

Visually Guided Attention is Neutralized when Informative Cues are Visible but Unperceived

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The ability to voluntarily shift the focus of visual attention away from the focus of gaze was investigated in a novel paradigm designed to elaborate the stages of processing underlying this ability. A basic experimental method used to investigate guided visual attention involves measuring response times to targets presented at positions of which the observer has been informed by an orienting cue. Binocular rivalry was utilized to dissociate presentation of the orienting cue from visual awareness of that cue. The findings indicated that when an informative cue was presented to an eye during the dominance phase, thus reaching visual awareness, manual response times were significantly affected by cue validity. In contrast, when the same cue was presented to an eye during suppression, and thus was not seen by observers, response times were not influenced by cue validity. We conclude that to guide attention, neural signals registering informative visual cues must be processed at stages lying beyond the site of rivalry suppression. Implications for investigating the neural basis of visual attention are discussed.

Attention Directed attention Visual attention Vision Binocular rivalry Binocular suppression
Response time

INTRODUCTION

We investigated the ability to covertly attend to arbitrary spatial locations without overt gaze shifts (e.g. Eriksen & Hoffman, 1972; Jonides, 1980; Posner, Snyder & Davidson, 1980). An intricate collection of brain structures is involved in the guidance of this form of visual attention (reviewed by Crick & Koch, 1990; Posner & Petersen, 1990). Analysis of the neural basis of such a complex cognitive phenomenon requires experimental dissection into constituent processes and subsystems. Such an approach has yielded useful insights. For example by analyzing the nature of the deficits in directing attention following inactivation or ablation of different structures, inferences have been made about the roles of those structures (reviewed by Posner & Petersen, 1990). Thus, it has been suggested that posterior parietal cortex serves to disengage attention, the superior colliculus and pretectum move the focus of attention, and the pulvinar processes the newly focused image. Also, recent studies of brain activation and metabolism in humans require sequences of tasks that allow investigators to attribute activation to different levels or stages of processing (e.g. Pardo, Pardo, Janer & Kaichle, 1990;

Corbetta, Miezin, Dobmeyer, Shulman & Petersen, 1991).

In this paper we report the use of a novel inferential strategy to study attention, one that exploits the phenomenon of binocular rivalry as a tool to dissociate presentation of an orienting cue from subjective awareness of the presence of that cue. Binocular rivalry occurs when the two eyes view dissimilar patterns (reviewed by Blake, 1989). At each instant one eye's pattern is perceived (dominant) while the other eye's pattern is not perceived (suppressed); the periods of dominance and suppression alternate stochastically as long as the stimuli are viewed. It is important to emphasize that rivalry is an interesting and experimentally useful phenomenon because the complementary stimuli are equally visible, i.e. capable of being seen, even though the phenomenal state of visual awareness alternates. Based on this, a number of studies have investigated the extent to which visual stimuli presented to the suppressed eye and thus not seen by observers are processed (Blake & Fox, 1974; Lehmkuhle & Fox, 1975; Wade & Wenderoth, 1978; White, Petry, Riggs & Miller, 1978; Walker & Powell, 1979; Zimba & Blake, 1983; Wiesenfelder & Blake, 1990, 1991).

The relationship between binocular rivalry and visual attention has been considered for many years (reviewed by Lack, 1978). Indeed, the alternation of perceptual states during rivalry was originally conceived as a form of visual attention (Helmholtz, 1865; see also James,

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1890). Recent work under more rigorously controlled conditions, however, has demonstrated the control that physical stimulus factors have on rivalry alternation (Levelt, 1965) and the limited control subjects can exert on alternation rate (Lack, 1978). More recently, it has been shown that guided attention is required to identify a rivalrous binocular stimulus among nonrivalrous binocular distractors in a visual search task (Wolf & Franzel, 1988).

The present study represents a new and different approach, using rivalry as a tool with which to investigate visual attention. This experiment utilizes the fact that during rivalry a normally salient stimulus is suppressed from conscious awareness for seconds at a time. We wanted to determine whether a stimulus suppressed from consciousness by rivalry might still serve as an effective cue for orienting attention. Because we can localize the site of rivalry suppression relative to other visual processes, the present results provide constraints on the type of information available to the neural mechanisms responsible for covert shifts of attention.

METHODS

We employed a modified version of the cueing paradigm wherein observers made a speeded response upon presentation of a target that appeared at either of two locations (e.g. Eriksen & Hoffman, 1972; Jonides, 1980; Posner *et al.*, 1980). Every appearance of the target was preceded by the brief presentation of a visual cue informing the observers of the likely target position. Many studies have found that when the cue validly predicts target location on a majority of trials (80–90%) response times (RTs) to the target are faster; on the occasional invalid trials when the target appears at the noncued location, RTs are elevated. In this experiment the cue was presented within the boundaries of a foveally viewed pattern that was in a specified state of binocular rivalry dominance. Thus, on the trials when the orienting stimulus was presented to the eye during dominance, observers perceived the cue; on the trials when the same visual cue was presented to the eye during suppression, it was not consciously registered.

Stimuli were generated by a Macintosh Iix computer on a 19" gray-scale monitor (P104 phosphor; 1152 × 882 resolution; 72 Hz) viewed through a mirror stereoscope at 1.07 m in a dark room; each pixel subtended 1 min arc. White portions of the display were 37 cd/m², and black portions were too dark to measure. Each eye's display was generated on half of the monitor. Observers viewed the display with heads stabilized in a head-and-chin rest. All observers had normal or corrected-to-normal acuity and good stereopsis. Each eye viewed a square-wave grating contained within a 0.4 deg diameter aperture (Fig. 1). The left grating was vertical, and the right, horizontal. Spatial frequency was 7.5 c/deg, and contrast was essentially unity. Use of small, high contrast rival targets insured that rivalry was unitary with few, brief periods of mixed dominance. The gratings were framed by brackets, and the display appeared

against a dark background textured with single pixel dots; the brackets and dots promoted stable binocular alignment of the stimuli. Nonius markers were available to monitor fixation disparity. The RT target was a small (4 × 4 pixel) gray spot appearing 2 deg to the left or right of the rival gratings; the target locations were framed by square outlines. The cue was a small (2 × 2 pixel) gray spot appearing in the left or right half of one of the rival gratings; the cue location relative to the center of the grating informed the observer of the probable location of the target.

The luminance and duration of the cue and target stimuli were adjusted according to response criteria. These critical stimulus values were determined using other tasks. First, by measuring RTs to the cue itself, the gray-level and duration of the cue were adjusted so that it was seen when superimposed on the dominant eye's pattern but was never seen when presented on the suppressed eye's pattern. Specifically, observers triggered presentation of the cue by depressing the spacebar when a specified eye's grating was exclusively dominant. The duration of the cue was adjusted to be less than the shortest rivalry dominance period. The gray level of the cue was adjusted so that when it was presented to the dominant eye, RTs were consistently shorter than 500 msec, and when presented to the suppressed eye, the RT time-out period of 2000 msec elapsed with no response. By these criteria the cue was fixed so that its presentation in the suppressed eye did not cause a

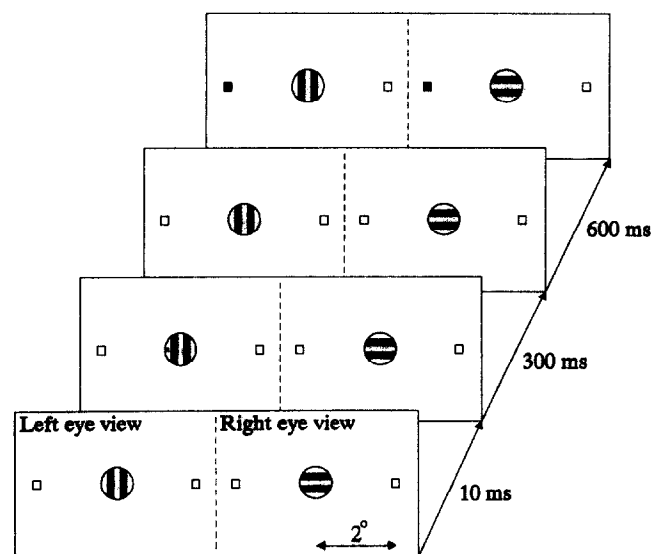


FIGURE 1. Sequence of trial events. Orthogonally oriented gratings within a circular aperture were presented binocularly to induce rivalry. When the specified eye became dominant, i.e. the grating presented to that eye became exclusively visible, observers pressed the spacebar on a keyboard. The orienting cue was then presented monocularly within one of the gratings for 300 msec; the brief exposure ensured that the rivalry state did not switch during presentation of the cue. The side of the grating on which the cue spot was positioned informed the observer of the likely location of the subsequent target. Following another delay the target was presented binocularly at an eccentric, marked location. Observers signaled detection of the target by releasing the spacebar. Response times were compared for validly and invalidly cued trials when the cue was presented during either dominance or suppression.

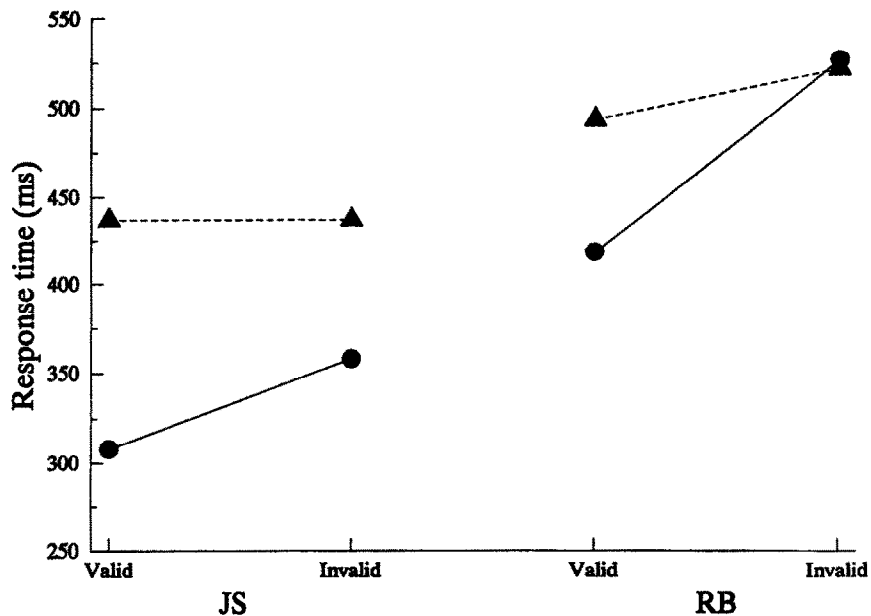


FIGURE 2. Response times with 90% valid trials during dominance and suppression. Mean RTs for validly and invalidly cued trials in which the cue was visible during dominance are illustrated with circles. Mean RTs for validly and invalidly cued trials in which the cue was not visible because it was presented during suppression are illustrated with triangles. Data from two observers are shown. For both observers RTs were significantly faster for validly cued trials than for invalidly cued trials when the cue was presented during dominance. For neither observer was there a difference in RTs for validly or invalidly cued trials when the cue was presented during suppression.

change in rivalry state. The optimum gray level for the cue was 21 cd/m^2 within a 37 cd/m^2 grating bar (28% contrast), and its duration was 300 msec. Second, the gray level and duration of the target and the cue-target presentation asynchrony were adjusted to yield reliable differences in the RTs on valid as opposed to invalid trials. For the purpose of determining these values, the gratings presented to the two eyes were of the same orientation and so did not invoke rivalry. The optimum gray level for the target was 26 cd/m^2 framed by a 37 cd/m^2 square, and its duration was also 300 msec with a cue-target asynchrony of 600 ± 10 msec.

The sequence of each experimental trial is illustrated in Fig. 1. For the duration of each trial the observer fixated the center of the rivalry gratings; after experiencing at least one cycle of dominance and suppression, the observer depressed the spacebar when the specified eye/grating was dominant. The monocular cue was then presented briefly; on half of the trials the cue was presented during the dominance phase, and on the remaining trials, it was presented during suppression. The target was presented binocularly. For two observers on 90% of the trials the cue was valid, i.e. the target appeared at the cued location; the remaining trials were invalid. Observers were instructed to release the spacebar as quickly as possible following presentation of the target. Eye of cue presentation, target location and cue validity were randomly selected and all combinations were uniformly presented in a block. One observer completed five blocks of 100 trials; a second completed 10 blocks. For a third observer 80% of the trials were valid; also, five blocks of 100 trials were run with the

right eye dominant, and five blocks, with the left eye dominant.

RESULTS

Anticipatory responses (RTs < 100 msec) were rejected from the analysis; these constituted < 5% of the trials. RTs to validly and invalidly cued targets were analyzed, accounting for whether cues were presented during dominance or suppression. Any difference between the RTs in validly and invalidly cued trials is interpreted as a measure of a shift of attention. Earlier studies included trials with a neutral cue, one that provided no information about target location; the cost and benefit in RT for invalid and valid trials could then be measured with respect to these neutral trials (e.g. Eriksen & Hoffman, 1972; Jonides, 1980; Posner *et al.*, 1980). Neutral trials were not included in this experiment for two reasons. First, given the compound factors of this experiment it was difficult to decide whether a neutral trial ought to be defined with reference to rivalry state, cue validity or target direction. Second, even though 90% of the trials were validly cued, only 50% occurred with the cue presented to the dominant eye. We were afraid that introducing a useful fraction of neutral trials would further dilute the effectiveness of the validly cued trials seen in the dominant eye. Concern about preserving the effectiveness of the validly cued trials also dissuaded us from using catch trials in which no target was presented.

Figure 2 illustrates the mean RTs of two observers tested with 90% validly cued trials. The RTs were submitted to a two-way analysis of variance with cue

validity and rivalry state as the factors. For JS there was a main effect of rivalry state [$F(1,1040)=60.59$, $P < 0.0001$]. The main effect of cue validity approached significance [$F(1,1040)=3.570$, $P = 0.0591$] as did the interaction of cue validity and rivalry state [$F(1,1040)=3.447$, $P = 0.0637$]. When the cue was presented during dominance, RTs on validly cued trials were significantly faster than those on invalidly cued trials [$t(545)=2.86$, $P < 0.01$]. For RB there were significant main effects of both cue validity [$F(1,477)=24.10$, $P < 0.0001$] and rivalry state [$F(1,477)=6.46$, $P = 0.0114$], and the interaction was also significant [$F(1,477)=8.14$, $P < 0.01$]. As with JS, when the cue was presented to the dominant eye, RTs on validly cued trials were significantly shorter than those on invalidly cued trials [$t(233)=5.06$, $P < 0.001$]. Thus, for both observers there was a significant effect on RTs of the validity of the cue when it was presented during the dominance phase of binocular rivalry. This result corresponds to the reliable cueing effect observed in numerous other studies (e.g. Eriksen & Hoffman, 1972; Jonides, 1980; Posner *et al.*, 1980) and represents the control condition for this investigation.

The condition of interest occurred when the cue was presented during the suppression phase. On such trials the main effect of validity was not significant. The RTs on valid and invalid trials when the cue was presented to the suppressed eye were not different for either JS [$t(495)=0.00$] or RB [$t(244)=1.59$]. This difference between dominance and suppression trials accounts for the interaction between cue validity and rivalry state. Thus, when the normally effective orienting stimulus (that was always potentially visible) was presented during suppression (and was therefore not seen), there was no reliable cueing effect, i.e. no indication of

a shift of attention. It should be stressed that the target itself was presented binocularly, far from the area of the eye undergoing rivalry; on every trial the target was easily seen and very reliably triggered RTs. It was the orienting cue that was rendered ineffective by suppression.

Figure 3 illustrates data collected from a third observer in which 80% of the trials were valid, and both eyes were tested during dominance in separate blocks. In the blocks of trials that were initiated when the right eye was in the dominance phase there was significant variation in RTs with cue validity [$F(1,574)=94.39$, $P < 0.0001$] and eye dominance [$F(1,574)=10.66$, $P < 0.01$]; the interaction was also significant [$F(1,574)=114.71$, $P < 0.0001$]. When the orienting cue was presented during dominance, the RTs on valid trials were significantly faster than those on invalid trials [$t(285)=14.78$, $P < 0.001$]. When the cue was shown to the suppressed eye, the RTs on valid and invalid trials were not different [$t(293)=0.73$]. Similar results were observed for blocks of trials initiated when the left eye was dominant. RT varied significantly with cue validity [$F(1,493)=59.51$, $P < 0.0001$] but not with eye dominance [$F(1,493)=0.01$]; the interaction, however, was significant [$F(1,493)=24.61$, $P < 0.001$]. When the cue was seen in the dominant eye, RTs were faster following validly cued trials than following invalidly cued trials [$t(246)=8.94$, $P < 0.001$]. In contrast, when the cue was unseen, being presented to the suppressed eye, RTs on valid and invalid trials were not different [$t(247)=1.96$].

The performance of the three observers differed in at least two notable ways. First, the magnitude of the differences in RTs following valid and invalid trials when the cue was presented during dominance were variable, ranging from a mean difference of 50 msec for JS to

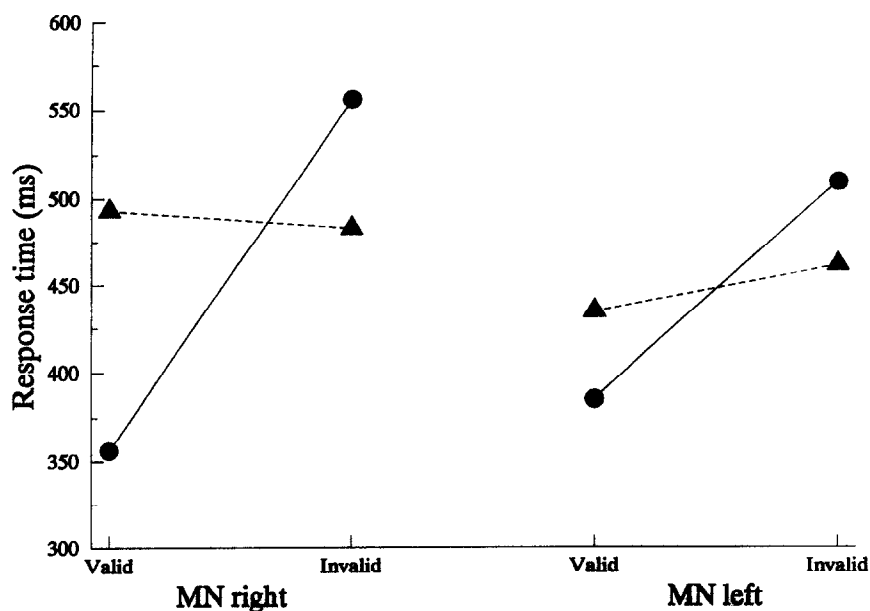


FIGURE 3. Response times with 80% validly cued trials during dominance and suppression. Conventions as in Fig. 2. Data are from another observer. In one block of trials the right eye was always dominant, and for another block, the left eye was dominant. The findings of a significant influence of cue validity when presented during dominance and no effect when presented during suppression were replicated under these conditions.

205 msec for MN. However, these magnitudes do not deviate from values reported previously which range from approx. 50 to 250 msec (e.g. Jonides, 1980; Posner *et al.*, 1980). A measure of the individual differences may be due to the addition of binocular rivalry to the cueing task. Recall that observers initiated trials only when a particular, predetermined state of rivalry dominance was achieved. Thus, some of the variability in the RT differences may be attributed to this added attentional load or the sustained vigilance required to perform well.

It is also of interest to compare the RTs on dominant invalid trials to the RTs when the cue was presented during suppression. Each possible pattern of results was observed in the three observers. For JS the RTs following all trials with the cue presented to the suppressed eye were elevated relative to the invalid dominant trial RTs. Perhaps the presentation of the orienting cue serves also as a warning signal which generates an enhanced state of readiness to generate the subsequent movement (reviewed by Niemi & Näätänen, 1981). Such an explanation does not generalize, however. The RTs following invalid dominant cue trials for RB were the same as his RTs following suppressed cue trials. For MN using his right eye as dominant the RTs following invalid dominant cue trials were longer than those measured when the cue was presented during suppression. The same pattern though in reduced magnitude was also evident when MN used his left eye as dominant. The quantitative difference between the results obtained with the two eyes of MN may be attributed to the fact that his right eye was stronger during rivalry (e.g. Coren & Kaplan, 1973).

DISCUSSION

This experiment used rivalry suppression as a tool for dissociating the physical presence of an effective visual cue from conscious awareness of that cue. We found that when an orienting cue was presented during the dominance phase of binocular rivalry, the information provided by the cue can be used to shift attention. But when that same cue was presented during the suppression phase of rivalry, no shift of attention occurred. Thus performance of this task was qualitatively under identical stimulus conditions, the contrast arising because of the alternate perceptual states occasioned by binocular rivalry. The interpretation and possible implications of this finding must be considered in the context of at least three issues.

First, the results might only pertain to attention guided by cues that symbolically designate the locus of the target. Earlier studies demonstrated that cues presented at the location of the peripheral target elicit a shift of visual attention that is more automatic than that resulting from a cue presented foveally (e.g. Posner, 1980; Jonides, 1981; Muller & Rabbitt, 1989; Shepherd & Muller, 1989; Reuter-Lorenz & Fendrich, 1992). It is not self-evident that the findings of this study generalize to conditions using peripheral cueing. In fact, we have attempted just such an experiment, but a number of

factors make it problematic. On the one hand, if the rivalry-inducing stimulus is large enough to enclose a sufficiently eccentric cue and target position (e.g. 3–4 deg), then the rivalry alternations become piecemeal with different retinal regions of the two eyes undergoing different phases of dominance and suppression asynchronously (Blake, O'Shea & Mueller, 1991). To initiate each trial, observers must wait long periods before one eye's pattern is fully dominant. With such prolonged vigilance, measures of response time differences become less reliable due to fatigue. Moreover, when it does occur, complete dominance of large patterns is fleeting. On the other hand, piecemeal rivalry can be reduced by using low spatial frequency, low contrast sinusoidal gratings. However, on such a dim background it is difficult to create a cue that cannot be detected by the suppressed eye because of the enhanced visual sensitivity conferred by adaptation and stimulation of parafoveal retina.

Second, the evaluation of the result obtained in this study should be interpreted in the broader context of other paradigms used to investigate the extent of processing of stimuli of which observers are not aware. A number of studies have found evidence for high level processing of stimuli of which observers were not aware. For example, in a priming paradigm the responses of patients with neglect were improved on the basis of stimuli presented to the neglected hemifield (Berti & Rizzolatti, 1992). In addition, evidence has been presented for semantic priming from words of which observers report being unaware because of masking (e.g. Marcel, 1983; but see Holender, 1986). Finally, the phenomenon of blindsight involves the ability of patients to behave appropriately in response to stimuli of which they were not aware (reviewed by Weiskrantz, 1986).

Third, the present finding must be considered in relation to the nature and locus of rivalry suppression. Clearly, the cue was visually conspicuous during dominance, but during suppression it was not. A skeptic could argue that our result is trivial because observers cannot utilize information specified by a cue they cannot see. After all, suppose observers had closed one eye on roughly half the cue presentations—certainly the potency of the cue would be abolished on these trials because it was not perceived. What, then, is different about not perceiving the cue because of rivalry suppression? The answer, of course, has to do with the respective mechanisms by which perception of the cue was prevented. In the case of rivalry suppression, unlike eye closure, neural information about the stimulus is registered by the retina and passed on to the brain. Thus, the cue was imperceptible for a very interesting reason—at some, as yet unknown stage of processing neural events normally elicited by the cue's presentation are disrupted. The orienting cue suffers the same fate as the suppressed rival stimulus upon which it is superimposed; it is temporarily erased from consciousness. We believe this lack of awareness of the cue is no less interesting or significant than is the lack of awareness of the suppressed rival target upon which it is superimposed.

The present results indicate, in other words, that the utilization of a foveal orienting cue to guide visual attention is mediated by events central to the locus of the neural process(es) responsible for binocular suppression because those events are disrupted during suppression. Given this conclusion, what can be said about the neural site of suppression? Psychophysical results from earlier experiments offer some indirect clues. For one thing, suppression has no effect on the build-up of several well-known visual aftereffects, including those produced by adaptation to translational motion (Lehmkühle & Fox, 1975; O'Shea & Crassini, 1981), spatial frequency (Blake & Fox, 1974) and contour orientation (Wade & Wenderoth, 1978; White *et al.*, 1978). For another, observers readily detect two-frame apparent motion even when the first frame is rendered invisible owing to suppression (Wiesenfelder & Blake, 1991; see also Walker & Powell, 1979, for a related effect). These results strongly suggest that certain aspects of visual information processing proceeds uninterrupted by (i.e. prior to the site of) suppression.

At the same time, suppression does interfere with aftereffect build-up under other conditions of adaptation. For example, Wiesenfelder and Blake (1990) discovered that the build-up of the spiral aftereffect (which involves rotation and expansion/contraction) was retarded when the inducing spiral was suppressed, with the strength of the resulting aftereffect proportional to the duration of phenomenal visibility. They concluded that spiral adaptation occurs at a later stage of motion processing relative to the site of suppression and to the site of adaptation to simple translational motion of the sort studied by Lehmkühle and Fox (1975). There is another published result showing that suppression affects adaptation to spatial frequency. Lehky and Blake (1991) found that the threshold elevation aftereffect produced by grating adaptation [the same aftereffect studied by Blake and Fox (1974)] was weakened when the adaptation pattern was suppressed for essentially the entire period of adaptation. They speculated that extreme monocular dominance may be necessary to evidence an effect of suppression on adaptation. At the same time, they noted that the results from their unusual paradigm were preliminary and required further investigation.

Considered together, the bulk of these psychophysical results imply that information about image primitives such as translational motion, spatial frequency and orientation is registered during both dominance and suppression phases of binocular rivalry. The specificity of receptive field properties of neurons in the visual cortex and the stimulus selectivities of these visual aftereffects, indicate that rivalry suppression occurs no earlier than visual cortex. This general conclusion has been instantiated in several contemporary neural models of binocular rivalry (Blake, 1989; Grossberg, 1987; Wolfe, 1986; Mueller, 1990). However, others have speculated that the neural concomitants of rivalry suppression could involve corticothalamic feedback that triggers interocular inhibition in the dorsal lateral gen-

iculate nucleus (Varela & Singer, 1987; Lehky & Blake, 1991), an idea more difficult to reconcile with the psychophysical evidence summarized above.

Can we conclude anything about the locus of rivalry suppression from neurophysiological studies employing rival targets? Unfortunately, no clear picture emerges. Recording from binocular neurons in striate cortex, several research groups (Blakemore, Fiorentini & Maffei, 1972; DeAngelis, Robson, Ohzawa & Freeman, 1992) have found no evidence for suppression of responsiveness under conditions that would elicit binocular rivalry. Others, however, do find such effects in binocular but not monocular striate neurons (Sengpiel, Harrad & Blakemore, 1992) as well as in cells in the LGNd (Varela & Singer, 1987). All of these experiments were performed on anesthetized cats, so it is impossible to say anything about possible fluctuations in monocular dominance upon presentation of dichoptic stimulation. Recording in awake, behaving monkeys, Logothetis and Schall (1989a, b) were able to relate the activity of single neurons in the cerebral cortex to the monkeys' subjective perceptual state during binocular rivalry. Monkeys viewed dichoptically presented horizontal gratings, with one eye viewing upward motion and the other downward motion. Activity evoked by these stimuli was recorded from neurons in the middle temporal (MT) visual area. Of the sampled neurons, the responses of 24% correlated with the direction of motion reported by the monkey. But the remaining neurons discharged whether their optimum stimulus was dominant or suppressed. So, a fraction of MT neurons carry a neural signature that could be construed as the concomitants of dominance and suppression. From the results of Logothetis and Schall, we do not know whether those MT neurons were simply mirroring response fluctuations arising at earlier cortical levels. But their results do indicate that suppression has left its mark on neural activity by the level of MT.

Returning to the question of visually guided attention, the observed qualitative difference in performance can come about only if the brain is in alternate states during presentation of the cue. In other words, certain neurons in the brain are activated by the cue when it is seen during dominance but those same cells do not respond when the cue is suppressed from visual awareness. Identification of such neurons would represent an important advance in the current understanding of the neural basis of visual attention because where such neurons are located is currently unknown. If suppression operates early in visual processing (e.g. Lehky & Blake, 1991), then such cells may be found in the LGNd. In fact, the possibility that rivalry suppression may limit the access of attention mechanisms to what is available in the LGNd has been anticipated by the hypothesis of thalamic regulation of guided visual attention (Crick, 1984). On the other hand, studies have demonstrated that the responsiveness of neurons in extrastriate cortical area V4 (Moran & Desimone, 1985; Fischer & Boch, 1985; Spitzer, Desimone & Moran, 1988; Haenny & Schiller, 1988), posterior parietal cortex (Bushnell,

Goldberg & Robinson, 1981; Mountcastle, Motter, Steinmetz & Sestokas, 1987) and the pulvinar (Petersen, Robinson & Keys, 1985; Peterson, Robinson & Morris, 1987) are modulated in relation to covert shifts of attention. Recordings from these and related structures using a rivalry paradigm like the one developed for the present experiment may contribute to unravelling the intricate processes responsible for guiding visual attention.

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