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A Primer on Binocular Rivalry, Including Current Controversies

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Abstract. Among psychologists and vision scientists, binocular rivalry has enjoyed sustained interest for decades dating back to the 19th century. In recent years, however, rivalry's audience has expanded to include neuroscientists who envision rivalry as a "tool" for exploring the neural concomitants of conscious visual awareness and perceptual organization. For rivalry's potential to be realized, workers using this "tool" need to know details of this fascinating phenomenon, and providing those details is the purpose of this article. After placing rivalry in a historical context, I summarize major findings concerning the spatial characteristics and the temporal dynamics of rivalry, discuss two major theoretical accounts of rivalry ("eye" vs "stimulus" rivalry) and speculate on possible neural concomitants of binocular rivalry.

Key words: binocular rivalry, conscious awareness, neural model, perceptual organization, suppression

1. Introduction

The human brain has been touted as the most complex structure in the known universe (Thompson, 1985). This may be true, but despite its awesome powers the brain can behave like a confused adolescent when it is confronted with conflicting visual messages. When dissimilar visual stimuli are imaged on corresponding retinal regions of the two eyes, the brain lapses into an unstable state characterized by alternating periods of perceptual dominance during which one visual stimulus or the other is seen at a time. This confusion is understandable, for the eyes are signalling the brain that two different objects exist at the same location in space at the same time. Faced with this physical impossibility, the brain, metaphorically speaking, entertains two alternative perceptual interpretations, changing its mind repeatedly. This fluctuation in perception, of course, is the phenomenon termed **binocular rivalry**, the focus of this special issue of *Brain and Mind.* Actually, in the early years after its discovery, the phenomenon sometimes was termed "retinal rivalry" in recognition of the fact that the two retinae were the source of the discordant binocular input. During the last century, that term was supplanted by "binocular rivalry." And very recently, some have advocated the even more neutral term "stimulus rivalry" because alternations in perceptual dominance can arise even when two competing stimuli are *not* unequivocally associated with the two eyes.

In this article I have four goals: (a) to provide a very brief historical account of binocular rivalry, (b) to summarize major findings concerning the spatial characteristics and the temporal dynamics of rivalry, (c) to discuss two major theoretical accounts of rivalry (“eye” vs “stimulus” rivalry) and the evidence bearing on those accounts, and (d) to speculate on possible neural concomitants of binocular rivalry. Several highly relevant topics are not included in this article, since they are covered by other contributors to this special issue of *Brain and Mind*; those timely topics include single-unit and brain imaging studies during rivalry and hemispheric specialization and rivalry.

From the outset, I want to forewarn readers that the literature on binocular rivalry is quite large, and a comprehensive review is beyond the scope of this article. I also wish to acknowledge the availability of several excellent reviews of work on binocular rivalry, including publications by Fox (1991), by Logothetis (1998), by Howard and Rogers (1995) and by Papathomas *et al.* (1999). Some of the content in this article echoes material covered in those reviews, and students of binocular rivalry will gain a balanced overview of the field by consulting those sources. As well, those interested in rivalry will find it worthwhile to capitalize on the very thorough, up-to-date reference list of papers on binocular rivalry maintained by Dr. Robert O’Shea – that list may be accessed on the world-wide web at:

hhttp://psy.otago.ac.nz/r_oshea/br_bibliography.html

Throughout this article, I will be describing aspects of rivalry that readers may want to experience first-hand. Toward that end, I have prepared a webpage with demonstrations that can be viewed using red/green filter glasses; the URL for that webpage is:

http://www.psy.vanderbilt.edu/faculty/blake/rivalry/BR.html

The webpage also lists several good commercial sources for purchasing effective, inexpensive anaglyphic glasses.

2. Background

Surveying the historical literature on vision and optics, one can identify a number of quotations indicating an appreciation of the perceptual consequence of discordant binocular stimulation. Indeed, the noted vision scholar Nicholas Wade, in his delightful book on *A Natural History of Vision* (Wade, 1998), describes no fewer than eight accounts of what can be construed as binocular rivalry. According to Wade, it is Porta (1593) who deserves credit for the first unambiguous description of rivalry. This description was based on Porta’s observation upon viewing separately with the two eyes different pages from two books. (Porta accomplished this simply by placing a partition between the two eyes, so that the left eye could only see the page on the left side of the partition and the right eye only the page before the right eye.) According to Porta, only one page was visible and, hence, available to consciousness for reading; according to Porta, it was the right eye, for him, that dominated in perception. So Porta's descriptions clearly capture one essential ingredient of binocular rivalry: the suppression from vision of one eye's view.

Following Porta, a number of vision scholars commented on the occurrence of rivalry, and some went so far as to invent more elaborate optical means (e.g., prisms) to promote the stimulus conditions for rivalry. However, it is Sir Charles Wheatstone (1838) who deserves credit for the first systematic study of rivalry, which can be found in his famous monograph on binocular stereopsis. Using his newly invented mirror stereoscope (Figure 1a), Wheatstone noted an odd breakdown in normal binocular cooperation when the two eyes separately viewed different alphabetic letters. To quote Wheatstone:

> If *a* and *b* [shown as S and A in Figure 1b] are each presented at the same time to a different eye, the common border will remain constant, while the letter within it will change alternately from that which would be perceived by the right eye alone to that which would be perceived by the left eye alone. At the moment of change the letter which has just been seen breaks into fragments, while fragments of the letter which is about to appear mingle with them, and are immediately after replaced by the entire letter. It does not appear to be in the power of the will to determine the appearance of either of the letters, but the duration of the appearance seems to depend on causes which are under our control: thus if the two pictures be equally illuminated, the alternations appear in general of equal duration; but if one picture be more illuminated than the other, that which is less so will be perceived during a shorter time.

So in this short passage Wheatstone offered several trenchant observations on key aspects of rivalry, including the complete suppression of one of two discordant stimuli, the alternations in dominance between the eyes, the spatial fragmentation of the two images during times of transition, and the dependence of predominance on the physical characteristics of the rival stimuli. These concise observations have been replicated and extended in subsequent work on rivalry.

Following Wheatstone's seminal essay, binocular rivalry captured the imagination of some of science's leading figures, including von Helmholtz, William James and Sir Charles Sherrington, and during the 20th century literally hundreds of papers were published on the topic. Earlier work on rivalry has been reviewed by Levelt (1965) and by Walker (1978), and more contemporary work is reviewed by Fox (1991) and by Howard and Rogers (1995). For purposes of relating rivalry to possible underlying neural mechanisms, it is useful to begin by summarizing a number of well supported generalizations about rivalry.

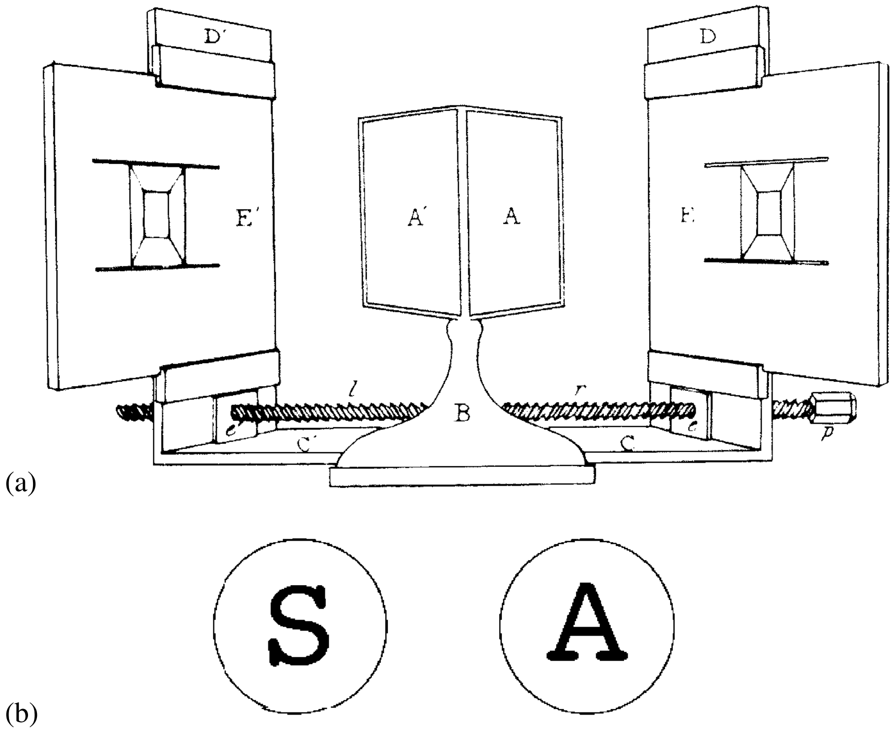

Figure 1. (a) A reproduction of the drawing of Sir Charles Wheatstone's newly invented mirror stereoscope, taken from his monograph on binocular vision (Figure 8 in Wheatstone, 1838). An observer would situate his head so that the right eye would see the image reflected in the right-hand mirror (A in the figure) and the left eye would see the image reflected in the left-hand mirror (A′). Each mirror would reflect whatever picture Wheatstone placed in the holders (E′ and E) attached to the upright boards (D′ and D) situated at opposite ends of the arms of the stereoscope. The arms are attached to two boards (C′ and C) that could be moved different distances from the mirrors. (b) A drawing reproduced from Wheatstone's monograph (Figure 25) showing a pair of dissimilar "half-images" that inspired Wheatstone's rather detailed descriptions of binocular rivalry.

3. Characteristics of Binocular Rivalry

These next several subsections summarize well-established characteristics of rivalry, with particular emphasis on factors that influence the spatial and temporal dynamics of rivalry.

3.1. WHAT STIMULUS DIFFERENCES TRIGGER RIVALRY?

Left- and right-eye differences along any one of a wide range of stimulus dimensions are sufficient to instigate binocular rivalry. These include differences in color, luminance, contrast polarity, form, size and motion velocity. Rivalry can be triggered by very simple stimulus differences (e.g., gratings differing only in orientation) and by complex differences (e.g., pictures of a human face viewed by one eye and a house viewed by the other). Rivalry can be observed over a very wide range of light levels, including scotopic, and it can be observed anywhere throughout the binocular visual field so long as the stimuli are adjusted for visibility. There appear to be only a few conditions of dichoptic stimulation (i.e., different monocular stimuli imaged on corresponding retinal areas) that resist rivalry; these include dichoptic differences in flicker rate (O'Shea and Blake, 1986), dichoptic differences in contrast level (to be distinguished from contrast polarity), large differences in left- and right-eye spatial frequency amplitude spectra (Yang *et al.*, 1992) and large differences in speed of random-dot motion (van de Grind *et al.*, in press). Liu *et al.* (1992) have reported that many seconds may be required before one experiences rivalry when both dichoptically viewed, orthogonally oriented gratings are near-threshold in contrast, particularly high spatial frequency gratings.

Alternations in perceptual dominance – the hallmark of binocular rivalry – can also be produced under some conditions of monocular viewing (Breese, 1899; Campbell and Howell, 1972), and, of course, there are many well-known ambiguous figures that produce fluctuations in perceptual interpretation (e.g., the vase/face figure). Some researchers believe that all these instances of perceptual fluctuation – binocular rivalry, monocular rivalry, ambiguous figures – result from common mechanisms (e.g., Andrews and Purves, 1997), an idea that deserves careful consideration. The present review will be confined to studies of patent binocular rivalry, where dissimilar stimuli are presented to corresponding regions of the two eyes.

3.2. SPATIAL EXTENT OF RIVALRY

In the literature, one often reads that binocular rivalry entails alternating periods of monocular dominance and suppression between discordant views seen by the left and right eyes. Particularly for large rival stimuli, however, this characterization is not entirely correct. Rather than alternating between periods of exclusive dominance of one eye's view and then the other eye's view, one often experiences a fluctuating patchwork consisting of intermingled portions of *both* eyes' views (Meenes, 1930); the incidence of "patchwork" rivalry increases with prolonged viewing of rival targets (Hollins and Hudnell, 1980). Sometimes dubbed "piecemeal" rivalry, these periods of mixed dominance suggest that rivalry transpires locally within spatially restricted "zones" and not globally between the eyes. How large are these putative zones? For foveally viewed rival stimuli, it has been estimated that exclusive, unitary rivalry (no periods of piecemeal rivalry) can be obtained only when rival stimuli do not exceed about 0.1 deg visual angle. However, this critical angular subtense increases with retinal eccentricity (Blake *et al.*, 1992) and with spatial frequency (O'Shea *et al.*, 1997), and the incidence of piecemeal rivalry is much reduced when rival targets are viewed at low light levels (O'Shea *et al.*, 1994). Figure 2a presents several pairs of rival figures, varying in

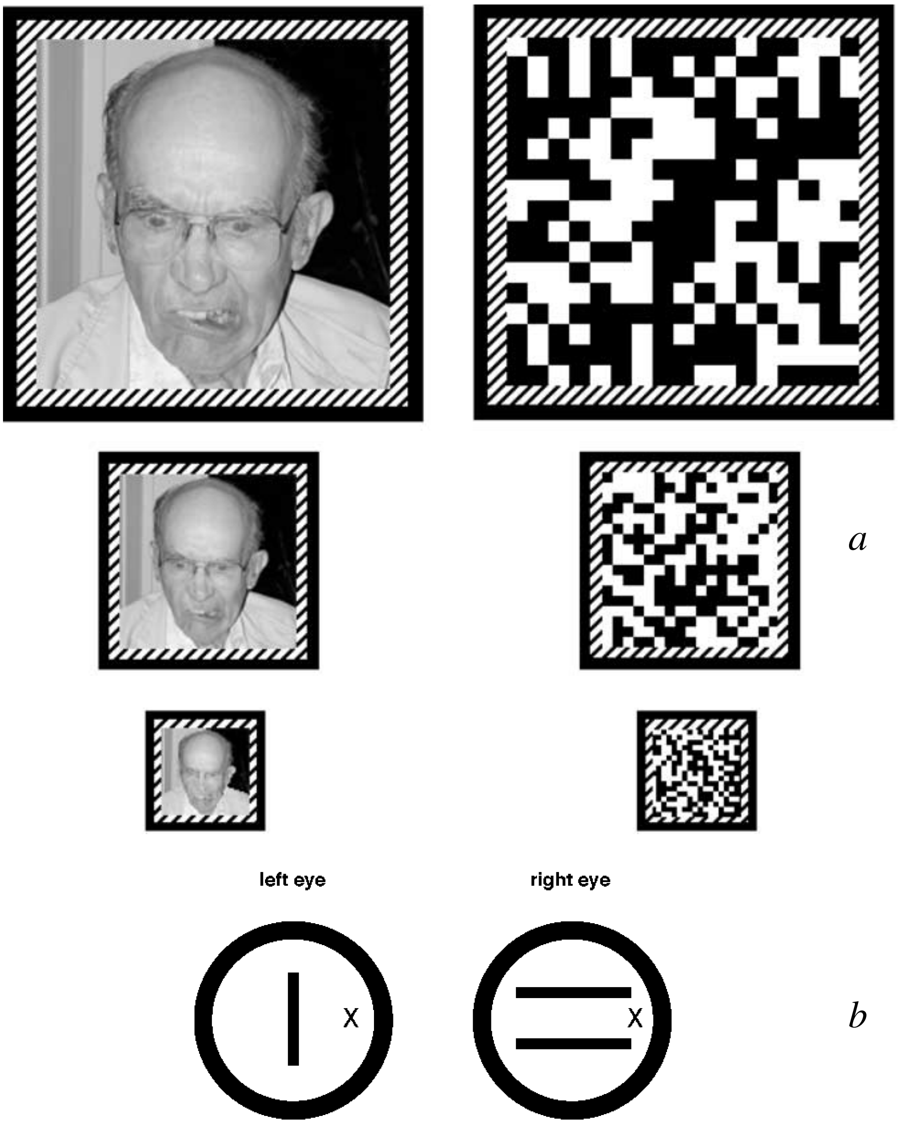

Figure 2. The three pairs of rival targets in panel *a* allow readers to experience how target size influences the incidence of piecemeal rivalry (i.e., rivalry in which different portions of targets seen by the two eyes can be dominant in perception simultaneously). Only with the smaller pair of rival targets do observers consistently experience exclusive dominance of one entire target or the other, with relatively few moments of piecemeal rivalry. The pair of rival targets in panel *b* allows readers to see how suppression spreads beyond the immediate location of conflict. After fusing the two half-images, fixate the x-mark and notice how the vertical contour often disappears in its entirety, even though the middle portion has no competing partner in the other eye.

their angular subtense. Readers capable of free-fusion can compare the incidence of piece-meal rivalry among these different pairs of figures. Also included in this Figure is a pair of rival targets (Figure 2b) demonstrating that suppression spreads some distance beyond the immediate regions of binocular conflict, again pointing to the possible existence of zones of suppression (Kaufman, 1963; Collins and Blackwell, 1974).

There is reason to believe that the spatial extent of rivalry is governed by the retinal angular subtense of the competing stimuli, not by the perceived size of those stimuli (Blake *et al.*, 1974). Specifically, when rival afterimages of small angular subtense are viewed against a surface located far from the observer, the rival targets appear quite large thanks to Emmert's law (perceived size of an object associated with a fixed size retinal image increases with perceived distance: Palmer, 1999). However, those apparently "large" afterimages in fact tend to rival in an all or none fashion in accordance with their small angular subtense. Conversely, rival afterimages of large angular subtense exhibit piecemeal dominance even when those afterimages are viewed against a very nearby surface which renders their apparent size quite tiny. Now, it is generally thought that variations in the perceived size of an afterimage of constant angular subtense reflect the operation of neural mechanisms that scale size in terms of distance. On this account, then, the spatial extent of rivalry must be determined by neural events uninfluenced by this putative size-scaling mechanism.

One intriguing, suggestive characteristic of rivalry concerns the spatial appearance during transitions in dominance between one stimulus and the other. Rather than being haphazard, these transitions often appear as spatially coherent waves of dominance wherein one stimulus appears to sweep the other from conscious awareness. This observation could be construed to imply that the putative "zones" of rivalry are not independent, which leads to the following question. Are fluctuations in rivalry within one portion of the visual field unrelated to rivalry fluctuations within other portions of the visual field? If local suppression zones were indeed completely independent, we would expect a relatively large stimulus viewed by one eye (i.e. one subtending many degrees of visual angle) to be visible, or dominant, in its entirety only very rarely. However, complete monocular dominance does occur significantly more often than would be expected based on chance alone (Blake *et al.*, 1992). In a similar vein, multiple small rival targets scattered throughout the visual field can engage in synchronized alternations, such that all targets of a given configuration (e.g. all the green circles) are dominant simultaneously (Whittle *et al.*, 1968; Dörrenhaus, 1975; Kovács *et al.*, 1996; Alais and Blake, 1999). This observation, too, implies that rivalry zones are not independent. Finally, it has been found that visual features located outside the boundaries of a rival target can influence the predominance of that rival target, as though the strength of the rival target was being modulated by its neighbors (Ichihara and Goryo, 1978; Mapperson and Lovegrove, 1991; Fukuda and Blake, 1992; Alais and Blake, 1998). This finding, likewise, points to spatial interactions beyond the boundaries of any putative local zones of rivalry.

3.3. TEMPORAL DYNAMICS OF RIVALRY

Binocular rivalry is not experienced when dissimilar monocular stimuli are very briefly exposed – instead, the perceptual result with brief exposure resembles the binocular superimposition of the two stimuli (Anderson *et al.*, 1978; Wolfe, 1983; Blake *et al.*, 1991). So, for example, a pair of briefly flashed, orthogonally oriented rival gratings looks like a plaid.[1] To experience complete dominance of one rival figure over another requires that both rival figures be presented simultaneously for at least several hundred milliseconds. Moreover, rivalry is disrupted if dissimilar monocular stimuli are flickered on-and-off rapidly and repetitively (O'Shea and Crassini, 1984). These observations suggest that rivalry is highly susceptible to transient stimulation. In fact, it is well known that, during rivalry, a phenomenally suppressed stimulus can be readily restored to dominance by maneuvers that create transient stimulation within the eye viewing that stimulus. Thus, for example, simply waving a pencil in front of a suppressed stimulus immediately brings it into dominance, erasing the other eye's view from consciousness (Grindley and Townsend, 1965); the same effect can be achieved by an abrupt increase in the contrast of a suppressed stimulus (Blake and Fox, 1974a) or by setting a suppressed stimulus into motion (Fox and Check, 1968; Walker, 1975; Walker and Powell, 1979).

What transpires when rival targets are viewed for periods lasting many seconds, without perturbation? In this case, individual periods of dominance and suppression are unpredictable in duration, being sequentially independent random variables (Levelt, 1965; Fox and Herrmann 1967; Blake *et al.*, 1971; Wade, 1975; Walker, 1975; Lehky, 1995). Individual dominance durations conform reasonably well to the gamma distribution, an example of which is shown in Figure 3. Comparable frequency distributions are found when monkeys experience binocular rivalry (Myerson *et al.*, 1981; Logothetis, 1998), a noteworthy finding that validates the use of non-human primates for the study of rivalry.

Aside from deploying oculomotor "tricks"[2] observers seem unable willfully to trigger immediate switches from suppression to dominance or to hold one stimulus dominant indefinitely (Blake, 1988).[3] There is quite a bit of evidence, however, that attentional manipulations can bias overall predominance in favor of one of two

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[1] Nor does a pair of rival targets "pop out" from an array of otherwise binocularly fused targets (Wolfe, 1988), implying that it takes time for the visual system to register monocularly incompatible stimuli.

[2] One can very easily terminate suppression of a stimulus by blinking the eye viewing the suppressed stimulus or by moving the eyes in a way that differentially creates transients from that stimulus (e.g., horizontal eye movements while a vertical grating is suppressed).

[3] Lack (1978) speculates that people might develop the ability to control rivalry completely if given sufficient practice. His speculation was stimulated by the observation that people can select-

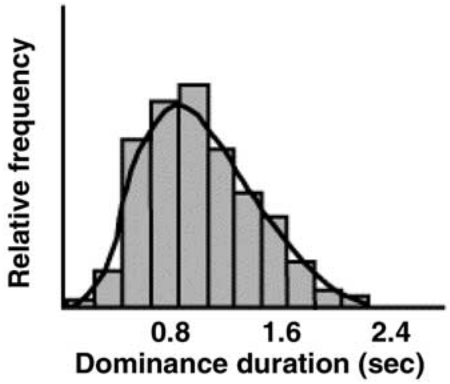

Figure 3. Histogram summarizing the durations of individual periods of dominance during binocular rivalry. Observers "tracked" dominance of two dissimilar patterns by pressing one of two keys, and the individual durations were tabulated, normalized (each value was divided by the grand mean) and plotted as a frequency histogram. The solid line shows the gamma function fit to the actual data. The skewness of this function varies with rivalry alternation rate, becoming more nearly gaussian when that rate is rapid (Myerson *et al.*, 1981). (Graph adapted with permission from Figure 2 of Fox, R. and Herrmann, J. 1967: Stochastic properties of binocular rivalry alternations, *Percept. Psychophys.* **2**, 432–436.)

rival figures during extended tracking periods. Helmholtz (1925) observed that he could bias dominance in favor of one rival target by concentrating his attention on that target using strategies like counting the number of lines in a given rival stimulus. Even then, however, Helmholtz found that attention's efficacy seemed to wane, for a dominant stimulus eventually gives way to suppression involuntarily after a period of time. Helmholtz's observations have since been documented in a number of studies showing that people can learn to influence the alternation rate of rivalry (e.g., Lack, 1969). The role of attention in determining rivalry predominance has been very systematically studied by Lack (1978) who, among other things, showed that control exerted over rivalry is not attributable solely to the operation of peripheral mechanisms such as blinking or accommodation. Instead, central neural processes are implicated. In addition to documenting that attention can promote dominance, Ooi and He (1999) showed that directing attention to the region of an eye where a rival target is currently suppressed can prematurely terminate suppression of that target.

Besides enhancing predominance and protecting a stimulus from suppression, attention to one of two rival targets may also promote exclusive dominance (i.e., minimize piecemeal rivalry) when those targets subtend a large angular subtense (Neisser and Becklen, 1975), an idea proposed by Ooi and He (1999). When local rivalry components are pieced together into a globally coherent, dominant image – a phenomenon discussed in the previous section (Kovács *et al.*, 1996) – perhaps

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ively control which of two dissimilar messages are heard during dichotic listening; selective listening, Lack points out, is a skill at which we're all well practiced.

attention is providing part of the neural glue. As we continue to get a clearer picture of how the responses of visual neurons are modulated by attention, including neurons at the very earliest cortical stages of processing, we will be in a better position to theorize about attention's modulatory effect on rivalry predominance and appearance.

The most straightforward means for influencing predominance is to vary some aspect of the competing stimuli. A large body of literature confirms that manipulation of stimulus variables such as luminance (Kakizaki, 1960; Fox and Rasche, 1969), contrast (Whittle, 1965; Hollins, 1980), contour density (Levelt, 1965), spatial frequency (Hollins, 1980; Fahle, 1982; Andrews and Purves, 1997), size (O'Shea *et al.*, 1997), velocity (Breese, 1899; Wade *et al.*, 1984; Blake *et al.*, 1998) and retinal eccentricity (Fahle, 1987), to name just a few, can produce pronounced variations in alternation rate and in stimulus predominance. As a generalization, a "stronger" rival target (e.g., one that is higher contrast than the other) enjoys enhanced predominance, defined as the total percentage of time that a given stimulus is visible during an extended viewing period. Moreover, there is evidence that this increased predominance is produced, in large part, by decreases in the durations of suppression periods of a given stimulus – "stronger" stimuli tend to stay suppressed for shorter periods of time while not necessarily staying dominant for longer periods of time (e.g., Levelt, 1965; Fox and Rasche, 1969; but see Mueller and Blake, 1989, and Bossink *et al.*, 1993, for evidence pointing to longer dominance durations, too). If both pairs of rival targets are bilaterally increased in strength (e.g., the contrasts of both are high), each target remains suppressed for more abbreviated periods of time and, consequently, the two targets alternate in dominance more rapidly (e.g., Levelt, 1965). Rivalry alternations measured with a given stimulus configuration slow markedly in older individuals, and this slowing of rivalry is only partially attributable to reduced retinal illumination (Jalavisto, 1964).

It is generally believed that transitions from dominance to suppression are mediated by neural adaptation, with the excitatory signals from the dominant stimulus weakening over time and eventually succumbing to the signals from the other, previously suppressed stimulus (e.g., Sugie, 1982; Lehky, 1988; Mueller, 1990). Consistent with this idea, a stimulus forced to remain dominant during rivalry (by incrementing its contrast the moment it becomes suppressed) generates increasingly brief dominance durations, as if being denied an opportunity to recover from adaptation (Blake *et al.*, 1990); once dominance is no longer forced, that stimulus remains suppressed for an unusually long period of time.

There is also some evidence purporting to show an influence of cognitive and motivational factors on stimulus predominance (see Walker, 1978 for a review of this evidence). In these kinds of studies, the two eyes view dissimilar monocular stimuli that vary in their emotional content or their meaningfulness to an observer. According to some studies, a more cognitively salient stimulus exhibits greater predominance during rivalry. For example, when Jewish and Catholic observers were asked to judge the relative predominance of symbols associated with their two religions (e.g., the star of David versus a cross) Jewish religious symbols tended to predominate for the Jewish observers while Catholic religious symbols tended to predominate for the Catholic observers (LoSciuto and Hartley, 1963). In a similar vein, upright pictures of a human face tend to predominate over inverted pictures of a face (Engel, 1956), and figures one has seen before tend to predominate over novel figures (Goryo, 1969). These and comparable results have been interpreted to mean that non-visual factors such as affective content influence the resolution of stimulus conflict during binocular rivalry (Walker, 1978). Such an influence would be very important in shaping our search for possible neural concomitants of binocular rivalry. Moreover, such an influence is not far-fetched given the evidence for attention's modulatory role in rivalry (Lack, 1978). There are, however, reasons to interpret these findings cautiously (Yu and Blake, 1992). Because they measured predominance using self-report, the measures of dominance were susceptible to demand characteristics. Moreover, these studies often used rival targets that were large and, therefore, prone to piecemeal rivalry, yet the judgements were binary in nature; observers had to adopt some criterion for declaring stimulus predominance, thus compounding the problem of response bias. It will be useful to see these kinds of experiments repeated using procedures that minimize these potential problems and, where possible, rely on more objective measures of rivalry dominance, such as the test probe method described in the following section.

3.4. WHAT IS SUPPRESSED DURING BINOCULAR RIVALRY?

When a given stimulus is suppressed during rivalry, the neural mechanisms underlying suppression perforce must be operating on the features composing that stimulus. But to what extent does suppression generalize to other stimulus features? The answer to this question depends on how it is framed experimentally. For one class of tasks (test probe tasks), suppression appears to be quite general, encompassing a wide range of stimulus conditions. For a second class of tasks (co-existence tasks), however, suppression appears more restricted. The following subsections briefly review results from these two categories of tasks, along with their implications.

3.4.1. *Test probe sensitivity*

Suppression periods of rivalry are accompanied by a general loss in visual sensitivity. Thus, a probe target superimposed on a stimulus engaged in rivalry is more difficult to detect when that probe is presented while the rival target is suppressed, compared to detection performance when the same probe is presented during rival target dominance (Wales and Fox, 1970; Fukuda, 1981; O'Shea and Crassini, 1981; Smith *et al.*, 1982). Moreover, it is not just psychophysically measured visual sensitivity that is impaired during suppression – a light stimulus presented to a suppressed eye evokes less pupillary constriction than does that same light presented to the eye during dominance (Barany and Hallden, 1948; Lorber *et al.*, 1965; Brenner *et al.*, 1969).

Impaired detection performance is found even when probes differ markedly from the suppressed target itself. Thus, for example, a test probe consisting of one of several possible alphabetic characters is difficult to recognize when briefly superimposed on a simple, uniform disk that was suppressed during rivalry (Fox and Check, 1972). In a similar vein, reaction times to highly visible probes are lengthened when those probes are presented to an eye during suppression (Fox and Check, 1968; O'Shea, 1987). This depression in visual sensitivity is also evidenced by an inability to detect changes in a suppressed rival target, so long as those changes are not accompanied by abrupt transients in luminance or contrast. Thus, for example, observers fail to detect large changes in the spatial frequency or the orientation of a suppressed grating (Blake and Fox, 1974a), and they fail to detect transitions from incoherent, random motion to coherent, structured motion (Blake *et al.*, 1998). Even when changes in orientation *are* accompanied by abrupt transients, reaction times for detection of those changes are lengthened (O'Shea and Crassini, 1981).

This nonselective loss in visual sensitivity represents a hallmark of suppression, and it has been construed to imply that suppression is operating not just on the stimulus features of the initially suppressed target but rather on the region of the eye upon which that target is imaged (Blake, 1989). It is important to keep in mind, however, that this region of nonselective suppression is limited in spatial extent and does not encompass an entire eye. Indeed, this is why piecemeal rivalry is often observed with large targets: different regions of an eye can be in different states of rivalry. It is also noteworthy that this general reduction in test-probe performance during suppression corresponds to only about 0.5 log-unit loss in sensitivity, relative to that measured during dominance (e.g., Holopigian, 1989).[4] This seems like a very modest sensitivity loss, compared to the wholesale loss in the visibility of the rival target itself. After all, a complex, high contrast image several orders of magnitude above detection threshold can disappear entirely for several seconds – here suppression seems to be depressing visibility by several log-units. However, a 0.5 log-unit range of stimulus energy (e.g., contrast) is sufficient under some conditions to span an entire psychometric function, ranging from chance to perfect performance. Viewed in this light, a 0.5 log-unit change in sensitivity could be sufficient to move a stimulus from reliably detectable to reliably undetectable. In any event, we presently have no idea why probes are difficult to detect during suppression, and we would like an answer to that question in order to know what the results from probe experiments are telling us about rivalry suppression.

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[4] It is worth noting that probe sensitivity during dominance is equivalent to monocular sensitivity measured under non-rivalry conditions, implying that there is nothing unusual about the dominance state of rivalry.

3.4.2. *Co-existence tasks*

What aspects of visual perception manage to co-exist with binocular rivalry, unperturbed by fluctuations in dominance and suppression? Answers to this question can have important implications for the issue of the selectivity of suppression (Blake, 1997). The following paragraphs highlight findings that bear on those answers.

3.4.2.1. *Stereopsis*. It is natural to wonder how stereopsis and rivalry relate to one another, since both phenomena involve binocular interactions between disparate monocular views. In the case of stereopsis, those disparities comprise slight perspective differences between the two eyes' views, disparities that can be resolved by synthesis of a stable, three-dimensional representation incorporating both views. In the case of rivalry, those disparities entail dissimilar monocular features incompatible with the existence of a single, three-dimensional view; the consequence, then, is a breakdown in stable, stereoscopic vision. It is interesting to note that dissimilar monocular stimulation does not inevitably yield rivalry – if dissimilar monocular stimulation is compatible with the pattern of stimulation one would experience while viewing partial occlusion of one object by another, binocular vision tends to be stable (Shimojo and Nakayama, 1990).

But what happens when stereo half-images are presented simultaneously with rival half-images? Can stereopsis co-exist in the face on ongoing rivalry? The evidence for coexistence is mixed. Several studies have reported that observers experience patent stereopsis even when the pair of stereo half-images are superimposed on dissimilar monocular figures undergoing vigorous binocular rivalry (Treisman, 1962; Ogle and Wakefield, 1967; Julesz and Miller, 1975; Mayhew and Frisby, 1976; Blake *et al.*, 1979). Several other studies, however, report the opposite: stereopsis is disrupted when stereo half-images are viewed during rivalry (Hochberg, 1964; Amira, 1989). In an attempt to reconcile these seemingly conflicting results, Harrad *et al.* (1994) measured stereo thresholds under conditions where one stereo half-image was presented continuously to one eye and a rival target was presented to the other eye. When the stereo half-image was suppressed in rivalry (as indicated by the observer's button press), the other stereo half-image was briefly superimposed on the other eye's dominant rival target (see Figure 4 for an example of one of these displays). By varying the exposure duration of the flashed half-image, Harrad *et al.* discovered that stereopsis was indeed impaired for the 150 milliseconds of exposure but, for durations longer than this, stereo performance was equivalent to that measured under nonrivalry conditions. This critical duration is the same order of magnitude as the threshold values reported by Julesz and Tyler (1976) for detecting transitions from rivalry stimulation to fusion stimulation. It appears, then, that stereopsis can defeat rivalry, after losing the initial, early stage of the battle.

3.4.2.2. *Visual adaptation*. Can a visual stimulus induce an adaptation aftereffect when that stimulus is suppressed from vision for a substantial portion of the adapt-

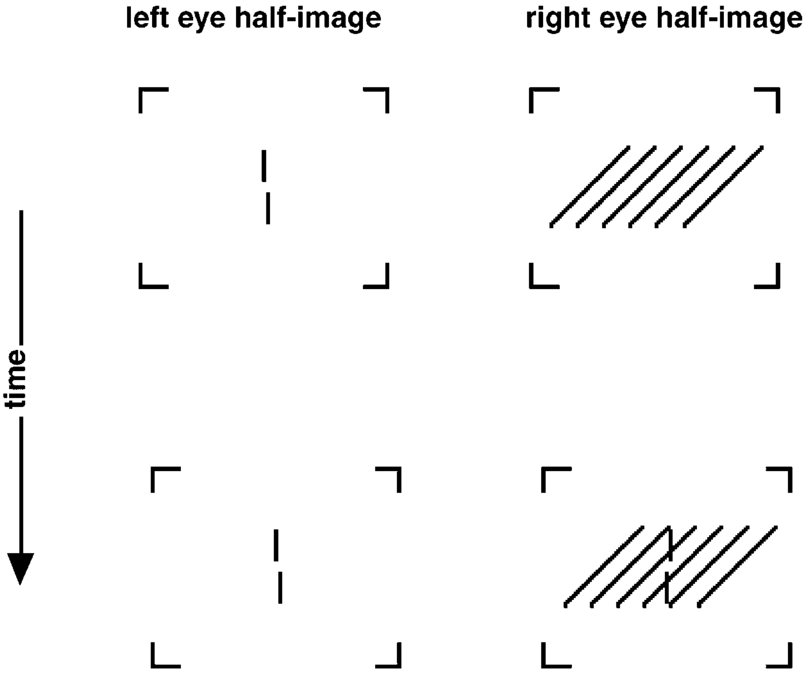

Figure 4. One of the several stimulus conditions used by Harrad *et al.* to study the interaction between stereopsis and binocular rivalry. Observers initially viewed the top pair of half-images, which produced rivalry between the pair of offset vertical lines seen by the left eye and the set of diagonal lines seen by the right eye. When the offset lines were suppressed in their entirety, observers depressed a key which triggered the brief presentation of the pair of offset vertical lines superimposed on the dominant diagonal lines in the right eye. This pair of offset lines, when paired with those imaged in the left eye, created the stimulus conditions for stereopsis (one line appears nearer than the other, in virtue of the relative disparities of the two). During blocks of trials the exposure duration of the briefly presented half-image was varied according to a method of constant stimuli, and duration thresholds for successful stereo performance were derived. For exposure duration less than 150 msec, thresholds measured during rivalry were elevated relative to thresholds measured under nonrivalry conditions. (Figure reproduced with permission from Harrad, R.A., McKee, S.P., Blake, R. and Yang, Y., 1994: Binocular rivalry disrupts stereopsis, *Perception*. **23**, 15–28. Copyright Pion Press.)

ation period? Several research groups have pursued this question, examining a variety of well-known visual aftereffects. With two exceptions, suppression has no effect on adaptation induction, meaning that a full-blown aftereffect is measured immediately following a period of adaptation during which the adapting stimulus is rendered intermittently invisible owing to binocular rivalry. Aftereffects (AE) that escape the sweep of suppression include the grating threshold elevation AE and the spatial frequency shift AE (Blake and Fox, 1974b), the translational motion AE (Lehmkuhle and Fox, 1975; O'Shea and Crassini, 1981) and the tilt AE (Wade and Wenderoth, 1978). Exceptions to this rule are the spiral AE (Wiesenfelder and Blake, 1990), the plaid aftereffect (van der Zwan *et al.*, 1993), subjective contour adaptation (van der Zwan and Wenderoth, 1994) and the square-wave illusion AE (Blake and Bravo, 1985). This pattern of results may reflect multiple, hierarchically arranged processing stages with rivalry suppression sandwiched between certain stages (Blake, 1995). Interpretation aside, these studies demonstrate that a stimulus is not necessarily rendered completely impotent when suppressed from conscious awareness during rivalry.

3.4.2.3. *Perceptual priming*. Prior exposure to a stimulus can subsequently facilitate judgments to other stimuli that are visually or semantically similar to the originally experienced stimulus. Called "priming," this facilitation can take the form of improved recognition, faster picture naming or speeded discrimination of words from nonwords. Two experiments performed in my laboratory have shown that a suppressed stimulus loses its potency as a priming source (Zimba and Blake, 1983; Cave *et al.*, 1998). To paraphrase the title from one of these articles (Zimba and Blake, 1983), a visual pattern out of sight is also a visual pattern out of mind.

This conclusion does not hold for motion priming, however. A clever experiment by Anstis and Ramachandran (1987) showed that people viewing an ambiguous apparent motion (AM) sequence experience one of two possible patterns of motion with equal likelihood when the lengths of the alternative motion paths are equivalent. Motion perception in this case is bistable. People can be biased, however, to see a given pattern of motion if the ambiguous AM sequence is preceded by "priming" motion consistent with that pattern of motion. Capitalizing on motion bistability, Blake, Ahlstrom and Alais (1998) found that motion perception could be biased even when the priming motion was presented within the confines of a suppressed rival target, thus rendering the priming motion completely invisible. This finding, incidentally, squares with earlier work showing that AM can be perceived even when the initial frame of the AM sequence comprises a suppressed rival target (Wiesenfelder and Blake, 1991), and work showing that motion signals from a suppressed eye can interact with those from the dominant eye to determine perceived direction of motion (Carney *et al.*, 1987; Andrews and Blakemore, 1999).

4. What Rivals during Rivalry?

Descriptively speaking, binocular rivalry involves a battle for dominance between conflicting patterns, with the temporary loser suppressed from consciousness for several seconds at a time. Moreover, the observer "sees" that pattern without any knowledge of which eye is dominant at any given moment during rivalry – the observer "sees" a stimulus without regard to its eye of origin. Based on appearances, then, it is entirely reasonable to believe that rivalry involves competition between alternative perceptual interpretations – indeed, this view has strong historical precedence, as summarized at the end of this section. Several lines of psychophysical evidence, however, imply that this belief may be incorrect and

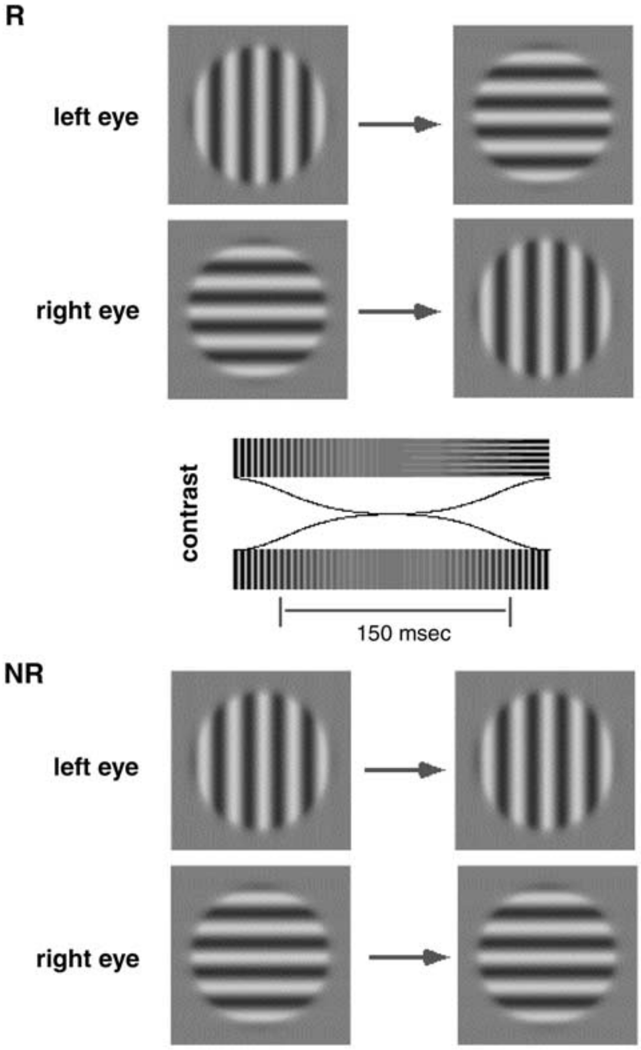

Figure 5. (a) Schematic of the eye swapping procedure deployed by Blake *et al.* (1980). At the start of each trial, observers dichoptically viewed a pair of orthogonally oriented gratings, shown here as horizontal and vertical. Observers depressed a key when the grating of one orientation was visible exclusively, with no hint of the other orientation. On “reversal” trials (R), button depression caused the two gratings to be interchanged between the eyes; to eliminate abrupt transients, the contrasts of the two gratings were ramped off and then back on over a 150 msec period, as indicated by the inset in the Figure. On “non-reversal” trials (NR), button depression caused the gratings to be ramped off and back on, but they were not exchanged between the eyes. On “ordinary” trials, the gratings remained present continuously when observers depressed a button to declare a grating dominant. Observers were instructed to release the button as soon as the suppressed grating achieved dominance. If a given *pattern* were dominant in rivalry, moving that pattern to the other eye should have no effect on its duration of dominance, which normally lasts at least several seconds. But if a region of a given *eye* is dominant during rivalry, swapping the orientations should produce an immediate transition in dominance, for the previously suppressed pattern would now be imaged in the currently dominant eye.

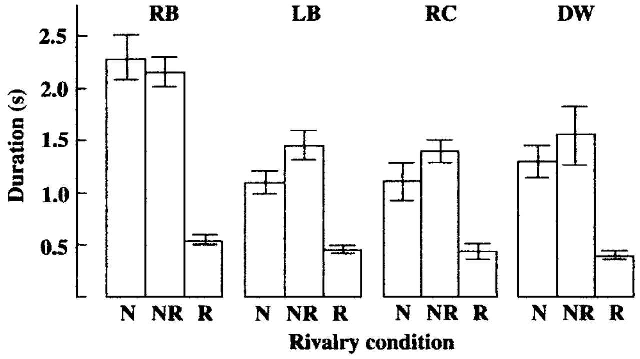

Figure 5. (b) Results showing that dominance durations during exchange trials (R) are significantly shorter than dominance durations during nonreversal trials (NR) and during ordinary trials where nothing happened at all (N). This pattern of results indicates that the visibility of a stimulus during rivalry depends on which eye is viewing that stimulus. (Figure 5b is reproduced with permission from Blake, R., Westendorf, D, and Overton, R., 1979: What is suppressed during binocular rivalry? *Perception* **9**, 223–231. Copyright Pion Press.)

that, instead, it is a region of one “eye” that is temporarily dominant, not a given “stimulus.” Consider the eye swapping procedure illustrated schematically in Figure 5.

An observer depresses a switch when the rival pattern shown to one eye is dominant exclusively, the other being completely suppressed from vision. If this keypress causes the two rival patterns to be swapped between the two eyes, the previously dominant pattern will now be shown to the previously suppressed eye and vice versa. When this happens, the outcome is clear (Blake *et al.*, 1980): the dominant pattern abruptly becomes invisible and the previously suppressed pattern becomes dominant, implying that it was the region of an eye that was dominant, not a particular stimulus. Control trials confirm that this outcome is not due simply to turning the patterns “off” and then back “on.”

Next, consider the stimulus change procedure. Here the orientation, the spatial frequency or the direction of motion of a stimulus is changed while that stimulus is suppressed. These changes, regardless how large, go unnoticed until seconds later when the suppressed eye returns to dominance – again, it seems not to be a particular pattern that is suppressed, but instead the region of an eye where a rival target is imaged (Blake and Fox, 1974a; Blake *et al.*, 1998). For “change” to go undetected during suppression, it is necessary to avoid sharp transients associated with replacement of one stimulus by another; as noted above, transients reliably break suppression (Walker and Powell, 1979).

A third piece of evidence pointing to a role for the “eyes” in rivalry comes from a study using stereo half-images that included regions in which corresponding retinal areas viewed dissimilar patterns (Shimojo and Nakayama, 1990). When that dichoptic stimulation was consistent with the partial occlusion (an ecologically valid situation), binocular vision was stable, but when dichoptic stimulation was inconsistent with partial occlusion binocular rivalry was experienced. In effect, these two alternative perceptual outcomes were dependent on which eye received which pattern of dichoptic stimulation, indicating that the rivalry process takes into account the eye of origin of monocular stimulation. A similar conclusion was reached by Ooi and He (1999), who found that a monocularly viewed “pop-out” array could bias dominance and could weaken suppression of a given eye during binocular rivalry; their results, too, require that the rivalry process have some record of which stimulus is being viewed by which eye.

On the other hand, several other pieces of evidence favor a “stimulus” based theory of rivalry. For example, rival targets differing in form and color can sometimes achieve states of dominance in which the color from one eye’s image combines in dominance with the form from the other eye’s image, temporarily creating a binocular impression that corresponds with neither monocular component (e.g., Breese, 1909; Creed, 1935; but see Hollins and Leung, 1978, for negative evidence on this point). These unusual periods of interocular combination could be construed as illusory conjunctions of the sort observed with briefly flashed arrays of colored objects (Treisman and Schmidt, 1982). Similarly, perceived direction of motion of a dominant stimulus can be influenced by the velocity of a suppressed stimulus (Andrews and Blakemore, 1999). In both of these instances, the perceptual experience during dominance phases of rivalry sometimes comprise an amalgam of attributes from *both* eyes’ views, which should be impossible if all information from a given region of one eye were lost during suppression.

Advocates of “stimulus” rivalry also point to “interocular grouping” during rivalry as evidence against “eye” rivalry (Kovács *et al.*, 1996). Figure 6 illustrates one particularly captivating instance of this phenomenon. With some practice viewing these patchwork rival figures, observers are able to see either of two globally coherent figures: the face of an ape or a complete array of text. These periods of coherent perception, of course, can only be achieved by very specific combinations of left-eye and right-eye components that are dominant simultaneously; obviously, one eye alone is not responsible for dominance. Evidence for simpler versions of interocular grouping have been reported by others as well (Diaz-Caneja, 1928, translated by Alais, O’Shea, Mesana-Alais and Wilson, 2000; Dörrenhaus, 1975; Alais and Blake, 1999).

Thus vision seems to be exploiting structural regularity to link distributed features in these kinds of displays, and one might be tempted to attribute these linkages to “top-down” processes signifying meaningful perceptual interpretations. This attribution, however, may be premature. Within early visual cortical areas, including V1, there exist long-range, lateral connections among orientation-selective neurons, with these connections arranged so as to strengthen responses among neurons signalling extended contours (Bosking *et al.*, 1997; Das and Gilbert, 1995). These lateral connections provide a possible neural substrate for embodiment of visual context effects, without the need for “top-down” feedback (Field *et al.*, 1993). Of course, there also is abundant evidence for feedback

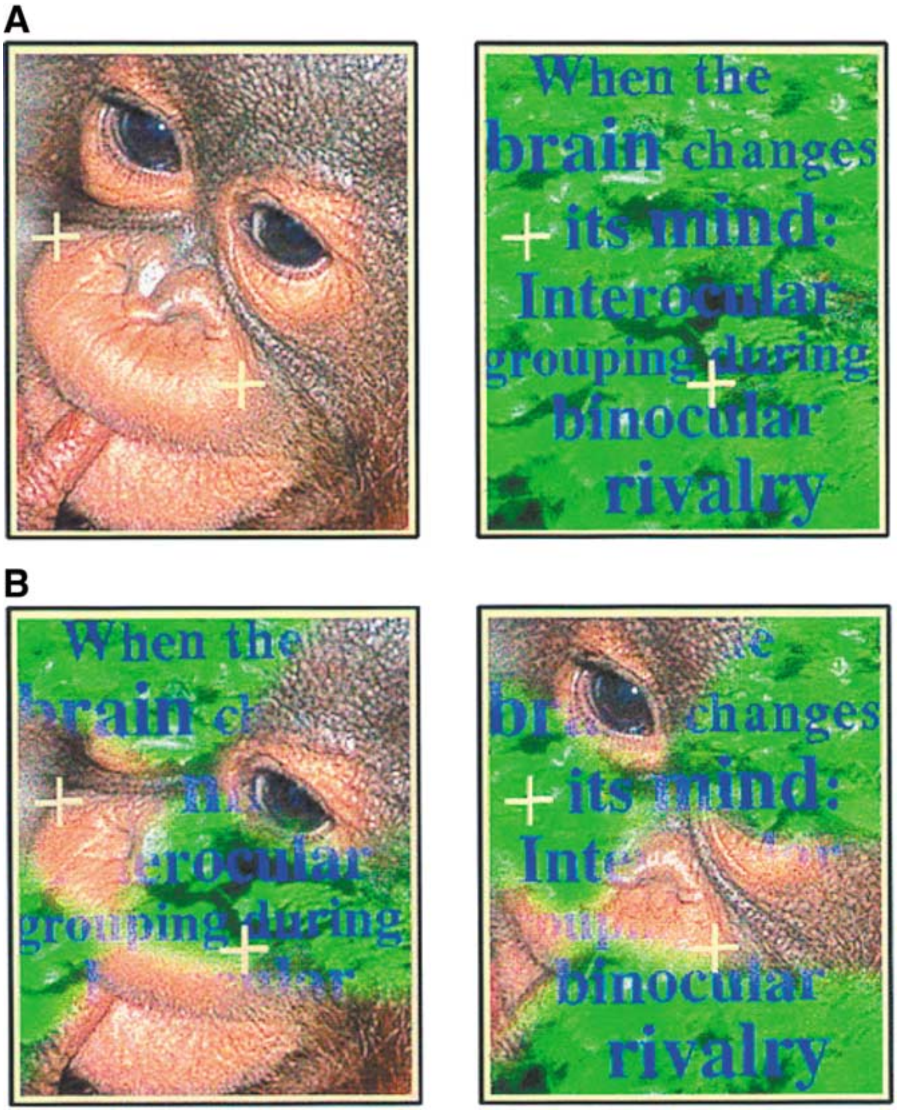

Figure 6. Rival targets used by Kovács *et al.* (1996). Shown in the upper part of the figure (A) is a pair of rival targets consisting of dissimilar pictures (in this case the face of an ape and a page of text) viewed by left and right eyes. Shown in the lower part of the figure (B) is a pair of rival targets each consisting of portions of the ape's face and portions of the text. Upon viewing these mixed rival targets, observers occasionally experience periods during which the ape or the text is dominant completely, an outcome that can only be achieved by the combination of image fragments from both eyes. Kovacs *et al.* found the incidence of complete dominance to be greater than that expected on the basis of chance alone. Readers may free-fuse these rival targets to judge the incidence of interocular grouping. (Figure reproduced with permission from Kovacs, I., Papathomas, T.V., Yang, M. and Fehér, A. 1997: When the brain changes its mind, Interocular grouping during binocular rivalry, *Proc. Natl. Acad. Sci. USA* **93**, 15508–15511. Copyright National Academy Press.)

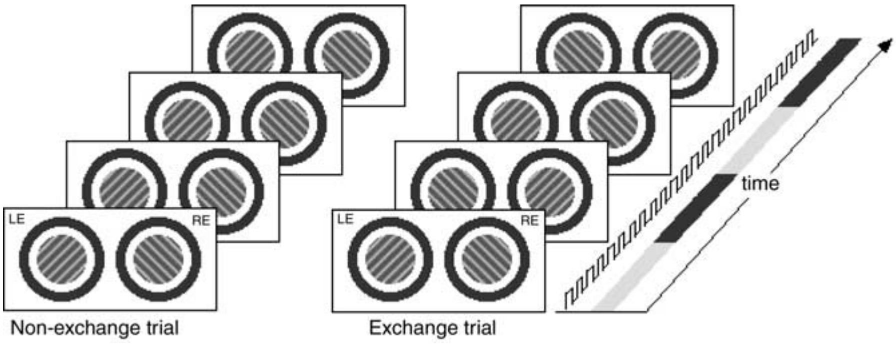

Figure 7. Schematic of stimulus displays used by Logothetis *et al.* (1996) and, subsequently, by Lee and Blake (1999). On some observation trials (exchange trial), orthogonally oriented rival gratings are flickered at 18 Hz and are intermittently exchanged between the eyes at a brisk rate (shown here as 3 Hz, the value used by Logothetis *et al.*); on other trials (non-exchange trial), the rival gratings flicker at 18 Hz but are not exchanged between eyes. (Figure reproduced with permission from Lee, S.H. and Blake, R., 1998: Rival ideas about binocular rivalry, *Vision Res.* **39**, 1447–1454. Copyright Elsevier Press.)

connections from higher cortical areas to lower ones. Thus, it stands to reason that feedback information registered during dominance phases of rivalry could impact neural events transpiring anywhere along the visual pathways, in a manner surmised by Papathomas *et al.* (1999). It remains for future work to reveal the extent to which visual image meaning per se can promote dominance during rivalry. In the meantime, these compelling interocular grouping phenomena certainly underscore that rivalry does not involve dominance of an entire eye; instead, spatially distributed image features can be cooperatively grouped to promote figural coherence. But interocular grouping does not rule out the possibility that the suppressed portions of an image are, in fact, linked to a given eye. Global dominance may be achieved by the spatial amalgamation of “eye” based features.

Perhaps the most influential piece of evidence favoring “stimulus” rivalry is provided by a paper published in *Nature* by Logothetis *et al.* (1996) in which they created novel stimulus conditions that unequivocally preclude eye rivalry. Using a variant of the eye interchange technique, they repetitively exchanged the two eyes’ patterns every 333 msec. In addition, both rival targets (low contrast, orthogonally oriented gratings) were rapidly flickered at 18 Hz (see right-hand drawing in Figure 7, labelled “Exchange trial”). Observers viewing this unique display experienced periods during which one grating was dominant for several seconds at a time, with dominance fluctuating between the two gratings in a slow, irregular time-course just like that experienced during conventional rivalry. Logothetis *et al.* referred to this outcome as “stimulus rivalry” because observers were perceiving a given stimulus for durations that exceeded the rate at which that stimulus was exchanged between the eyes – clearly, these extended periods of stimulus dominance could not be attributable to “eye” rivalry. Generalizing from their results, Logothetis *et al.* concluded that rivalry under conventional conditions, wherein stimuli are not swapped between the eyes, also entails alternations in dominance between competing stimuli, not between competing eyes. According to Logothetis (1998), "the dominance and suppression of a pattern during rivalry reflects the excitation and inhibition of cell populations in the higher visual areas, which are directly involved in the representation of visual patterns." He echoes this view in a later essay (Logothetis, 1999) by saying, "rivalry occurs because alternate stimulus representations compete in the visual pathway (p. 73)."

Intrigued by Logothetis *et al.*'s report and their conclusions, members of my laboratory felt it important to test the generality of these findings. Accordingly, Sang-Hun Lee and I created modified versions of the unique displays used by Logothetis *et al.*, including ones that examined "eye" vs "stimulus" rivalry over a wider range of spatial and temporal conditions (Lee and Blake, 1999). Specifically, we repetitively interchanged left and right eye rival targets while, at the same time, flickering those targets at 18 Hz ("exchange trials" in Figure 7). We also intermixed conventional, "non-exchange" trials on which rival targets were flickered at 18 Hz but were *not* rapidly swapped between the eyes ("Non-exchange trials" in Figure 7). On any given trial observers did not know which type of presentation was being presented – eye swapping or not – and following each trial observers indicated whether they experienced "slow, irregular" changes in dominance, "rapid, regular changes" in dominance, or "mixed and patchy" dominance. All four observers, including three who were naive about the purpose of the experiment, experienced "slow, irregular" changes in dominance under the conditions tested by Logothetis *et al.*, i.e., low contrast, high spatial frequency gratings interchanged between the eyes at 3 Hz. At slower exchange rates and at lower spatial frequencies, however, these observers experienced "rapid, regular" fluctuations in dominance, indicating that they were perceiving the regular flips in orientation presented to a given eye (i.e., "eye" rivalry). At the lowest spatial frequencies tested, observers primarily experienced piecemeal rivalry. In other words, "stimulus" rivalry is confined to a rather narrow range of spatial and temporal conditions (see Figure 8). We also found that the incidence of "stimulus rivalry" within this restricted, optimal region of spatio-temporal space was markedly dependent on the nature of the 18 Hz flicker. We picked the best spatial frequency and the best eye exchange rate for producing "stimulus rivalry" and then tested using different conditions of temporal modulation. When the rapid, 18 Hz flicker was eliminated, the incidence of "stimulus rivalry" dropped from 68% to 30%. Moreover, when the non-flickering gratings were exchanged at 3 Hz between the eyes in a manner that eliminated abrupt transients (gaussian contrast modulation rather than square-wave modulation), the incidence of "stimulus rivalry" dropped to 10%.

Based on the results from this study, we (Lee and Blake, 1999) concluded that the narrow range of conditions yielding "stimulus rivalry" effectively overrides normal rivalry, perhaps because of the complex train of transient events accompanying rapid flicker and eye exchange. After all, it is known from the study by

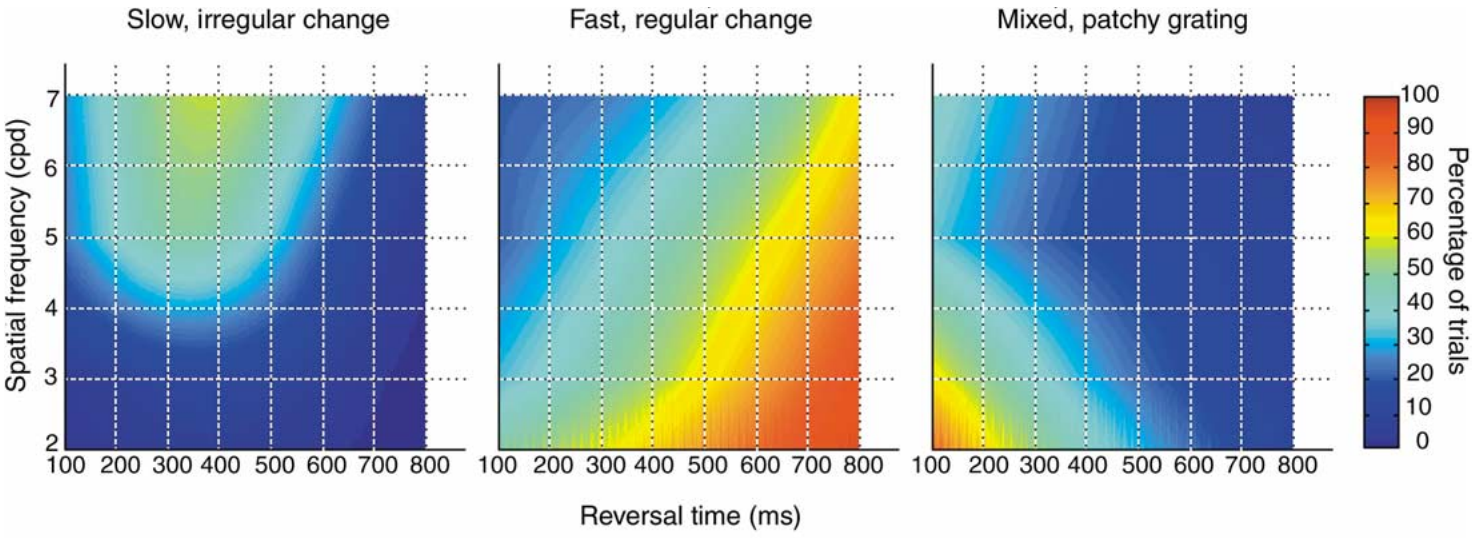

Figure 8. These three graphs show the relative incidence of "stimulus" rivalry, conventional rivalry and piecemeal rivalry for different conditions of dichoptic stimulation measured using the exchange technique illustrated in Figure 5. For these measurements, the two eyes viewed orthogonally oriented gratings that flickered on/off at 18 Hz and were interchanged between the eyes at a rate that varied over blocks of trials (duration shown along the abscissa). Grating contrast was constant at 25% and spatial frequency of both gratings varied over the range shown on the ordinate. Evidence for "stimulus" rivalry (slow, irregular change) was observed almost exclusively at high spatial frequencies and at fast rates of eye exchange; throughout most of the spatio-temporal space, observers experienced either conventional rivalry (fast, regular change) or piecemeal rivalry (mixed, patchy grating). (Figure reproduced with permission from Lee, S.H. and Blake, R., 1998: Rival ideas about binocular rivalry, *Vision Res.* **39**, 1447–1454. Copyright Elsevier Press.)

O'Shea and Crassini (1984) that transients can disturb rivalry, and the same conclusion is implied by test probe experiments showing that abrupt stimulus changes disrupt the normal course of rivalry (Fox and Check, 1968; Walker and Powell, 1984; Blake *et al.*, 1990). It is important to note that the results of Lee and Blake do not discredit the existence of "stimulus rivalry" but, instead, indicate that "stimulus rivalry" represents yet another intriguing form of perceptual bistability that can arise when normal binocular rivalry is disengaged.

Despite this limitation on the generality of the findings of Logothetis *et al.* (1996), the "stimulus" view of rivalry is widely accepted in the field of visual neuroscience, having been embraced by a number of investigators interested in perceptual organization and in conscious awareness. Thus, for example, Andrews and Purves (1997) opine that "when the stimulus is an ambiguous figure or dichoptically rivalrous, then perception fluctuates between various possible associations in an ongoing effort to find a definite meaning (p. 9908)." According to this view, then, binocular rivalry is just one member of a large class of multistable phenomena all involving fluctuations in alternative object interpretations. Included in that class along with rivalry are Rubin's vase/face illusion, the Necker cube, the "old woman/young girl" figure, kinetic depth reversals, the Schroeder staircase and the Hering bent card illusion. Certainly at the descriptive level, rivalry does behave like the rest of these, with fluctuations in alternative interpretations over time. And there is some evidence that successive durations of these alternative perceptual states are independent random variables. However, this resemblance does not necessarily mean that all these phenomena arise from a common visual mechanism involving the generation of object descriptions. Indeed, there is evidence (Struber and Stadler, 1999) that "top-down" influences (an instruction to "control" the reversal rate) are more successful for contrast-reversal figures (e.g., the "duck/rabbit" figure) than for perspective-reversal figures (e.g., the Necker cube). In addition, the reversal rate tends to increase throughout prolonged viewing of ambiguous figures (e.g., Brown, 1955) while the rate tends to decrease during prolonged viewing of binocular rivalry. The observation that different multistable phenomena, including binocular rivalry, exhibit comparable temporal fluctuations may reflect a fundamental property of neural dynamics, but not necessarily a common neural mechanism.

Besides the influential study by Logothetis *et al.* (1996), there is another strong reason for the growing popularity of the "stimulus" view of rivalry: it seems to have the force of neurophysiological evidence behind it. In "higher" temporal lobe areas thought to mediate visual object recognition, all neurons show modulations in activity in synchrony with a monkey's report of fluctuations in perceptual dominance (Sheinberg and Logothetis, 1997); cell activity, in other words, closely mirrors an animal's perceptual experience. In contrast, relatively few neurons in "early" visual areas exhibit such tight coupling between firing rate and perception, including neurons in area MT (Logothetis and Schall, 1989) and monocular neurons in area V1 (Leopold and Logothetis, 1996). This pattern of neurophysiological data has been interpreted by some as evidence against "eye" rivalry, since eye-of-origin information is maintained only within V1 neurons whose activity is mostly unrelated to fluctuations in dominance. But with all due respect to neurophysiology, data from single-cell recordings cannot dictate how psychophysical experiments must turn out. A failure to find neurophysiological evidence favoring "eye" rivalry can not negate perceptual evidence implicating "eye" rivalry; instead, that failure implies that it may be necessary to rethink the nature of the neural concomitants of rivalry.

Incidentally, the phrase "eye" rivalry is sometimes used synonymously with "early" rivalry, meaning that the neural events triggering and controlling rivalry transpire at "early" stages of visual processing. It should be noted, however, that "early" rivalry does not necessarily mean that competition occurs between corresponding regions of the two eyes. One could imagine an "early" rivalry process that operates on local image features registered among binocular neurons. Distinguishing "early" from "late" rivalry using psychophysical techniques is tantamount to determining the extent to which rivalry is governed by cognitive factors, including object semantics. The brain imaging techniques of functional magnetic resonance imaging (fMRI) and magnetic encephalography (MEG) can also be employed fruitfully to address this issue of early vs late rivalry (Lumer *et al.*, 1998; Tong *et al.*, 1998; Srinivasan *et al.*, 1999; Polansky *et al.*, 2000); elsewhere in this special issue, these techniques are discussed by Tong (2001).

As an historical aside, it is interesting to note that this currently popular view – stimulus rivalry – is reminiscent of a position championed by several noted authorities of their time, including Helmholtz, William James and Charles Sherrington. Although they didn't use these exact words, they construed rivalry as a high-level, central process in which fully elaborated monocular views competed for mental dominance. For example, Sherrington (1906) wrote:

> Only after the sensations initiated from right and left corresponding points have been elaborated, and have reached a dignity and definiteness well amenable to introspection, does interference between the reactions of the two eye-systems occur. The binocular sensation attained seems combined from right and left uniocular sensations elaborated independently .... In retinal rivalry we have an involuntarily performed analysis of this sensual bicompound. The binocular perception in that case breaks down, leaving phasic periods of one or other of the component sensations bare to inspection (p. 379).

This view seems to have survived well into the latter part of this century, as exemplified by Walker's widely cited review of the binocular rivalry literature in which he endorses the classical, cognitive view (Walker, 1978). It was Levelt's influential monograph (Levelt, 1965) that introduced an alternative conceptualization of rivalry, one treating it as a relatively "low level" process responsive to unrefined image primitives such as luminance contrast and contour density. Although it took some years for Levelt's ideas to catch on, by the mid-70's vision scientists were beginning to construe rivalry as arising from reciprocal inhibition between featuredetecting neurons in early vision (Blakemore *et al.*, 1972; Wade, 1974; Abadi, 1976; Lehky, 1988; Blake, 1989). In the last decade, however, the pendulum has begun to swing back to the classic, "cognitive" view.

5. On the Neural Bases of Binocular Rivalry

A major purpose of this special issue of *Brain and Mind* is to highlight binocular rivalry's potential usefulness as a "tool" for discovering the neural concomitants of conscious awareness. It is appropriate, therefore, to conclude this article with some speculations on those concomitants, including some caveats about what to look for and where to look.

5.1. BINOCULAR FUSION VS BINOCULAR RIVALRY

What is rivalry's relation to normal binocular single vision? An enduring idea in the vision literature posits that rivalry occurs all the time, not just when the two eyes receive dissimilar stimulation (e.g., Asher, 1953). According to this idea, alternating suppression is *the* mechanism responsible for single vision; it's always occurring but we fail to realize it because the two monocular views are normally identical. Known as suppression theory, this idea has had adherents as recently as the late twentieth century (e.g. Wolfe, 1986).

The weight of the evidence now, however, goes against strict suppression theory (e.g., O'Shea, 1987), although binocular suppression may play a role in eliminating diplopia for images formed by objects located far away from the horopter (Ono *et al.*, 1977). A major reason for believing that binocular single vision is not attributable solely to suppression is that normal single vision is not accompanied by transient losses in visual sensitivity that are the hallmark of suppression phases of binocular rivalry (e.g., Wales and Fox, 1970). For this and other reasons, it is now believed that binocular fusion takes precedence over binocular rivalry (Blake and Boothroyd, 1985). Only when the visual system fails to find left- and right-eye matching features does vision lapse into reciprocal periods of dominance and suppression. This conclusion is important, for it implies that one should expect to find the neural concomitants of rivalry only when an observer is explicitly experiencing rivalry and not when experiencing stable binocular single vision.

5.2. IS RIVALRY A PROPERTY OF JUST ONE OF THE "MULTIPLE" VISUAL PATHWAYS?

It is widely accepted that primate vision comprises multiple neural pathways, each specialized to some degree in terms of its selectivity to spatial and temporal frequency, color, motion and luminance contrast. There remains active debate concerning the particulars of these pathways and the extent to which they interact, but the general notion of multiple pathways is deeply ingrained in contemporary visual neuroscience. Is there reason to believe that the neural events underlying binocular rivalry arise within just one of these putative pathways?

Based on the spatial frequency range yielding the most clear-cut rivalry, Hollins (1980) speculated that rivalry is crucially dependent on activity in what at that time was dubbed the "transient" channel and which today we would call the "magnocellular pathway." The same conclusion was reached by Livingstone and Hubel (1987), who thought that stimulation favoring the parvocellular pathway yielded fusion of dissimilar monocular stimuli, not rivalry. In subsequent work, however, this conclusion has not received support. For one thing, we know that rival targets "seen" primarily by the parvocellular pathway can nonetheless yield clear binocular rivalry (Kulikowski, 1992; O'Shea and Williams, 1996). For another, at least some stimulus conditions that should strongly activate the magnocellular pathway in fact fail to generate binocular rivalry (O'Shea and Blake, 1986; Liu *et al.*, 1992) or yield weak rivalry at best (Carlson and He, 2000). Certainly, the limited fMRI data on fluctuations in neural activity during rivalry points to strong modulation in neural activity within ventral stream structures typically associated with the "form" or parvocellular pathway (Tong *et al.*, 1998). The weight of evidence today is against the hypothesis that rivalry is a property primarily of the magnocellular pathway.

Is there reason to believe that it is the parvocellular pathway that makes the more robust contribution to rivalry, as proposed by some (Ramachandran, 1991; Carlson and He, 2000)? As mentioned above, there are good reasons for believing that rivalry can be experienced under stimulus conditions that activate just the parvocellular pathway. Moreover, several psychophysical studies indicate that motion information can be integrated between the two eyes while, at the same time, those eyes are engaged in form rivalry (Andrews and Blakemore, 1999; Carlson and He, 2000) or in color rivalry (Carney *et al.*, 1987). Recall, too, that motion information associated with a suppressed rival target can nonetheless generate the translational motion aftereffect (Lehmkuhle and Fox, 1975), can support perception of apparent motion (Wiesenfelder and Blake, 1991) and can bias perception of otherwise ambiguous motion (Blake *et al.*, 1998). All these observations are consistent with the hypothesis that rivalry transpires mainly in the parvocellular pathway, with aspects of vision associated with the magnocellular pathway escaping rivalry's vicissitudes. Still, there are studies reporting vigorous binocular rivalry when the two eyes receive incompatible directions of motion (Blake *et al.*, 1985), including motion at speeds strongly favoring magnocellular activation (van de Grind *et al.*, in press). Moreover, observers can experience binocular rivalry even between competing motion aftereffects, provided that those aftereffects are elicited by real motion (Blake *et al.*, 1998). It is commonly thought that the MAE arises from neural signals within the magnocellular pathway (e.g., Tootell *et al.*, 1995). It is not immediately obvious how to reconcile these latter findings with the idea that rivalry is the exclusive consequence of parvocellular activity.

5.3. DOES RIVALRY RESULT FROM DISTRIBUTED NEURAL PROCESSES?

Simply observing rivalry, one is fascinated and intrigued that a highly visible, complex, interesting stimulus can disappear from conscious awareness for several seconds at a time. Though still imaged on the retina, that stimulus behaves visually as if it intermittently ceased to exist. Based on this phenomenology, one might be tempted to conclude that the neural events underlying rivalry are as profound as those accompanying intermittent physical removal of a stimulus. However, this temptation may be misleading – relatively modest shifts in the balance of neural activity between different populations of neurons may be sufficient to promote dramatic fluctuations in the visual appearance of the objects represented by that activity. In this regard, we are reminded that, during suppression phases of rivalry, visual sensitivity is not dramatically depressed but, instead, is reduced by a very modest degree. The neural concomitants of suppression, in other words, do not engender a complete blockade of information transmission but, instead, seem to embody a rather modest gain change. To the extent that this view is correct, neurophysiologists searching for those neural concomitants may need to look for more subtle changes in cellular responses coincident with fluctuations in dominance and suppression.

By the same token, psychophysical studies of rivalry may need to rethink how to predict the effect of suppression on other visual phenomena such as adaptation aftereffects. In much of the past work on this question, including studies by me, the effects of intermittent suppression during rivalry have been contrasted with intermittent physical removal of that rival target (e.g., Blake, 1995). But this comparison may be misleading if the neural concomitants of suppression, in fact, are tantamount merely to attenuating, not eliminating, neural signals associated with a given stimulus. To illustrate, consider suppression's failure to reduce the magnitude of the conventional motion aftereffect (Lehmkuhle and Fox, 1976), which has been interpreted to indicate that registration of information about translational motion is unaffected by suppression. Perhaps suppression does not block registration of that information, thereby reducing the overall duration of adaptation, but instead dilutes the effective contrast of the adapting stimulus by an amount insufficient to impact the magnitude of the resulting aftereffect. So, in brief, we should not necessarily equate phenomenal suppression of a stimulus with physical removal of that stimulus. To paraphrase an idea advanced by Ramachandran (1991), rivalry need not involve a complete occlusion of one eye's signals.

In a related vein, it may also be an oversimplification to speak of rivalry "occurring" at any one particular neural locus (another oversimplification of which a number of researchers are guilty, including me). Indeed, brain imaging studies of humans experiencing rivalry (Polansky *et al.*, 2000; Tong *et al.*, 1998; Lumer *et al.*, 1998; Tononi *et al.*, 1998) and single-unit studies from awake, behaving monkeys experiencing rivalry (Logothetis, 1998) both imply that traces of the neural signature of rivalry are detectable at early stages of visual processing, with those traces then being amplified at subsequent, higher stages. Rivalry may result from a cascade of neural events transpiring at multiple sites along the visual pathways, with no single site constituting "the" locus of rivalry (e.g., Ooi and He, 1999).

There is another sense in which rivalry could result from distributed processes, not a single mechanism operating at one level of vision. As noted above, binocular rivalry can be characterized in terms of its spatial extent, its temporal dynamics and its generality beyond those conditions triggering rivalry. These aspects of rivalry are not necessarily tied to a single, omnibus process, although one frequently encounters the phrase "rivalry mechanism" in discussions of binocular rivalry. The stimulus determinants of fluctuations in dominance and suppression (i.e. temporal dynamics) are not necessarily those governing the spatial extent of rivalry. Similarly, it is conceivable that the well-established stimulus determinants of suppression phases (i.e., energic variables like luminance and contrast) differ from those controlling dominance durations (e.g., context, meaning). Indeed, to reconcile the diverse findings concerning rivalry – including controversial results on the role of meaning and context in rivalry – it may be important to distinguish between processes responsible for initiation of rivalry and selection of one eye's input for dominance from processes responsible for the implementation and maintenance of suppression. It is entirely plausible that suppression and selection are the result of separate mechanisms operating at different stages in the visual system. In a sense, selection involves the comparison of information presented to the two eyes to establish the degree of correspondence and, perhaps, the relation of a given stimulus to other features within the visual field. Once selection has been accomplished, one stimulus (or portions of it) is temporarily "rejected" (i.e. suppressed) while another stimulus dominates. The fate of the suppressed stimulus – and other, new information presented within its immediate vicinity – can be determined by neural events different from those registering the initial incompatibility of monocular stimuli. This idea of rivalry being a dual process has been elaborated by Fox (1991), and it offers a potentially useful scheme for reconciling seemingly conflicting results within the rivalry literature.

6. Concluding Remarks

To close on a personal note, twenty six years ago when I published my dissertation work on binocular rivalry (Blake and Fox, 1974a,b), the phenomenon was considered by some to be a laboratory curiosity of questionable relevance for an understanding of perception.[5] Since that time, however, binocular rivalry has been "rediscovered" by the neuroscience community, undoubtedly because of its potential as a tool for studying the neural concomitants of visual awareness using both single cell responses (Logothetis, 1998; Engel *et al.*, 1999) and brain imaging techniques (Tong *et al.*, 1998; Polansky *et al.*, 2000). Accompanying rivalry's rediscovery has been a flurry of clever psychophysical studies of rivalry that,

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[5] J.J. Gibson (1966) colorfully characterized rivalry as "optical trickery."

among other things, challenge models positing that rivalry is based on competing eyes (Blake, 1989) and strengthen the case for the involvement of context, attention and meaning in the promotion of dominance. For seasoned aficionados of binocular rivalry, it is gratifying, not to mention invigorating, to experience a resurgence of interest in this fascinating and still enigmatic phenomenon.

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