The Neural Site of Binocular Rivalry Relative to the Analysis of Motion in the Human Visual System

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Neural processing is disrupted during suppression phases of binocular rivalry, as evidenced by the temporary invisibility of an otherwise complex, high-contrast visual stimulus. This paper investigates the locus of this disruption relative to the processing of information about image motion. In one experiment, observers tracked binocular rivalry between a stationary textured field and a plaid composed of 2 drifting cosine gratings, with the angle between components varied to produce different pattern speeds. (Plaid speed is given by the ratio of the component speed to the cosine of the angle between the 2 directions of motion.) Predominance of the moving plaid increased with pattern speed, even though the speed of the individual components remained constant. Control measures verified that this influence of plaid speed was not attributable to specific component orientations. Information about coherent motion influences the rivalry process, implying that the site of coherent motion analysis, presumably the middle temporal area (MT), received input during dominance phases of rivalry. A second experiment investigated the effect of suppression on the processing of complex, nonlinear motion. Observers tracked rivalry phases for a rotating spiral, then indicated the duration of the subsequently perceived spiral aftereffect (SAE) for both rivalry and nonrivalry conditions. The SAE was reduced when adaptation occurred under the rivalry condition, with aftereffect duration proportional to the total duration of spiral visibility during adaptation. Earlier work places rivalry after the site of the linear motion aftereffect, and the present results show that rivalry suppression occurs prior to the site of spiral motion processing. Together with physiological evidence, these findings place the neural site of rivalry beyond the primary visual cortex but no later than MT or one of its afferent target sites.

The human binocular visual system is remarkably adept at discovering matches between corresponding left- and right-eye image features, as evidenced, for instance, by our ability to perceive complex surface shapes defined solely by disparity in random-dot stereograms (Julesz, 1971). Equally remarkable is the disruption in perception that occurs when the binocular visual system fails to establish correspondence between the 2 eyes'

views. In this case, stable binocular single vision gives way to unstable monocular vision: only one eye's view or the other's is consciously experienced at any given moment, and these periods of monocular dominance alternate over time in an unpredictable, uncontrollable fashion. This breakdown in stable single vision, the phenomenon termed "binocular rivalry," is intriguing in that a complex, high-contrast image may be suppressed from conscious perception for seconds at a time. Indeed, it is this suppression of vision that makes binocular rivalry a potentially powerful tool for relating visual perception to underlying neural processes. We may attempt to learn, in other words, how and where neural transmission of information is disrupted during suppression phases of binocular rivalry.

No clear picture emerges about the neural concomitants of binocular rivalry. The earliest stage at which inhibitory interactions between the 2 eyes might conceivably occur is the lateral geniculate nucleus (LGN), which receives input from both retinæ and from the visual cortex. The existence of interocular inhibitory interactions within the LGN is well established (Sanderson et al., 1971; Marrocco and McClurkin, 1979), and some investigators (Blakemore et al., 1972b) have speculated that it is these inhibitory interactions that underlie binocular rivalry. Varela and Singer (1987) have shown that the LGN cells exhibiting interocular inhibitory effects are those receiving input from higher cortical areas, not cells receiving input solely from the retina. Surprisingly, evidence is lacking for interocular inhibitory effects in primary visual cortex (V1) in response to dissimilar monocular stimulation that would promote binocular rivalry when viewed by human observers. Ohzawa and Freeman (1986) found that the responses of simple cells in cat area V1 area to monocular presentation of the cells' preferred stimuli (i.e., appropriately oriented contours) were uninfluenced by stimulation of the other eye by a nonpreferred stimulus. Blakemore et al. (1972a) reported essentially the same result. Both of these studies involved single-unit recordings from paralyzed, anesthetized cats. Recent physiological recordings from alert, behaving monkeys trained to monitor eye dominance indicate that the activity in some cells in the middle temporal area (MT) varies in a manner mirroring the perceptual reports of the animal (Logothetis and Schall, 1989). These findings suggest that the neuronal events responsible for rivalry may transpire by this level of processing.

Psychophysical data can also shed light on this question of the locus of the neural events underlying suppression. For instance, it has been established that several of the well-known visual aftereffects of adaptation can be induced even when the adapting stimulus is suppressed from vision for substantial portions of the adaptation period. This is true for the tilt aftereffect

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(Wade and Wenderoth, 1978), the linear motion aftereffect (MAE) as measured both intraocularly (Lehmkuhle and Fox, 1975) and interocularly (O'Shea and Crassini, 1981), and the threshold elevation aftereffect produced by adaptation to spatial frequency gratings (Blake and Fox, 1974). Evidently, information about those various adapting patterns continues to reach the site(s) of adaptation in an unperturbed state, implying that suppression occurs after the neural site(s) of adaptation. Now it is generally thought that these simple visual aftereffects arise from neural events early in visual processing, perhaps in area V1 based on physiological measures of the neural aftereffects of adaptation (Maffei et al., 1973; Vautin and Berkley, 1977; von der Heydt et al., 1978; Movshon and Lennie, 1979; Hammond et al., 1985, 1986, 1988; Hammond and Mouat, 1988).

Thus, considering both these psychophysical and physiological data, it is tempting to conclude that the neural concomitants of binocular rivalry occur somewhere between V1 and higher cortical areas (e.g., area MT). This idea is, of course, highly speculative and in need of further testing, which is the purpose of the experiments reported in this paper. The present study employs 2 complementary strategies. In one series of experiments, we measured the influence of coherent motion on the predominance of an eye during binocular rivalry. In the other series of experiments, we determined the effect of rivalry on processing of motion stimuli. The stimuli used in these experiments included complex motion vectors thought to be synthesized at stages of visual processing later than V1. To qualify the scope of our experiments, it is thought by some (e.g., Livingstone and Hubel, 1988) that the neural pathway involved in the processing of motion information (the so-called magno-stream) differs from that pathway (the parvo-stream) underlying certain other aspects of vision (e.g., detailed form vision). To the extent that this distinction is real, the conclusions from the present psychophysical analysis of binocular rivalry may pertain only to neural events in those pathways concerned with the analysis of information about motion.

Experiment 1: Plaid Motion and Rivalry

During binocular rivalry, the total dominance time (i.e., predominance) of a stimulus viewed by a single eye is governed by its physical characteristics, such as contrast, intensity, and contour density (Levitt, 1965). One very potent determinant of monocular predominance is motion: Moving targets tend to predominate over stationary ones (e.g., Breese, 1899), and the strength of this predominance increases, within limits, with motion speed (Wade et al., 1984). It is this latter characteristic of rivalry that serves as the point of departure for our first experiment.

Suppose one eye views a stationary target while the other views a plaid composed of 2 drifting cosine gratings differing in orientation. The speed of the plaid can be considered either in terms of the speed of the individual component gratings or in terms of the speed of the plaid pattern as a whole. This distinction arises because it is possible to vary the speed of the plaid (hereafter called the "pattern speed" or "plaid speed") without varying the speed of the components (hereafter called the "component speed"). This is accomplished by changing the relative angles of orientations of the 2 drifting cosine gratings (Welch, 1989; Ferrera and Wilson, 1990). Given this distinction, then, suppose we use a plaid as the rival target and systematically vary the plaid's speed (by changing the angle of the pattern components) while holding the component speed constant. What

will be the effect on binocular rivalry predominance? Answering this question was the motive for this first series of experiments.

Materials and Methods

Displays. All visual displays used in these experiments were generated by a Macintosh II computer on 2 matched gray-scale video monitors (640 horizontal $\times$ 480 vertical resolution, 66.7 Hz noninterlaced frame rate, P4 phosphor). The monitors were viewed separately by the 2 eyes through a mirror stereoscope, from a distance of 145 cm in an otherwise dark room. Details of luminance calibration appear elsewhere (Wilson et al., 1990). In brief, a look-up table stored in computer RAM corrected monitor nonlinearities and allowed the display of 120 different gray levels. The mean luminance of the display was 15.0 cd/m².

The rival targets appeared within circular regions 1.54° in diameter located in the centers of the 2 monitors (see Fig. 1). A distinct, black border (0.12° width) framed each eye's rival target, which was itself centered within a 1.66° square. This contour-rich display, along with the borders of the video screen, provided a strong stimulus for maintenance of accurate binocular alignment of the 2 displays. A pair of superimposed, drifting cosine gratings was generated on one monitor; we shall refer to this stimulus as a "plaid." The drift rate, orientation, and contrast of either cosine grating could be varied independently; the spatial frequency of each component was always 4.5 cycles/degree. Smooth motion of the plaid was achieved by phase-shifting the gratings successively over frames in small steps. The other rival target was a stationary, high-contrast "noise" pattern consisting of a random array of black squares scattered over a white background (see Fig. 1).

Observers. Four adults with normal or corrected-to-normal visual acuity participated in 1 or more of these experiments. All of these individuals were highly experienced observers of binocular rivalry, but only 2 (the authors) were aware of the hypotheses under test.

Procedure. Throughout a 60-sec test period, the observer manually tracked the fluctuations in dominance of the 2 rival targets, using a pair of keys on the computer keyboard. The observer depressed one key when the moving plaid was dominant entirely, another key when the stationary noise display was dominant entirely, and neither key when portions of both targets were visible simultaneously. The computer recorded the durations of these successive dominance periods during the 60-sec test trial. Rival targets were removed between trials, and the observer was allowed to rest as long as desired. In these tracking experiments, the measure of interest was the predominance of an eye viewing a particular kind of target.¹ To define predominance, one could simply calculate the fraction of the total time that a given key was depressed (i.e., a given eye/target was dominant). This definition fails to take into account, however, possible variations in the incidence of mixed dominance. The preferable definition of predominance expresses the total duration of dominance of one eye/target relative to the total duration of dominance of the other eye/target. Following the convention developed by Wade et al. (1984), we defined predominance as the ratio of the total right-eye dominance to the sum of the total dominances [$R/(R + L)$], a ratio whose value can range from 0 (complete dominance of one eye) to unity (complete dominance of the other eye).

Results

Component speed

In a preliminary experiment, 2 observers tracked rivalry between the stationary noise display (left eye) and a plaid (right eye) whose component gratings were oriented 45° and 135°. Over blocks of trials, the drift rate of both components was randomly varied from 0.27 to 1.01 degree/sec. For both observers, predominance increased monotonically within this range of drift rates (observer RB: $r = 0.881$, $p < 0.001$; HW: $r = 0.372$, $p < 0.01$). Data from one observer are shown in Figure 2. Analysis of the individual dominance durations for the 2 eyes revealed that the average dominance duration for the left eye (i.e., the noise target) decreased significantly (RB: $r = 0.847$, $p < 0.001$;

¹ In these tracking experiments, the same target was always presented to the same eye over blocks of trials, so we may speak of eye dominance or target dominance interchangeably. In pilot work, we established that the results described here were independent of which eye received which target.

Figure 1. Schematic of rival targets used in Experiment 1. One eye viewed a "noise target" consisting of black spots against a white background, and the other eye viewed a pair of drifting cosine gratings that formed a plaid.

HW: $r = 0.291$, $p < 0.05$) as the speed of the plaid increased (not shown in Fig. 2). This means, in other words, that the plaid remained suppressed for shorter and shorter durations as its speed increased. This result is in general agreement with earlier work showing that increases in stimulus strength reduce the average duration of suppression of a rival target (Levelt, 1965; Fox and Rasche, 1969; Blake, 1977; Mueller and Blake, 1989). In addition, the mean dominance duration of the moving plaid tended to increase with its speed (RB: $r = 0.296$, $p = 0.064$; HW: $r = 0.299$, $p = 0.039$; not shown).

This increase in predominance with component speed merely replicates the earlier finding of Wade et al. (1984) and thus sets the stage for our main experiment.

Plaid speed

In the main experiment, the drift rate of the plaid components was held constant at 0.37 degree/sec, while the angle between the 2 gratings, and hence plaid speed, was varied. Plaid speed can be calculated by dividing the component speed by the cosine

Figure 2. Predominance of eye viewing plaid as a function of plaid speed (which always equaled component speed). The component gratings of the plaid differed in orientation by 90°, and speed was manipulated by varying the drift rate of both components.

of the angle between the 2 directions of motion. The pairs of angles, measured in degrees counterclockwise from vertical, were 12, 168; 19, 161; 30, 150; and 45, 135. These pairs of components resulted in plaids with pattern speeds that were 5, 3, 2, and 1 times the component speed, respectively. Data from 4 60-sec tracking trials were obtained at each of the 4 plaid speeds, yielding a total of 16 trials; the order of conditions was random.

Results from this experiment, which appear as open squares in Figure 3, show that predominance of the eye viewing the plaid increased with the speed of that plaid. This increase in predominance was caused largely by a significant increase in the average duration of dominance of the eye viewing the plaid (for all correlations, $p < 0.001$). No reliable change was found in the average duration of suppression of the plaid.

Component angle

To vary plaid speed in the above experiment, we varied the angle of the component gratings. Could the change in predominance found in that experiment be attributable to the angle per se, not to the speed of the plaid? To test this possibility, we had observers track rivalry between the stationary noise and a single cosine grating drifting at 0.37 degree/sec, with the angle of the grating varied over trials (across the range of angles used in the plaid experiment). Four 60-sec trials at each of 4 angles were administered in a random order.

Results from this experiment (solid diamonds in Fig. 3) revealed no trend for predominance to vary in a manner that could account for the plaid speed results. Accordingly, we conclude that the variation in predominance with plaid speed is attributable to the speed of the plaid, not just to the angle of the gratings.

Discussion

The pattern of results from these experiments indicates that information about plaid speed is registered during binocular rivalry and influences the predominance of one eye over the other. Given this conclusion, what can be said about the neural processing of these kinds of 2-dimensional moving patterns? Adelson and Movshon (1982) proposed that this processing occurs in 2 stages, the first devoted to analysis of the individual components of motion, and the second, to the nonlinear com-

Figure 3. Predominance of eye viewing plaid as a function of plaid speed (open squares) and as a function of orientation of single component grating (solid diamonds). For the plaid stimuli, the orientations of the component gratings were varied to change plaid speed without altering drift rate of the components. Observer MB was tested on the plaid condition only. For the plaid speed condition, significance levels were $p < 0.001$ (RB, HW), $p = 0.004$ (GH), and $p = 0.02$ (MB). Note that, for the component orientation condition, correlations were negative, with significance levels of $p = 0.244$ (GH), $p = 0.515$ (RB), and $p = 0.03$ (HW).

bination of these components. This multistage model has received support from subsequent psychophysical experiments (Ferrera and Wilson, 1987, 1990; Welch, 1989). Concerning the actual neural sites of these 2 processing stages, it is thought that cells in area V1 register component motion only (e.g., the individual cosine components of a plaid), while a significant number of neurons in area MT respond selectively to the direction of pattern (e.g., plaid) motion (Movshon et al., 1985). According to this account, then, MT is the site at which information about plaid speed is analyzed, and the neural locus of rivalry would receive input from this analysis. What can be said about the relation of these 2 neural sites, rivalry and pattern motion?

On all accounts, the neural events underlying rivalry must occur at a site more central than that involved in the registration of component motion (i.e., the first stage posited by Adelson and Movshon, 1982), for we know that information about linear motion is processed fully even during suppression phases of binocular rivalry (Lehmkuhle and Fox, 1975). There are, however, different ways to conceptualize the relation of rivalry to the second stage of motion analysis, putatively area MT. The neural events underlying rivalry could occur at a site more central than MT, as depicted in Figure 4*a*. On this hypothesis, the variation in predominance with plaid speed occurs because information processed in MT flows forward (i.e., more centrally) to the site of rivalry. It is also possible, though, that the site of rivalry occurs before MT, and that information processed in MT is fed back to that site, as depicted in Figure 4*b*. The existence of feedback connections from MT to lower cortical areas has been confirmed by several studies (e.g., Krubitzer and Kaas, 1989), so the hypothesis depicted in Figure 4*b* is not inconsistent with neuroanatomy.

Can we distinguish between these 2 possibilities from the present data? Recall that the increase in predominance with plaid speed was reflected in a lengthening of the periods of time

that the plaid was dominant; the durations of suppression showed no consistent change with plaid speed. For 2 subjects, suppression duration showed a significant but small (RB: $r = -0.387$, $p = 0.029$; HW: $r = -0.253$, $p = 0.006$) decrease, while for the other 2, no relation between plaid speed and suppression duration was found. This pattern of results could mean that information about the components constituting the plaid was registered in MT only during dominance phases of rivalry, which in turn would mean that the feedback from MT to lower visual areas (including the site of rivalry) was active only during dominance phases of rivalry. If, however, the site of rivalry occurred after MT, both dominance and suppression durations should have been affected by plaid speed, as they were when the actual speed of the components was varied (recall the results from the first experiment). This was not reliably the case, however. Thus, there is at least circumstantial evidence favoring the alternative depicted in Figure 4*b* involving feedback from MT to the site of rivalry. The experiments described in the next section were designed to test these 2 alternatives more directly.

Experiment 2: Effect of Rivalry on Complex Motion

If rivalry occurs prior to a given processing site, then stimulus information from a suppressed eye should not reach that site during rivalry or should reach it in a perturbed state. Thus, visual aftereffects occurring prior to the site of rivalry should remain unaffected by suppression during adaptation, but those that occur beyond the level of rivalry suppression should be weakened while the aftereffect-inducing stimulus is suppressed. As mentioned above, the buildup of the simple linear MAE remains unaffected by suppression of the adapting motion (Lehmkuhle and Fox, 1975). Evidently, then, the site of rivalry resides beyond the neural locus of the linear MAE, which is thought to be V1 (e.g., Vautin and Berkley, 1977). Applying this

Figure 4. Schematic diagrams showing possible site of binocular rivalry suppression relative to putative stages of processing of motion information. This diagram undoubtedly oversimplifies the actual neuroanatomical pathways involved in the analysis of image motion and is meant merely to illustrate the connections between visual areas and the possible sites of rivalry relative to these areas (after Maunsell and Newsome, 1987).

logic to test the alternative hypotheses summarized in Figure 4 requires identifying an aftereffect that presumably occurs at or beyond MT. An excellent candidate is the well-known spiral aftereffect (SAE). Following prolonged inspection of, say, a clockwise rotating spiral that appears to be expanding, a stationary spiral will subsequently appear to rotate anticlockwise and to contract for a number of seconds. If the adaptation spiral rotates anticlockwise and contracts, the stationary spiral will appear to rotate clockwise and to expand. This SAE occurs even when the adapting stimulus is viewed by one eye and the test stimulus is viewed by the other eye, implying that the site of the SAE occurs after information from the 2 eyes has been combined.

Several lines of evidence suggest that spiral motion is processed at a relatively late cortical stage, beyond area V1. For one thing, Cavanagh and Favreau (1980) found that the SAE occurs even when the test spiral is the mirror image of the adapting spiral. In this situation, the contours of the 2 spirals are all at right angles, so that local motion vectors provide no

basis for the aftereffect. Rather, the SAE must result from a more global, presumably higher-level, analysis. For another, an SAE can be experienced in retinal regions unstimulated by motion during the adaptation period (Hershenson, 1984). For simple linear motion under analogous conditions, such as "phantom" MAEs are not experienced (Weisstein et al., 1977). Again, this finding implies more global, spatially extended processing underlying the SAE. Finally, it can be shown that the motion of a rotating spiral can be decomposed into 2 orthogonal components: radial motion (manifested as either expansion/contraction or motion-in-depth) and rotational motion (Hershenson, 1987). Recent physiological experiments suggest that neurons in higher cortical areas are responsive to both rotation and expansion/contraction. Specifically, Albright (1989) has found that MT cells show a bias for motion in a centrifugal direction, that is, motion away from the fovea. Saito et al. (1986), Tanaka et al. (1989a), and Tanaka and Saito (1989) found that certain classes of cells in the medial superior temporal area (MST), which receives inputs from MT, respond selectively to

Figure 5. Schematic of rival targets used in Experiment 2. One eye viewed a field of "noise dots" while the other viewed a spiral that either expanded (during adaptation) or was stationary (during postadaptation testing). During postadaptation testing, the untested eye viewed a blank circular region rather than dots.

rotation or to expansion/contraction. Cells in the posterior parietal association cortex (area PG, which receives input from the MST) respond to rotational motion (Sakata et al., 1986) and to components of motion involved in expansion/contraction (Motter and Mountcastle, 1981; Motter et al., 1987; Steinmetz et al., 1987). These are aspects of motion not uniquely signaled by neurons at early visual stages.

Hence, there are sound reasons to believe that the SAE and the linear MAE are distinct, with the SAE arising at a more central site in the visual pathways. Does rivalry suppression, which has no effect on the linear MAE, affect the buildup of the SAE? Answering this question was the motive for the next experiment.

Materials and Methods

Displays. The apparatus employed was the same as that used in Experiment 1. In the present experiment, one eye viewed a spiral target while the other viewed a noise pattern. The spiral consisted of a single-throw, $4\frac{1}{2}$ -turn Archimedes spiral, with an arm width of approximately 0.7° min arc (see Fig. 5). It was generated within a circular window 1.34° in diameter, with a 0.12° thick circular border. With continuous presentation of a single image of the spiral, it of course appeared stationary. By rapidly presenting successive images, or frames, with the spiral advanced slightly clockwise in each frame, it was possible to portray a continuously rotating spiral that appeared to be expanding. The animation sequence was timed to yield rotation at 150 rpm.

The rival target viewed by the other eye consisted of small (2-min-wide) black polygons randomly scattered throughout the circular region. By displaying different frames of noise successively over time, the black "blobs" appeared to jump randomly from position to position. When a single frame was displayed continuously, the blobs were stationary.

Observers. Seven adults with normal or corrected-to-normal visual acuity participated in 1 or more of these experiments. All of these individuals were highly practiced at both the tracking task and the recording of motion aftereffects, but only 2 (the authors) were aware of the hypotheses being tested. All observers showed increases in SAE duration as adaptation duration was increased up to 60 sec, and all showed a maximal SAE of at least 10 sec.

Procedure. To determine whether suppression retards the buildup of the SAE, we measured the duration of the SAE following 3 conditions of adaptation: (1) In the *nonrivalry condition*, one eye viewed the rotating spiral while the other eye viewed a blank field; under these conditions, the rotating spiral was continuously visible throughout the adaptation period. (2) For the *weak suppression condition*, the nonadapted eye viewed the stationary blobs. During the adaptation period, this blob target engaged in rivalry with the rotating spiral, though the moving spiral tended to predominate over the stationary blobs, meaning that the adapting spiral was suppressed for a relatively small fraction of the entire adaptation period. (3) In the *strong suppression condition*, the noise blobs viewed by the nonadapted eye underwent continuous random motion throughout the adaptation period. Not surprisingly, this dynamic stimulus increased the predominance of the nonadapted eye, meaning that the spiral was suppressed for a greater percentage of the adaptation period.

Observers viewed the adaptation display for 60 sec, fixating the center of the circular display (and thus the center of the spiral) throughout the adaptation period. During this period, observers tracked the visibility of the spiral by depressing a computer key at all times it was dominant. Thus, it was possible to relate the duration of spiral visibility during adaptation to SAE strength following adaptation. Immediately following the adaptation period, the blob target viewed by the other eye was removed, and the spiral ceased to rotate. The observer depressed a key for as long as the stationary spiral appeared to rotate/contract. Six observers were tested 4 times for each condition, while a seventh observer (GH) was tested 12 times for each; the order of conditions was randomized.

Results

In a preliminary control experiment, 6 different adaptation durations—10, 20, 30, 40, 50, and 60 sec—were employed in the nonrivalry condition to confirm that the duration of the SAE

Figure 6. Magnitude of spiral aftereffect as a function of adaptation duration.

increased with adaptation duration. Representative results are shown for one observer in Figure 6, with 7 trials for each duration. This experiment merely confirms an underlying assumption of the main experiment: Longer exposure during the adaptation period produces a longer aftereffect. Results from the 3 conditions constituting the main experiment appear in Figure 7, which shows scatterplots of SAE duration as a function of the cumulative duration of dominance of the spiral during adaptation. Best-fit lines reveal a strong positive correlation between SAE strength and the duration of spiral visibility during adaptation. Clearly, binocular suppression interferes with the buildup of the SAE. Our result is consistent with the finding of Lack (1978) that the aftereffect produced by adaptation to a rotating field of dots was reduced under conditions of rivalry suppression.

Now one could argue that the moving blobs viewed by the nonadapted eye during rivalry somehow combined with the spiral to yield a weakened motion signal, thereby effectively reducing the strength of the spiral motion. This argument fails, however, to explain why the *stationary* blobs also reduced the strength of the SAE. Moreover, we tried but failed to observe any sort of MAE following 60 sec of adaptation to the moving blobs alone. This failure implies that the randomly moving blobs have no differential effect on the cells adapted by prolonged exposure to the rotating spiral. We are confident, therefore, that the reduced effectiveness of the rotating spiral is attributable to suppression of information about that spiral for a substantial portion of the adaptation period. These results, then, imply that rivalry suppression occurs prior to the site of the SAE, which can be putatively identified as a visual area at or beyond MT, and because MST receives its input from MT, these results favor the hypothesis depicted in Figure 4b.

General Discussion

Emerging from the present series of experiments is a picture of the neural locus of rivalry suppression sandwiched between sequential stages of motion analysis, with feedback from the higher stage(s) onto the rivalry process. This conceptualization is admittedly oversimplified, for a couple of reasons. First, we know that a given visual area (e.g., V1) comprises a complex pro-

Figure 7. Magnitude of SAE as function of total duration of visibility of spiral during adaptation. Each panel shows results from one subject. All correlations between spiral visibility and SAE duration were highly significant.

cessing architecture involving different classes of cells richly interconnected (Gilbert and Wiesel, 1979; Ferster and Lindstrom, 1983; Martin and Whitteridge, 1984). It is conceivable that one form of motion analysis (e.g., local analysis of linear motion) transpires at one level of this architecture while rivalry arises within another. Thus, to place rivalry suppression completely outside of V1 or prior to MT overstates the conclusion. Second, it is possible that rivalry itself involves multiple distributed neural processes. For instance, the neural events responsible for registering the presence of dissimilar images on corresponding retinal areas could transpire at a site different from that at which the inhibitory concomitants of suppression take place (e.g., Fox, 1990). The experiments in this paper focus primarily on the neural events determining predominance and suppression, not on the mechanisms involved in the establishment of binocular correspondence. Moreover, our conclusions may pertain only to binocular rivalry involving motion; rivalry between stationary patterns or between dissimilar colors may

engage inhibitory processes in other pathways. Still, we can say with confidence that suppression does not retard the processing of motion information by direction-selective units responsive to linear motion within local regions of the visual field, whereas it does interfere with processing of contraction/expansion information.

It makes sense that the neural events underlying rivalry would arise prior to a stage where information from the 2 eyes had become inextricably combined. On logical grounds, it can be argued that, when confronted with dissimilar monocular stimulation, the visual system *must* rely on monocular signals to instigate binocular rivalry (Sloane, 1985; Blake, 1989), for binocular signals cannot unambiguously distinguish the conditions for rivalry from the conditions for fusion (i.e., matched inputs to the 2 eyes). In addition, we know from psychophysical experiments that, during binocular rivalry, it is a region of an eye that is suppressed, not a particular stimulus feature (Blake et al., 1980). This monocular suppression would be very difficult

to accomplish if rivalry transpired after a level of processing where information from the 2 eyes had been combined into binocular signals. Eye-of-origin information, in other words, is an essential ingredient in the rivalry process. Now, from physiological experiments, it is known that neurons in V1 vary widely in ocular dominance (e.g., Hubel and Wiesel, 1968; Schiller et al., 1976), while neurons in extrastriate areas, including visual area 3 (V3; Felleman and Van Essen, 1987) and MT (Maunsell and Van Essen, 1983), are predominantly binocular, with roughly equal excitatory drives from the 2 eyes. On these grounds, then, rivalry would be simpler to accomplish at stages prior to MT and/or V3. Of course, the small proportion of monocular cells in MT may be sufficient to detect the conditions for binocular rivalry. From the experiments of Logothetis and Schall (1989, 1990), we know that the activity of about 25% of neurons in the MT is modulated in synchrony with an animal's behavioral report of dominance during binocular rivalry. It appears, in other words, that a reliable neural concomitant of fluctuations in dominance is expressed by this level of the visual nervous system. That finding is, of course, in good agreement with the present psychophysical results.

Thus far, our discussion of the neural bases of rivalry suppression has focused on possible loci of suppression. Indeed, we hope that the present results may provide guidance to physiologists interested in those neural bases. Also of importance to physiologists, however, is the nature of the neural events underlying suppression, wherever those events transpire. To illustrate what we have in mind, consider a situation where the left eye views stationary dots, and the right eye views a drifting plaid. Suppose the plaid is temporarily dominant, and the dots are suppressed entirely. From the observer's viewpoint, this situation is essentially identical, albeit temporarily, to one where only the right eye receives a plaid and the left eye is unstimulated. In other words, when the plaid is exclusively dominant in rivalry, the invisibility of the dots is just as compelling as when those dots are physically absent. Indeed, this is the profound quality of rivalry: the occasional complete invisibility of a complex, suprathreshold stimulus. Are we to conclude from the perceptual equivalence of "stimulus absent" and "stimulus suppressed" that these 2 perceptual states are mediated by equivalent neural states?

For a couple of reasons, this conclusion seems mistaken. First, it is well established that probe targets presented to an eye during suppression phases of rivalry are more difficult to detect than probes presented to that same eye during its dominance phases (Fox and Check, 1968; Wales and Fox, 1970; Westendorf et al., 1982). Surprisingly, however, the elevation in probe thresholds during suppression is only a small fraction of a log-unit. Suppression, in other words, is not occasioned by a dramatic reduction in visual sensitivity, suggesting that the inhibition producing suppression is relatively modest. Moreover, evoked potential studies reveal that reductions in the amplitude of the response evoked by a suppressed stimulus are quite small (e.g., Regan, 1989) compared to the large amplitude reductions in the evoked potential when the visibility of the evoking stimulus is reduced by physical means (e.g., Campbell and Maffei, 1970). These differences imply that the neural events underlying suppression are not equivalent to those associated with real manipulations of the stimulus.

To end on a speculative note, we are inclined to believe that rivalry suppression involves a rather subtle shift in the pattern of neural activity within an ensemble of neurons that, for the

reasons spelled out above, vary in their ocular dominance (Blake, 1989). According to this model, modulations in neural activity associated with shifts in perceptual dominance occur only within that subset of those neurons that is strongly dominated by one eye or the other. On this view, the paradox of binocular rivalry is that such compelling swings in perceptual dominance could be mediated by quite small swings in neural activity.

References

- Adelson EH, Movshon JA (1982) Phenomenal coherence of moving visual patterns. *Nature* 300:523-525.
- Albright TD (1989) Centrifugal directional bias in the middle temporal visual area of the macaque. *Vis Neurosci* 2:177-188.
- Blake R (1977) Threshold conditions for binocular rivalry. *J Exp Psychol* 3:251-257.
- Blake R (1989) A neural theory of binocular rivalry. *Psychol Rev* 96:145-167.
- Blake R, Fox R (1974) Adaptation to invisible gratings and the site of binocular rivalry suppression. *Nature* 249:488-490.
- Blake R, Westendorf D, Overton R (1980) What is suppressed during binocular rivalry? *Perception* 9:223-231.
- Blakemore C, Fiorentini A, Maffei L (1972a) A second neural mechanism of binocular depth discrimination. *J Physiol (Lond)* 226:725-749.
- Blakemore C, Iverson SD, Zangwill OL (1972b) Brain functions. *Annu Rev Psychol* 23:413-456.
- Breese BB (1899) On inhibition. *Psychol Monographs* 3:1-65.
- Campbell FW, Maffei L (1970) Electrophysiological evidence for the existence of orientation and size detectors in the human visual system. *J Physiol (Lond)* 207:635-652.
- Cavanagh P, Favreau OE (1980) Motion aftereffect: a global mechanism for the perception of rotation. *Perception* 9:175-182.
- Felleman DJ, Van Essen DC (1987) Receptive field properties of neurons in area V3 of macaque monkey extrastriate cortex. *J Neurophysiol* 57:889-920.
- Ferrera VP, Wilson HR (1987) Direction specific masking and the analysis of motion in two dimensions. *Vision Res* 27:1783-1796.
- Ferrera VP, Wilson HR (1990) Perceived direction of moving two-dimensional patterns. *Vision Res* 30:273-287.
- Ferster D, Lindstrom S (1983) An intracellular analysis of geniculocortical connectivity in area 17 of the cat. *J Neurophysiol* 342:181-215.
- Fox R (1990) Binocular rivalry. In: *Binocular vision and psychophysics Vol 9* (Regan DM, ed). London: MacMillan, in press.
- Fox R, Check R (1968) Detection of motion during binocular rivalry suppression. *J Exp Psychol* 78:388-395.
- Fox R, Rasche F (1969) Binocular rivalry and reciprocal inhibition. *Percept Psychophys* 5:215-217.
- Gilbert CD, Wiesel TN (1979) Morphological and intracortical projections of functionally characterized neurones in the cat visual cortex. *Nature* 280:120-125.
- Hammond P, Mouat GSV (1988) Neural correlates of motion aftereffects in cat striate cortical neurones: interocular transfer. *Exp Brain Res* 72:21-28.
- Hammond P, Mouat GSV, Smith AT (1985) Motion aftereffects in cat striate cortex elicited by moving gratings. *Exp Brain Res* 60:411-416.
- Hammond P, Mouat GSV, Smith AT (1986) Motion aftereffects in cat striate cortex elicited by moving texture. *Vision Res* 26:1055-1060.
- Hammond P, Mouat GSV, Smith AT (1988) Neural correlates of motion aftereffects in cat striate cortical neurones: monocular adaptation. *Exp Brain Res* 72:1-20.
- Hershenson M (1984) Phantom spiral aftereffect: evidence for global mechanisms in perception. *Bull Psychonom Soc* 22:535-537.
- Hershenson M (1987) Visual system responds to rotational and size-change components of complex proximal motion patterns. *Percept Psychophys* 42:60-64.
- Hubel DH, Wiesel TN (1968) Receptive fields and functional architecture of monkey striate cortex. *J Physiol (Lond)* 195:215-243.
- Julesz B (1971) *Foundations of cyclopean perception*. Chicago: University of Chicago Press.

- Krubitzer LA, Kaas JH (1989) Cortical integration of parallel pathways in the visual system of primates. *Brain Res* 478:161–165.
- Lack LC (1978) Selective attention and the control of binocular rivalry. New York: Mouton.
- Lehmkühle SW, Fox R (1975) Effect of binocular rivalry suppression on the motion aftereffect. *Vision Res* 15:855–859.
- Levelt WJM (1965) On binocular rivalry. Soesterberg: Institute for Perception RVO-TNO.
- Livingstone M, Hubel D (1988) Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science* 240:740–749.
- Logothetis NK, Schall JD (1989) Neuronal correlates of subjective visual perception. *Science* 245:761–763.
- Logothetis NK, Schall JD (1990) Binocular motion rivalry in macaque monkeys: eye dominance and tracking eye movements. *Vision Res* 30:1409–1419.
- Maffei L, Fiorentini A, Bisti S (1973) Neural correlates of perceptual adaptation to gratings. *Science* 182:1036–1039.
- Marrocco RT, McClurkin JW (1979) Binocular interaction in the lateral geniculate nucleus of the monkey. *Brain Res* 168:633–637.
- Martin KAC, Whitteridge D (1984) Form, function and intracortical projections of spiny stellate neurones in the striate visual cortex of the cat. *J Physiol (Lond)* 353:463–504.
- Maunsell JHR, Newsome WT (1987) Visual processing in monkey extrastriate cortex. *Annu Rev Neurosci* 10:363–401.
- Maunsell JHR, Van Essen DC (1983) Functional properties of neurons in middle temporal visual area of the macaque monkey. II. Binocular interactions and sensitivity to binocular disparity. *J Neurophysiol* 49:1148–1167.
- Motter BC, Mountcastle VB (1981) The functional properties of the light-sensitive neurons of the posterior parietal cortex studied in waking monkeys: foveal sparing and opponent vector organization. *J Neurosci* 1:3–26.
- Motter BC, Steinmetz MA, Duffy CJ, Mountcastle VB (1987) Functional properties of parietal visual neurons: mechanisms of directionality along a single axis. *J Neurosci* 7:154–176.
- Movshon JA, Lennie P (1979) Pattern selective adaptation in visual cortical neurones. *Nature* 278:850–852.
- Movshon JA, Adelson EH, Gizzi MS, Newsome WT (1985) The analysis of moving visual patterns. In: *Pattern recognition mechanisms* (Chagas C, Gatass R, Gross C, eds), pp 117–151. New York: Springer.
- Mueller TJ, Blake R (1989) A fresh look at the temporal dynamics of binocular rivalry. *Biol Cybern* 61:223–232.
- Ohzawa I, Freeman RD (1986) The binocular organization of simple cells in the cat's visual cortex. *J Neurophysiol* 56:221–242.
- O'Shea RP, Crassini B (1981) Interocular transfer of the motion aftereffect is not reduced by binocular rivalry. *Vision Res* 21:801–804.
- Regan D (1989) Human brain electrophysiology: evoked potentials and evoked magnetic fields in science and medicine. New York: Elsevier.
- Saito H, Yukie M, Tanaka K, Hikosaka K, Fukada Y, Iwai E (1986) Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *J Neurosci* 6:145–157.
- Sakata H, Shibutani H, Ito Y, Tsurugai K (1986) Parietal cortical neurons responding to rotary movement of visual stimulus in space. *Exp Brain Res* 61:658–663.
- Sanderson KJ, Darian-Smith I, Bishop PO (1971) The properties of the binocular receptive fields of lateral geniculate neurons. *Exp Brain Res* 13:178–207.
- Schiller PH, Finlay BL, Volman SF (1976) Quantitative studies of single-cell properties in monkey striate cortex. II. Orientation specificity and ocular dominance. *J Neurophysiol* 39:1320–1333.
- Sloane ME (1985) Binocular rivalry: a psychophysics in search of a physiology. In: *Models of visual cortex* (Rose D, Dobson VA, eds), pp 211–222. Chichester: Wiley.
- Steinmetz MA, Motter BC, Duffy CJ, Mountcastle VB (1987) Functional properties of parietal visual neurons: radial organization of directionalities within the visual field. *J Neurosci* 7:177–191.
- Tanaka K, Saito H (1989) Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *J Neurophysiol* 62:626–641.
- Tanaka K, Fukada Y, Saito H (1989) Underlying mechanisms of the response specificity of expansion/contraction and rotation cells in the dorsal part of the medial superior temporal area of the macaque monkey. *J Neurophysiol* 62:642–656.
- Varela FJ, Singer W (1987) Neuronal dynamics in the visual corticocortical pathway revealed through binocular rivalry. *Exp Brain Res* 66:10–20.
- Vautin RG, Berkley MA (1977) Responses of single cells in cat visual cortex to prolonged stimulus movement: neural correlates of visual aftereffects. *J Neurophysiol* 40:1051–1065.
- von der Heydt R, Hanny P, Adorjani C (1978) Movement aftereffects in the visual cortex. *Archiv Ital Biol* 116:248–254.
- Wade NJ, Wenderoth P (1978) The influence of color and contrast rivalry on the magnitude of the tilt aftereffect. *Vision Res* 18:827–835.
- Wade NJ, De Weert CMM, Swanston MT (1984) Binocular rivalry with moving patterns. *Percept Psychophys* 35:111–122.
- Wales R, Fox R (1970) Increment detection thresholds during binocular rivalry suppression. *Percept Psychophys* 8:90–94.
- Weinstein N, Maguire W, Berbaum K (1977) A phantom motion aftereffect. *Science* 198:955–958.
- Welch L (1989) The perception of moving plaids reveals two motion-processing stages. *Nature* 337:734–736.
- Westendorf DH, Blake R, Sloane M, Chambers D (1982) Binocular summation occurs during interocular suppression. *J Exp Psychol [Hum Percept]* 8:81–90.
- Wilson HR, Blake R, Halpern DL (1990) Coarse spatial scales constrain the range of binocular fusion on fine scales. *J Opt Soc Am*, in press.