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A Neural Theory of Binocular Rivalry

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When the two eyes view discrepant monocular stimuli, stable single vision gives way to alternating periods of monocular dominance; this is the well-known but little understood phenomenon of binocular rivalry. This article develops a neural theory of binocular rivalry that treats the phenomenon as the default outcome when binocular correspondence cannot be established. The theory posits the existence of monocular and binocular neurons arrayed within a functional processing module, with monocular neurons playing a crucial role in signaling the stimulus conditions instigating rivalry and generating inhibitory signals to implement suppression. Suppression is conceived as a local process happening in parallel over the entire cortical representation of the binocular visual field. The strength of inhibition causing suppression is related to the size of the pool of monocular neurons innervated by the suppressed eye, and the duration of a suppression phase is attributed to the strength of excitation generated by the suppressed stimulus. The theory is compared with three other contemporary theories of binocular rivalry. The article closes with a discussion of some of the unresolved problems related to the theory.

This article presents a neural theory of binocular rivalry. The theory consists of a set of propositions that account for major features of binocular rivalry. Some of these propositions are based on empirical evidence, whereas others are more axiomatic in form. A concise statement of each proposition follows a short introductory section. Next, the detailed reasoning underlying each proposition is elaborated upon, and evidence consistent with the proposition is outlined. A comparison of the present theory with several other recent models that include rivalry within their domains follows. The article closes by describing certain phenomena that are presently inconsistent with the theory and by proposing some possible, testable reconciliations of theory and data.

Background of the Theory

Binocular rivalry refers to the alternating periods of dominance and suppression occassioned by stimulation of corresponding retinal areas with dissimilar monocular stimuli. Rivalry was actually described several centuries ago by Dutour (1760), who noted alternations in perceived color when the two eyes viewed different colors. It remained, however, for Wheatstone (1838) to study the phenomenon systematically, which he did in the course of his seminal work on stereopsis. To my knowledge, Wheatstone was the first to publish a stereogram demonstrating contour rivalry. Around the turn of the century, Breese (1899, 1909) published a couple of influential monographs detailing the stimulus conditions that trigger rivalry, and many of Breese's careful observations remain definitive today. Probably the single most significant piece of recent work on rivalry is Levelt's (1965) monograph. In his work, Levelt drew the important distinction between rivalry suppression (the temporary invisibility of a monocular stimulus occasioned by contour stimulation of the corresponding area of the other eye) and Troxler's effect (the perceptual fading of a nonfoveally viewed monocular stimulus). Levelt also formalized a set of rules specifying the relation between rivalry alternation rate, average duration of dominance, and the strength of the competing monocular stimuli.

In the last 20 years, most of the work on binocular rivalry has been empirical in nature. Fox and his colleagues (Blake & Fox, 1974a; Fox & Check, 1966; Wales & Fox, 1970) have pursued a program of research aimed at elucidating the extent to which information presented to a suppressed eye is lost at an early stage of processing. Results from Fox's research has inspired others (Lack, 1978; O'Shea & Crassini, 1981a; Walker & Powell, 1979) to examine this question, too. At the same time, several laboratories have studied the stimulus determinants of suppression within the context of spatial frequency analysis (Blake, 1977; Fahle, 1982; Hollins, 1980) and other neural analytic mechanisms (Abadi, 1976; Blake, Zimba, & Williams, 1985; Wade, 1974; Wade, de Weert, & Swanson, 1984). Still others have examined patterns of eye movements during episodes of suppression and dominance, looking for possible visuomotor events that influence the alternations of rivalry (e.g., Sabrin & Kertesz, 1983). There has even been some progress in developing psychophysical procedures for studying binocular rivalry in nonhuman mammals (Myerson, Miezin, & Allman, 1981).

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In contrast to this vigorous empirical activity, there have been few major theoretical developments concerning binocular rivalry. Kaufman (1964) has tried to champion the idea that rivalry suppression underlies ordinary binocular single vision, but his writings have not dwelled on possible mechanisms of rivalry. Several contemporary models of stereopsis (e.g., Sperling, 1970) make reference to rivalry in their formulations, but binocular rivalry clearly is not the focus of those theories. The most recent theoretical work on rivalry is Wolfe's (1986) model, which attempts to combine elements of suppression theory and fusion theory, and Lehky's (1988) model, which concentrates on the temporal dynamics of rivalry. Also, Grossberg (1987) includes binocular rivalry in his general theory of visual perception based on self-organizing neural networks. These three models will be discussed in some detail after presentation of the present theory. Finally, Sloane (1985) has provided a succinct review of the properties of binocular rivalry that must be incorporated into a comprehensive theory of rivalry; those properties will be reiterated in this article, as the present theory unfolds.

This article represents an attempt to develop a neural theory of binocular rivalry. The effort is inspired, in part, by the conviction that further advances (both physiological and psychophysical) in our understanding of binocular rivalry will be facilitated by an explicit, provocative theoretical treatment of this curious and fascinating phenomenon. From the outset it should be stressed that some of the concepts (e.g., the existence of cortical neurons that vary in their ocular dominance) are themselves not novel, and some of the neural processes integral to the theory (e.g., interocular inhibition) have been proposed by others (e.g., Abadi, 1976; Cogan, 1987; Sloane, 1985; Sugie, 1982). It is the alliance of these ideas into a comprehensive set of propositions that makes the theory unique.

The theory consists of a set of seven propositions. Some of these are inspired by psychophysical observations that will be described in the context of the appropriate proposition. Other propositions follow from logical considerations. An overview of the seven propositions is provided to help the reader form a general impression of the theory before each proposition is developed in detail.

An Overview of the Seven Propositions

Proposition 1: Binocular Fusion Takes Precedence Over Binocular Rivalry

The binocular visual nervous system attempts to identify matched primitives (e.g., oriented contours) in the two eyes' views. This matching process embodies the assumption that only a single object can occupy a given location in visual space. When the two eyes both fixate that object, left- and right-eye feature descriptions of that object match, except perhaps for slight positional disparities related to the shape and volume of the object. Establishment of binocular matches yields stable binocular single vision (i.e., fusion). Failure to find matching features on corresponding or near-corresponding retinal areas leads to reciprocal periods of dominance and suppression of nonmatching features (i.e., the phenomenon of binocular rivalry).

Proposition 2: Rivalry Suppression Operates Within Delimited Regions of the Cortical Image

The matching process operates locally and in parallel over restricted regions of the neural representation of the binocular visual field. Matches can be established within one set of corresponding monocular areas, although matches are impossible within other corresponding monocular areas. Where matches are established, binocular fusion occurs; where matches prove impossible, rivalry ensues.

Proposition 3: Cortical Neurons Vary in Their Ocular Dominance

It is assumed that cortical neurons vary in the extent to which they may be activated by the two eyes, with some neurons excited only by right-eye stimulation, others excited only by left-eye stimulation, and the remainder excited to varying degrees by stimulation of either eye. The first two classes of neurons are termed *monocular neurons* and the latter class, *binocular neurons.* Note that these categories are defined exclusively in terms of excitatory input from one or both eyes onto cortical neurons. It is further assumed that monocular neurons innervated by the left eye can indirectly exert inhibitory influence over monocular neurons innervated by the right eye, and vice versa. Monocular neurons, in other words, receive excitatory input from one eye and may receive inhibitory input from the other eye. For purposes of the theory, it is further assumed that all neurons involved in the rivalry process are selective for orientation.

Proposition 4: Monocularly Innervated Cortical Neurons Instigate Binocular Rivalry

Binocular neurons cannot distinguish the stimulus conditions (i.e., dissimilar monocular features) that produce rivalry from those stimulus conditions (i.e., matched monocular features) that produce stable single vision, whereas monocular neurons can distinguish between these two conditions. It is monocular neurons, therefore, that signal unambiguously the set of feature primitives existing at a given region of the neural representation of visual space.

Proposition 5: Rivalry Suppression Entails Inhibition of Activity Within All Monocular Neurons Innervated by a Given Retinal Area of One Eye

During a suppression phase of binocular rivalry, neural activity is inhibited within *all* monocular neurons innervated by the eye viewing the currently suppressed stimulus, not just those neurons selective for the features specifying that stimulus. In other words, it is a region of an eye that is suppressed during rivalry, not information about a particular set of stimulus features.

Proposition 6: Strength of Inhibition Underlying Suppression Is Directly Related to the Size of the Pool of Monocular Neurons Receiving Inhibition

When corresponding areas of the two eyes view dissimilar stimuli, the pool of monocular neurons activated by the currently dominant eye exerts an inhibitory influence on the pool of monocular neurons activated by the currently suppressed eye. The strength of that inhibition is determined by the size of the pool of monocular neurons innervated by the suppressed eye, not by the characteristics of the stimulus activating the pool of neurons innervated by the dominant eye. Activity within the pool of binocular neurons is largely unaffected by the inhibitory interactions between the pools of monocular neurons.

Proposition 7: The Time Needed for the Currently Inhibited Pool of Monocular Neurons to Overcome Inhibition (and Hence Terminate Suppression of That Eye) Is Directly Related to the Strength of the Stimulus Viewed by the Suppressed Eye

An eye's transition from suppression to dominance occurs when the activity produced by the stimulus viewed by that eye offsets the inhibition affecting that pool of neurons. Because excitatory activity is directly related to stimulus strength, a weak monocular stimulus remains suppressed, on average, for longer periods of time; that weak stimulus generates less activity per unit time and, hence, takes longer to overcome interocular inhibition. Furthermore, any manipulation of the suppressed stimulus that boosts the level of activity generated by that stimulus hastens the termination of suppression; any manipulation of the suppressed stimulus that lowers its evoked activity lengthens the duration of suppression.

The reasoning behind each of these seven propositions is discussed next.

Proposition 1: Precedence of Binocular Fusion Over Binocular Rivalry

Background

There is an obvious advantage to frontal eye placement: By viewing a common region of the visual scene from slightly different vantage points, the two eyes provide the brain with positional disparity information that can specify with great precision the relative positions of objects in three-dimensional space. This keen sense of depth perception based on retinal disparity is known, of course, as stereopsis. Not only is stereoscopic depth information quite useful for visually guided behavior (e.g., Sheedy, Bailey, Buri, & Bass, 1986), it can also contribute significantly to the segregation of objects from their backgrounds. This stereoscopic segregation process is most dramatically illustrated by the emergence of form from random-dot stereograms (Julesz, 1971).

To use the potential information provided by positional disparities provided by the two eyes' views, it is first necessary for the brain to discover features in the left-eye's view that correspond to (i.e., match) features in the right-eye's view. Expressed in the parlance of computational theories (Marr, 1982), the brain must solve the correspondence problem. In its search for corresponding features, the binocular visual system may exploit an axiomatic property of the physical world: A given region of visual space may be occupied by one and only one object at any given moment in time (cf. Marr & Poggio, 1976). This property, which I shall refer to as the *existence property*, dictates that when a person with normal eye alignment binocularly fixates an object, the foveae of the two eyes will receive matching images of that object. In other words, corresponding areas of the two eyes (the foveae in this case) will be stimulated by similar images.

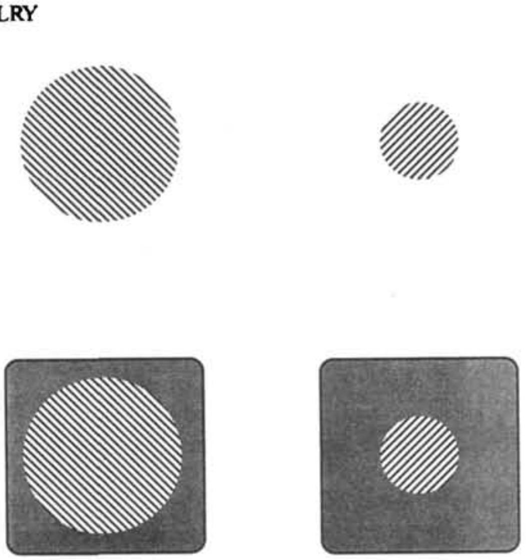

Figure 1. Readers capable of free fusion may experience the stabilizing effect that fusion contours have on vergence eye movements. (While dichoptically viewing the upper pair of rival targets, notice how the two targets slip back and forth in position relative to one another. Compare this behavior with the bottom pair of rival targets, which are surrounded by identical patterns that should promote stable binocular alignment and, hence, minimize the visual consequences of vergence changes.)

Suppose left-eye and right-eye foveal images do not match. In effect, the two eyes are providing the brain with conflicting information about the object situated at a given region of visual space. This conflict, of course, represents a violation of the existence property. Several things may occur in this circumstance. The binocular visual system may signal visuomotor centers to alter the vergence angle of the two eyes, in an attempt to bring matching images onto the two foveae. Anyone who has observed binocular rivalry between dissimilar monocular targets of large angular subtense will have noticed how the two images appear to be sliding back and forth constantly over one another; this is the visual consequence of vergence instability caused by the absence of matching features anywhere close to the fovea. It is possible, incidentally, to minimize the vergence response to conflicting monocular input by providing matching features in the immediate vicinity of the fovea. By viewing the two pairs of rival targets in Figure 1, the reader may compare what happens when matching features are lacking (top pair of rival targets in Figure 1) and when they are present (bottom pair of rival targets in Figure 1).

As an alternative solution, the brain may temporarily resolve an interocular conflict by suppressing one of the two discrepant images. Metaphorically speaking, the brain momentarily accepts one of the two monocular assertions about the nature of the object existing at the contested region of visual space.

So, to reiterate, the binocular visual system first attempts to solve the correspondence problem (i.e., the matching of left- and right-eye features). The search for matching features is limited to retinal regions in the immediate vicinity of corresponding areas of the two eyes, a strategem that minimizes the occurrence of false matches. Where feature matches are established, stable binocular single vision results; following convention, I shall refer to this state of stability as *binocular fusion*. Moreover, the establishment of matching features on horizontally disparate retinal areas typically gives rise to the perception of stereoscopic depth. Where matches cannot be established, single vision gives way to binocular rivalry. Construed in this way, then, binocular rivalry represents the default outcome when binocular fusion fails.

Two questions are raised by this conceptualization of binocular rivalry: (a) What monocular features are used in the brain's attempt to solve the correspondence problem? and (b) what is the evidence that fusion takes precedence over rivalry? Let's consider each of these two questions in turn.

Matching Features

By studying the stimulus conditions that cause binocular rivalry, it is possible to get at the question of *binocular correspondence*, at least as that concept applies to the establishment and maintenance of stable binocular single vision (i.e., binocular fusion). Note, incidentally, that binocular fusion and stereopsis are not strictly synonymous, as evidenced by the fact that the two phenomena may be dissociated. In particular, stereopsis can be experienced even with horizontal disparities too large to be fused; under these conditions, observers perceive diplopic images in front of or behind the plane of fixation, the direction of depth depending on the sign of the disparity. Stereopsis can also be experienced when horizontally disparate retinal areas are stimulated by dissimilar monocular images that resist binocular fusion (Mitchell, 1969). Conversely, one may experience fusion of disparate images without an accompanying sense of stereoscopic depth—this can occur when viewing horizontal contours that are vertically disparate between the two eyes. This dissociation between these two phenomena of binocular vision implies that the matching process underlying stereopsis may differ from that underlying binocular fusion. Because rivalry is conceived as a breakdown in fusion, it is the fusion matching process that is more relevant here.

Table 1 lists for different stimulus dimensions the maximum interocular stimulus difference that can be tolerated before stable single vision gives way to binocular rivalry. It should be stressed that these represent average values; because of hysteresis, fusion limits can vary depending on whether interocular differences start at some negligible value and increase until fusion is lost versus start at some large value and decrease until fusion is achieved. These particular interocular feature matching values are not critical to the theory developed here; they are given simply to illustrate the range of interocular tolerance exhibited by the binocular visual system. Nor can we be sure that these truly represent the feature primitives utilized by the binocular matching process (see, e.g., Mayhew & Frisby, 1981). To the extent that the correspondence problem is tackled early in visual processing, however, we would expect the matching primitives to correspond to those features (i.e., orientation, spatial frequency, direction of motion) implicitly represented at an early stage of visual processing.

Precedence of Fusion Over Rivalry

The theory advanced here asserts that binocular rivalry is the default outcome when interocular features differ by an amount too great to be fused. This assertion is tantamount to rejection of suppression theories of binocular vision (e.g., Asher, 1953), which argue that rivalry is ongoing, albeit inconspicuously, under *all* conditions of binocular stimulation. According to my theory, the presence of matching features in the two eyes' images makes those features exempt from binocular suppression. Several lines of evidence support this aspect of the theory.

The most direct piece of evidence that fusion takes precedence over rivalry comes from a study by Blake and Boothroyd (1985). In that study, observers were required to give reaction time (RT) responses to a decrement in the contrast of a monocularly viewed grating pattern viewed under various conditions. The rationale for this study is based on the fact that changes in a monocular target are much more difficult to detect when that target is suppressed during binocular rivalry, compared with when the target is dominant. In the case of the RT task, RTs to a contrast decrement are fast when the grating is dominant in rivalry and are quite long when the grating is suppressed.

With this observation in mind, consider the results from the following set of conditions (which are summarized schematically along with the results in Figure 2). When both eyes view identical vertical gratings (the fusion condition), RTs to a decrement in the contrast of one eye's grating are fast and distributed unimodally. When one eye views vertical and the other eye views horizontal (the rivalry condition), RTs are slower on average and are much more variable, with some RTs several seconds in duration. Reaction time is affected in this condition because the monocular contrast decrement is occuring sometimes during dominance and other times during suppression. When one eye views a blank field and the other eye views a composite pattern generated by the superimposition of horizontal and vertical, RTs to decrements in either component are fast and unimodal. Finally, and crucially, when one eye views the horizontal–vertical composite and the other eye views just vertical, RTs to contrast decrements in any one of the component gratings are fast and unimodal. Note that this last condition contains the stimulus conditions for fusion (vertical to both eyes) as well as the stimulus conditions for rivalry (vertical to one eye and horizontal to the other). There is no evidence for an effect of suppression in this last condition, compared with the genuine rivalry condition, indicating that the presence of matching features (vertical contours) in the two eyes' views has stabilized the binocular percept. Essentially the same conclusion has been reached by O'Shea (1987a) using a rather different RT task.

There are other, more circumstantial bits of evidence that support the conclusion that fusion takes precedence over rivalry. For instance, Julesz and Tyler (1976) found that the transition from correlated monocular images (fusion condition) to uncorrelated monocular images (rival condition) was detected more quickly than the transition from uncorrelated to correlated. This finding could be interpreted to imply that suppression does not operate when monocular images are correlated, making changes in those images easier to detect; uncorrelated monocular images engage suppression that retards the detec-

Table 1
Maximum Disparity Yielding Binocular Single Vision for Various Stimulus Dimensions

Reference	Stimulus dimension	Maximum interocular difference
Blakemore (1970)	Spatial frequency	20% difference in cycles/degrees
Kertesz & Jones (1970)	Orientation	15 angular degrees
Braddick (1979)		
Wade, deWeert, & Swanson (1984)	Direction of motion	30 angular degrees
Blake, Zimba, & Williams (1985)		
Blake et al. (1985)	Velocity	50% difference in degrees per second
Hollins & Leung (1978)	Wave length	Varies with reference nanometer

tion of changes in the degree of correspondence between those images.

Then there is a large body of evidence showing that two eyes are better than one on a variety of threshold tasks, a phenomenon referred to as *binocular summation* (Blake & Fox, 1973). This superiority of binocular viewing is greater than that predicted on the basis of probability summation (i.e., an enhancement in performance attributable solely to the statistical advantage of two chances to detect). Binocular summation in excess of probability implicates cooperative neural interactions between the two eyes. Moreover, the magnitude of binocular summation is significantly reduced when one eye's threshold target is presented to that eye during explicit periods of binocular rivalry suppression (Westendorf, Blake, Sloane, & Chambers, 1982). In other words, when an observer views dissimilar monocular stimuli (and, hence, experiences binocular rivalry), the detectability of identical monocular targets (binocular summation probes) is impaired, relative to the condition in which those same targets are presented while the observer is viewing identical monocular stimuli (and, hence, does not experience patent binocular rivalry). This difference in the magnitude of binocular summation implies the operation of a suppression effect under conditions of rivalry that is not operative under nonrivalry conditions.

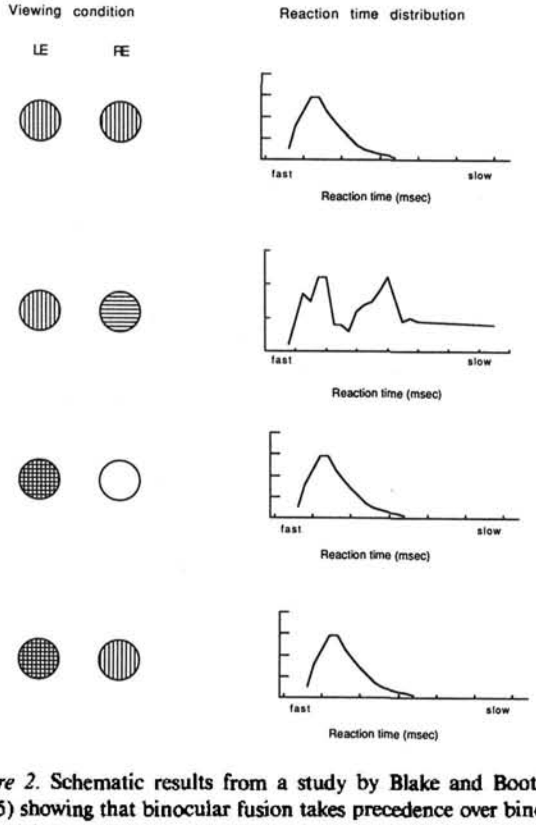

Figure 2. Schematic results from a study by Blake and Boothroyd (1985) showing that binocular fusion takes precedence over binocular suppression. (On the left are various conditions of dichoptic stimulation, and on the right are frequency histograms for reaction times measured under those various stimulus conditions; these distributions are stylized representations of the actual results. Reaction times were measured in response to an abrupt increase in the contrast of one of the component gratings.)

Finally, there are several experiments showing that monocular probe targets are detected more readily under conditions of fusion than under conditions of rivalry (see O'Shea, 1987a, for a review of these experiments). This class of experiments, too, indicates that fusion normally occurs except when monocular inputs fail to match.

It should be acknowledged, however, that several contemporary workers (Makous & Sanders, 1978; Wolfe, 1986) continue to embrace the notion that binocular suppression operates under all conditions, including dioptic stimulation (i.e., in which the two eyes receive identical stimulation). Readers who are interested in this debate should consult the exchange between Blake and O'Shea (1988) and Wolfe (1988) that appeared in this journal.

Proposition 2: Rivalry Suppression Operates Within Delimited Regions of the Cortical Image

Background

Simply observing rivalry between conflicting monocular targets makes it evident that suppression is piecemeal in nature. Only when foveally viewed rival targets are very small (less than 1° visual angle) does an observer experience complete dominance of one target for appreciable amounts of time. With larger rival targets, one rarely sees an entire monocular target dominate completely over its rival counterpart.

To appreciate this property of rivalry, take a look at the three pairs of rival targets shown in Figure 3, noting in each case how frequently the binocular percept resembles a dynamic mosaic of the two targets. The limited spatial extent of rivalry suppres-

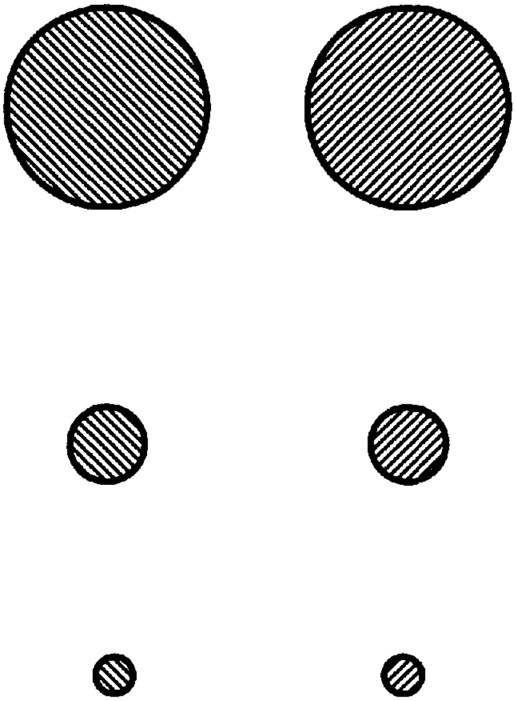

Figure 3. Three pairs of rival targets that demonstrate that the incidence of complete monocular suppression depends on target size. (In the upper pair of large targets, note how infrequently one entire target dominates the other; compare this with the frequency of complete dominance experienced with the other pairs of targets.)

sion has been commented on frequently in the literature (e.g., Meenes, 1930).

What is the evidence indicating that the spatial extent of suppression is based on retinal image size? When rival targets subtending a small angular subtense are viewed as after images against a distant surface, rivalry tends to be unitary even though the targets appear quite large by virtue of Emmert's law (Blake, Fox, & Westendorf, 1974). By the same token, after-image targets large in angular subtense that appear small (because they are viewed against a very close surface) still engage in piecemeal rivalry only. In other words, when apparent size and retinal size are pitted against one another, it is retinal size that determines the extent to which suppression is piecemeal.

Zones of Suppression

In recognition of the fact that suppression is local, the theory hypothesizes the existence of regional zones of suppression. These zones may be defined as portions of the cortical representation of the two retinae within which monocular features compete for dominance. Incidentally, there is some evidence that the sizes of these zones are smallest in the fovea and increase with retinal eccentricity (Blake, O'Shea, & Halpern, 1988).

It is tempting to equate a suppression zone with the aggregate receptive field sizes of neurons composing a hypercolumn in visual cortex (Frisby, 1980; Hubel, Wiesel, & Stryker, 1978; Koenderink & van Doorn, 1987). As defined by Hubel and Wiesel (1962), a hypercolumn consists of a group of cortical cells that together provide a complete representation of orientations for both eyes; a hypercolumn encompasses about 1 mm^2 on the cortical surface, and its boundaries run the full 3–4-mm depth of the cortical layers. Each and every hypercolumn occupies approximately the same area of cortex, but the size of the retinal area (and hence the region of visual space) innervating a given hypercolumn grows dramatically from fovea to periphery, owing to the systematic increase in receptive field size with retinal eccentricity. Each hypercolumn, in other words, examines a patch of retina whose area is determined by the receptive field coverage of the constituent neurons. In effect, each hypercolumn must send to subsequent processing stages a "statement" about the nature of the feature primitives occupying the region of the retina innervating the constituent neurons. During rivalry, the hypercolumn receives from the two eyes conflicting input concerning those feature primitives, causing the local neural network within that hypercolumn to lapse into an unstable state in which the hypercolumn's output varies over time. Because foveally innervated cortical neurons have much smaller receptive fields, the hypercolumn is processing information within a much more restricted region of visual space; consequently, the zones of suppression associated with the fovea are correspondingly small.

Note that this concept of local zones of suppression does not preclude interactions among neighboring suppression zones (e.g., among neighboring hypercolumns), interactions that could serve to synchronize outputs signaled by a given eye. During the course of observing rivalry, there are certainly times when one experiences transitions from dominance to suppression that have a wavelike quality, such that suppression seems to sweep across and engulf one eye's target. This qualitative aspect of rivalry could be interpreted as evidence for cooperative interactions among neighboring rivalry zones. Now, the notion of spatial cooperativity is not novel—it appears in Julesz's (1971) dipole model of stereopsis, in Williams, Phillips, and Sekuler's (1986) model of the perception of motion direction and in Grossberg and Mingolla's (1985) theory of form perception. Before incorporating spatial cooperativity into the current model, however, it is necessary to demonstrate definitively that rivalry exhibits behaviors diagnostic of a cooperative network. At this time, the notion of spatial cooperativity among suppression zones is speculative.

Proposition 3: Cortical Neurons Vary in Their Ocular Dominance

Background

The theory assumes that the cortical neurons composing a hypercolumn (see Proposition 2) differ in the extent to which they receive excitatory input from the two eyes. For purposes of exposition, the theory posits three classes of neurons: those receiving excitatory input from the left eye only, those receiving excitatory input from the right eye only, and those receiving excitatory input from both eyes. The first two classes of neurons will be termed *monocular* and the third class, *binocular.* The assumption of just three ocular dominance groups undoubtably oversimplifies the true state of affairs; physiological evidence reveals more of a continuum defining the extent to which one eye or the other excites a cortical cell (e.g., Hubel & Wiesel, 1962). But, as will be argued in the next section, the crucial aspect of the present theory is the existence of monocular neurons; the essence of the theory would not be changed by breaking the binocular group into further categories based on more finely graded degrees of binocularity.

The rest of this section is devoted to a summary of some of the psychophysical evidence for the existence of binocular and monocular neurons in human vision.

Binocular neurons. The phenomenon most frequently cited as evidence for binocular neurons is interocular transfer of visual aftereffects. It is well established that most of the classic aftereffects, including the tilt aftereffect (Gibson, 1933), the motion aftereffect (Wohlgemuth, 1911), the threshold elevation aftereffect (Blakemore & Campbell, 1969), and the spatial frequency shift aftereffect (Blakemore & Sutton, 1969), can be induced in one eye and subsequently observed in the other eye. Moreover, it has been shown that some of these aftereffects transfer interocularly even when the adapted eye is pressure blinded following adaptation, a result that definitively places the site of adaptation at a postretinal stage of the visual pathways (e.g., Blake & Fox, 1972). Besides being used to distinguish retinal from central sites of adaptation, interocular transfer has now become a popular psychophysical tool for investigating reduced binocularity in people with histories of eye misalignment and other visual disorders (Lema & Blake, 1977; Mitchell & Ware, 1974; Selby & Woodhouse, 1981).

Although interocular transfer unequivocally demonstrates binocular neural interaction, it cannot be concluded with certainty that this interaction is excitatory in nature. Dealy and Tolhurst (1974) have argued that at least some aftereffects are the consequence of prolonged inhibition generated during adaptation, and not the result of neural fatigue from prolonged excitation. Neurophysiological studies, although clearly demonstrating that prolonged stimulation reduces responsiveness, have not been performed to distinguish these two alternative theories of adaptation (Vautin & Berkley, 1977; Maffei, Fiorentini, & Bisti, 1973). So on its own, interocular transfer is not conclusive proof for excitatory binocular interaction of the sort posited by the present theory. Interocular transfer could be the aftereffect of prolonged inhibition of one eye by the other, an idea that has been advanced recently by Cogan (1987).

Besides visual aftereffects of adaptation, there are other visual phenomena that exhibit interocular effects and, hence, can be construed as evidence for the existence of binocular neurons. Most notable of these is dichoptic masking, in which a pattern flashed to one eye impairs the visibility of a similar pattern briefly presented to the other eye (e.g., Legge, 1979). Again, however, this psychophysical result is equivocal with respect to the nature—excitatory versus inhibitory—of the underlying binocular interactions.

Another visual phenomenon that points to the existence of binocular neurons is binocular summation, the superiority of binocular over monocular performance on a host of visual tasks. As mentioned earlier, this binocular superiority exceeds that expected on the basis of probability summation (i.e., the performance expected from two independent detectors). Consequently, it is generally agreed that binocular summation reflects the operation of genuine neural summation between the two eyes, a conclusion tantamount to positing the existence of binocular neurons. In the case of binocular summation, it seems entirely reasonable to assume that the underlying binocular neural interaction is excitatory, not inhibitory.

This overview of phenomena that exhibit binocular effects underscores that binocular interactions can be either excitatory or inhibitory. Now, the ocular dominance scheme originated by Hubel and Wiesel (1962) focused entirely on excitatory input to cortical cells, with their seven categories defined solely in terms of the extent to which a given eye could activate a cortical cell. Other neurophysiologists (e.g., Ferster, 1981; Henry, Bishop, & Coombs, 1969) later emphasized that some cortical cells receiving excitatory input from only one eye (i.e., a monocular neuron in Hubel and Wiesel's scheme) nonetheless received inhibitory input from the other eye. Strictly speaking, then, these monocular cortical neurons *are* binocular, in that their activity levels can be influenced by stimulation of either eye. As will be seen in a subsequent section, these inhibitory interactions among monocular cortical neurons play a key role in the present theory of binocular rivalry.

For sake of completeness, note that binocular interactions may also arise in a feedback loop in which cells receiving excitatory input from both eyes (i.e., conventional binocular cells) innervate cells receiving direct input from only one eye. To give a specific example, it is widely recognized that cells of the lateral geniculate nucleus (which receive monocular excitatory input) receive heavy feedback from cells in layer VI of visual cortex (some of which are binocularly excited). This means, therefore, that "monocular" cells in the lateral geniculate nucleus receive binocular input via feedback pathways projecting down from the cortex. In fact, Singer (1977) has proposed that this corticogeniculate feedback loop plays an important role in the transmission of neural signals arising from corresponding areas of the two retinae. In the present theory, however, interocular inhibition via corticogeniculate feedback does not play a crucial role in mediating binocular rivalry. Corticogeniculate inhibition is discounted because of psychophysical evidence (Wade & Wenderoth, 1978) indicating that orientation specific adaptation occurs even during suppression phases of binocular rivalry, implying that the site of suppression cannot be prior to the neural stage at which orientation selectivity emerges. It is generally recognized that orientation selectivity first arises within the visual cortex, not at the level of the lateral geniculate nucleus.

As a final comment in this discussion of binocular interaction, a word should be said about the possible existence of another category of binocular neurons, those activated only by simultaneous stimulation of both eyes. Because such cells would behave like logical AND gates, this putative category of cells has been termed *binocular AND cells* (Wolfe & Blake, 1985). There is disagreement concerning the importance of such cells in human binocular vision (Blake & O'Shea, 1988; Wolfe, 1986). In any case, binocular AND cells play no role in the theory developed here, and their existence, if proven, would not change the details of the theory because by definition, binocular AND cells would not be engaged during conditions that instigate binocular rivalry.

Now we are ready to consider the other class of neurons posited by the theory, monocular neurons.

Monocular neurons. Before considering phenomena that point to the existence of monocular neurons in human vision, the definition of this class of neurons needs to be clarified. The existence of monocular neurons in the human visual system is unarguable—retinal neurons, for instance, are most certainly monocular. The concept of monocular neurons used here refers to cortical cells receiving excitatory input from one eye (and possibly inhibitory input from the other), existing within an ensemble of cells that also includes neurons receiving excitatory binocular input. The critical notion, then, is an ensemble of neurons at a common site in the nervous system, some that receive binocular input and others that receive monocular input. To the extent that certain visual phenomena depend crucially on activity within this pool of neurons, it should be possible to distinguish monocular and binocular contributions to those visual phenomena.

The evidence most frequently cited for the existence of monocular neurons comes from measures of the interocular transfer of visual adaptation. Almost invariably, transferred aftereffects are weaker than the same aftereffects measured in the adapted eye (monocular adaptation followed by monocular testing of that same eye is referred to as *direct adaptation*). To illustrate, adaptation of, say, the left eye to motion may yield a motion aftereffect that lasts 15 s when the adapted left eye views the test stimulus, but lasts only 10 s when the unadapted right eye views the stimulus. The stronger aftereffect measured under the direct condition is typically attributed to the involvement of adapted monocular neurons that are not engaged during interocular testing. In other words, direct testing (i.e., testing the adapted eye) engages both binocular and monocular neurons, all of which were also stimulated during the adaptation episode. Interocular testing, in comparison, engages binocular neurons that were stimulated during adaptation and monocular neurons that were not stimulated during adaptation. Hence, at the time of postadaptation testing, all neurons engaged by direct testing are adapted, whereas neurons engaged during interocular testing include some that are adapted and and others that are unadapted. The involvement of unadapted neurons presumably dilutes the strength of the transferred aftereffect. This line of reasoning is analyzed in detail elsewhere (Blake, Overton, & Lema-Stern, 1981; Moulden, 1980).

A second, related piece of evidence for monocular neurons comes from an ingenious experiment by Anstis and Moulden (1970). They adapted the right eye to rotational motion in a clockwise (CW) direction and the left eye to motion in a counterclockwise (CCW) direction. A stationary test display subsequently appeared to rotate CW when viewed with the left eye but appeared to rotate CCW when viewed with the right eye; binocular viewing of the test display yielded no motion aftereffect. This pattern of results can be explained by assuming the existence of monocular and binocular neurons within the pool of neurons responsible for this motion aftereffect. According to this scheme, the effects of adaptation are canceled within neurons receiving input from both eyes because those neurons would receive equal but opposite stimulation during adaptation. Monocular neurons, however, would see only the direction of motion signaled by the eye providing input to those neurons, resulting in an aftereffect defined by the direction of rotation experienced by that eye. Similar conclusions were reached by Lehmkuhle and Fox (1975a) using somewhat different procedures.

Besides visual aftereffects, there is another phenomenon that can be interpreted as evidence for the existence of monocular neurons. Blake and Cormack (1979a) have shown that observers can reliably discriminate which eye has received brief monocular stimulation under certain conditions, and they argue that this ability must entail reliance on a neural signal that is labeled as to eye of origin. That people with reduced binocular vision can perform this task with even greater ease than observers with good binocular vision (Blake & Cormack, 1979b) supports this interpretation, although others (Loshin, Klein, & Levi, 1983) have presented alternative explanations for that particular finding.

It will be argued in the next section that the phenomenon of binocular rivalry itself argues for the existence of monocular neurons.

Proposition 4: Monocularly Innervated Cortical Neurons Instigate Binocular Rivalry

Proposition 4 arises from logical considerations that are most easily developed within the context of a specific example. For simplicity's sake, imagine a hypercolumn containing some neurons selective for horizontally oriented contours and other neurons selective for vertically oriented contours. Furthermore, suppose that within the group responsive to horizontal and within the group responsive to vertical there exist neurons from the three ocular dominance classes described in the previous section. These various types of neurons are depicted schematically in Figure 4.

Now consider the patterns of activity produced within this population of neurons to different stimulus conditions. Suppose just the right eye views a set of vertical contours, with the left eye unstimulated. In this case, the binocular neurons tuned to vertical and the monocular, right-eye neurons tuned to vertical will respond. Perceptually, an observer experiences a stable vertical pattern. Suppose instead that just the left eye views a set of horizontal contours. Now the binocular neurons tuned to horizontal will respond as will the monocular, left-eye neurons tuned to horizontal. An observer perceives a stable set of horizontal contours. Needless to demonstrate, complementary predictions follow from the situation in which only the right eye views horizontal or only the left eye views vertical.

Next, consider a more complicated monocular stimulus, one composed of vertical contours superimposed on horizontal contours; this pattern will be termed a *gingham*. If the gingham is viewed by the left eye only, binocular neurons tuned to horizontal and binocular neurons tuned to vertical should be activated, as their preferred stimuli are present in the pattern. (Whether the binocular responses to the composite are equivalent to responses to the single components is an interesting question that I shall return to in a moment.) Monocular, left-eye neurons tuned to vertical will be activated, as will monocular, left-eye neurons tuned to horizontal. The same line of reasoning, of course, can be worked out for the gingham viewed by the right eye. And in either case, an observer experiences a relatively stable percept of the gingham; vertical and horizontal are visible simultaneously, with perhaps some fluctuations in

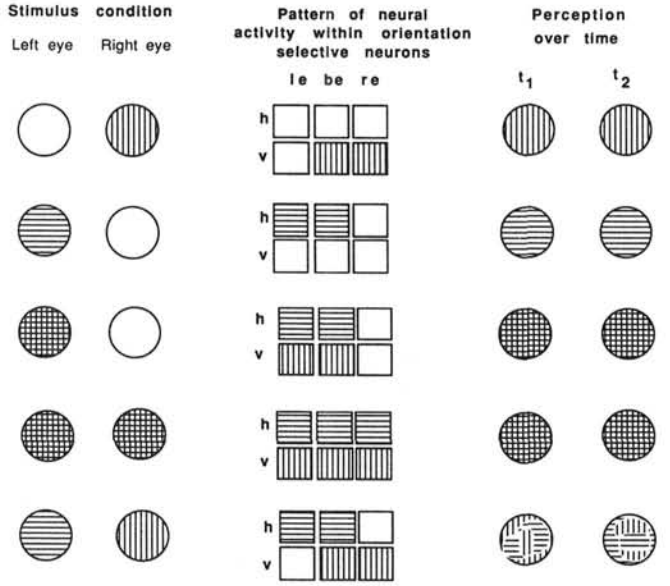

Figure 4. Patterns of neural activity and perceptual outcomes associated with different combinations of left-eye and right-eye stimulation. (The left-hand column shows various pairs of targets viewed by the left eye and by the right eye; the middle set of boxes represent pools of orientation-selective neurons. Boxes in the rows labeled *h* are meant to represent neurons selective for horizontal; boxes in the rows labeled *v* represent neurons selective for vertical. The three columns of neurons represent pools of neurons innervated by the left eye only (LE), by both eyes (be) and by the right eye only (re). The right-hand column depicts the perceptual outcome at two moments in time (t_1 and t_2) associated with dichoptic viewing of the targets pictured in the corresponding part of the left-hand column.)

apparent contrast of the two orientations (Campbell & Howell, 1972).

Now suppose the gingham pattern is viewed by both eyes. In this case, binocular neurons tuned to vertical and binocular neurons tuned to horizontal will be activated. Also activated will be monocular, left-eye and monocular, right-eye neurons tuned to horizontal and monocular, left-eye and monocular, right-eye neurons tuned to vertical. All neurons in the ensemble, in other words, will be activated. Under this condition of dioptic stimulation, an observer perceives a stable gingham pattern.

Finally, consider what happens when the right eye views vertical and the left eye views horizontal. From the viewpoint of the binocular neurons, this condition is no different than the ones described earlier for monocular stimulation: Binocular neurons tuned to horizontal should be activated, in response to their preferred stimulus, and binocular neurons tuned to vertical should also be activated by their preferred stimulus. (At this point, one might question whether these binocular responses would be equivalent to activity produced under monocular stimulation, but evidence supporting this contention is presented later.) Looking at the monocular neurons within the pool, monocular, left-eye neurons tuned to horizontal will respond and monocular, right-eye neurons tuned to vertical will respond. Yet we know that this stimulus condition produces an unstable, fluctuating percept consisting of portions of one eye's view and portions of the other eye's view. Obviously, then, the pattern of activity among neurons within the hypercolumn ensemble must be different and more unstable compared with any of the patterns of activity produced by the other stimulus conditions.

It is particularly instructive to compare the pattern of activity produced by the binocularly viewed gingham with the pattern of activity produced by the rivalry condition. Note that the state of the binocular neurons is comparable in the two situations. Of course, dioptic stimulation with the gingham might produce greater activity within the binocular neurons, because of neural summation between the two eyes. However, these kinds of differences in level of activity within the binocular neurons could, in principle, be canceled by changing the contrast of the vertical or horizontal contours, or both. It should be possible, in other words, to produce a gingham that elicits a pattern of activity among the binocular neurons that is, *upon initial viewing,* indistinguishable from the pattern of activity produced by the rival targets. I stress *upon initial viewing,* for it may be that the pattern of activity within the binocular neurons eventually becomes influenced by the pattern of activity within the monocular neurons. Also, with extended viewing, eye movements could differentially affect the pattern of activity produced by the rival targets versus the binocularly viewed gingham. Initially, though, it is only the pattern of activity within the monocular-left and monocular-right neurons that unequivocally distinguishes the stimulus conditions for rivalry and fusion. In effect, the monocular-left neurons and the monocular-right neurons are in agreement that both vertical and horizontal are present when both eyes view the gingham pattern. These two pools of monocular neurons are in disagreement, however, when the two eyes view rival patterns. The ensemble of monocular-left neurons signals the presence of horizontal contours (not vertical) at a given region of visual space, whereas the ensemble of monocular-right neurons signals the presence of vertical (not horizontal) at that same region of visual space. This state of affairs thus violates the existence principle stating that one and only one object can exist at the same time and same place in visual space. Note that it is the *absence* of activity within subsets of the monocular neurons (i.e., the monocular-left verticals and the monocular-right horizontals) that instigates the conflict between the ensemble of monocular-left neurons and the ensemble of monocular-right neurons.

So, according to the theory, it is conflicting patterns of activity within the ensemble of orientation selective monocular neurons that signal the presence of incompatible monocular stimulation (i.e., stimulus conditions that cause binocular rivalry). Once the conditions for rivalry have been realized, so to speak, by the monocular neurons, the entire hypercolumn ensemble lapses into an unstable state that underlies the fluctuations in monocular dominance and suppression. Incidentally, there is evidence that it takes some time for the hypercolumn network to register the presence of rival stimulation: Investigators have noted that rival targets briefly flashed for only a few hundred milliseconds are seen superimposed, with no hint of dominance of one target over the other (Anderson, Bechtoldt, & Dunlap, 1978; Goldstein, 1970; O'Shea & Crassini, 1984; Wolfe, 1983);

only when rival targets are presented for 400 ms or longer does one target dominate the other.

This proposition asserts that the activity within binocular neurons in response to a monocularly viewed gingham is indistinguishable from the activity in those neurons in response to vertical contours viewed by one eye and horizontal contours viewed by the other eye. There is physiological evidence to support this assertion. Recording from binocular cells in cat visual cortex, Ferster (1981) found that the activity level produced by monocular stimulation with a cell's preferred orientation was unaffected when the other eye simultaneously received an orientation orthogonal to the preferred orientation (i.e., stimulus conditions that yield robust rivalry). Blakemore, Fiorentini, and Maffei (1972) found essentially the same result. In other words, both studies found that the responses of cortical cells to dichoptic stimulation (i.e., orthogonal orientations to the two eyes) was more or less equivalent to that produced by monocular stimulation with the cells' preferred orientations. These physiological findings support the idea that binocular neurons cannot unambiguously signal the stimulus conditions yielding binocular rivalry.

A Possible Neural Circuit for Registering Dissimilar Monocular Input

So far I have argued that monocular neurons are critically involved in the instigation of binocular rivalry. This raises an important question: What kind of neural circuitry might enable monocular-left-eye and monocular-right-eye neurons to register that the two eyes are receiving discrepant monocular inputs (e.g., vertical to one eye and horizontal to the other)? Borrowing an idea from digital logic circuitry, monocular incompatibility could be signaled by a neural network that functions like an exclusive OR gate (XOR). An XOR gate is a device whose output is low (i.e., not "on") whenever all inputs to the gate are on or whenever all inputs are "off"; the output of the gate is high whenever different inputs to the gate are in different states (i.e., some are on and others are off). How might such a gate be realized in the visual nervous system?

One possible circuit for achieving XOR behavior is diagrammed in Figure 5. The two presynaptic units are monocular neurons (one innervated by the right eye and the other innervated by the left eye) whose preferred orientation is the same (vertical for this particular local circuit). Each monocular neuron makes excitatory synaptic connection with an inhibitory interneuron. Furthermore, each monocular neuron makes a nonrecurrent reciprocal inhibitory connection onto the interneuron activated by the other eye. Now, the strengths of the inhibitory and excitatory synapses can be adjusted such that the pair of nonrecurrent inhibitory signals produced by binocular vertical stimulation cancels the excitatory input from each monocular neuron onto its associated interneuron. Stimulation of just one eye with vertical, however, will activate the interneuron innervated by the stimulated eye. For instance, stimulation of the left eye by vertical would inhibit the right-eye vertical cell and would excite the interneuron innervated by the left-eye vertical cell. The circuit thus exhibits XOR behavior because output from one of the two interneurons is generated only when one eye or the other, but not both, receives stimulation.

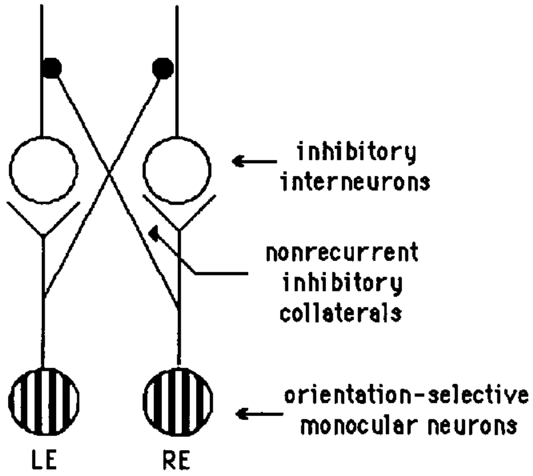

Figure 5. A simple neural circuit that can exhibit XOR behavior. (The direct connection from monocular cell to interneuron, shown by the "v," is excitatory, whereas the connection from monocular cell to contralateral interneuron, shown by the "●," is inhibitory.)

The circuit uses nonrecurrent (i.e., feed-forward) inhibition, not recurrent inhibition, to preclude disinhibition (i.e., the decreased capacity of Neuron LE to inhibit Neuron RE when Neuron LE itself receives inhibition). Recurrent inhibition would create a feedback loop that could transiently disrupt the XOR-like gating property of the circuit. The theory does not specify particulars of the putative inhibitory signals (e.g., their equilibrium potential), nor is the microstructure of the synaptic contacts detailed; psychophysical data (the grist for this theory) shed no light on these matters.[1]

In Figure 6, several of these XOR circuits are replicated for different preferred orientations. The axons of the interneurons form inhibitory synapses onto orientation selective cells innervated by the contralateral eye; in the diagram these connections are shown for just the interneurons associated with the vertical XOR circuit, but in fact *all* interneurons synapse on orientation selective monocular neurons. According to the theory, these inhibitory connections provide the substrate for suppression of one eye's image. This contralateral inhibition is spread over all orientations for reasons to be discussed in the following section.

Note incidentally that a given XOR circuit is activated by dissimilar stimulation of the two eyes, regardless of whether that involves rival stimulation or exclusive monocular stimulation (i.e., when one eye alone views a pattern). Activation of an inhibitory interneuron under nonrival, monocular stimulation represents a useful by-product of the model because there is evidence indicating that under conditions of monocular stimu-

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[1] Suggestive ideas for future, more detailed modeling of underlying synaptic architecture of the XOR gate may come from the theoretical work of Koch and Poggio (1985). To account for direction selectivity in cortical cells, they have designed a *veto circuit* involving nonlinear interactions between excitation and shunting inhibition. Their model was based on information about the branching structure of neurons that is simply not available for the putative circuits envisioned in Figures 5 and 6.

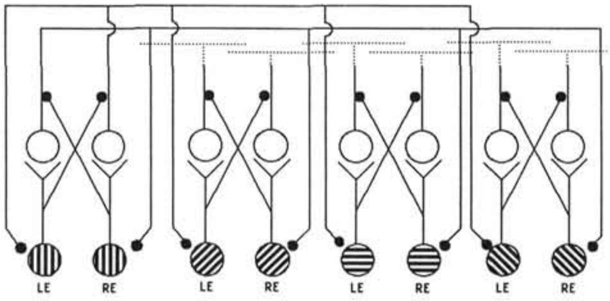

Figure 6. An array of XOR circuits with projections from inhibitory interneurons spreading to all orientation-selective neurons activated by the eye contralateral to the one innervating a given interneuron. (Shown are interneuron projections for just one pair of monocular cells, those selective for vertical. In the model, inhibitory interneurons from each XOR circuit project to monocular neurons in all other XOR circuits.)

lation, the nonstimulated eye is inhibited by the stimulated eye (e.g., see Blake & Camisa, 1978). This possibility needs to be examined in more detail, however, as there is some circumstantial evidence to the contrary (D. H. Westendorf, personal communication, August 1988).

It is instructive to reconsider the response of this XOR network under conditions of gingham stimulation. What happens when, say, the left eye views a gingham and the right eye views only vertical contours? Under this condition, the XOR network devoted to left- and right-eye vertical would be inactive, thus signaling the condition for fusion; the other XOR network connecting left- and right-eye horizontal, however, would be active, signaling the condition for rivalry. In a sense, the situation is comparable to strict monocular stimulation with horizontal, yet there is no evidence for rivalry under this gingham–vertical condition (Blake & Boothroyd, 1985). It remains to be seen how this putative network allows fusion to take precedence over rivalry. It could be that rivalry and fusion would be experienced simultaneously if both eyes contained both matching and nonmatching features (e.g., vertical to both eyes, diagonal CW to one eye, and diagonal CCW to the other). Grossberg (1987) has discussed how fusion and rivalry can coexist at different spatial scales, and it is conceivable that a comparable sort of coexistence occurs in the case of orientation.

It is natural to assume that the XOR network is composed of intrinsic connections within the cortex. This aspect of the theory seems plausible, for there is good evidence that the cortex contains a rich network of inhibitory interneurons (e.g., Benevento, Creutzfeldt, & Kuhnt, 1972). Moreover, it is noteworthy that intracortical inhibition is strongest between cells separated by somewhere between 200 and 400 μm (e.g., Legendy, 1985), a distance sufficient to span one complete set of ocular dominance columns in primate visual cortex (Hubel, Wiesel, & LeVay, 1975). (An ocular dominance column is a stacklike grouping of cortical cells, all of which are comparably dominated by one eye or the other.) It remains to be determined, however, whether those interneurons connect monocular neurons in the orientation-specific manner required by the theory. Similar ideas concerning intracortical inhibition and rivalry have been advanced by Sloane (1985).

The monocular neurons diagrammed in Figures 5 and 6 presumably also make excitatory connections with other neural elements besides the inhibitory neurons. Those other elements would form part of the output pathways from the hypercolumn to further processing stages. It is also worth noting that a network exhibiting XOR-like behavior, besides registering the conditions for rivalry, could serve the useful function of signaling the oculomotor system to change the vergence angle of the eyes, in the interests of establishing feature matches on corresponding retinal areas.

As a final comment on this part of the theory, I must acknowledge that individual neurons are not simple logic gates that behave in an all-or-none fashion. Rather, they are information-processing devices whose underlying biophysical properties give rise to graded (i.e., analog) voltage changes. Even at the level of action potentials (which can be construed as all-or-none events), a neuron's firing rate varies over a significant range, thereby conveying more information than does a simple logic gate. As I have tried to stress, employment of the concepts of OR, AND, and XOR "neurons" and "interneurons" is meant to approximate network properties exhibited by aggregates of neurons. This digital characterization of neural networks composed of analog elements is not novel; for instance, Adelson and Movshon (1982) hypothesized the existence of logic AND detectors to resolve ambiguous motion. The present theory posits neural interactions whose logiclike behavior detects the absence of correspondence between stimuli viewed by the two eyes.

Proposition 5: Rivalry Suppression Entails Inhibition of Activity Within All Monocular Neurons Innervated by a Given Retinal Area of One Eye

Proposition 4 described the crucial role played by monocular neurons in the initial registration of incompatible monocular stimulation. Once that state of affairs has been registered, how is suppression of one eye's input effected within the hypercolumn network?

The theory posits the existence of reciprocal inhibitory connections between monocular-left-eye and monocular-right-eye neurons. The exact neuroanatomical basis of these inhibitory connections is not critical for the theory, although the circuitry diagrammed in Figure 5 is not structurally unreasonable. What is critical is that these inhibitory connections, when activated, operate nonselectively on the entire group of monocular neurons innervated by a given eye, not just on a subset of those monocular neurons tuned to a particular feature. This nonselectivity property is included to account for the psychophysical finding that suppression operates on all information presented to a suppressed eye, not just on those features composing the originally suppressed target (Blake & Fox, 1974b; Blake, Westendorf, & Overton, 1980; Fox & Check, 1968; O'Shea & Crassini, 1981a; Zimba & Blake, 1983). This issue of nonselectivity is sufficiently important to warrant further comment. After that, I will present evidence indicating that nonselective inhibition is confined primarily to monocular neurons.

Nonselectivity of Suppression

The concept of nonselective suppression was originated by Fox and colleagues (Fox & Check, 1966, 1968; Wales & Fox,

1970) to account for results from test probe experiments. In those studies, observers tracked the fluctuations of dominance and suppression between rival targets. In addition, observers were required to detect probe targets presented to an eye during periods of dominance and during periods of suppression. It was consistently found that probes were more difficult to detect when presented to a suppressed eye, with thresholds elevated anywhere from 0.3 to 0.5 log-units, relative to thresholds measured during dominance. It was also consistently found that thresholds for probes presented during dominance phases of rivalry were equivalent to those measured under nonrivalry conditions.

In nearly all of Fox's studies, the probe target was radically different in form from the rival target on which it was superimposed. In effect, then, suppression both rendered the rival target invisible and made an entirely different stimulus—the test probe—also harder to see. The effect of suppression, in other words, was not confined to the initially suppressed target, which led Fox to develop the concept of *nonselective suppression.* This nonselectivity was most dramatically demonstrated in a study that showed that large changes in the spatial frequency or the orientation of a suppressed target went undetected for long periods of time, whereas these same changes were readily detected during dominance (Blake & Fox, 1974b).

It is important to realize that nonselectivity, at least as that term is used by Fox and by myself, is not meant to imply that an eye is literally blind to all new information presented to the suppressed region of that eye. It is quite simple to ensure that a probe target is reliably and quickly detected when presented to a suppressed eye: Make the probe high in contrast and/or intensity and/or present the probe with an abrupt temporal onset. In brief, any strong, transient stimulus seems able to overcome suppression. Indeed, abruptly raising the contrast of a suppressed stimulus itself will terminate suppression (Blake & Fox, 1974b; Mueller & Blake, 1988), although this abrupt increase in the contrast of a suppressed target takes a few hundred milliseconds longer to detect than when the increase occurs while the target is dominant.

So, according to the present conceptualization, evidence for selective suppression would consist of showing that suppression has no influence whatsoever on detection or recognition thresholds for new information presented to a suppressed eye—performance during suppression would be equivalent to performance during dominance. To my knowledge, the only article describing such an absence of influence is one by Smith, Levi, Harwerth, and White (1982), in which it is reported that the intensity threshold for detection of short wave-length test probe is the same during dominance and during suppression. Detection thresholds for medium and long wave-length probes, in contrast, were elevated during suppression. Using a complicated argument based on chromatic adaptation, Smith et al. (1982) concluded that suppression is selective within the opponent-process chromatic channel, but not in the luminance channel. This conclusion certainly deserves further testing.

In any event, it is clear that the detectability of all sorts of probe targets is impaired during suppression, so the theory is forced to posit that the inhibition underlying suppression operates on all monocular neurons innervated by a given eye, not just those activated by features composing the presently suppressed target.

The Fate of Binocular Activity During Suppression

Why does the theory posit that inhibition operates on monocular neurons, not binocular neurons? What, in other words, is the evidence that the responsiveness of binocular neurons is not dramatically altered during suppression phases of rivalry? For one thing, we know it is possible to obtain interocularly transferred aftereffects even under conditions in which the monocularly viewed adapting pattern is suppressed for a substantial portion of the adaptation period (threshold elevation aftereffect: Blake & Overton, 1979; motion aftereffect: O'Shea & Crassini, 1981b). Moreover, these transferred aftereffects produced by a suppressed adaptation pattern are just as strong as the transferred aftereffects produced under nonrivalry conditions. This indicates that binocular neurons mediating these aftereffects continue to respond during suppression, in a manner comparable with their responsiveness during monocular adaptation under nonrivalry conditions. Now, one could argue that the binocular neurons involved in interocular transfer reside at a locus prior to the site of suppression or in a pathway parallel to that in which suppression occurs. So, the failure of suppression to weaken interocular adaptation, although suggestive, leaves open the possibility that suppression affects activity in only certain classes of binocular neurons. In this regard, recall that binocular interaction (and perhaps interocular transfer) could arise from prolonged interocular inhibition (e.g., Cogan, 1987) or from corticogeniculate feedback (e.g., Singer, 1977).

It is also known that binocular summation is obtained even when one of the two monocular probe targets is presented to a suppressed eye (Westendorf et al., 1982). In this case, summation is reduced somewhat, but according to the present theory this reduction is attributable to the inhibition of activity within the ensemble of monocular neurons. This point is developed in a subsequent section. Finally, there is evidence indicating that stereopsis can be experienced even during binocular rivalry, implying that the binocular machinery responsible for disparity processing remains active during rivalry (Blake et al., 1980; Julesz & Miller, 1975). Whether the operating efficiency of that binocular machinery is reduced during suppression remains debatable (e.g., Amira, 1988).

In general, the evidence that suppression spares activity in binocular neurons is somewhat circumstantial. This is an aspect of the theory that deserves testing.

While discussing Proposition 5, I want to explore an interesting distinction concerning the physical absence of a stimulus versus the phenomenal absence of that stimulus. This distinction has important bearing on the inhibitory events underlying suppression.

Suppression Versus Absence of a Stimulus

Let us reconsider a couple of the stimulus conditions depicted in Figure 4, paying particular attention to the similarities in perceptual state and the differences in underlying patterns of neural activity.

Think back to the situation in which the left eye views a set of horizontal contours and the right eye views a blank field. Here, neither eye views vertical so it stands to reason that neurons tuned to vertical will not be activated, and it is certainly no surprise that an observer sees horizontal but not vertical. But next, think about the situation in which the left eye views horizontal and the right eye views vertical, the rivalry condition. Moreover, assume that horizontal is temporarily dominant and vertical is suppressed entirely. Now from the observer's viewpoint, this situation is essentially identical—albeit temporarily—to the one in which just the right eye receives horizontal. In other words, when horizontal is exclusively dominant in rivalry, the invisibility of vertical is just as compelling as when vertical is physically absent. Indeed, the profound quality of rivalry is this complete invisibility of a complex, suprathreshold stimulus for several seconds at a time.

Are we to conclude from the perceptual equivalence of stimulus absent and stimulus suppressed that these two perceptual states are occasioned by equivalent neural states? According to the theory, the underlying patterns of neural activity are quite different, as can be seen by inspection of Figure 4. Invisibility during suppression phases of rivalry is not accomplished by lowering the level of activity within all neurons innervated by the suppressed eye to a level comparable to that associated with the absence stimulation of that eye. It is only activity within the monocular neurons innervated by the suppressed eye that is lowered. And even here, it is doubtful that activity within those neurons is depressed to the background level associated with total absence of stimulation. This doubt is based, in large part, on the rather modest losses in visual sensitivity that accompany periods of suppression, losses that are typically no greater than a fraction of a log-unit. The visual system, in other words, manages to render an otherwise salient monocular stimulus completely invisible by generating an inhibitory signal that operates nonselectively on all inputs to the suppressed eye and yet only modestly impairs visual sensitivity. Indeed, this is one of the paradoxes of binocular rivalry.

To end this section on a speculative note, perhaps the paradox is resolvable by assuming that dominance of an eye during rivalry is achieved by temporarily tipping the balance of activity within the hypercolumn in favor of those stimulus features signaled by the eye whose monocular neurons are currently active. On this hypothesis, the left-eye and right-eye monocular neurons operate like weights on opposing ends of a seesaw. Small differences in those weights (i.e., the activity levels within the ensembles of left-eye and right-eye monocular neurons) can produce large swings in the position of the seesaw.

Proposition 6: Strength of Inhibition Underlying Suppression Is Directly Related to the Size of the Pool of Monocular Neurons Receiving Inhibition, Not to the Characteristics of the Stimulus Activated by the Pool of Neurons Innervated by the Dominant Eye

Background

The strength of inhibition can be estimated psychophysically in one of several ways. One possibility is to measure the amount by which suppression elevates threshold for probe targets presented to the suppressed region of an eye; with this strategy, a large elevation in threshold would be interpreted as evidence for strong inhibition. This was Fox and Check's (1972) line of reasoning in their investigation of the relation between rivalry suppression duration and magnitude of suppression. They found, incidentally, that the elevation in probe threshold was constant throughout a suppression period, suggesting that inhibition does not dissipate over time.

A second, arguably more direct procedure for estimating strength of inhibition is to determine the increase in the strength of the suppressed stimulus necessary to break suppression. Here, it is an increase in the intensity or contrast of the suppressed target itself that serves as the probe; large increases in stimulus strength required to break suppression would indicate strong inhibition. This is the strategy used by Holopigian, Blake, and Greenwald (1988) in their study of the magnitude of suppression in normal observers and in individuals with varying degrees of amblyopia. Those investigators found a significant negative correlation between depth of amblyopia and strength of inhibition, a finding I shall return to shortly.

Strength of Interocular Inhibition

What actually determines the strength of inhibition responsible for suppression? An obvious possibility is the activity level within the neural ensemble generating the inhibitory signal. According to this idea, a strong monocular stimulus would generate potent inhibition, whereas a weak monocular stimulus would generate a correspondingly weak inhibitory signal. Although this is a conventional way to think about inhibition (see, e.g., Cornsweet, 1970, pp. 290–301), there are reasons to doubt its applicability to rivalry. For one thing, Blake and Camisa (1979) found that the impairment in probe detectability during suppression is unrelated to the contrast of the inducing rival targets. For another, Blake (1977) found that a pattern whose contrast was just at the visibility threshold could suppress temporarily a contralateral pattern 1 log-unit higher in contrast; moreover, the average duration of suppression of the high contrast pattern did not vary with changes in the contrast of the rival target seen by the other eye. Both of these findings are difficult to reconcile with the notion of recurrent inhibition.

Assuming that rivalry involves something other than recurrent inhibition, what alternatives come to mind? To borrow an idea from electrical engineering, rivalry inhibition seems to operate like a current-limiting device in which input overload (dissimilar monocular images in the case of rivalry) triggers an open-loop clamp circuit that simply attenuates all activity within a set of monocular neurons. This analogy, of course, leaves unanswered the question of what *does* determine the magnitude of inhibition, if not stimulus strength. The following paragraphs develop the idea that the strength of inhibition is directly related to the size of the pool of monocular neurons receiving inhibitory input.

The point of departure for this aspect of Proposition 6 comes from a consideration of individual differences in the magnitude of suppression. A survey of the rivalry experiments that have measured probe thresholds reveals that the elevation in probe sensitivity during suppression averages about 0.25 log-units. This number summarizes the sensitivity loss during suppression measured in observers with good acuity and normal stereopsis. When probe sensitivity is measured in observers with histories of disordered binocular vision, a rather different pattern of results is obtained. The magnitude of the elevation in threshold during suppression varies greatly among clinical observers and is strongly related to the difference in acuities between the two eyes (Holopigian et al., 1988). In people with deep amblyopia (i.e., large interocular acuity differences), test probe sensitivity of the amblyopic eye is practically equivalent during dominance and during suppression. Suppression, in other words, has essentially no deleterious effect on probe detectability, implying that the amblyopic eye receives a very weak inhibitory effect from the dominating eye. (Unfortunately, it is impossible to estimate the strength of inhibition exerted by the amblyopic eye on the nonamblyopic eye because one cannot measure probe sensitivity of the nonamblyopic eye during suppression—the amblyopic eye hardly ever dominates in rivalry; in fact, to measure probe thresholds in the amblyopic eye while it is dominant requires removing all pattern information from the nonamblyopic eye.)

Contrast this result to that obtained in nonamblyopic clinical suppressors, people with good acuity in both eyes who nonetheless chronically suppress the input to the fovea of one eye (such individuals typically have a history of strabismus). In this class of observers, probe sensitivity during suppression may be depressed as much as 1 log-unit, relative to performance when the same eye is probed during dominance. A suppression effect of such large magnitude implies very strong inhibition from the dominating eye. It is important to note that all of these clinical observers—amblyopic and nonamblyopic—had essentially no foveal stereopsis.

So, to reiterate, people with deep amblyopia evidence very little interocular inhibition, nonamblyopic people with deficient stereopsis give evidence of unusually large interocular inhibition, and nonamblyopic people with good stereopsis show an intermediate level of interocular inhibition. What might account for this range of individual differences? The key to this mystery may be provided by considering plausible differences in the ocular dominance distributions among these groups of observers. (By ocular dominance distributions, I mean the relative numbers of monocular-left-eye neurons, monocular-right-eye neurons, and binocular neurons.) Let's work through this reasoning, one group at a time, starting with the nonclinical observers with good stereopsis and good acuity.

In visual cortex of normal, adult monkeys and cats, the majority of neurons can be activated by either eye (Categories 2–6 in Hubel & Wiesel's, 1962, scheme), and the remaining monocular neurons (Categories 1 and 7) are more or less equally divided between the left eye and the right eye. (There is reason to believe that the actual proportions of binocular and monocular neurons vary with receptive field type—simple vs. complex—as well as with retinal eccentricity—foveal vs. parafoveal cortical representation. These details, however, do not compromise the idea being developed here.) So within a hypercolumn in visual cortex of a human observer with normal vision, let us assume that binocular neurons outnumber monocular neurons and that monocular neurons innervated exclusively by the left eye are no more numerous than monocular neurons innervated exclusively by the right eye. The histogram at the top of Figure 7 summarizes this idea. Keep in mind that this ocular dominance distribution is associated with people who evidence modest interocular inhibition during rivalry suppression.

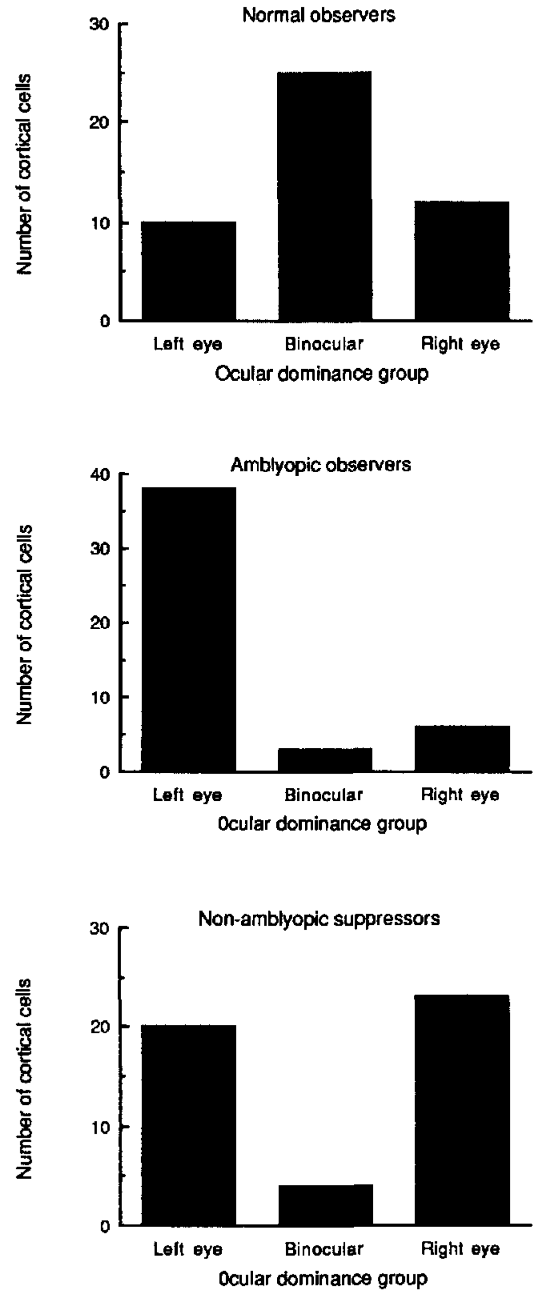

Figure 7. Prototypical ocular dominance histograms. (Hubel & Wiesel's, 1962, Categories 2–6 are combined into the single BE category in these histograms. The top histogram is characteristic of the ocular dominance pattern found in the cortex of a normally reared animal; the middle histogram is typical of that found in animals deprived of vision in one eye early in life; the bottom histogram is typical of that found in animals given visual experience through each eye separately, but without simultaneous bincular vision early in life.)

Next, consider the ocular dominance distribution for amblyopic individuals. From neurophysiological studies in animals, it is well established that amblyopia is associated with two neural abnormalities, a reduction in cortical binocularity and a shift in the proportion of monocular neurons in favor of the nonamblyopic eye (e.g., Chino, Shansky, Jankowski, & Banser, 1983). These two outcomes are summarized by the hypothetical ocular dominance distribution in the middle of Figure 7. Note that this ocular dominance distribution is presumably characteristic of clinical observers who show very weak interocular inhibition.

To complete the picture, look at the ocular dominance distribution illustrated at the bottom of Figure 7. This represents the typical result found in animals reared such that each eye alone receives adequate stimulation, whereas at the same time the two eyes together never receive simultaneous binocular stimulation. This rearing condition leads to a breakdown in binocularity, with the resulting monocular cortical cells more or less evenly divided between left and right eyes. Significantly, animals exhibiting this ocular dominance profile typically have good acuity in both eyes, although they lack stereopsis (e.g., Blake & Hirsch, 1975). This ocular dominance profile, then, may be associated with people who exhibit the greatest degree of interocular inhibition.

Looking at the three hypothetical distributions in Figure 7, note that (a) the strongest interocular inhibition effect is measured in that group of observers with the largest pool of monocular neurons, (b) an intermediate level of inhibition is associated with the group of observers with an intermediate number of monocular neurons, and (c) the smallest interocular inhibition effect is found in observers with the fewest monocular neurons innervated by the suppressed eye. It is this pattern of results that leads to the proposition that strength of inhibition is directly related to the size of the pool of monocular neurons receiving inhibition.

Now, at first glance, this conclusion may seem counterintuitive—should not the strength of inhibition be related to the size of the pool of monocular neurons that *generates* the inhibitory signal, not the size of the neural pool receiving inhibition? Keep in mind, though, that the hypercolumn network, under conditions of rivalry, operates to depress activity within a pool of monocular neurons. So it stands to reason that the inhibitory effort needed to accomplish this operation will be related to the size of that pool. Considered in this way, the explanation advanced earlier makes sense.

This proposition also accounts for the reduction in binocular summation during rivalry (Westendorf et al., 1982). To describe this finding briefly, binocular sensitivity exceeds monocular even when one member of a pair of binocular targets is presented to an eye during suppression. The magnitude of binocular summation during rivalry, however, is less than that measured under nonrivalry conditions. The level of binocular summation measured during rivalry corresponds to that expected from the binocular integration of the normal sensitivity of the dominant eye and the attenuated sensitivity of the suppressed eye. According to the theory, the drop in binocular summation during rivalry is attributable to the reduced participation of monocular neurons on the summation task. Conceived in this way, binocular summation consists of two components, neural summation within binocular cells and probability summation from the contribution of monocular cells. Reducing the level of activity within one pool of monocular neurons will weaken the contribution of probability summation and, therefore, reduce the magnitude of binocular summation. This conceptualization also squares with the observation that binocular performance in stereoblind individuals (who presumably lack binocular neurons) corresponds to the level predicted on the basis of probability summation alone (Blake, Martens, & DiGianfillipo, 1980; Westendorf, Langston, Chambers & Alleegretti, 1978). Stereoblind observers benefit solely from the statistical advantage that accrues from stimulation of independent pools of monocular neurons.

It is recognized that this proposition may be the most controversial aspect of the theory. Hence, efforts to test this proposition will provide a particularly strong evaluation of the theory.

Proposition 7: The Time Needed for the Currently Inhibited Pool of Monocular Neurons to Overcome Inhibition (Thereby Terminating Suppression) Is Directly Related to the Strength of Stimulation Received by the Suppressed Eye

Background

Rivalry is a dynamic phenomenon, meaning that dominance shifts from eye to eye over time. The two previous propositions have focused on putative neural events responsible for suppression of one eye's view. This last proposition addresses the question of how a suppressed eye overcomes the inhibitory influence triggering suppression.

The key to this question comes from studies showing that the duration of suppression is related to the strength of the suppressed stimulus. It has long been known that a strong stimulus will predominate over a weak one (e.g., Breese, 1899). It was Levelt (1965), however, who first formalized this observation by operationally defining stimulus strength in energic terms. Moreover, Levelt made the important observation that the increase in predominance of a strong rival target actually occurs because such a target remains in the suppressed state for a relatively short period of time, compared with a weak rival target. It is the average duration of suppression, in other words, that varies with the strength of a rival target. This observation led Levelt to propose that some small, fixed number of implicit neural events must transpire for a suppressed eye to regain dominance. Levelt reckoned that these events might be generated by microsaccadic eye movements. However, the eye-movement hypothesis was subsequently disproved when it was shown that rivalry between afterimages is comparable in time course to rivalry between ordinary, unstabilized rival targets (Blake, Fox, & McIntyre, 1971). Still, Levelt's idea of implicit neural events overcoming suppression remains viable and constitutes the essence of this proposition (see also Walker & Powell, 1979).

According to the theory, inhibition lowers the level of activity within an entire pool of monocular neurons during suppression. Of course, the suppressed eye still transmits neural signals up to the visual cortex, so the inhibited pool of monocular neurons continues to receive a stream of excitatory input. It is assumed that the effects of this excitation accumulate over time, eventually overcoming the effects of interocular inhibition and thereby triggering a transition to dominance. One can envision this accumulation as involving the buildup of excitatory postsynaptic potentials (EPSPs) that eventually overcome the hyperpolarization caused by inhibition. Sugie (1982) has shown how stochastic fluctuations in excitatory input could account for the random variations in successive suppression durations. For a transition from suppression to dominance to occur, however, we must further assume that the inhibition generated by the pool of monocular neurons innervated by the currently dominant eye wanes over time, perhaps because of fatigue within the inhibitory interneurons (see Grossberg, 1987, for other ideas about the neural dynamics of dominance fluctuations). Without this additional assumption, excitation from the currently suppressed eye might never overcome inhibition from the currently dominant eye.

Note that a strong stimulus generates excitatory input at a faster rate than a weak stimulus, thus explaining the relation between stimulus strength and average suppression duration. Once a sufficient level of excitation has been achieved, the previously inhibited pool of monocular neurons activates their associated interneurons (recall Figure 6), which then inhibit the entire pool of monocular neurons driven by the contralateral eye. This shift in the relative activity levels in the two pools of monocular neurons tips the balance of hypercolumn activity in favor of the stimulus viewed by the previously suppressed eye, producing an alternation in dominance. There is some reason to believe, incidentally, that the rate of buildup of excitation triggering a transition from suppression to dominance may vary with retinal eccentricity (Fahle, 1987).

Besides accounting for the effect of stimulus strength on average suppression duration, this proposition explains several other phenomenon of rivalry. It has been noted, for example, that a briefly flashed probe target that appears superimposed on a suppressed rival stimulus frequently triggers dominance of that stimulus (e.g., Fox & Check, 1968). This makes sense in the context of this proposition because the probe target itself adds excitatory input to the pool of inhibited neurons. It has also been found that when a suppressed rival target is replaced by a different target, the duration of suppression is now determined by the strength of that new target (Blake & Fox, 1974a; Mueller & Blake, 1988). This finding, too, implies that it is the excitatory strength of input from the suppressed eye that determines how quickly that eye regains dominance.

While considering the concept of stimulus strength, one should note that prior adaptation of an eye to its own rival target weakens the predominance of that stimulus in rivalry (Blake & Overton, 1979; Kakizaki, 1950; O'Shea, 1987b). In terms of its effect on rivalry predominance, in other words, prolonged exposure to a pattern is comparable with reducing the actual stimulus strength of that pattern. This finding implies that the neural events underlying adaptation precede the locus of suppression. Note, though, that this concept of locus need not imply different nuclei or distinct cortical areas. It is conceivable that the neural events underlying adaptation and the neural events underlying suppression both occur within the hypercolumn module, with adaptation being presynaptic to suppression (e.g., see Wade & deWeert, 1986).

Comparison With Other Theories

In this section the present theory is compared with several other recent models that make explicit theoretical statements about binocular rivalry. Two of these theories—Wolfe (1986) and Lehky (1988)—focus specifically on rivalry, whereas a third—Grossberg (1987)—is a more general theory of form, color, and brightness vision that includes rivalry within its scope.

Wolfe's Model

Wolfe's (1986) theory posits the existence of two parallel pathways, one mediating stereopsis and the other mediating binocular rivalry. The rivalry pathway, according to Wolfe, is active at all times, even when the two monocular views are identical. In this sense, Wolfe's model incorporates the essence of suppression theory, that is, the chronic suppression of one eye's view under normal viewing conditions (see Kaufman, 1974, for a more complete description of suppression theory). Furthermore, to implement the rivalry process, Wolfe posits the existence of an AND gate that receives input from two sources, monocular neurons and binocular OR cells; the AND gate signals an output to the obligatory rivalry process only when the OR cells and the monocular cells tuned to the same orientation are simultaneously active.

Wolfe's theory differs from the present theory in several significant ways. Recall that Proposition 1 of the present theory treats rivalry as a default outcome that occurs only when binocular fusion fails; so, unlike in Wolfe's theory, rivalry is not obligatory. Concerning the implementation of rivalry, Proposition 4 of the present theory places the responsibility for rivalry exclusively on monocularly innervated neurons, with no appeal to the involvement of binocular OR cells. It is interesting to note, however, that a more complicated version of the XOR network described as a possible mechanism for signaling the stimulus conditions for rivalry can be implemented by using the null output from an AND gate (i.e., the "on" signal from an XOR gate is equivalent to the "not on" signal from an AND gate). In general, DeMorgan's theorem (Mano, 1984) states that any logic function using AND circuitry can be accomplished using OR functions with inverted output; inverted output can be simply accomplished in nervous systems using inhibitor interneurons. The circuit sketched in Figure 5 is simpler than Wolfe's AND gate.

Wolfe's theory does not deal with the spatial extent of suppression nor the inhibitory mechanisms that govern the temporal dynamics of rivalry. So, in his theory, there are no counterparts to Propositions 2, 5, 6, and 7. In summary, the present theory concentrates on the neural basis of binocular rivalry, whereas Wolfe's theory focuses on the putative coexistence of rivalry and stereopsis. The fundamental difference between the two theories concerns the question of the precedence of fusion/stereopsis over rivalry, a question that is considered in detail in a recent exchange in this journal (Blake & O'Shea, 1988; Wolfe, 1988).

Lehky's Theory

Lehky (1988) has proposed a model of rivalry involving reciprocal feedback inhibition between monocular signals, prior to the point of binocular combination. Because the strength of inhibition is related to the relative differences in stimulus strength between the two monocular images, the circuit can exhibit either stability (i.e., fusion) or instability (i.e., rivalry), but not both at the same time. This aspect of the model is consistent with Proposition 1 of the present theory. Unlike the present theory, Lehky's model largely ignores the question of the spatial extent of suppression, although it would be straightforward to replicate Lehky's feedback network over neighboring cortical areas to achieve the behavior dealt with in Proposition 2. Nor does Lehky deal with the problem binocular correspondence (Proposition 4), although he acknowledges that spatial congruence between the two images must somehow influence the strength of binocular inhibitory couplings. A real strength of Lehky's model is its ability to simulate the temporal dynamics of rivalry, including the changes in monocular predominance associated with unilateral changes in stimulus strength. In his model, this behavior is achieved by reciprocal inhibitory connections, with stimulus strength governing the potency of inhibition. In my discussion of Proposition 6, I enumerated reasons for questioning the relation between stimulus strength and inhibition. Lehky's theory does not account for the nonselectivity of suppression, and it predicts that visual sensitivity during dominance phases of binocular rivalry should be less than sensitivity measured under nonrival, monocular conditions. Proposition 4 of the present theory predicts that sensitivity should be equivalent under the two conditions, a prediction consistent with some (Blake & Camisa, 1978; Wales & Fox, 1970), although not all (Makous & Sanders, 1978), results.

Grossberg's Theory

Grossberg's ideas about binocular rivalry form a small part of his more comprehensive theory of visual perception, and that complete theory exceeds the scope of this article; suffice it to say that Grossberg's (1987) latest theory, which has evolved out of earlier theoretical work (e.g., Grossberg, 1983), represents a remarkably ambitious effort to account for numerous visual phenomena within a unified neuro–computational framework.

Integral to Grossberg's (1987) theory is the notion of a "boundary contour system" that synthesizes "perceptual boundaries" as they are called; these are boundaries that delimit the global configuration of objects and texture discontinuities. The front end of this boundary contour system consists of two serially ordered processing stages, each containing competitive (i.e., inhibitory) interactions among cells selective for orientation. It is within this portion of the boundary contour system that rivalry occurs, according to Grossberg. Actually, Grossberg envisions two distinct kinds of rivalry, one occurring when corresponding retinal areas receive dissimilar spatial patterns (e.g., dissimilar orientations) and the other triggered when identical spatial patterns impinge on retinal areas too disparate to yield fusion. The theory outlined in this article deals explicitly with the first kind of rivalry (pattern rivalry), and it is our respective theoretical treatments of pattern rivalry that I shall focus on here.

Grossberg (1987) considers pattern rivalry and fusion to be mutually exclusive events, with fusion being the stable state sought by the visual system. My Propositions 1 and 2 square with this aspect of Grossberg's theory. We disagree, however, on what exactly is suppressed during rivalry. According to Grossberg, pattern rivalry results when binocularly activated cells tuned to different orientations at the same retinal locus inhibit one another. Grossberg's theory thus implies that it is a given stimulus feature that is suppressed during rivalry. In contrast, Proposition 5 asserts that it is a region of an eye that is suppressed, not information about a particular stimulus feature. Evidence favoring this assertion was presented earlier.

Grossberg handles the temporal dynamics of rivalry by positing that stronger stimuli generate larger signals within the boundary contour system, giving those stimuli an advantage in the competitive stage in which different orientations vie for dominance. Neural habituation associated with prolonged stimulation produces instability in this competitive network, yielding the alternations of rivalry. The present theory also incorporates the notion of fatigue, whereby activity within inhibitory interneurons decays (Proposition 7); this idea is in the same spirit as Grossberg's neural habituation. However, unlike Grossberg's theory, the present model stresses the strength of excitation generated by the *suppressed* image as the causal agent in controlling the duration of dominance of the other eye; this is the essence of Proposition 7.

The two theories are in agreement on the spatially local nature of rivalry (Proposition 2), and both invoke the involvement of monocular and binocular neurons that can be activated by stimulation of either eye (Proposition 3). In his explication of the theory, Grossberg doesn't go into the details of the processes responsible for distinguishing rivalry conditions from nonrivalry conditions (i.e., the gingham problem illustrated in Figure 4). But, generalizing from his discussion of the interactions between the boundary contour system and the so-called feature contour system, the neural hardware for distinguishing rivalry from nonrivalry is in place.

Unresolved Issues

Evidence in support of the present theory has been presented in the context of the various propositions composing the theory. There are, however, some experimental results that cannot be reconciled with the theory in any simple manner or that go beyond the scope of the theory. This section discusses those findings.

Visual Aftereffects

One of the most difficult results confronting any theory of rivalry is suppression's failure to influence any of the conventional aftereffects of visual adaptation. It has been found that suppression of an eye during adaptation does not retard the growth of the threshold elevation aftereffect (Blake & Fox, 1974b; Blake & Overton, 1979), the spatial frequency shift aftereffect (Blake & Fox, 1974a), the tilt aftereffect (Wade & Wenderoth, 1978), or the motion aftereffect (Lehmkuhle & Fox, 1975b; O'Shea & Crassini, 1981b). Evidently in all of these instances, information about the adaptation stimulus reaches the site of adaptation during suppression.

One could argue that the neural site of adaptation and the neural site of suppression are located in noninteracting, parallel pathways. From other results, however, we know this argument is incorrect. As mentioned earlier, adaptation *does* affect the predominance of a stimulus during rivalry, implying that the rivalry mechanism receives neural input that has passed through the site of adaptation.

So the conclusion seems inescapable that adaptation precedes suppression. Yet according to the theory, suppression is occasioned by inhibition of activity within an ensemble of monocular neurons. Are we to conclude that those neurons contribute nothing to the magnitude of a visual aftereffect? This conclusion seems wrong because monocular neurons are presumably the reason why an interocularly transferred aftereffect is weaker than the aftereffect measured in the adapted eye (recall the discussion of Proposition 3).

At present, we have no firm theory about the neural events responsible for the build up of visual aftereffects. Until that question is resolved, it may be premature to speculate about the relation of adaptation and suppression. Clearly, though, this is a weakness of the theory that must be remedied.

Magnitude of Inhibition During a Suppression Period

Recall that Proposition 7 assumes that a transition from suppression to dominance occurs when the build up of excitation within the pool of monocular neurons exceeds the level of inhibition exerted upon those neurons. There is one result that seems inconsistent with Proposition 7. Fox and Check (1972) found that the magnitude of the elevation in probe threshold during suppression was invariant throughout the suppression phase. In other words, probes presented late in a suppression period were no more detectable than probes presented early in a suppression period. Yet the theory proposes that relative level of excitation and inhibition within the pool of inhibited monocular neurons changes during a suppression period, as excitation overcomes inhibition. Why isn't this graded change reflected in probe detectability?

In Fox and Check's (1972) study, the probe target was considerably different from the rival target viewed by the probed eye. Perhaps graded effects could be measured if the probe were an increment in the contrast or intensity of the rival target itself. However, the nonselectivity of suppression (Proposition 6) implies that any and all probes should be subject to the same inhibitory influence. The discrepancy between Proposition 7 of the theory and the data of Fox and Check remains to be resolved. Incidentally, this paradox of graded changes in neural activity yielding all-or-none switches in dominance is deftly handled in Grossberg's (1987) theory by a thresholding device with hysteresis that yields discrete jumps in the balance of activity within the boundary contour system.

Meaning and Predominance

Proposition 7 of the theory proposes that the predominance of a stimulus in rivalry depends on the rate at which excitation generated by that stimulus overcomes interocular inhibition. According to this conceptualization, the major determinant of predominance should be the energic quality of the suppressed stimulus. Yet there are data in the rivalry literature that have been interpreted to indicate that predominance is significantly influenced by cognitive variables and even by personality and cultural factors. To give a few examples, Engel (1956) found that an upright picture of a face viewed by one eye dominated an inverted face picture viewed by the other eye; Bagby (1957) found that the predominance of two conflicting scenes—one a Mexican scene and the other an American scene—was related to an observer's nationality—Mexican versus American; Davis (1959) found that familiar words dominated less familiar words in a stereoscope; and Kohn (1960) reported that emotional words related to sex or aggression, or both, were seen frequently by hospitalized patients who scored relatively high on a hostility questionaire. In a related vein, Lack (1978) reported that observers can learn to control the rate of rivalry alternations. This literature dealing with the effects of meaning and practice on rivalry has been reviewed by Walker (1978), who concluded that "the meaningful content of a suppressed stimulus is being discriminated" (p. 386). Although evidence contrary to this conclusion does exist (Zimba & Blake, 1983), the weight of evidence for semantic effects on predominance is too large to be ignored.

In thinking about the role of meaning in rivalry, it is important to distinguish between meaning's potential effect on dominance and its potential effect on suppression. When a monocular stimulus is dominant in rivalry, information about that stimulus obviously passes to higher visual centers where its semantic content is extracted. Now, it is conceivable that this semantic content in turn guides top-down processes that somehow operate to prolong dominance durations. At present, the theory incorporates no such top-down influence during dominance; the dominance duration of a stimulus is, on this theory, determined entirely by the duration of suppression of the partner eye's stimulus. The theory could be modified, however, to introduce some form of top-down influence that enhances the salience of the dominant stimulus. As one possibility, eye movements that scanned the borders of a dominant stimulus could conceivably influence the pattern of excitation generated by that dominant stimulus and, thereby, amplify its inhibitory effect on the partner eye.

Although an influence of meaning on dominance duration is conceivable within the theory, any influence of meaning on the suppression duration of a stimulus is proscribed. Suppression is accomplished at a relatively early stage in the visual system in which only information about feature primitives has been extracted. Thus, the semantic content of a suppressed stimulus cannot amplify the excitatory signals necessary to overcome the inhibition producing suppression.

A testable prediction follows from this discussion: Any influence that meaning exerts on rivalry predominance must be expressed in the duration of dominance of the meaningful stimulus, whereas the suppression duration of a stimulus can be affected only by the energic qualities of that stimulus, not by its semantic content.

Color Rivalry

On the basis of anecdotal observation, it has been reported that contour rivalry and color rivalry sometimes slip out of synchrony (Breese, 1899; Creed, 1935). For instance, suppose one eye views vertical contours appearing against a red background, whereas the other eye views horizontal contours against a green background. Occassionally, the contours seen by one eye (e.g., vertical) will predominate simultaneously with the color seen by the other eye (e.g., green). (Also recall that Smith et al., 1982, found evidence for selective suppression of color information but nonselective suppression of luminance information.) Quite recently, Carney, Shadlen, and Switkes (1987) described a novel motion illusion that crucially depends on binocular integration of monocular motion information. Carney et al. reported that this binocular motion illusion occurs even when the monocular components are displayed in different colors that rival, indicating that color and motion information are analyzed in parallel.

This dissociation of contour and color information and the dissociation of motion and color information during rivalry could be interpreted to imply that separate cortical areas analyze different dimensions of the retinal image and that each such area contains neural machinery for implementing binocular rivalry. Although the present theory does not rule out this possibility, it would seem more efficient to implement rivalry at a stage in visual processing in which all information from a given region of an eye is contained within an anatomically restricted processing module (i.e., a hypercolumn). Nonselective suppression would certainly be simpler to coordinate within a single hypercolumn, compared with distributed processing modules located in different visual areas of the brain. Still, this question of dissociation of different stimulus attributes during rivalry is an intriguing one that deserves more careful study.

Is Rivalry a Property of the Magno Pathway?

In a recent, provocative article, Livingstone and Hubel (1987) assigned different visual phenomena to one of several anatomically distinct visual pathways. These assignments were made on the basis of similarities between the physiological properties of cells in a particular pathway (e.g., the lack of color opponency) and psychophysical properties of a given visual function (e.g., the disappearance of a phenomenon at equiluminance). Included in their roster of phenomena was binocular rivalry, which was ascribed to the so-called magno system, so named because the thalamic input to this pathway comes from the magnocellular layers of the lateral geniculate nucleus. This association between the magno system and rivalry was based on two psychophysical observations: (a) the loss of binocular rivalry under conditions in which the two half images, although different in color, were equiluminant, and (b) the loss of rivalry at very high spatial frequencies. These two observations dovetailed with physiological evidence showing that neurons composing the magno system are not color selective and exhibit only moderate spatial resolution (e.g., Hubel & Livingstone, 1987).

For several reasons, this linkage between rivalry and the magno system is questionable. First, the observation that rivalry fails at high spatial frequencies is unprecedented and inconsistent with unpublished observations from this laboratory (Mueller & Blake, 1988). Second, binocular rivalry breaks down under conditions of temporal flicker (O'Shea & Blake, 1986) that should robustly stimulate the magno system. And third, there remain questions concerning the stimulus properties of neurons that compose the various parallel pathways envisioned by Livingstone and Hubel (1987; e.g., see Desimone, Schein, Moran, & Ungerleider, 1985). At this juncture, then, it is fair to conclude that Livingstone and Hubel's theory is controversial, albeit eminently testable.

Rivalry Suppression and Clinical Suppression

Some individuals habitually suppress foveal vision in one eye under ordinary viewing conditions. Typically this chronic suppression is an adaptive response that eliminates diplopia or confusion, or both, arising from eye misalignment (Burian & von Noorden, 1974). Are chronic suppression and binocular rivalry suppression in fact equivalent, as proposed by some investigators (e.g., Fahle, 1983)? Certainly the instigating conditions—dissimilar monocular images striking corresponding retinal areas—are comparable in the two cases. However, rivalry suppression in normal individuals seems invariably to involve alternations in dominance between the two eyes, whereas chronic suppression in people with eye misalignment is often unilateral. Among individuals with histories of eye misalignment are some who are able to control which eye is suppressed, but these so-called alternating suppressors typically use one eye for near vision and the other for distance vision. So these alternations in suppression are not really comparable to the alternations experienced by a person with normal vision who views rival targets in a stereoscope.

Are there other differences between rivalry suppression and the suppression experienced by people with disorders of binocular vision? Holopigian (1987) has recently investigated this question in some detail. Her results show that in several respects the two categories of suppression are equivalent. For instance, the depth of rivalry suppression and the depth of chronic suppression are both invariant with contrast as well as with background luminance. As already described, Holopigian et al. (1988) did find that the depth of suppression varies greatly among individuals with chronic suppression, although it varies little among normal observers. Recall, though, that this observation actually serves as the point of departure for Proposition 6; this difference between chronic suppression and rivalry suppression is an important ingredient in the theory. Smith et al. (1985) have reported that chronic suppression operates nonselectively on all test probes, regardless of probe wave length, whereas rivalry suppression has a selective impairment on probe detectability. This pattern of results implies that the two forms of suppression are not strictly comparable. Finally, Blake and Lehmkuhle (1972) found that neither chronic suppression nor rivalry suppression had any influence whatsoever on the growth of the threshold elevation aftereffect. This finding implies that the two forms of suppression occur early in the visual pathways, although not necessarily at the same neural locus.

This question of the relation between chronic suppression and rivalry suppression, although not central to the present theory, is potentially significant in understanding the neural bases of chronic suppression in people with disordered binocular vision.

Role of Rivalry Suppression During Normal Binocular Vision

No one doubts that binocular rivalry is a fascinating phenomenon: To watch an otherwise clearly visible stimulus disappear for seconds at a time is truly remarkable. This alone, however, doesn't mean that rivalry is a fundamental aspect of normal vision. In fact, one could argue that binocular rivalry is a curious laboratory artifact that occurs under conditions ordinarily never experienced by most observers.

It is true that the left and right foveae rarely receive dissimilar stimulation for any length of time—indeed, the oculomotor system actively tries to avoid this situation by altering vergence angle until matching features are imaged on the two foveae. There are, however, multiple locations on the two retinae in which dissimilar monocular images strike corresponding retinal areas; this is an inevitable consequence of the geometry of binocular vision. Objects located well in front of or well behind the horopter will, by definition, cast images on distinctly different areas of the two eyes, and the resulting disparities will be too large for the binocular visual system to resolve. This means, therefore, that for a significant region of visual space, dissimilar monocular images will be cast on corresponding areas of the two eyes. Yet an observer ordinarily does not experience the consequences—confusion and diplopia—of this dissimilar monocular stimulation. In fact, areas of a binocularly viewed display in which matches are impossible (and in which rivalry occurs) appear to lie at a different depth plane than regions of the display that are fused (O'Shea & Blake, 1987). This observation implies that dissimilar stimulation of corresponding retinal areas, besides triggering rivalry, also signals depth of a magnitude outside the disparity limits for binocular single vision.

So, it is reasonable to conclude that binocular single vision is accomplished by two processes, binocular fusion (which operates over those regions of visual space in which matching features are present) and binocular suppression (operating over regions in which matching features are absent); this is essentially the same conclusion reached by Ono, Angus, and Gregor (1977) on the basis of studies of perceived visual direction under conditions of dichoptic viewing. The idea that fusion and suppression coexist at different regions of the visual field should be distinguished from Wolfe's (1986) proposal, whereby rivalry and fusion occur simultaneously throughout the binocular visual field; Wolfe's idea is inconsistent with Proposition 2 of the present theory.

Conclusion

In recent years we have witnessed major advances in our understanding of binocular stereoscopic vision. These advances were sponsored, in large measure, by the development of sophisticated neural (Nelson, 1975; Sperling, 1970) and computational (Marr & Poggio, 1976; Mayhew & Frisby, 1981) theories of stereopsis that have guided thinking and research on this problem. During the same period of time, our understanding of the mechanism of binocular rivalry has progressed rather little. It is hoped that the availability of a comprehensive theory of rivalry now will spark renewed interest in the phenomenon and, more important, will serve as a framework for generating revealing experimental results. The theory includes several counterintuitive propositions, predictions from which are readily testable. The success of the theory, in this author's mind, will be marked by the vigor with which it is critically examined.

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Calls for Nominations for *JCCP, Educational, JPSP: Attitudes,* and *JPSP: Interpersonal*

The Publications and Communications Board has opened nominations for the editorships of the *Journal of Consulting and Clinical Psychology,* the *Journal of Educational Psychology,* and the Attitudes and Social Cognition section and the Interpersonal Relations and Group Processes section of the *Journal of Personality and Social Psychology* for the years 1991–1996. Alan Kazdin, Robert Calfee, Steven Sherman, and Harry Reis, respectively, are the incumbent editors. Candidates must be members of APA and should be available to start receiving manuscripts in early 1990 to prepare for issues published in 1991. Please note that the P&C Board encourages more participation by members of underrepresented groups in the publication process and would particularly welcome such nominees. To nominate candidates, prepare a statement of one page or less in support of each candidate.

- For *Consulting and Clinical,* submit nominations to Martha Storandt, Department of Psychology, Washington University, St. Louis, Missouri 63130. Other members of the search committee are Bernadette Gray-Little, Frederick Kanfer, and Hans Strupp.
- For *Educational,* submit nominations to Richard Mayer, Department of Psychology, University of California, Santa Barbara, California 93106. Other members of the search committee are Robert Glaser, Jill Larkin, Sigmund Tobias, and Noreen Webb.
- For *JPSP: Attitudes,* submit nominations to Don Foss, Department of Psychology, University of Texas, Austin, Texas 78712. Other members of the search committee are Marilyn Brewer, David Hamilton, Melvin Manis, and Richard Petty.
- For *JPSP: Interpersonal,* submit nominations to Frances Degen Horowitz, Department of Human Development and Family Life, University of Kansas, Lawrence, Kansas 66045. Other members of the search committee are Kay K. Deaux, Phoebe C. Ellsworth, and Robert M. Krauss.

First review of nominations will begin February 15, 1989.