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Landmarks in the History of Binocular Rivalry

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Why, in recent years, have so many perceptual psychologists, cognitive neuroscientists, neurophysiologists, philosophers, and the occasional Nobel laureate gotten excited about binocular rivalry? Why has the study of rivalry developed into a veritable industry occupying the time and resources of some of our best and brightest? It is true that many used to think that rivalry was fundamental to vision, occurring all of the time for all of us (Asher, 1953). But the weight of evidence now runs against this so-called suppression theory (O'Shea, 1987), at least the more radical version equating binocular single vision with wholesale monocular dominance (for a more refined version of suppression theory, see Wolfe, 1986). So, except for some individuals with eye misalignment, binocular rivalry is a laboratory artifact—the result of “optical trickery,” as Gibson (1966) put it. Why, then, the upsurge of interest in the phenomenon?

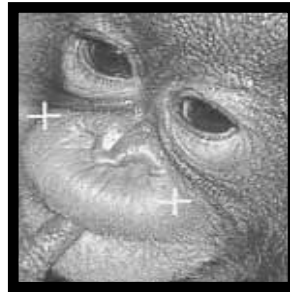
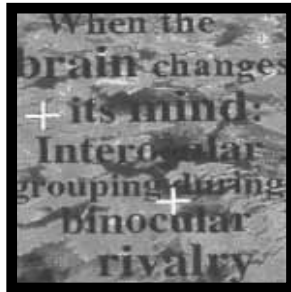
These days a single answer to this question echoes throughout the vision literature: binocular rivalry provides a potentially powerful tool for learning about the neural concomitants of visual awareness or, as some have dubbed it, the “neural correlates of consciousness” (Crick and Koch, 1998). To illustrate rivalry's utility, consider the pair of dissimilar pictures shown in figure 1.1a (see also plate 1). Suppose the picture of the house is viewed by one eye and the picture of the face is viewed by the other eye. Even though these pictures are continuously imaged on the two retinas, we tend to see only one of the two at any given moment—the temporary “winner” dominates perception and the loser is vanquished, or suppressed, from conscious awareness.

Of course, victory by one image is only temporary, for sooner or later the suppressed image will achieve dominance and the previously dominant image will be erased from awareness; these alternations in perceptual dominance will continue for as long as the dissimilar images are viewed,

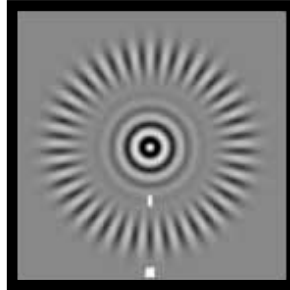
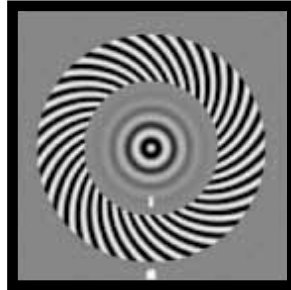
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d



with the rate of alternations varying markedly among individuals (for more discussion of individual differences, see chapter 15 in this volume). Figures 1.1b–d show other examples of dichoptic half-images that produce vigorous rivalry; some of those rival figures are also shown as anaglyphs in color plate 1. Readers with access to red/green viewing glasses can experience rivalry without having to free-fuse the two rival pairs.

These fluctuations in perception during rivalry must surely result from fluctuations in neural activity associated with the two alternative perceptual outcomes. In principle, then, it should be possible to identify the nature and locus of those fluctuating neural events, thereby revealing something about the neural concomitants of visual awareness. The same line of reasoning can be applied to forms of perceptual ambiguity besides rivalry, including reversible figures such as Rubin’s vase/face illusion (see chapter 11 in this volume) and bistable motion stimuli such as plaids (see chapter 8 in this volume). In these cases, too, unchanging visual stimulation triggers changing visual perception, again implicating fluctuating neural activity.

Thus this potential link between visual awareness and underlying neural events represents a chief reason for the recent, growing interest in binocular rivalry and other forms of perceptual ambiguity (Blake and Logothetis, 2002). In a related vein, there is a school of thought saying that rivalry in fact reveals a fundamental aspect of human cognition. According to this idea, human vision is routinely faced with weak, ambiguous sensory information that necessarily requires active interpretation guided by knowledge, experience, and intentions. According to this view, binocular rivalry represents a patent manifestation of this interpretative process (e.g., Leopold and Logothetis, 1999) and, for this reason, provides a promising means for isolating and studying brain areas involved in attention and selection. Chapters 7, 9, and 13 in this volume develop this notion in more detail.

◀ **Figure 1.1** Four examples of pairs of dissimilar images that, when viewed dichoptically, trigger binocular rivalry; some of these rival targets are also produced as anaglyphs in plate 1. (a) House/human face rival targets used by Frank Tong and colleagues to study brain activation during dominance and suppression phases of rivalry (work detailed in chapter 4). (b) Monkey/jungle scene targets used by Kovács et al. (1996) to examine spatial grouping in binocular rivalry (work described in chapter 9). (c) Concentric radial grating and spiral grating used by Wilson, Blake, and Lee (2001) to measure the spread of dominance at the time of rivalry transitions (work described in chapter 17). (d) Photographs of different individuals that, when viewed dichoptically, yield binocular rivalry despite similarities in global facial structure; in reality, the two individuals pictured here experience stable friendship, with their differences of view resolved harmoniously. See plate 1 for color version.

On the other hand, there is another school of thought that distinguishes between binocular rivalry and other forms of perceptual ambiguity, with rivalry attributed to reciprocal inhibition among neurons at relatively early stages of visual processing involved in stereoscopic vision (e.g., Blake, 1989). Evidence bearing on this alternative viewpoint appears in chapters 3, 4, and 16 of this volume.

This opening chapter sidesteps the controversies concerning the nature of binocular rivalry and, instead, provides an overview of the major characteristics of rivalry, characteristics that must be accommodated by any successful theoretical account of rivalry. Rather than simply catalog these characteristics of rivalry, as done elsewhere (Blake, 2001), this chapter presents them within a historical context that highlights some of the landmark discoveries about rivalry and acknowledges the individuals who made them.

WHEATSTONE ON BINOCULAR RIVALRY

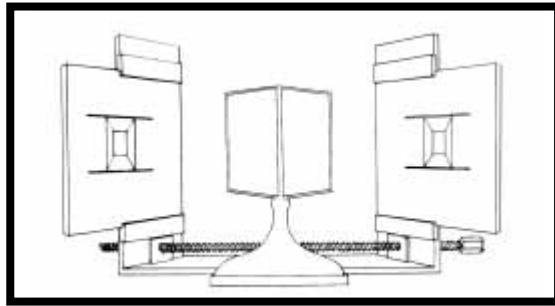
Among vision scientists, Sir Charles Wheatstone (figure 1.2a) is appropriately celebrated for his invention of the stereoscope, the optical device by which the two eyes can receive independent stimulation (technically called “dichoptic” stimulation). With the stereoscope (figure 1.2b), Wheatstone was able to show convincingly that two-dimensional, right- and left-eye views could harmoniously blend into a stable, three-dimensional impression of the visual world, and the geometry underlying this cooperative interaction formed the core of his famous paper (Wheatstone, 1838). Also that paper is the first systematic description of binocular rivalry, the vigorous, unremitting conflict in visual perception instigated when the left eye and the right eye receive radically different views. As Wade (1998) has documented, others had observed and commented on binocular rivalry before the nineteenth century.

But it is Wheatstone who deserves credit for bringing this fascinating outcome of dichoptic stimulation to the foreground of vision science. Indeed, the importance of his observations cannot be overemphasized, for without doubt they played a key role in stimulating the thinking of later giants in the field of vision, including Helmholtz (1925), William James (1891), and Sherrington (1906). Moreover, it was his invention of the stereoscope that facilitated the scientific exploration of binocular rivalry. In chapter 2 of this volume, Wade provides a colorful account of the controversy surrounding Wheatstone’s simple, clever invention and the ensuing arguments over the novelty of his observations concerning stereopsis;

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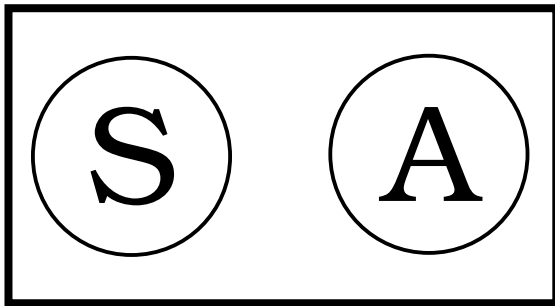


Figure 1.2 (a) Drawing of Sir Charles Wheatstone, whose invention of the stereoscope brought the phenomenon of binocular rivalry to the attention of the scientific community. (b) Schematic of stereoscope invented by Wheatstone and used to observe rivalry. (c) Schematic of rival letter targets described by Wheatstone.

in the next few paragraphs of this chapter, I will concentrate on Wheatstone's seminal contributions to binocular rivalry.

In the span of two paragraphs in Wheatstone's 1838 paper, one finds succinct descriptions of three key features of binocular rivalry, made in reference to dichoptic viewing of the rival figures shown in figure 1.2c:

If *a* and *b* 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. (p. 386)

Here Wheatstone is commenting on the fragmentary appearance of rivalry during transitions in dominance as well as on the factors that can, and cannot, influence the pattern of predominance during rivalry. Concerning transitions in the rivalry state, it is typical for one small region of the suppressed figure to break through into dominance and spread wave-like throughout the rest of the region of rivalry. Ordinarily, it is impossible to anticipate exactly which portion of a previously suppressed figure will break through into dominance, but Wilson, Blake, and Lee (2001) devised unique rival targets (see figure 1.1c) along with a novel technique for triggering dominance waves at a given spatial location. This, in turn, made it possible to measure the propagation speed of the dominance waves. The results from those measurements, along with their implications, are described in chapter 17 of this volume. For our purposes it is sufficient to note that the speed and behavior of dominance waves point to a retinotopically organized visual area as the site of dominance wave propagation.

In commenting on rivalry transitions, Wheatstone noted that small patches of one figure ("fragments," as he called them) often appear intermingled with patches of the other figure—the resulting impression resembles a dynamic mosaic made up of bits and pieces of both figures. These states of mixed dominance are all the more likely when the rival figures are large in angular subtense (Meenes, 1930); other factors that influence the incidence of mixed dominance include retinal eccentricity (Blake, O'Shea, and Mueller, 1992), spatial frequency (Schor, 1977; Hollins, 1980;

Yang et al., 1992; O’Shea, Sims, and Govan, 1997), and the overall global context in which a rival target appears (e.g., Kovács et al., 1996; Alais and Blake, 1999). In chapter 6 of this volume, Kovács and Eisenberg document developmental trends in the incidence of mixed rivalry dominance and use these data to draw conclusions about changes in cortical connectivity during early childhood.

Turning to another of his seminal observations on rivalry, Wheatstone also observed an inability to use willpower to force dominance of one rival figure over the other—rivalry alternations, in other words, seem to occur spontaneously and unpredictably. Actually, opinions differ on the question of voluntary control of rivalry. Unlike Wheatstone, Helmholtz (1925) felt that he was able to hold one rival figure in dominance indefinitely:

I am able to concentrate my attention on either of the two systems [rival figures], whichever I choose, and to see it for a while exclusively, without seeing the other one at all. One way of doing it is by counting the lines in one system. (p. 498)

In keeping with his adversarial relationship with Helmholtz, Hering (1964) was skeptical of Helmholtz’s claim. Hering conjectured that Helmholtz’s “act of will” in fact was attributable to patterns of eye movements that favored one rival figure over the other. Evidence in favor of Hering’s conjecture was subsequently reported by Breese (1899), who showed that intentional eye movements could indeed promote increased predominance of one figure over the other during rivalry. Is it possible that eye movements also play a role in triggering switches in dominance from one rival figure to the other? The answer here appears to be “no”—Peckham (1936) failed to find any correlation between fluctuations in dominance and the occurrence of eye movements, and decades later Blake, Fox, and McIntyre (1971) documented normal binocular rivalry alternations even when the rival targets were perfectly stabilized on the two retinas.

The most systematic assessment of the role of voluntary control in rivalry is provided by Lack (1978). In a series of carefully performed experiments, he convincingly showed that naïve observers could exert a degree of control over the rate of rivalry alternations, especially following relatively small amounts of practice. Moreover, Lack proved that rivalry control was not mediated by peripheral mechanisms such as changes in pupil size, accommodation, or blink rate; instead, he attributed rivalry control to a central “switching” mechanism of the sort proposed by Fox and Rasche (1969). It is noteworthy that none of Lack’s observers developed an ability to completely arrest the alternations of rivalry, and

on this point there seems to be consensus throughout the literature. It may well be that this inability to arrest rivalry alternations was what Wheatstone was talking about in his descriptions of willpower and binocular rivalry.

While “willpower” as exercised by Wheatstone proved ineffective in the control of rivalry, he did observe that significant control over rivalry *could* be exerted through manipulations of the relative “strengths” of the two rival figures. Specifically, a more weakly illuminated stimulus was perceived for a shorter time, according to Wheatstone. This aspect of rivalry—the relation of predominance and stimulus strength—is one of the most widely studied properties of the phenomenon. For an overview of what is known about this relation, we turn now to the seminal work by Breese (1899), a leading early figure in the study of binocular rivalry.

B. B. BREESE

B. B. Breese (figure 1.3) completed a master’s degree at Harvard under the supervision of William James and a Ph.D. at Columbia, where he was a student of James McKeen Cattell. His dissertation was on the general concept of inhibition, and this was the source of his interest in binocular rivalry. Published as a monograph in 1899, Breese’s dissertation devoted many pages to discussion of what he termed “physiological” inhibition (e.g., the willful attenuation of an otherwise reflexive muscle contraction) and “psychological” inhibition (e.g., the squelching of one idea by another). With this as background, Breese turned to binocular rivalry (“inhibition of one sensation by another”) as a paradigm case for studying the relation between physiological and psychological inhibition.

Using a prism stereoscope, Breese presented a red grating to one eye and a green grating to the other eye; the grating lines were oriented counterclockwise for one eye and clockwise for the other. With this basic configuration Breese was able to identify a number of conditions that influenced the dominance durations for the two rival figures. As already noted, observers could influence dominance durations simply through “willpower,” but in every case Breese found that the effect of “willpower” was unwittingly accomplished by eye movements.

By having people press keys to track successive dominance periods for the two rival figures, Breese was able to quantitatively assess the effect of “strength” on rivalry predominance (defined as the percentage of total observation time that a given rival figure was dominant). Initially, he observed that, all things being equal, each rival figure was dominant



Figure 1.3 B. B. Breese, whose early monograph on binocular rivalry described several key features of the phenomenon. (Courtesy of Robert Frank, University of Cincinnati.)

approximately 50% of the time. He also documented that increasing the luminance intensity of both figures by an equal amount led to a four-fold increase in the rate of alternations while, at the same time, maintaining the relative parity in predominance between the two figures. In a similar vein, bilateral increases in the distinctness of the lines of the gratings increased the alternation rate without affecting relative predominance. This in itself is a remarkable set of observations, for it reveals that the process responsible for selection (i.e., predominance) is distinct from the process responsible for alternations.

When some property of one of the rival targets was varied, Breese observed changes in predominance. Specifically, unilateral fourfold decrease in luminance intensity reduced the predominance of the dimmer figure, giving its brighter competitor almost a 2:1 advantage in total dominance time. Although Breese did not comment at length on it, this decrease in predominance came about largely through an increase in the average duration of suppression of the weaker stimulus (compare tables XV and XVII in Breese, 1899).

Breese also found that the predominance of one rival figure was markedly enhanced when the contours in that figure moved. (His simple but clever method for introducing unilateral motion was to attach one stimulus card to a pendulum that swung the card back and forth behind an aperture.) Remarkably, the moving contours were visible almost continuously, with the orthogonal, stationary contours appearing and disappearing just as they did when pitted against a stationary competitor (when visible, the stationary contours appeared superimposed on the moving ones). The salience of motion during binocular rivalry has since been well documented by others (e.g., Grindley and Townsend, 1965; Blake, Yu, et al., 1998).

Breese made two other intriguing observations that warrant mention. In one experiment, he had observers tense the arm and leg on one side of the body while tracking alternations in rivalry between figures of equal strength. He found no systematic influence of muscle contraction on predominance and concluded that activation of the motor centers had no influence on activation of the visual centers. This is perhaps not so surprising, for Breese's observers relied on central fixation of the rival figures, guaranteeing that "visual centers" in both hemispheres would be engaged during rivalry.

Breese's second remarkable observation concerned the perceptual consequence of presenting the two rival figures—the red grating and the green grating—to a single eye (which was optically accomplished by using a prism). Under these conditions, Breese observed what he termed "monocular rivalry":

... a rivalry of the colors was perceptible. Neither disappeared entirely: but at times the red would appear very distinctly while the green would fade; then the red would fade and the green appear distinctly. The two sets of lines showed the same fluctuation, keeping pace with the changing of the intensities of the colors. Sometimes one of them would disappear altogether. This rivalry of the colors and of the lines was much slower than the rivalry in binocular vision. (p. 43)

This intriguing observation seems to have gotten lost in the mists of time for decades, but the phenomenon of monocular rivalry was rediscovered and nicely documented in the mid-1970s by Fergus Campbell and colleagues (Campbell and Howell, 1972; Campbell et al., 1973; Atkinson et al., 1973; Rauschecker, Campbell, and Atkinson, 1973); readers may be able experience monocular rivalry by viewing the overlapping red/green radial and spiral gratings in color plate 1. Whether monocular rivalry and binocular rivalry have a common neural foundation remains debatable.

Following publication of Breese's monograph, interest in binocular rivalry waned during the first half of the twentieth century. According to Lack's (1978) tally, only a handful of papers on rivalry appeared between 1909 and 1950. This lack of interest in rivalry was undoubtedly a consequence of psychology's infatuation with behaviorism and its accompanying disdain for all things mental—one sees a parallel trend in papers dealing with attention. In the case of rivalry, it was not until the middle of the twentieth century that interest in the phenomenon reemerged, although even then many publications on rivalry simply exploited the phenomenon as a tool for studying individual differences (e.g., Bagby, 1957), sex differences (Kaufer and Riess, 1960), and various kinds of "top-down" influences on perception (e.g., Bokander, 1966). However, studies aimed at learning about binocular rivalry itself did begin to appear (e.g., Wallach and Adams, 1954; Kakizaki, 1960), and some of those studies sought to place rivalry within the broader context of binocular fusion and stereopsis (Treisman, 1962; Hochberg, 1964; Ogle and Wakefield, 1967; Kaufman, 1963).

All of these studies certainly contributed to a renewed interest in the phenomenon of rivalry. In my view, however, rivalry's reappearance on the perception landscape was most forcefully promoted by work coming out of three doctoral dissertations completed within two years: one in the United States (Fox, 1963), one in England (Whittle, 1963), and one in the Netherlands (Levelt, 1965). The following sections provide an overview of the characteristics of rivalry which were illuminated by those three influential bodies of work and by the studies they spawned.

ROBERT FOX AND THE SUPPRESSION EFFECT

During the 1940s there emerged a school of thought called "new look" psychology whose central theme was the role of motivational variables in perception. This research tradition generated experimental evidence that perception is shaped by an individual's needs, both physiological (e.g., hunger) and psychological (e.g., achievement), as well as by the

individual's impulses and anxieties (Dember, 1965). Among the phenomena studied by "new look" students was perceptual defense, operationally defined as decreased perceptual awareness of words or pictures with negative connotations for the perceiver (Postman, Bruner, and McGinnies, 1948; Erdelyi, 1974). But how can one selectively avoid perception of a threatening stimulus without first perceiving what that stimulus is (Howie, 1952)? This seeming paradox was resolved by positing multiple stages of processing, with inputs reaching consciousness only after elaborate perceptual processing (Erdelyi, 1974). And given this perspective, the challenge was to develop psychophysical strategies for interrupting the processing of stimulus information at intermediate stages prior to the emergence of awareness.

It was toward that end that Robert Fox (figure 1.4) began his investigations of binocular rivalry suppression. Working at the University of Cincinnati (where, incidentally, B. B. Breese was chair of the Psychology Department for decades), Fox wanted to find a way of studying rivalry

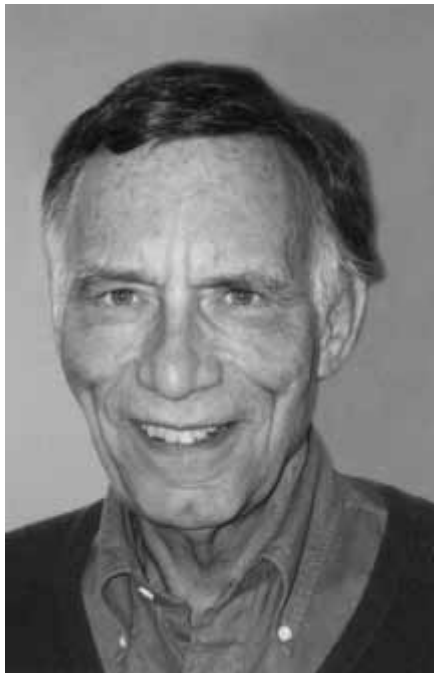


Figure 1.4 Recent photograph of Robert Fox, who developed and refined several important psychophysical strategies for studying binocular rivalry suppression.

that went beyond phenomenological report and its attendant susceptibility to response bias. It was in this spirit that he developed and refined the test-probe procedure, whereby visual sensitivity is assessed by briefly presenting “probe” targets to an eye during dominance and suppression phases of rivalry.

In a series of experiments beginning with his dissertation and continuing for several decades thereafter, Fox and his students documented that visual sensitivity during dominance phases is equivalent to that measured during ordinary monocular viewing, whereas visual sensitivity is depressed during suppression phases. Thus, for example, when presented during suppression phases, brief spots of light are more difficult to detect (Wales and Fox, 1970), letter forms are harder to identify (Fox and Check, 1972), and the onset of visual motion produces abnormally long reaction times (Fox and Check, 1968).

This pattern of results led Fox to characterize rivalry suppression as “nonselective,” meaning that the inhibitory events underlying suppression are not specially tailored to the configuration of the rival figure; instead, those inhibitory events act more generally, or nonselectively, on all information presented within the boundaries of a suppressed stimulus. At least in Fox’s mind, this property of rivalry undermined its utility as a means for introducing emotionally charged words or pictures outside of awareness—the putative inhibitory events underlying suppression were affecting all information introduced within the boundaries of the suppressed figure, making it impossible for semantic information to survive and influence perceptual judgments.¹

In subsequent studies carried out in collaboration with Fox and others, I used a variant of the test-probe procedure to show that normally conspicuous changes in a rival figure can go undetected for several seconds when those changes are introduced during suppression. Thus, observers fail to see large changes in the spatial frequency or the orientation of a suppressed grating (Blake and Fox, 1974a); observers do not notice variations in the coherence of kinematic events (Blake, Yu, et al., 1998); and observers are “blind” to changes in the emotional expressions of human faces (Kim, Grossman, and Blake, 2002).

In fact, suppression is sufficiently broad in scope that when the dominant and suppressed stimuli are exchanged between the eyes, suppression immediately affects the previously dominant stimulus (Blake, Westendorf, and Overton, 1980). These findings, besides reaffirming the nonselectivity of suppression, were interpreted to imply a relatively “early” locus for the neural site of suppression, with “early” meaning processing stages

where a wide range of visual features are compactly represented within retinotopic coordinates.

The nonselective nature of rivalry, together with evidence implying that it is an eye—not a stimulus—that is suppressed during rivalry (Blake, Westendorf, and Overton, 1980), led me to develop a neural model of rivalry based on reciprocal inhibition among orientation selective neurons varying in their ocular dominance (Blake, 1989). This model was certainly not the first to envision this kind of underlying circuitry; seeds of this idea can be identified in the writings of others (Wade, 1974; Grossberg, 1987; Sugie, 1982). The model did, however, make some rather specific predictions that stimulated subsequent work on rivalry, both psychophysical (Logothetis, Leopold, and Sheinberg, 1996) and physiological (Leopold and Logothetis, 1996; Tong and Engel, 2001). Chapters 3, 4, 9, 11, and 17 in this volume summarize some of the evidence—positive and negative—bearing on the model.

While suppression's effect is quite broad, encompassing all manner of stimulation presented within the suppressed region of an eye, suppression is at the same time quite fragile (i.e., easily perturbed). It is well known that a suppressed stimulus can be restored to dominance by abruptly increasing the contrast of that stimulus (e.g., Wilson, Blake, and Lee, 2001) or by suddenly moving the stimulus (e.g., Walker and Powell, 1979). For that matter, simply flicking a finger in front of a suppressed rival figure can trigger that figure's return to dominance (a maneuver responsible for the "Cheshire cat" illusion popularized by the San Francisco Exploratorium).

In general, suppression is highly susceptible to these kinds of transient events, and for that reason we have always been careful in our experiments to employ "ramped" contrast variations when introducing changes to a suppressed stimulus. Because of suppression's vulnerability to transients, the measured loss in visual sensitivity to briefly flashed test probes presented during suppression is only a fraction of a log-unit in magnitude. This modest loss in sensitivity could be construed to imply that the underlying inhibitory events are more subtle than one might imagine based on the wholesale invisibility of a normally salient, easily perceived stimulus (see chapter 3 in this volume).

Given suppression's nonselective breadth, does a suppressed stimulus retain any of its normal effectiveness? Scattered evidence bearing on this question existed prior to Fox's documentation of nonselective suppression. Thus, for example, Treisman (1962) reported that the positional information associated with a suppressed contour could nonetheless

contribute to stereopsis. However, the most systematic work on the residual effectiveness of a suppressed stimulus was launched in Robert Fox's laboratory at Vanderbilt University. Blake and Fox (1974b) showed that several of the aftereffects associated with grating adaptation could be generated even though the adapting pattern was suppressed from vision for a substantial portion of the adapting period. Similarly, Lehmkuhle and Fox (1975) found that the translational motion aftereffect could be generated by motion signals rendered invisible by suppression.

Exploiting this approach in the study of suppression, a number of investigators have since assessed suppression's effect on the buildup of other visual aftereffects, including the tilt aftereffect (Wade and Wenderoth, 1978), the McCollough effect (White et al., 1978), the spiral motion aftereffect (Wiesenfelder and Blake, 1990), the phase-specific aftereffect (Blake and Bravo, 1985), and the plaid motion aftereffect (Van der Zwan, Wenderoth, and Alais, 1993). Summaries of the outcomes of those studies can be found elsewhere (Blake, 1995; Logothetis, 1998; Blake and Logothetis, 2002). Suffice it to say that suppression has no effect on the generation of "low-level" visual aftereffects but retards the buildup of "higher-level" aftereffects.

PAUL WHITTLE AND GLOBAL DOMINANCE

At the same time that Fox was completing his dissertation in the United States, Paul Whittle (figure 1.5) was working at Cambridge University on an extensive series of dissertation experiments examining temporal and spatial characteristics of binocular rivalry. Some of his experiments extended Breese's earlier observations on the effect of size and blur on rivalry predominance, and other studies examined the possible role of eye movements in rivalry and the relation of rivalry alternation rate to stereoscopic acuity; some of that work was subsequently published (Whittle, 1965).

The most novel contribution of Whittle's dissertation, and the one with greatest impact, concerned his documentation of the role of figural grouping in rivalry. In these experiments, published subsequently as a journal article (Whittle, Bloor, and Pocock, 1968), Whittle sought to learn why a single, large rival target was seen in its entirety for much of the viewing period (up to 80% of the time), whereas two small, nearby rival targets seemed to rival independently of one another. Whittle reckoned that synergistic interactions among similar features forming a single "object" might promote synchronous dominance in rivalry of those features, and he set out to test this conjecture in a series of experiments.



Figure 1.5 Recent photograph of Paul Whittle, whose dissertation work highlighted the contribution of figural organization to rivalry dominance.

Whittle had observers press buttons to indicate when multifeature rival targets assumed a given state of dominance (an outcome Whittle called synchronous rivalry). He found that spatial proximity on its own was insufficient to promote synchronous rivalry of two targets—such targets were simultaneously dominant no more frequently than chance alone would dictate *when* those targets appeared to comprise separate objects. In contrast, the incidence of synchronous rivalry was greater than that expected on the basis of chance when local rival targets were arranged in a configuration suggesting the presence of an extended contour.

This, to Whittle's mind, explained why all the component parts of a large rival target could be dominant at the same time. To quote from his dissertation: "If part of a rivaling figure is visible, the rest may have a tendency to become so. This would make a patchy mixture of two figures an unstable state which would tend towards the temporary equilibrium of complete dominance of one or the other stimulus" (Whittle, 1963, p. 26). Incidentally, Whittle pointed out that these results argue against a crucial role of eye movements in rivalry, for eye movements would affect stimulus

features throughout the visual field of a given eye, not just spatially adjacent, collinear features. Instead, Whittle believed that rivalry occurs within local zones throughout the visual field, with the states of these zones being independent except when local contours in adjacent zones form a single “compound object.”

Thus, Whittle deserves credit for underscoring the role of figural processes in binocular rivalry.² In recent years, his seminal observations have been refined and extended by several research groups. In one widely cited paper, Kovács and colleagues (1996) devised “composite” rival targets consisting of bits and pieces of two complex images distributed between the two eyes in a complementary arrangement. With practice, observers can experience periods during which one image or the other is visible in its entirety (requiring interocular grouping), and these periods of complete dominance are greater than one would predict based on chance alone (see chapter 9 in this volume for further discussion of interocular grouping).

Alais and Blake (1999) showed that contour collinearity is a major factor in the production of global, figural grouping during rivalry, and Sobel and Blake (2002) discovered that global motion coherence influences dominance in the case of motion rivalry. In general, results from these and other studies (e.g., Dörrenhaus, 1975; Rogers, Rogers, and Tootle, 1977; Logothetis, 1998; Mapperson and Lovegrove, 1991) show that the pattern of global rivalry dominance depends, in part, on the structural regularity of spatially distributed rival features, even when those features are distributed between the two eyes (thereby requiring interocular grouping). This grouping propensity no doubt does play a role in promoting complete dominance of large rival figures, just as Whittle thought.

LEVELT ON PREDOMINANCE

The last of the three landmark dissertations on rivalry was completed in 1965 by W. J. M. Levelt (figure 1.6), working at Leiden University in the Netherlands. Published in monograph form, Levelt’s dissertation is still widely cited. From the outset it is worth noting that Levelt was an unabashed advocate of the view that rivalry occurs at an “early” stage in visual processing; reading his dissertation, it is clear that his thinking was influenced by the very recent physiological experiments by Hubel and Wiesel (1962) documenting the existence of cortical cells varying in their ocular dominance and demonstrating the importance of contours in evoking responses from those neurons.



Figure 1.6 Recent photograph of W. J. M. Levelt, whose dissertation on binocular rivalry documented the statistical properties of rivalry alternations and the effects of stimulus “strength” on those properties. (Photograph by Erik van ‘t Hullenaar.)

Following several introductory chapters that provide a thorough review of extant literature on binocular rivalry is a set of chapters devoted to the determinants of binocular brightness averaging (“Fechner’s paradox,” as it is known) and binocular contour rivalry. For our purposes, we may focus on several significant discoveries concerning the dynamics of rivalry.

First, Levelt deserves credit for documenting the stochastic properties of successive rivalry durations. He was the first to show that individual durations of dominance phases of rivalry together comprised a gamma distribution. Noting that the best gamma fit was obtained when the parameter λ equaled 5, Levelt interpreted this parameter as indexing the number of implicit events (“excitation spikes,” as he called them) necessary for triggering a transition from suppression to dominance. He further speculated that the timing of these implicit events might be related to “flicks” in eye movements leading to a switch in dominance, but subsequent

experiments showed that the optimal λ value remained 5 even when eye movements were eliminated as causal agents in rivalry alternations (Blake, Fox, and McIntyre, 1971).

Inspired by Levelt's characterization of rivalry as a stochastic process, subsequent investigations have looked in more detail at the statistical properties of dominance distributions, using various tests all of which confirm that (1) successive durations are statistically independent (Fox and Herrmann, 1967) and (2) rivalry durations do not behave as if driven by deterministic, chaotic attractors (Lehky, 1995). There are weak, second-order effects showing a trend toward longer dominance durations over the course of an extended viewing period, but these effects are probably attributable to contrast adaptation and not some property intrinsic to the alternation process itself (Lehky, 1995; Blake, Westendorf, and Fox, 1990).

The gamma distribution, first established by Levelt, has become the hallmark signature validating indirect measures of binocular rivalry in humans (Fox, Todd, and Bettinger, 1975) and in animals (e.g., Myerson, Miezin, and Allman, 1981). Moreover, there is evidence that the gamma distribution generalizes to perceptual state durations associated with bistable motion associated with viewing plaid patterns (see chapter 8 in this volume), as well as with other forms of perceptual bistability (De Marco et al., 1977; but see Strüber and Stadler, 1999).

Important as the discovery of the gamma distribution may be, Levelt's most revealing discovery concerned the lawful behavior of dominance and suppression durations with variations in the relative strengths of the rival figures. To embody these effects in a single variable, he developed the concept of "stimulus strength" and related it to "the amount of contour per area" and, for a constant amount, with the "strength of those contours" (1965, p. 74). He was able to scale stimulus strength based on measurements performed in a brightness averaging paradigm, wherein a given eye's contribution to the binocular impression of brightness was dependent on the contour density and luminance of the stimulus viewed by that eye. With "strength" gauged in this manner, Levelt was able to formulate four propositions concerning the dynamics of rivalry:

1. Increasing the stimulus strength in one eye will increase the predominance of the stimulus.
2. Increasing the stimulus strength in one eye will not affect the average duration of dominance of that eye.

3. Increasing the stimulus strength in one eye will increase the rivalry alternation rate.
4. Increasing the stimulus strength in both eyes will increase the alternation rate.

Propositions 1, 3, and 4 make intuitive sense, and at the time of Levelt's work there was ample evidence to confirm those outcomes (e.g., recall the results of Breese, 1899). But proposition 2 is counterintuitive, as Levelt himself acknowledged, for it implies that varying the strength of a stimulus has no effect on the dominance durations of that stimulus but, instead, affects the dominance durations for the contralateral stimulus. At that time, there were no data bearing on this second proposition (although tables XV and XVII in Breese, 1899, provide hints), so Levelt performed three experiments in which "strength" was manipulated unilaterally by varying blur, contrast, and average luminance.

As expected, all three manipulations produced variations in predominance, with the "stronger" stimulus being visible for a greater percentage of the overall viewing period. And, consistent with proposition 2, the average dominance durations were unaffected by changes in stimulus strength. Subsequent studies have replicated this finding (e.g., Fox and Rasche, 1969), although the independence of strength and dominance durations may break down when the disparity between monocular strength values is extreme (Mueller and Blake, 1989).

The importance of the dynamical property implied by proposition 2 cannot be overstated. For one thing, it implies that variations in predominance with stimulus strength arise from variations in the durations of suppression of a stimulus: on average, a weaker stimulus remains suppressed for a longer period of time. For that reason, varying the strength of a stimulus while it is suppressed will influence the duration of that suppression phase (Blake and Fox, 1974a), which may help us understand why transients are potent disrupters of suppression. Proposition 2 also implies that dominance and suppression are not necessarily two sides of the same coin—indeed, we now know that stimulus factors influencing suppression durations differ from those factors influencing dominance durations (Sobel and Blake, 2002).

This fact, in turn, may go some way toward reconciling seemingly conflicting views concerning the neural bases of binocular rivalry: to the extent that rivalry involves multiple processes, some governing dominance and others governing suppression, we may find that the neural events underlying those processes are distributed among visual areas within the brain (Blake and Logothetis, 2002). Finally, Levelt's proposition 2

may generalize beyond rivalry alternations, as Rubin and Hupé discuss in chapter 8 of this volume.

Levelt, along with Whittle (1963), also deserves credit for highlighting the distinction between rivalry suppression (the temporary invisibility of one monocular stimulus owing to the presence of a dissimilar stimulus imaged on the corresponding region of the other eye) and Troxler's effect (the spontaneous fading from visibility of a continuously viewed stimulus, independent of the stimulation received by the other eye). In recognition of this distinction, rivalry experiments subsequent to Levelt and Whittle's work have taken care to use stimulus conditions that preclude Troxler's effect (e.g., foveal viewing and/or flickering rival targets) or have explicitly measured the incidence of Troxler's effect and used those measures to "correct" rivalry predominance data.

BINOCULAR RIVALRY TODAY

The historical overview provided here is by no means exhaustive—many papers on binocular rivalry not mentioned here were published during the second half of the twentieth century. To get an idea of the volume of this work, interested readers are directed to Robert O'Shea's up-to-date reference list accessible at http://psy.otago.ac.nz/r_oshea/br_bibliography.html. Moreover, much of the most revealing, provocative research on binocular rivalry has appeared since about 1990, including research on possible neurophysiological concomitants of binocular rivalry. In addition, alternative theoretical views about rivalry have been advanced recently (Logothetis, Leopold, and Sheinberg, 1996; Andrews and Purves, 1997; Lee and Blake, 1999; Pettigrew, 2001), and these theoretical accounts have sharpened the focus of recent empirical work on rivalry. Indeed, a major purpose of the following chapters is to document these exciting, recent developments, both empirical and theoretical. This chapter is intended to set the stage for what appears in the following pages and to provide the reader with a deeper appreciation of the intellectual roots of contemporary work on binocular rivalry and bistable perception.

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NOTES

1. Experiments carried out years later confirmed that semantic information—whether linguistic or pictorial—is indeed neutralized during suppression phases of rivalry (Zimba and Blake, 1983; Blake, 1988; Cave, Blake, and McNamara, 1998).
2. The importance of perceptual grouping in rivalry, a major theme in Whittle’s work, was presaged by Diaz-Caneja (1928), a little-known paper introduced to the English-speaking scientific community by Alais et al. (2000).

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