract involuntary attention to its location. Other studies have shown that attention summoned in this way acts to facilitate visual processing at the cued location. For example, in a detection task, the detection of a test stimulus at the cued location is improved (Krose and Julesz 1989; Nakayama and Mackeben 1989). It has been suggested that the facilitation, or cueing effect, is due to the cue attracting attention to its location prior to the onset of the test stimulus. Consequently, the availability of attention at this cued location helps to facilitate the subsequent visual task.

We hypothesized that when a cue attracts involuntary attention to a momentarily suppressed image, the suppressed image reverts to dominance. To test this hypothesis, one needs to cue the visual system while it is undergoing binocular rivalry. A straightforward (but potentially confounding) design of a candidate experiment is shown in figure 3a. First, the observer views a pair of rivalry gratings. Then, when one stimulus, say the one in the left eye, is in the suppressed state, a cue stimulus (rectangular frame) is presented to that eye. If the cue is effective in attracting attention to its location, we would expect the suppressed left eye's stimulus which is in the vicinity of the cue to become dominant upon being cued.

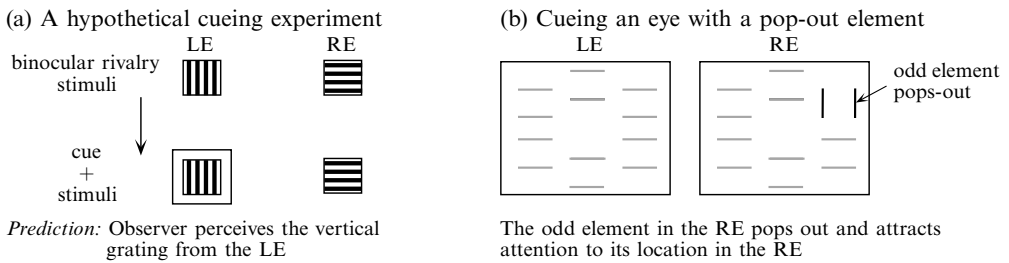


Figure 3. Theoretical considerations. (a) A possible test paradigm to reveal the impact of involuntary attention. A pair of rivalry gratings is first presented to the observer to initiate binocular rivalry. Some interval later, a cue (rectangular frame) is presented to the grating in the left eye (LE) to attract involuntary attention to it. The attention hypothesis predicts that, if the grating in the LE is in the dominant state prior to the cue presentation, it will simply remain dominant. However, if the grating in the LE is in the suppressed state prior to the cue presentation, involuntary attention summoned by the cue will revert the grating to dominant. Note, however, that the cue used in this paradigm can also be argued to contribute contour strength to the LE according to the contour hypothesis. (b) An alternative pop-out cue paradigm to attract attention. The right eye (RE) is presented with a display consisting of an odd element (a pair of gray vertical lines) among common elements (five pairs of red horizontal lines). Meanwhile, the LE is presented with a display consisting simply of common elements, of which five pairs are placed at corresponding retinal points to their counterparts in the RE. The odd element will be detected quickly, ie pop-out, and attract attention to its location in the RE.

However, this hypothetical experiment (figure 3a) runs into an interpretive problem if the cueing effect is found. This is because the cueing effect can be accounted for both by the attention hypothesis (ie the cue brings attention to the left eye), and by the contour hypothesis (ie the cue adds contour strength to the left eye). Thus, to precisely prove the role of attention, the proper experimental design has to discount or balance the possible contour contribution from the cue.

To achieve this, our present experiment capitalized on the established odd-element pop-out phenomenon (Treisman and Gelade 1980). In a typical pop-out display, when an odd element is presented among a group of common elements (eg a gray element among red elements) it will be detected quickly. Further, it has been shown that the pop-out (odd) element can facilitate detection of a target that is subsequently presented at the pop-out element's location. Presumably, the pop-out element acts as an attention cue to draw attention to its location (Joseph and Optican 1996; Neisser 1967; Treisman and Gelade 1980; Yantis 1993).

Figure 3b illustrates how the pop-out cueing phenomenon can be used for our purpose. To attract attention to a particular location of an eye, a 'pop-out cue' display is presented to it, while the fellow eye is presented with a display consisting of common elements, ie no pop-out cue. Thus, as shown in the figure, the right eye is stimulated by a pair of gray vertical lines which acts as the odd element (pop-out cue), and five pairs of red horizontal lines which act as the common elements. Meanwhile, the left eye is presented with six pairs of common elements. The placements of these common elements, except the one in the vicinity of the corresponding pop-out cue in the right eye, are at corresponding retinal points to ensure fusion. With this arrangement, attention will be preferentially drawn to the location of the gray pop-out cue in the right eye, while in the left eye the attention resource will be evenly distributed over the six common elements (six pairs of red horizontal lines). Consequently, attentional concentration at the pop-out cue location in the right eye is stronger than that at the corresponding element location in the left eye. Notably, the target pops out not because of its stronger contours, but because of its image property difference from the remaining elements.

The pop-out cue display as conceived above was employed in our current experimental strategy to undermine the critical influence of the contour mechanism in binocular rivalry. As shown in figure 4a, six pairs of rivalry grating stimuli were first presented to the observer to elicit binocular rivalry. This was followed by the display of the pop-out cue, which consisted of an odd pair of gray vertical lines among five common pairs of red horizontal lines (gray pop-out cue condition) in one eye (RE in figure 4a). The fellow eye (LE) was presented with six common pairs of red horizontal lines.

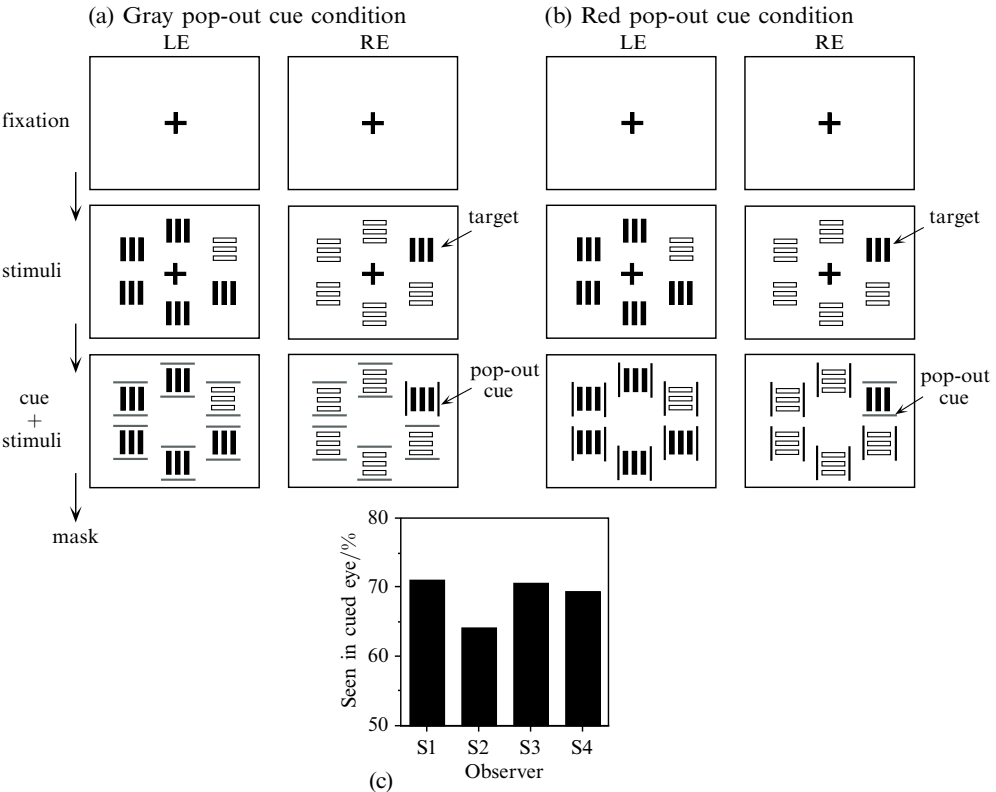


Figure 4. Reverting a suppressed image to dominance with attention cueing. (a) Gray pop-out cue condition. Upon maintaining fixation at the cross the observer initiates the trial which begins with the display of six patches of orthogonal red and green rivalry gratings for 500 ms. The fixation cross is then removed. 200 ms later, the gray pop-out cue display is added to the rivalry stimulus display. The pop-out cue display consists of an odd pop-out cue (a pair of vertical gray lines) and six pairs of common elements (horizontal red lines) in the cued eye (RE in this case), and six corresponding common elements in the uncued eye (LE). Refer to the text for detailed descriptions of the pop-out cue display. The trial terminates with a visual mask (not shown). (b) Red pop-out cue condition: similar to (a) except that the pop-out cue display now consists of red horizontal lines as the pop-out cue and gray vertical lines as the common elements. (c) The percentage correct performances of four observers in identifying the color of the grating at the pop-out cue location (average results from both the gray and red pop-out conditions) are shown in the bar graph. The observers performed above chance level (> 50%), indicating that an attention cueing effect occurred, ie attention cueing can revert a suppressed eye to dominant.

As discussed in conjunction with figure 3b, attention will be summoned to the location of the eye viewing the pop-out cue. Predictably, if attention can affect the rivalry stimulus in its vicinity (and same eye), the observer will perform above chance level (50%) when asked to identify the color of the grating (red or green) at this pop-out cue location. Otherwise, the observer will perform at the 50% chance level. This is because, if the grating is already dominant during the presentation of the gray

pop-out cue, it will simply remain dominant. But, if the grating is suppressed while the gray pop-out cue is presented, the attention evoked by the pop-out cue will cause it to become dominant, leading to an above-chance-level performance ($> 50\%$) in identifying the color of the rivalry grating.

Arguably, even if the observer performs above chance level in the gray pop-out cue condition (figure 4a), it can still be attributed to the contour mechanism. This is because the experiment in figure 4a above has not accounted for (or balanced) the contour strength between the gray and red elements. It is possible that the gray pop-out cue carries a higher contour strength than the common red elements. To empirically address this possibility, a control experiment in which the pop-out cue was now a pair of red horizontal lines and the common elements were pairs of gray vertical lines was performed (figure 4b: red pop-out cue condition). Thus, if the common gray elements now have stronger contour strength, the contour hypothesis would predict that the observers will perform below chance level ($< 50\%$) in this red pop-out cue condition. Meanwhile, the attention hypothesis will still predict an above-chance-level ($> 50\%$) performance since the red cue, being the odd element, will command more attention.

5.1 *Apparatus and stimuli*

The physical dimensions of the stimuli used in our experiment, illustrated in figures 4a and 4b, were as follows. The fixation cross occupied an area of approximately $34\text{ min} \times 39\text{ min}$ in the center of the gray background (0.17 cd m^{-2}) which filled the entire computer screen. The dimensions of the elements in the cue display were as follows: the paired red lines were 93 min long, 8.5 min thick, and 82 min in vertical separation; the paired gray lines were 98 min long, 8.5 min thick, and 76 min in horizontal separation. The luminances of the gray and red lines were about 0.4 cd m^{-2} and 1.0 cd m^{-2} , respectively. The elements in the cue display that were located directly above and below the fixation cross were 127 min away from the fixation cross, while the remaining elements were located 149 min away. The binocular rivalry stimuli consisted of six square-wave grating patches ($3.5\text{ cycles deg}^{-1}$). The size of each grating patch was $67\text{ min} \times 59\text{ min}$. In each eye, all except an odd grating had similar orientation (horizontal or vertical) and color (red or green; depicted in the figure in outline or black, respectively) which were reversed in the fellow eye. Before commencing the cueing experiment, the monocular luminances of the red and green gratings were adjusted appropriately for each eye to ensure equal competitiveness, so that each eye had about equal chance of becoming dominant during binocular rivalry (without the cueing frames) (Ooi and He 1994). These luminance levels ranged from 0.4 to 2.2 cd m^{-2} .

Under our test conditions the pop-out cue could be seen either in its entirety or in fragments even when the grating in the proximity of the cue was suppressed. Thus our observers were not uncertain of the pop-out cue location. Both the gray and the red pop-out cue conditions were tested on each observer with 200 trials in each condition. During the experiment, the eye receiving the pop-out cue display was randomized, as were the cue location and the color/orientation of rivalry gratings.

5.2 *Procedure*

Figures 4a and 4b illustrate the stimuli employed in this experiment. During the experiment the binocular rivalry stimuli (six square-wave grating patches) were presented for 500 ms to elicit binocular rivalry. After this, the fixation cross was removed, and the cue display was presented 200 ms later. The entire display remained on the screen for a further 1000 ms before a mask (not shown) appeared to terminate the trial. At the end of the trial, the observer, whose task was to report the color of the grating (red or green) at the pop-out cue location, responded by pressing one of two keys on the keyboard. Throughout the trial, the observers were instructed to always maintain steady fixation at the previous location of the fixation cross.

The initial rivalry stimulus duration of 500 ms (figures 4a and 4b) was chosen for two reasons. First, to ensure that binocular rivalry was already underway by the time the cue display was presented, for it has been shown that binocular rivalry latency is only about 150 ms (Wolfe 1984). Second, to ensure that the observer's perception was not confounded by the perceptual alternation of binocular rivalry that occurs with prolonged stimulation. On a separate issue, the fixation cross was removed before the cue display was presented to allow attention to disengage from it (Fischer 1987; Mackeben and Nakayama 1993).

5.3 Observers

The two authors and two other observers, who were naive to the purposes of the study, participated in the experiment. All observers had normal color vision, stereoacuity of at least 40 s of arc with the Stereo Fly test, and normal or corrected-to-normal visual acuity.

5.4 Results and discussion

The bar graph in figure 4c shows our observers' results. The data from the gray and red pop-out cue conditions obtained from each observer were combined and plotted individually in the graph. Clearly, all observers performed well above chance level ($> 50\%$) in both the red and the gray pop-out cue conditions (t -test, $p < 0.05$). This suggests that cue-mediated, involuntary attention can cause a suppressed image to become dominant during binocular rivalry.

This finding cannot be explained by the contour hypothesis, which predicts an even 50% performance level. This is because, according to the contour hypothesis, if the pop-out cue, say gray lines in figure 4a, had stronger contour (contrast energy) than the red lines, the observers would perform above the 50% chance level. But, when the gray and red lines were switched in the second condition (figure 4b) the eye viewing the gray lines (common elements) and not the eye viewing the red lines (pop-out cue) had the stronger contrast energy. In this case, the rivalry grating enclosed by the red cue was less likely to be dominant (ie performance $< 50\%$). Consequently, the combined performance from the gray pop-out cue condition ($> 50\%$) and red pop-out cue condition ($< 50\%$) would be about 50%, which it is not (figure 4c). Thus, our result in figure 4c is consistent with the prediction of the attention hypothesis, that the pop-out cue attracts involuntary attention to its location to cause the rivalry stimulus in its proximity (and eye) to become dominant.

At this juncture, we are reminded of experiments by others who have employed various other manipulations to force a suppressed eye to dominance during binocular rivalry. As mentioned in section 1, Walker and Powell (1979) and Blake et al (1990) induced eye dominance by perturbing the suppressed eye with an abrupt reversing contrast stimulus. Wolfe (1984) and Ooi and Loop (1994) induced eye dominance by allowing the eye to be suppressed to preview the rivalry stimulus. Thus, there is no question that using special perturbation methods in combination with the binocular rivalry paradigm can lead to eye dominance. Instead, the critical issue here is the underlying mechanism. In this regard, we attribute our particular finding in figure 4c to an attentional mechanism.

6 Experiment 4. Preparing an eye for dominance by prior cueing for attention

To recapitulate, we have found in experiment 2 that voluntary attention helps to retain the dominant state of an image during rivalry. Then in experiment 3 we showed that when involuntary attention is summoned by a cue to a suppressed image during rivalry, it can revert that image to dominance. Notably, these two experiments demonstrate the actions of attention *during* binocular rivalry. In the current experiment, we wondered if attention can affect the fate of binocular rivalry, even *before* the rivalry begins. Specifically, can the attention summoned by a pop-out cue prior to the onset of the

rivalry stimulus pave the way for a rivalry stimulus in its vicinity (and eye) to become dominant in the subsequent rivalry event?

Thus, in the present experiment, the pop-out cue display was presented to the observer before the rivalry stimulus. The stimuli used in the experiment (figures 5a and 5b) were similar to those employed in experiment 3, with one exception. Here, the design of the cue display was slightly modified so that the eye viewing the pop-out cue display received only the odd cue without the common elements. This measure was taken as a further control against the argument that the pop-out cue display in the previous experiment consisted of second-order contour information, owing to the proximity of the pop-out cue to its neighboring common elements (in the same eye).

As in experiment 3, both the red pop-out cue condition (figure 5a) and the gray pop-out cue condition (figure 5b) were tested on each observer, with instruction to identify the color of the rivalry grating (red or green) at the pop-out cue location. The prediction of the current experiment for the attention hypothesis is also similar, in that the observer will perform above chance level ($> 50\%$) in both the red and gray

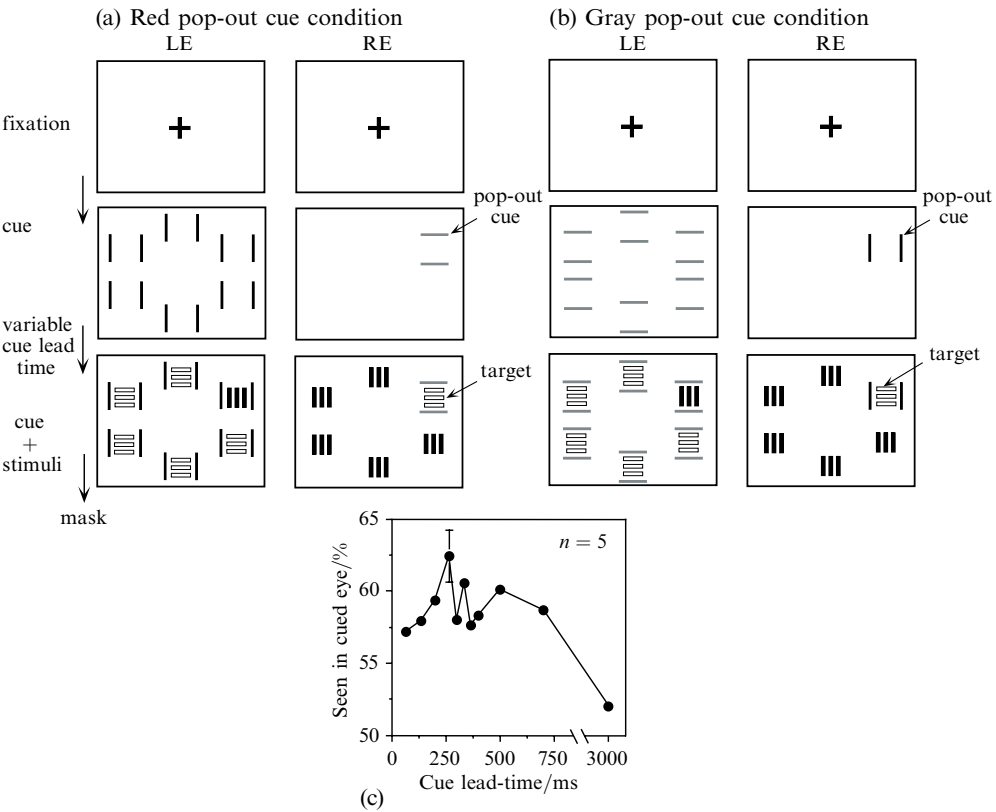


Figure 5. Encouraging binocular rivalry dominance by prior cueing for attention. (a) Red pop-out cue condition. The trial begins with the display of a fixation cross which is removed after a random period of 500–1000 ms. This is followed 200 ms later, by the cue display which consists of an odd pop-out cue (a pair of horizontal red lines in one eye) and six common elements (pairs of vertical gray lines in the fellow eye). After some predetermined cue lead-time interval (67–3000 ms), six patches of orthogonal red and green rivalry gratings are presented, followed by a mask (not shown). (b) Gray pop-out cue condition. This is similar to (a) except that the pop-out cue is a pair of gray vertical lines and the common elements are pairs of red horizontal lines. (c) The combined average results from both red and gray pop-out cue conditions, plotted as a function of cue lead-time, show performance in seeing the grating enclosed by the cue as above chance level ($> 50\%$). This indicates that an attention cueing effect occurred. The vertical bar represents the average standard error of all cue lead-time intervals.

pop-out cue conditions. On the other hand, the contour hypothesis predicts that the observer will perform above chance level in one pop-out cue (eg gray) condition and below chance level in the counter pop-out cue (eg red) condition.

By varying the interval between the presentation of the cue and the rivalry stimulus in different trials, ie having variable cue lead-time, the present experiment also allows us to gauge the effectiveness of the pop-out cue as a function of time (Nakayama and Mackeben 1989).

6.1 *Stimulus and procedure*

6.1.1 Red pop-out cue condition (figure 5a). A trial began with the display of a fixation cross. Then the observer pushed the mouse button, upon which the fixation cross disappeared after a random period (0.5–1.0 s). Two hundred milliseconds later, the cue display consisting of a pop-out cue (red horizontal lines in one eye) and six common elements (gray vertical lines in the fellow eye) appeared. After some cue lead-time interval (67, 133, 200, 267, 300, 333, 367, 400, 500, 700, 3000 ms), six patches of orthogonal red/green rivalry gratings were presented for 500 ms, followed by a mask (not shown). (As mentioned in the earlier experiment, this particular stimulus duration was chosen to ensure that ample time was given for rivalry to occur but not too long to produce rivalry alternation.) For each cue lead-time interval (11 intervals in total), the observer performed 100 trials. During the experiment, the eye receiving the pop-out cue was randomized, as were the cue location, color/orientation of the rivalry gratings, and cue lead-time interval. The observers were instructed to always maintain fixation at the former location of the fixation cross. Their task was to report the color of the rivalry grating seen at the pop-out cue location. Before commencing the cueing experiment, the monocular luminances of the red and green gratings were adjusted appropriately for each eye to ensure equal competitiveness, so that each eye had about equal chance of becoming dominant during binocular rivalry (without the cueing frames).

6.1.2 Gray pop-out cue condition (figure 5b). This condition was similar to the red pop-out cue condition except that the pop-out cue was represented by a pair of gray vertical lines and the common elements by six pairs of red horizontal lines.

6.2 *Observers*

The two authors and three other observers, who were naive concerning the purposes of the study, participated in the experiment. They had normal or corrected-to-normal visual acuity, normal color vision, and a stereoacuity of at least 40 s of arc with the Stereo Fly test.

6.3 *Results and discussion*

The mean performances of the five observers from both pop-out cue conditions were combined and their average data are plotted in figure 5c, as the percentage of seeing the rivalry grating in the cued eye as a function of cue lead-time. Statistical analysis reveals that the observers performed significantly above chance level (50%) for all cue lead-times (t -test, $p < 0.05$) except for the one at 3 s ($t_4 = 1.13$; $p > 0.05$). As in experiment 3, this finding cannot be explained by the contour hypothesis which predicts an even 50% performance level. Thus, the current result supports the prediction that, when involuntary attention is attracted to the proximity of a rivalry stimulus, it promotes the chances of that stimulus to become dominant.

7 Experiment 5. Discouraging eye dominance by distracting attention

To further verify the role of attention in binocular rivalry, in the next experiment we adopted a complementary approach. In experiment 4, we showed that prior cueing of an eye can promote the chances of a rivalry stimulus in that eye to become dominant. This finding, according to the attention hypothesis, is due to the cue-mediated attention paving the way for rivalry dominance to occur. If this explanation is correct,

the attentional cueing that promotes dominance should be hampered when attentional resources at the cued location are diverted.

We tested this prediction in two conditions. First, in a focal-attention condition (figure 6a) an attentional cue (rectangular frame) was presented to one eye, followed by a pair of rivalry gratings. The observer was asked to report the color (red or green) of the perceived grating. Second, in a divided-attention condition (figure 6b), a binocular Vernier target was added to the display after the cue was presented, but before the rivalry gratings were presented. The observer now had to report both the color of the dominant grating and the relative displacement of the upper limb of the Vernier target (right or left), while maintaining steady fixation at the center of the monitor (as in the first condition).

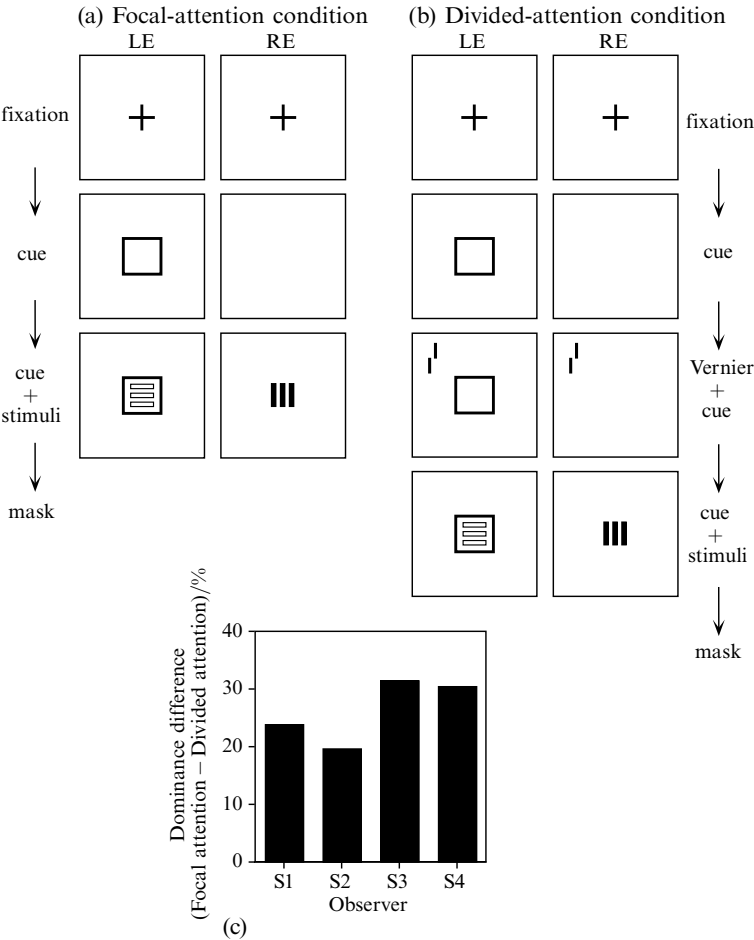


Figure 6. Discouraging binocular rivalry dominance by distracting attention. (a) Focal-attention condition. A trial begins with the observer fixating a cross which is removed 1000–1500 ms thereafter. Then the cue (rectangular frame) is presented for 2200 ms, before a pair of orthogonal red and green rivalry gratings is added to the cue display for a further 533 ms. The trial ends with a mask display (not shown). (b) Divided-attention condition. This is almost similar to (a) except that, 200 ms before the display of the rivalry gratings, a binocular Vernier target is presented randomly at one of six peripheral locations. In addition to reporting the color of the rivalry grating, the observer now has to report the relative displacement of the upper limb of the Vernier target while maintaining fixation at the center of the rectangular frame (cue). (c) The difference in percentage dominance of the cued eye (focal-attention condition – divided-attention condition) is plotted for each observer. The positive difference indicates that less dominance occurred in the cued eye under the divided-attention condition.

It is important to note the critical difference between these two conditions in terms of attention deployment. In the focal-attention condition (figure 6a), the attention resource is concentrated at the cue (rectangular frame) location. Thus the chances of seeing the grating from the cued eye should be increased. But in the divided-attention condition (figure 6b), having to attend to the Vernier target means that some attentional resources are diverted from the cue (rectangular frame) location. Consequently, the chances of seeing the grating from the cued eye in the divided-attention condition should be reduced, if the involuntary-attention hypothesis applies. On the other hand, the contour hypothesis predicts no difference in performance between the two conditions, since their local contour contents are unchanged.

7.1 *Stimulus and procedure*

7.1.1 Focal-attention condition (figure 6a). A trial began with the observer fixating a cross on a 0.17 cd m^{-2} gray background. He then pushed the mouse button to replace the fixation cross 1.0–1.5 s later with a rectangular frame cue (size = $93 \text{ min} \times 98 \text{ min}$; line thickness = 8.5 min), while maintaining steady fixation at the center of the monitor for another 2.2 s. Thereafter, a pair of orthogonal red/green rivalry gratings ($3.5 \text{ cycles deg}^{-1}$; $67 \text{ min} \times 59 \text{ min}$) was displayed within the rectangular frame for 533 ms. The trial ended with a mask display (not shown). The observer's task was to report the color of the grating perceived by pressing one of two keys on the keyboard.

Throughout the experiment, the eye receiving the cue and the color/orientation of the rivalry gratings were randomized. As in experiments 3 and 4 earlier, before commencing the cueing experiment, the monocular luminances of the red and green gratings were adjusted appropriately for each eye to ensure equal competitiveness, so that each eye had an equal chance of becoming dominant during binocular rivalry (without the cueing frame).

7.1.2 Divided-attention condition (figure 6b). This condition is similar to that shown in figure 6a, except that 200 ms before the display of the rivalry gratings a binocular Vernier target (each line = $8.4 \text{ min} \times 29.5 \text{ min}$; lateral Vernier shift = 12.6 min) was randomly placed at one of six peripheral locations 127–149 min away from the fixated center. Now the observer had to identify the directional displacement (right or left) of the upper limb of the Vernier target relative to its lower limb by pressing one of two keys on the keyboard. In addition, the observer had to report the color of the grating seen by pressing one of two separate keys on the keyboard. The observer performed 100 trials each in this and the above condition.

7.2 *Observers*

The two authors and two other observers, who were naive to the purposes of the study, participated in the experiment. They had normal color vision, stereoacuity of at least 40 s of arc with the Stereo Fly test, and normal or corrected-to-normal visual acuity.

7.3 *Results and discussion*

Figure 6c shows the difference in dominance of the cued eye between the two conditions (ie focal attention minus divided attention) for each observer. All observers showed a positive difference in performance (*t*-test, $p < 0.01$), indicating that they perceived the rivalry grating from the cued eye more frequently in the focal-attention condition than in the divided-attention condition. This confirms the prediction that, when involuntary attention is distracted from the cue, its ability to promote rivalry dominance at the cued location is reduced.

Additionally, since the Vernier stimulus in the divided-attention condition was displayed binocularly and was about 2–2.5 deg away from the binocular rivalry target, the results in figure 6c are unlikely to be due to (second-order) contour interaction between the Vernier stimulus and rivalry target (Polat and Sagi 1993). Thus the current

results further eliminate the argument raised in experiments 3 and 4 that the pop-out cue stimulus was possibly confounded by second-order contour information.

Collectively, our findings from experiments 3–5 provide empirical proof for the involvement of an involuntary form of attention in inducing binocular rivalry dominance. Experiments 3 and 4 reveal that cueing of attention during or before rivalry commences helps to increase the dominance of the rivalry stimulus at the cued location (and eye). Experiment 5 further reveals that the primary role of the cue is to attract attention and not to merely add contour strength to the eye. Indeed, the view that attention can aid in the perception of visual scenes is not new, but echoes those of the early selective-attention theories which argue that selective attention acts as a bottleneck between the early and the later (higher) stages of visual information processing (Anderson and Van Essen 1987; Koch and Ullman 1985; Nakayama 1990).

8 General discussion

In summary, our experiments reveal that voluntary attention has a role in retaining the dominant state of a rivalry stimulus, while involuntary attention has a role in promoting the ability of a stimulus to become dominant. These findings provide empirical evidence for the hypothesis that visual attention influences binocular rivalry (Helmholtz 1910/1962).

Still at issue is how binocular rivalry dominance is actually realized at the neuronal level. Also, how does our understanding of binocular rivalry fit into the broader issues of binocular vision and visual awareness? Here, we shall capitalize on the implications of our findings and those from other laboratories to offer some speculations.

It has been suggested that the eye-of-origin information plays a critical role in binocular vision (Blake 1989; Gillam and Borsting 1988; Helmholtz 1910/1962; Nakayama and Shimojo 1990a; Shimojo and Nakayama 1990). With regard to binocular rivalry, this idea has been convincingly demonstrated by Shimojo and Nakayama (1990). In their experimental display, each eye viewed a stimulus with an unpaired region consisting of nonidentical patterns to induce rivalry. Of significance was their careful placement of the unpaired regions within the rivalry stimulus to simulate either a real-world partial occlusion situation (ecologically valid case) or otherwise (ecologically invalid case). The authors found that robust rivalry occurred between the unpaired regions in the ecologically invalid case, while the unpaired region in the ecologically valid case almost always escaped rivalry suppression and alternation. This finding indicates that the visual system is able to utilize real-world occlusion constraints to distinguish between a biologically possible and impossible situation. When the stimulus situation is deemed impossible in an ecologically invalid case, binocular rivalry is instigated. Most importantly, this means that the visual system must rely on the eye-of-origin information to make the distinction (Nakayama and Shimojo 1990a, 1990b).

But how is the eye-of-origin information represented by the cortical neurons? One possible coding method, pointed out by several researchers in the past, is by using the monocular neurons (eg Blake 1989; Nakayama and Shimojo 1990a, 1990b; Shimojo and Nakayama 1990). Here we suggest a second hypothetical coding method, which is based on the characteristic group response from an ensemble of binocular neurons that weight the relative inputs from the two eyes (ie population coding). According to this population-coding scheme, some binocular neurons within the ensemble would receive more inputs from the left eye, while other binocular neurons would receive more inputs from the right eye. In this way, the eye-of-origin information can be computed by comparing the responses of these binocular neurons. Further, the two possible coding methods might not be mutually exclusive, and each or both strategies could be utilized by the visual system at the various levels of visual processing. Particularly, since the vast majority of neurons beyond V1 are binocular neurons (Burkhalter and Van Essen 1986;

Hubel and Livingstone 1987; Maunsell and Van Essen 1983), the population-coding method for representing the eye-of-origin information might be an alternative.

Accordingly, does this mean that the eye-of-origin information is registered at all cortical levels? We speculate that it does not, at least not as high as the level of visual awareness, which is presumed to be 'quite high' (Crick and Koch 1995). This is because psychophysical observations have suggested that the eye-of-origin information probably exerts its impact implicitly in a manner akin to Helmholtz's *unconscious inference*. In fact, both common experience and laboratory research reveal that, in a dichoptic viewing condition, one cannot tell what stimulus is viewed by which eye (Fox 1991; Ono and Barbeito 1985; Wolfe and Franzel 1988). Furthermore, one cannot voluntarily direct one's attention to an eye whose stimulus is not momentarily perceived (Schall et al 1993).

The representation of the eye-of-origin information by cortical neurons is fundamental to the classical notion of binocular rivalry being a competition between the two eyes (eye competition). Of late, however, this view has been challenged. In its place is a new notion that rivalry is due to a competition between two dissimilar stimuli which happened to be viewed by the two eyes (stimulus competition) (Kovács et al 1996; Logothetis et al 1996). For example, Logothetis et al (1996) found that, when two orthogonal gratings that were flickered at 18 Hz were swapped between the two eyes every 333 ms, the observer perceived the same oriented grating over several stimulus exchanges. This led them to conclude that rivalry is due to stimulus competition; otherwise the observer would have perceived very rapid alternation between the gratings at a rate comparable to the swapping of the two gratings. More recently, however, Lee and Blake (1998) reported that Logothetis et al's observation of 'stimulus competition' could only be obtained under very limited experimental conditions. Specifically, the rivalry stimuli had to be of low spatial frequency, low contrast, and be exchanged at a rapid rate. Under other conditions, the perceived alternation was consistent with the eye-competition notion.

We think that the argument whether the eyes or stimuli compete for dominance in binocular rivalry can be overcome by discovering, instead, the limiting factors responsible for instigating rivalry. At least two considerations are warranted. First, let us assume that the biological significance of binocular rivalry is for the visual system to achieve a stable and coherent surface perception (of the dominant image). In the real-world viewing condition, dissimilar objects beyond fixation (horopter) project onto corresponding points of the two eyes, resulting in a situation not unlike the binocular rivalry condition artificially created in the laboratory. Thus, a suppression mechanism can also be used to solve the potential problem of *confusion* (ie an unstable mixture of two drastically different images, which is meaningless). To determine what should be suppressed, and hence what should be selected for conscious perception, the visual system could rely on constraints related to real-world visual surfaces, such as smoothness, texture, contrast polarity, occlusion, etc (Gillam and Borsting 1988; Marr and Poggio 1979; Nakayama and Shimojo 1990a; Shimojo and Nakayama 1990). Now, since it has been shown that the eye-of-origin information is a vital factor in occlusion (Gillam and Borsting 1988; Nakayama and Shimojo 1990a), it is likely that the same information is utilized by the visual system for binocular rivalry.

The second consideration relates to the possibility that the notions of eye competition and stimulus competition in binocular rivalry refer to operations that occur at different cortical levels. As mentioned earlier, contemporary neurophysiological studies have shown that binocular rivalry is mediated by cortical neurons both at the lower levels (eg V1, V2) and at the higher levels (eg MT, V4, and IT) (Leopold and Logothetis 1996; Logothetis and Schall 1989; Sengpiel and Blakemore 1994; Sengpiel et al 1995; Sheinberg and Logothetis 1997). Thus the notion of eye competition could be appropriate

when referred to the earlier levels, where local image properties and explicit eye-of-origin information are represented. But at the higher cortical levels—where image integration becomes the mainstay, and cortical neurons there are concerned with issues pertaining to perceptual grouping, meaningfulness, surface properties, and attentional modulation—the notion of stimulus competition may be applicable.

The idea that binocular rivalry is processed at multiple levels also facilitates our understanding of how attentional modulation operates at various cortical levels to determine rivalry dominance. Returning to our experimental findings, we speculate that the impact of attentional modulation is felt at multiple cortical levels, including the eye-of-origin level. This proposal is consonant with our findings from experiments 3–5, which deployed involuntary attention. Recall that involuntary attention itself is an early form of attention that is driven by a bottom–up stimulus and is quite independent of the conscious will of the observer. Thus it is likely that involuntary attention can easily access the eye-of-origin information and vice versa, as both are rather automatic processes that are not totally dependent on the observer's conscious will.

More neurons in the higher cortical levels, particularly in area IT, are modulated according to the monkey's on-line perceptual report of image dominance. This implies that the selection process for which rivalry image is perceived is likely to be completed at or by area IT (Sheinberg and Logothetis 1997). In view of the known neurophysiology, our psychophysical finding of voluntary-attention modulation of binocular rivalry, though unique, is not totally unexpected since others have shown that neurons in the extrastriate cortical areas are subjected to attentional modulation (Chelazzi et al 1993; Moran and Desimone 1985; Treue and Maunsell 1996; also see review by Desimone and Duncan 1995).

On the other hand, our finding is both intriguing and surprising when one considers the fact that the human observer is incapable of telling which eye is being stimulated in a dichoptic situation (Fox 1991; Ono and Barbeito 1985; Schall et al 1993; Wolfe and Franzel 1988). Then, how can we explain our psychophysical finding that voluntary attention can modulate the eye-of-origin information which is not explicitly represented by neurons related to visual awareness? We speculate that, even though an observer can only willfully attend to neural images at the visual-awareness level, the impact of voluntary attention on the perceived image can be extended to the earlier unconscious cortical levels via feedback mechanisms or recurrent excitatory network. Presumably, in our voluntary-attention experiment (figure 2) attending to a (dominant) neural image at the visual-awareness level activates a feedback loop to the earlier cortical levels such as the primary visual cortex, where the eye-of-origin information is intact or explicit. Consequently, in our cue-valid condition (figure 2a) the information regarding the dominant image viewed by one eye is preferentially 'captured' by the attention-selection process, resulting in its ability to resist the perturbing AM.

Remarkably, this presumed attention-selection-feedback process can induce neural activities at the earlier cortical levels, even though we have no direct awareness of these activities. Indeed, such attention feedback or top–down processing might be analogous to those findings where the primary visual cortex is found to be active during visual imagery and attentive motion tasks (Kosslyn et al 1996; Watanabe et al 1998). Thus, this explanation is consistent with the suggestion by Crick and Koch (1995) that the primary visual cortex is not the site of visual awareness.

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