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Binocular Rivalry and the Illusion of Monocular Vision

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A primate's visual impression of the world is shaped by highly refined cortical mechanisms for registering and interpreting images cast on the retinas. The act of seeing is normally so efficient and effortless that one seldom considers the inherent difficulty in the process. The eyes and brain, presented with a two-dimensional image of light, dark, and color, must extract the structure and spatial relationships of objects from which illuminating light is reflected. In particular, the visual cortex is thought to employ diverse stages of processing that together integrate the detection of sensory motifs in a scene with mechanisms that actively interpret and understand the physical structures from which they arise. Interestingly, among these multiple levels of representation, some of the neural elements critical in securing robust perception are not themselves enlightened as to the ultimate percept.

AMBIGUITY IN VISION

The problem of local ambiguity in vision is illustrated in figure 13.1, which demonstrates that even a well-posed visual problem is, at some level, composed of many smaller ambiguous ones. An apparently important task in perceptual organization¹ is the disambiguation of local information based upon global and configural properties of a scene, to generate unified perception of shapes and objects (Gregory, 1997; Koffka, 1935; Purves et al., 2001). Local analysis is implemented at many levels of visual processing. For example, a neuron in the primary visual cortex (V1) monitors only a small portion of the world (its receptive field), and responds only if a particular feature is present there. Such neural responses, when considered in isolation, are inherently ambiguous. For example, suboptimal stimulation of a typical V1 cell can be achieved by any number of combinations of

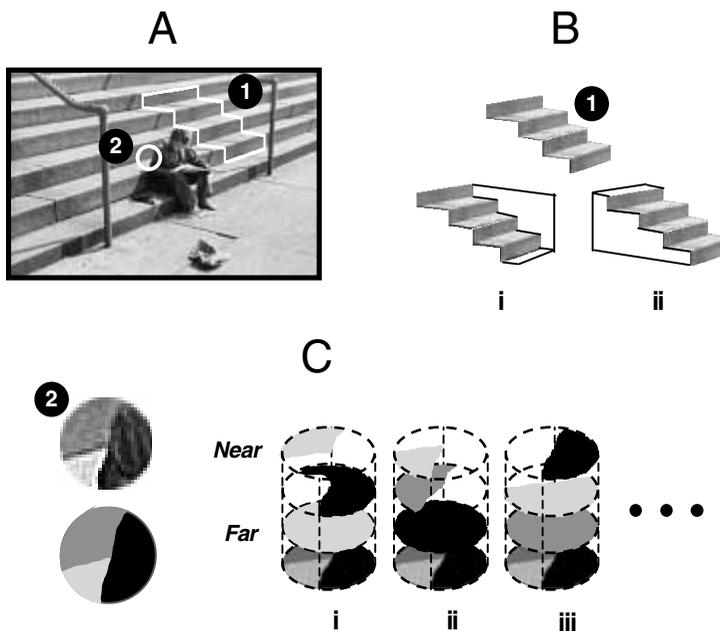


Figure 13.1 Illustration of local ambiguity present in a natural scene. (A) Unambiguous photograph of a boy sitting on steps, with two local regions of the image denoted (1 and 2). (B) The extracted portion of the stairway (1), having lost its global context, is ambiguous. The brain alternately interprets this pattern in the configurations indicated by (i) and (ii). (C) Small portion of the scene (2), comparable to that monitored by a spatially localized receptive field. The three intersecting texture regions arise from a combination of local 3-D geometry, occlusion, and shading. However, in the absence of global information, the depth-ordering problem is entirely ambiguous. Three of many possible solutions are shown (i, ii and iii). Note that despite the abundance of local ambiguity, the global information ensures that this ambiguity does not reach perceptual awareness.

orientation, contrast, and spatial frequency. Second, even if the neuron's optimal feature is present in the receptive field, it might belong to any of an infinite number of global shapes and objects. The activation of such "feature detectors," while subject to moderate cognitive influences, is generally assumed to be an automatic consequence of the underlying connectivity, and their activity can be demonstrated even when an animal is under general anesthesia.

It is interesting to note that normally visual ambiguity is completely hidden from our perception, because global and redundant information generally ensures the uniqueness of a single, "correct," holistic impression of a scene. Nonetheless, it is relatively simple to create artificial stimuli

that are ambiguous for all levels of visual processing and thus do not provide a unique interpretation see figure 13.1B). Confronted with such patterns, our visual impression does something highly uncharacteristic—it begins to waver. The result is a percept that is multistable in nature, adopting a certain configuration for a period, then often abruptly switching to an alternative interpretation. These perceptual alternations are thought to reflect a frequent reevaluation of activity in the visual cortex due to an inherently ambiguous or conflicting visual input. The class of multistable patterns is diverse, involving changes in visibility (Bonneh, Cooperman, and Sagi, 2001; Campbell and Howell, 1972; Levelt, 1965; Pritchard, 1961; Troxler, 1804), perceived depth (Necker, 1832; Rubin, 1921), or motion (Schiller, 1933; Wallach and O’Connell, 1953). While opinions regarding the basis of this phenomenon are varied, multistable stimuli have been valuable in the arsenal of tools employed by visual scientists to study interpretive elements of vision (Gregory, 1997; Koffka, 1935; Rock, 1984).

But how do visually responsive neurons in the early cortical areas fare when observing a multistable pattern, such as that shown in figure 13.1B? Are they active participants in the perceptual alternations, with their activity changes driving perception, or do they simply provide an impartial sensory signal upon which higher perceptual mechanisms can draw? A number of recent neurophysiological studies in monkeys using multistable stimuli suggest that the answer to this question may be quite complicated. While some neurons in the early cortical areas clearly modulate their responses according to perception, a larger fraction appears to respond purely on the basis of the physical structure of the stimulus, regardless of the perceptual state (Bradley, Chang, and Andersen, 1998; Dodd et al., 2001; Grunewald, Bradley, and Andersen, 2002; Leopold and Logothetis, 1996; Logothetis and Schall, 1989). In other studies examining the disambiguation of local features by applying different global contexts, neuron responses were similarly divided (Albright and Stoner, 2002; Heider, Meskenaite, and Peterhans, 2000; Lamme, Rodriguez-Rodriguez, and Spekreijse, 1999; Lee et al., 2002; Pack and Born, 2001; Rossi, Rittenhouse, and Paradiso, 1996; Sugita, 1999; Zhou, Friedman, and Von der Heydt, 2000). These and other experiments illustrate the complexity inherent in interpreting the perceptual relevance of signals in the sensory areas. Namely, in most cases of normal vision, activity in the visual cortex appears to consist of a mixture of local sensory processing, global contextual effects, and additional response modulation whose expression is not uniquely defined by the retinal input.

BINOCULAR RIVALRY

In recent years, the bistable phenomenon of binocular rivalry has been studied extensively, using a variety of psychophysical and physiological techniques (Blake and Logothetis, 2002). As described in previous chapters, rivalry refers to the spontaneous alternation between periods of left- and right-eye dominance that emerges when conflicting stimuli are presented separately to the two eyes. At any point in time, a stimulus in one of the eyes is seen to dominate perception while that in the other eye is completely invisible. Yet this condition is only temporary, since after a few seconds the other eye becomes dominant, and visibility switches to the previously suppressed pattern. Perception during binocular rivalry is so “monocular” in nature that under appropriate conditions, it can be closely approximated by alternate closure of the two eyelids. Experiments testing the generality of rivalry suppression revealed that it was indiscriminate with regard to particular stimulus features, adding support to the notion that the entire eye’s input is uniformly blocked (Blake, Westendorf, and Overton, 1980; Fox and Check, 1966a, 1968; Wales and Fox, 1970; but see Smith et al., 1982).

Yet while these observations support the notion of pure monocular vision during rivalry, other psychophysical experiments suggest that information from the perceptually suppressed eye penetrates deep into the cortical processing machinery. For example, in many cases, unperceived stimuli can generate adaptational aftereffects² that are of the same strength as continually visible stimuli (Blake and Fox, 1974; Lehmkuhle and Fox, 1975). Furthermore, interocular transfer³ of such aftereffects is unattenuated during rivalry (Blake and Overton, 1979; O’Shea and Crassini, 1981), while the monocular component of such aftereffects can cause rivalry between monocular stimuli that are identical (Blake et al., 1998).

These results suggest that the mechanisms responsible for binocular rivalry lie at a relatively advanced stage of sensory processing, beyond both monocular and binocular mechanisms responsible for simple adaptational aftereffects. Thus psychophysical experiments have long called into question the intuitive notion that perception during rivalry stems from monocular processing. More recent studies have demonstrated that high-level organizational principles can override interocular alternation (Kovács et al., 1996; Logothetis, Leopold, and Sheinberg, 1996). Although such “stimulus rivalry” occurs only under a restricted set of conditions (Lee and Blake, 1999), it nonetheless presents additional difficulty for rivalry theories rooted in monocular suppression.

Neurophysiological investigation of the mechanisms of rivalry has suggested that the activity of many neurons, particularly those at the earliest stages of processing, is entirely unaffected by the perceptual state. For example, in the lateral geniculate nucleus (LGN), where monocular signals are segregated, extracellular recordings failed to demonstrate any perception-related modulation during rivalry (Lehky and Maunsell, 1996; Sengpiel, Blakemore, and Harrad, 1995). A similar indifference was displayed by monocular neurons in the primary visual cortex of monkeys reporting their spontaneous perceptual changes (Leopold and Logothetis, 1996). In that study, the activity of a minimal fraction of binocular neurons in areas V1 and V2 correlated directly with the monkey's changing interpretation of the rivalry stimulus. Ascension in the cortical hierarchy revealed an ever-increasing fraction of neurons whose responses were in agreement with perception (Leopold and Logothetis, 1996; Logothetis and Schall, 1989; Sheinberg and Logothetis, 1997; for a review, see Leopold and Logothetis, 1999).

Interestingly, perception-modulated neurons were often neatly interwoven with those whose responses were dictated only by the sensory stimulus. These results suggest that binocular rivalry is not the consequence of a highly specialized mechanism imposed upon incoming monocular information (but see Polonsky et al., 2000; Tong and Engel, 2001). Interestingly, subsequent neurophysiological studies using bistable (structure-from-motion) 3-D object rotation have revealed very similar results (Bradley, Chang, and Andersen, 1998; Dodd et al., 2001; Grunewald, Bradley, and Andersen, 2002). Thus binocular rivalry appears to be related to other multistable phenomena (see chapter 8 in this volume) that have long been thought to employ principles of perceptual organization derived from natural vision.

We have previously reviewed the many parallels between binocular rivalry and other multistable stimuli, with particular attention paid to the nature of the alternation process (Leopold and Logothetis, 1999). In the next sections, we ignore for a moment those aspects of rivalry related to alternation, and focus instead on the mechanisms responsible, at any point in time, for the perceptual dominance of one stimulus over another. Specifically, we ask whether this subjective condition is dictated by, or at least reflected in, the activity of neurons in the early cortical visual areas. We address this question using an offshoot of binocular rivalry termed flash suppression (see also chapters 11 and 12 in this volume), which allows one to deterministically bestow perception during rivalry with a particular state of dominance (Wolfe, 1984).

NEURAL ACTIVITY DURING FLASH SUPPRESSION

Flash suppression refers to the sudden and persisting perceptual dominance achieved when two rivalrous patterns are presented asynchronously to the two eyes (figure 13.2). Under these conditions, the latter pattern dominates perceptually over the first, as long as they differ sufficiently in their structure (Wolfe, 1984). This paradigm, which affords the experimenter excellent control over the subject's perceptual state, is of great value in neurophysiological experiments, and was previously used to study perception-related single-cell responses in cats (Sengpiel, Blakemore, and Harrad, 1995; see also chapter 11 in this volume), monkeys (Sheinberg and

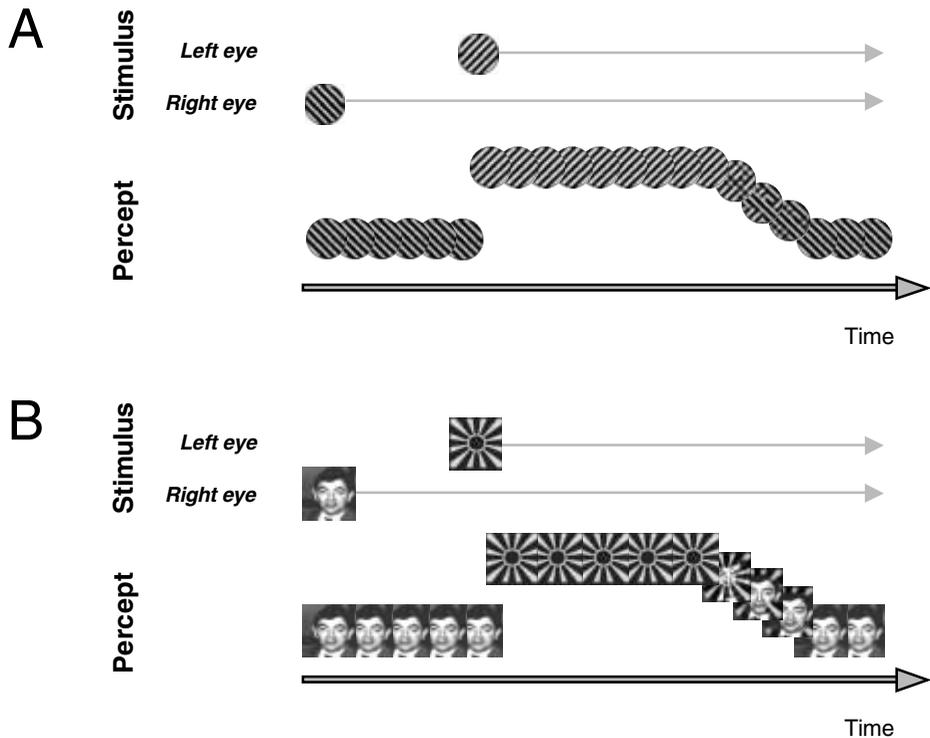


Figure 13.2 Flash suppression paradigms using (A) small grating patterns and (B) large complex patterns and natural images. In all cases, monocular stimuli were presented for at least 500 msec before the addition of the rivalrous stimulus in the other eye. This asynchronous presentation reliably results in the immediate and persistent perception of the second stimulus, accompanied by complete suppression of the first.

Logothetis, 1997; Leopold, 1997), and, most recently, humans (Kreiman, Fried, and Koch, 2002; see also chapter 12 in this volume). For two identical rivalry presentations (except for the immediate history), flash suppression thus allows the experimenter to impose two very different perceptual states.

Methods

To examine the expression of the alternate perceptual states during rivalry, we recorded activity in the visual cortex of three monkeys—A (90013), B (90004), and C (K97)—as they experienced flash suppression. The animals were required to fixate a small spot during two testing conditions. In the first, the position and extent of receptive fields were mapped. In the second, two conflicting stimuli were presented asynchronously to the two eyes, resulting in flash suppression. Monkey C was additionally required to report his percept following the flash. For monkeys A and B, stimuli consisted of small ($^{\circ}$) orthogonal grating patterns at the center of gaze (figure 13.2A), which are known to elicit excellent flash suppression in humans. Single units were isolated in the foveal representations of V1, V2, and V4, and recorded one at a time. The gratings were optimized in their orientation and spatial frequency to maximally stimulate each neuron's receptive field. Stimuli were presented separately to each eye by means of a polarization shutter system (see Leopold and Logothetis, 1996).

For monkey C, flash suppression was induced between diverse patterns, such as the image of a face and a geometrical pattern (figure 13.2B). The stimuli were large ($^{\circ}$), and optimized not according to the specific neural preferences but, rather, to perceptual criteria. Stimuli were presented separately to the two eyes by means of a mirror stereoscope. Extracellular single- and multiple-unit signals were conducted, using multiple electrodes distributed anterior to and posterior to the lunate sulcus. For most recording sites, the receptive fields' centers were located between 0 and 3 of the fixation spot.

Single-Unit Responses During Flash Suppression

The responses of single neurons during flash suppression are shown for several visual areas in figure 13.3. Data from monkeys A and B are combined in the first three quadrants, corresponding to responses in V1, V2, and V4. The last quadrant presents data redrawn from Sheinberg and Logothetis (1997), showing equivalent data from IT. In each quadrant, the

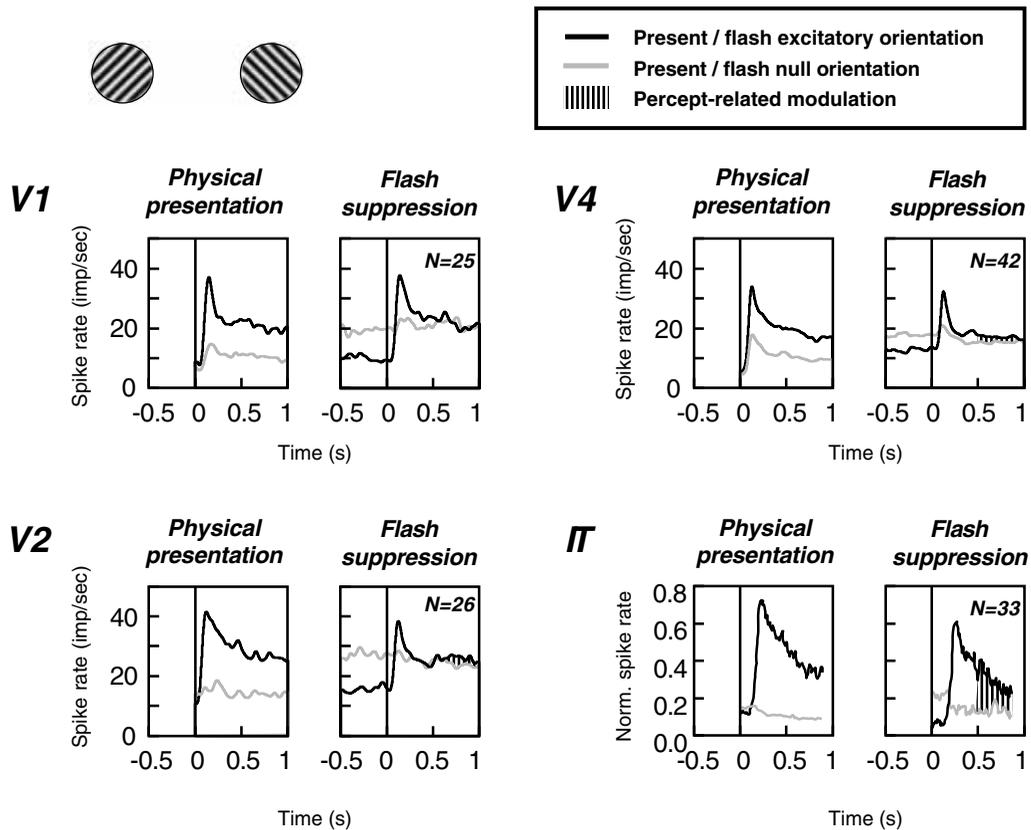


Figure 13.3 Single-unit responses during physical presentation and flash suppression in several cortical visual areas. Excitatory and nonexcitatory patterns consisted of the preferred orientation and null (orthogonal) orientations in areas V1, V2, and V4, and of images or complex patterns in IT. Prior to testing, the excitatory and nonexcitatory stimuli were tailored to the preferences of each neuron. Physical presentations consisted of monoptic (or dioptic) placement of the stimulus in the neuron’s receptive field for at least 1 sec. During flash suppression, the two patterns were shown dichoptically and asynchronously, with a 500 msec interval, resulting in perception of the second pattern. The hatched regions illustrate the difference in neural activity corresponding to the very different perceptual states. Note that this activity difference is markedly higher in the inferotemporal cortex (IT) than in the earlier visual areas (V1, V2, V4). (IT data adapted from Sheinberg and Logothetis, 1997.)

left panel shows mean responses over all neurons to the presentation of neurons’ preferred (black line) versus null (gray line) orientations. Stimuli used for the inferotemporal cortex in the bottom right quadrant did not consist of oriented grating patterns, but of images and patterns similar to those shown in figure 13.2B. The right panels compare the flash suppression

responses when the preferred (black line) and null stimuli (gray line) became dominant.

Perceptually, the conditions portrayed in the left and right panels, corresponding to the nonrivalry and rivalry conditions, respectively, are nearly identical, a fact that might lead one to speculate that the underlying neural activity is similar in the two cases. Nonetheless, figure 13.3 shows that the cells in the early cortical areas responded very differently during nonrivalry and rivalry, and generally showed less discrimination between the two orientations during perceptual, as compared to physical, stimulus changes. This was particularly true for cortical areas V1, V2, and V4, where perception-related modulation following flash suppression was modest compared to the preferred and null stimuli presented alone. Following initial transients (whose relevance to the perceptual state is difficult to assess, and which are put aside in the present analysis in favor of more sustained responses reflecting the prolonged perceptual state), activity in V1 was nearly indistinguishable for the two perceptual conditions during flash suppression. Areas V2 and V4 demonstrated a small but significant persisting difference between preferred and null dominance (hatched areas).

Thus, although the percepts experienced during the physical presentation and flash suppression conditions are highly similar, the unseen suppressed stimulus has a marked influence on the firing of neurons in the visual cortex. Responses in the inferotemporal cortex during flash suppression bore a much stronger resemblance to those seen during physical presentation of effective and ineffective stimuli (bottom right panel of figure 13.3) (Sheinberg and Logothetis, 1997). In contrast to the earlier areas, neural responses in IT reflected perception during flash suppression in a manner predicted by the neural selectivity.

While we have previously speculated that such differences among areas during free-running rivalry reveals their respective roles in natural vision, direct comparison is difficult because of the dissimilar nature of the stimuli used in flash suppression. Although binocular rivalry, including flash suppression, is highly robust to different stimulus types, it might be possible that the expression of perceptual dominance throughout the visual cortex depends on the types of stimuli used. For example, natural or complex patterns might produce fundamentally different global activity patterns, which could contribute to the differences observed. To test the effects of stimulus type directly, we next recorded from the early visual areas, using stimuli that were similar in nature to those used in the previous inferotemporal study.

Flash Suppression with Natural Stimuli

Data were collected from the early visual areas in monkey C during flash suppression, using a variety of patterns of the type shown in figure 13.2B. The stimuli were optimized according to perceptual criteria, to provide uniform and reliable flash suppression. In addition to monitoring single-unit activity, we collected multiunit activity (MUA), corresponding here to the absolute value of the band-pass-filtered raw signal (500 Hz–3 kHz). Average MUA data for all recording sites in areas V1, V2, and V4 are shown in figure 13.4 during physical reversal between the two stimuli (left panels) and flash suppression (right panels). As with the data reported above, these two conditions were perceptually highly similar. For each recording site, the two competing stimuli were divided into effective and ineffective, based upon responses during physical reversal only (i.e., without regard to responses during flash suppression). Physical presentation of the effective stimulus (black lines) thus always resulted in higher activity than the ineffective stimulus (gray lines).

The corresponding patterns of responses during flash suppression were, as before, substantially different. In area V1, for example, there was no significant activity difference during perceptual dominance of the effective versus ineffective stimuli, as long as both were simultaneously present. This is consistent with the single-unit data presented above. In contrast, area V2, and particularly area V4, displayed an increased activity difference related to the perceptual state (hatched areas). Thus, consistent with flash suppression with gratings above, as well as with our earlier binocular rivalry results (Leopold and Logothetis, 1996), neural activity related to perception increased at higher stages of cortical processing.

Discussion

The single-unit and multiunit results, taken together, demonstrate that the neural expression of a given perceptual state following flash suppression is distinctly different from that observed in the absence of interocular competition. In other words, in accordance with the psychophysical results described above, the unperceived, “suppressed” pattern continues to have a large impact on neurons throughout early striate and extrastriate cortical processing stages. Given the similarity in the single-unit and multiunit data, as well as in flash suppression between pairs of simple and

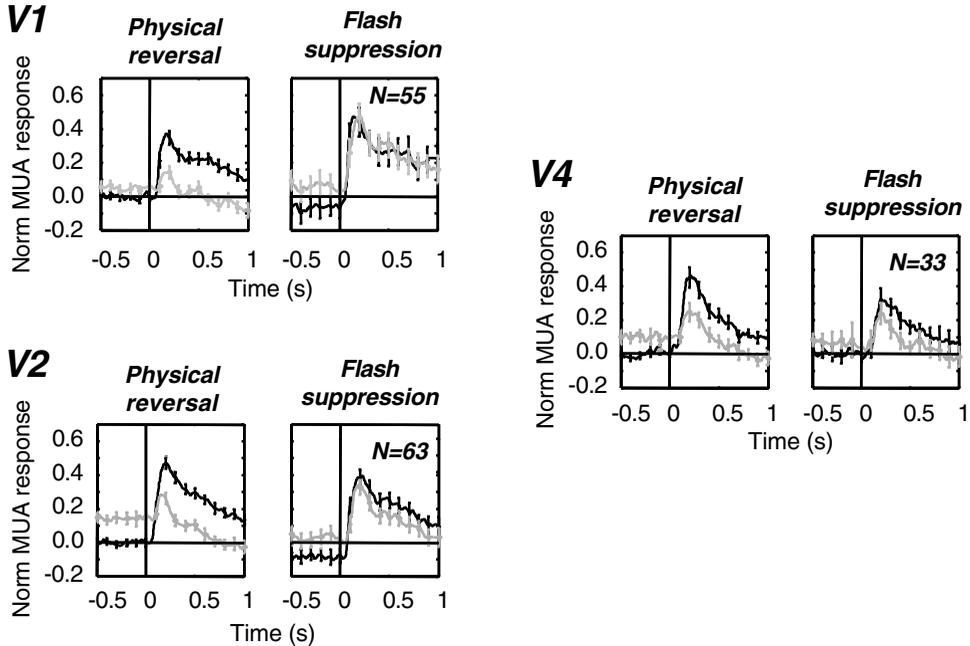
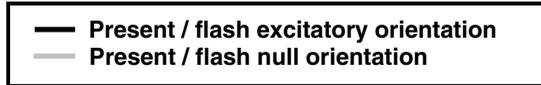


Figure 13.4 Multiunit responses collected in areas V1, V2, and V4 during physical reversal and flash suppression of complex patterns. In this case, complex stimuli were selected based on perceptual criteria, and sorted into effective and ineffective based upon the responses during the physical reversal trials. During physical alternation trials (left panels), one pattern was shown monocularly for at least 1.0 sec (0.5 sec is shown to the left of the vertical line), and then replaced by the other pattern in either the same or the opposite eye (at time $t = 0$ sec). In the flash suppression trials, the second pattern was always shown to the opposite eye after at least 0.5 sec, while the first pattern remained. This manipulation resulted in a percept that was very similar to the physical reversal condition, although both stimuli were simultaneously present after the flash. The mean responses at each recording site were normalized by the nonrivalry, preferred responses. The baseline before presentation of the preferred stimulus (when the nonpreferred was present) was first subtracted in all conditions, and this trace was divided by the magnitude of the preferred response. The error bars represent the standard error of the mean among sites normalized in this way.

pairs of complex stimuli, what might account for the stark differences between early and late areas of visual processing?

The answer may lie in a fundamental difference in the roles of the various areas regarding the disambiguation of local stimulus information. Neurons responding to local visual primitives in the primary visual cortex necessarily pass ambiguous information on to higher processing stages. While their responses may be subject to modification by lateral interactions within the same area (Kapadia, Westheimer, and Gilbert, 2000; Stettler et al., 2002) and by feedback from higher visual areas (Angelucci et al., 2002; Hupé et al., 1998; Lamme and Roelfsema, 2000), these influences are limited. The increased perception-related responses in the extrastriate areas may signify their increasingly interpretive role in vision.

This finding parallels those of several other recent studies demonstrating that activity in area V2 more closely matches the perception of a locally ambiguous region than of primary visual cortex (Bakin, Nakayama, and Gilbert, 2000; Heider, Meskenaitė, and Peterhans, 2000; Zhou, Friedman, and Von der Heydt, 2000). In the inferotemporal cortex, neural responses may play a distinctly different role in perception. Since inferotemporal neurons sit beyond cortical stages where ambiguous features are represented explicitly, their activation may reflect a visual problem for which a solution has already been found. This is one explanation that could account for the high fraction of neurons which modulate with perception in the inferotemporal cortex during binocular rivalry (Sheinberg and Logothetis, 1997).

While this is likely to be an oversimplified view of a process in which there is great interaction between diverse brain areas, it is possible to consider that the responses of IT neurons already represent a “commitment” on the part of the visual system, and are therefore much more closely linked with perception than responses in other areas which, by nature, remain ambiguous. But it is important to emphasize that even if IT were the first stage of cortical processing in which neural responses consistently match the perceived stimulus, it would not be implicated as being the site of binocular rivalry. On the contrary, the results presented here, taken in the context of other neurophysiological and psychophysical results, suggest that binocular rivalry does not have a single site in which it is implemented, but instead reflects competitive and interactive processes distributed over many levels of visual processing (Blake and Logothetis, 2002; Logothetis, 1998). In the next section, we consider how, given this distribution of neural activity in the cortex during rivalry, perception takes the form that it does.

THE NATURE OF BINOCULAR RIVALRY

The flash suppression results shown here, taken together with several other psychophysical and physiological studies, suggest that most binocular neurons in the striate and early extrastriate areas continuously receive input from both eyes during binocular rivalry. But why, then, do we have the subjective impression that we only see one eye's stimulus at a time? What, then, is responsible for this monocular perception? If, as we have previously speculated, perception during rivalry is a product of central competitive mechanisms, why does it default to a form that could, in theory, be implemented in a much simpler way? Here we explore these points by drawing upon examples of interocular conflict present in natural vision. We first show that during normal binocular vision, the brain is frequently forced to resolve interocular conflict arising from diverse factors, and that it generally does so by defaulting locally to a monocular view. We then propose that perception during binocular rivalry is governed by similar principles, dictated by perceptual constraints and implemented well beyond the site of binocular combination in primary visual cortex.

Interocular Conflict in Natural Vision

Primates, with their frontally mounted eyes separated by several centimeters, necessarily process two slightly different monocular views of the three-dimensional world. Discrepancies in the two eyes' images can arise from numerous factors, some of which are illustrated in figure 13.5 (see plate 4), which shows monocular and binocular regions of a human's horizontal plane of view. Note that each monocular field, for example, has a sharp discontinuity at its medial border representing the edge of the nose. With the eyes aimed straight ahead, these discontinuities define the horizontal borders of the binocular visual field, which subtends roughly 114, and produce two monocular flanks extending an additional 37 in each direction (figure 13.5A) (Howard and Rogers, 2002). Despite the abrupt transition from monocular to binocular, there is no perceptual discontinuity at the edges of the binocular zone. This cannot be accounted for solely by the eccentric position of the border, since visual experience is similar even when the center of gaze is shifted directly into an unpaired monocular zone (figure 13.5B).

In this condition, the contralateral eye is aimed at the nose and cannot see the target. While introspection can bring us to notice the faint outline of our nose, we are generally unaware that our vision is monocular, a fact

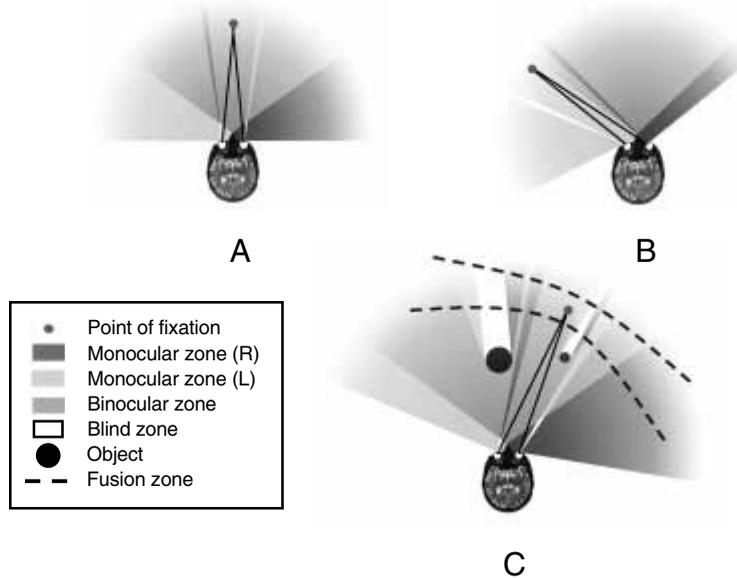


Figure 13.5 Monocular and binocular regions of the visual field are mixed during natural vision. (A) During normal viewing of an object, a portion of each eye's view is blocked by the nose. For straight-ahead viewing, this results in a binocular field of roughly 114 visual angle centered on the object of interest. In addition to the unpaired temporal crescents, each eye's blind spot adds a monocular region nearer to the center of gaze. (B) A gaze shift (version) results in a smaller binocular visual field due to enhanced obstruction from the nose. Shown here is a large version in which the center of gaze is itself monocular. (C) Cluttered scenes lead to a highly inhomogeneous field of monocular, binocular, and blind zones, even in Panum's fusional area (dashed lines). See plate 4 for color version.

that can be easily verified by closing the contralateral eye. Other monocular regions in the visual field correspond to the blind spot representations on the horizontal meridian, arising from the receptor-free optic disk on each retina. These monocular zones are depicted by the thin blue and yellow streaks protruding at 12–15° from the gaze center in figure 13.5A. As with the monocular flanks, there are virtually no perceptual consequences to these unpaired zones during binocular vision, since we simply see that region of the world through the eye that is able. Finally, and perhaps most important, the presence of nearby objects in the real world differentially occludes the eyes, and thereby casts different images on the retinas.

Figure 13.5C demonstrates that in addition to the factors mentioned above, the presence of objects in a scene leads to large, unpaired monocular

zones, which are also largely unnoticed. Thus, in considering the information originating within regions of space corresponding to Panum's fusional zone⁴ (processing outside of Panum's area, while also potentially of great interest, is not discussed here), our natural vision often contains a complex constellation of monocular, binocular, and blind regions. Experiments have demonstrated that in binocular vision without interocular conflict, singleness of vision is due to the fusion of images from both eyes rather than suppression of one (Blake and Camisa, 1978; Fox and Check, 1966b). But how are the unpaired monocular zones treated? Clearly they cannot be fused, since they have no counterpart in the other eye. This commonly encountered situation in cyclopean vision⁵ may be a fundamental problem of perceptual organization, in which the brain hides the complexity of the underlying binocular problem in favor of seeing continuous objects and surfaces.

Many observations have underscored the need for the intervention of higher-order perceptual principles to contend with interocular conflict, in particular the unpaired monocular zones that occur during binocular object vision. Leonardo da Vinci, for example, was aware of their existence, and was continually frustrated that they, along with the alternate perspectives afforded by the two eyes, prevented him from directly translating a binocularly viewed scene onto a flat canvas (Howard and Rogers, 2002; Ono, Wade, and Lillakas, 2002). Recently, models of stereoscopic vision have incorporated these zones as a means to disambiguate three-dimensional structure (Anderson and Nakayama, 1994; Gillam and Borsting, 1988; Nakayama and Shimojo, 1990). Interestingly, Shimojo and Nakayama demonstrated that during stereoscopic viewing, monocular zones which are "ecologically valid" (i.e., those which correspond to the geometry of natural vision) escape binocular rivalry entirely (Shimojo and Nakayama, 1990), and that points lying in these zones are assigned depth based upon global occlusion constraints rather than on local binocular matching (Shimojo and Nakayama, 1994). Thus, these and other experiments have revealed a strong link between fundamental mechanisms of binocular vision and other aspects of perceptual organization concerned with object and surface properties.

How, then, might the visual cortex draw upon this patchwork of monocular and binocular zones to synthesize a continuous and accurate percept? The need for an eye-of-origin signal has prompted speculation that such real-world constraints of binocular vision are implemented early in the visual system, where information from the two eyes is still largely

segregated (Shimojo and Nakayama, 1990, 1994). At higher processing stages, binocular neurons would be unable to discriminate between right-eye and left-eye stimulation, and thereby could not judge whether a visual feature should be dominant or suppressed.

Similar arguments have been put forth for other aspects of stereoscopic vision as well, including the detection of binocular disparity. Since the seminal work of Julesz (1960), binocular disparity has been recognized as a sufficient cue for the perception of depth. Following the discovery of disparity-tuned neurons in the primary visual cortex (Barlow, Blakemore, and Pettigrew, 1967), and the subsequent demonstration that edges defined by disparity alone could activate orientation-selective neurons (Poggio et al., 1985), the convergence of monocular signals in the primary visual cortex has been thought to be an important contributor to the mechanisms underlying our stereopsis (for a review, see Cumming and DeAngelis, 2001).

Yet it is important to emphasize that even for aspects of perception that depend upon detecting large or small interocular discrepancies, there is no a priori reason to believe that problems of binocular vision must be resolved at the earliest stages of binocular combination. First, while humans' poor performance on utrocular discrimination⁶ suggests that eye-of-origin information is inaccessible to perception, experiments in monkeys have revealed that many neurons carry eye-specific information well beyond the primary visual cortex. Although the vast majority of neurons in extrastriate cortex are binocular, meaning that they do not respond exclusively to stimuli placed in one eye or the other, a fraction of neurons in most areas tested display biases in their ocular preferences (Burkhalter and Van Essen, 1986; Maunsell and Van Essen, 1983; Uka et al., 2000). Even more pervasive in extrastriate areas is selectivity for interocular disparity, which is commonly found in the extrastriate areas (Burkhalter and Van Essen, 1986; Felleman and Van Essen, 1987; Hinkle and Connor, 2002; Janssen, Vogels, and Orban, 2000; Maunsell and Van Essen, 1983; Taira et al., 2000; Uka et al., 2000).

The role of ocular biases in interpreting the structure of objects and scenes is unknown, although recent evidence obtained with cortical microstimulation provides compelling evidence that extrastriate disparity responses are directly linked to the perception of stereoscopic depth (DeAngelis and Newsome, 1999). Most important, regardless of where interocular conflict is detected, its resolution must be smoothly integrated with diverse information arising from many other aspects of vision,

including global cues applied in the reconstruction of three-dimensional structure (Cavanagh, 1987). A number of studies, including those mentioned above, suggest that neural activity bears increasing resemblance to perception as one moves beyond primary visual cortex. Recent physiological recordings assessing neural responses to absolute versus relative disparity⁷ suggest that this principle is true even for stereopsis itself (Cumming and Parker, 1999; Thomas, Cumming, and Parker, 2002). In that study, many neurons in cortical area V2, but not in primary visual cortex, responded according to the relative disparity in a binocular pattern, capturing the aspect of stereopsis for which humans are most sensitive. This finding parallels several other recent studies demonstrating that activity in area V2 more closely matches stereoscopic perception and figure-ground depth ordering than that in primary visual cortex (Bakin, Nakayama, and Gilbert, 2000; Heider, Meskenaitė, and Peterhans, 2000; Zhou, Friedman, and Von der Heydt, 2000).

Thus, close examination of natural binocular vision reveals an abundance of interocular mismatches. Small horizontal disparities, which are registered in the activity of neurons throughout the visual cortex, are generally exploited to provide information about three-dimensional structure. Resolution of larger interocular conflicts, whose explicit representation in extrastriate areas is less clear, generally takes the form of exclusive monocular dominance, although this is largely hidden from our perception. In all cases, interocular conflict arising in natural vision is coordinated with interpretive elements of vision to generate a unified and robust percept. In the final section, we return to binocular rivalry, and explore the possibility that its monocular percept is due to similar high-level organizational principles that guide the resolution of interocular conflict during normal vision.

Binocular Rivalry and Perceptual Organization

When patterns in the two eyes are beyond reconciliation, binocular rivalry arises and perception becomes monocular. But given the evidence presented earlier, what is the neural basis of this monocular vision? Above we discussed evidence that interocular conflict is a common feature of natural vision, whose “monocular” resolution is smoothly integrated with other aspects of perceptual organization. Here we propose that vision during binocular rivalry derives from similar processes, and that its suppression, while powerful in shaping our percept, is in many respects only apparent.

One characteristic of rivalry consistent with this hypothesis is the surprisingly small magnitude of changes in sensitivity during suppression. Experiments measuring the effect of rivalry on perceptual thresholds have generally found that the sensitivity of the suppressed eye is impaired by only 0.3–0.5 log unit (Blake and Camisa, 1978; Blake and Logothetis, 2002; Fukuda, 1981; Norman, Norman, and Bilotta, 2000; Wales and Fox, 1970). This dissociation—strong perceptual suppression despite weak impairment of probe detection—is consistent with monocular perception being implemented at a central stage of processing. This point is further underscored by similar results obtained from other experiments, unrelated to binocular vision, in which basic visual sensitivity is shown to vary according to subjective figure/ground organization. In the “context superiority effect,” test probes are more difficult to detect when a region is perceived as background than when it is perceived as figure (Weitzman, 1963; Wong and Weisstein, 1982). Most important, the sensitivity changes measured in such experiments are very similar to those measured during dominance and suppression phases of binocular rivalry, where the visibility of the stimulus is continually changing.

These experiments, taken together, suggest that the small changes observed in test probe detectability occurring in the suppressed eye during rivalry reflect a decrease in the perceptual prominence of its context (i.e., the suppressed stimulus) rather than a general disruption of monocular information. Such context effects are thought to be important in influencing not only the sensitivity but also the balance of dominance and suppression during multistable perception (Alais and Blake, 1999; Peterson and Gibson, 1993; Yu and Blake, 1992). An additional example of the similarity between rivalry and figure/ground reversals is shown in figure 13.6, which compares different effects of manipulating stimulus salience in binocular rivalry and a classic ambiguous figure (Rubin, 1921). Note that in the rivalry condition, the mean duration of rivalry dominance is determined by the contrast of the suppressed, rather than the visible, stimulus (Levelt, 1965), indicating that the brain can extract even quantitative information from an unperceived pattern. Even in the pathological condition of strabismic suppression, in which misalignment of the eyes results in a percept that is always monocular, evidence suggests that suppression is superficial. While distinct from rivalry, strabismic suppression affects test probe sensitivity by roughly the same small magnitude (Smith et al., 1985). Furthermore, strabismic suppression, like binocular rivalry, is similarly incapable of preventing the formation of adaptational aftereffects (Blake and Lehmkuhle, 1976).

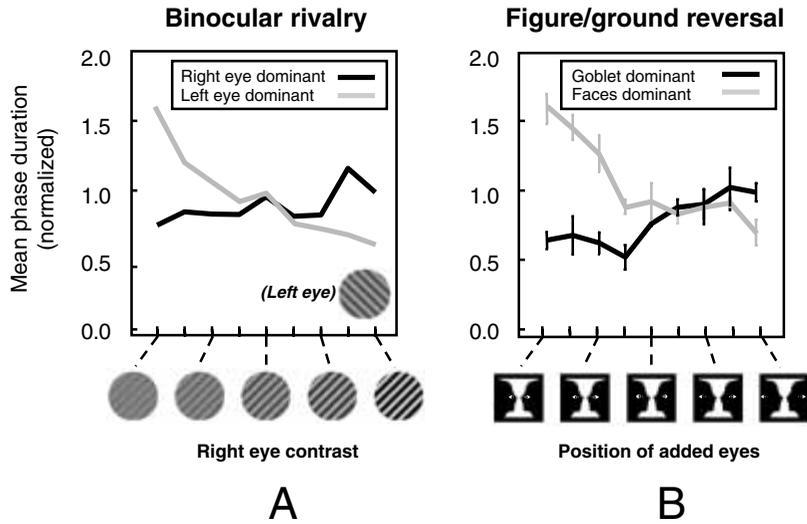


Figure 13.6 Parametrically changing one stimulus during multistable perception can alter the balance of dominance and suppression. (A) For binocular rivalry, this is traditionally demonstrated by changing the contrast of a pattern in one eye while leaving that in the other eye constant. These data, from one subject, are typical, and demonstrate that the mean dominance of the unchanged stimulus is primarily affected. (B) The alternation dynamics can also be influenced by stimulus manipulations in other forms of multistable perception. Here, changing the position of two eyes added to Rubin’s faces/vase pattern systematically changes the mean dominance time (τ).

These results, taken together, demonstrate that state-dependent changes in sensitivity are not unique to binocular rivalry, but appear to represent a more general mechanism related to perceptual organization. Nor is perceptual suppression dependent upon interocular conflict, since many phenomena exist in which complete visual suppression, often resembling binocular rivalry, exist in the absence of interocular conflict (Andrews and Purves, 1997; Bonnef, Cooperman, and Sagi, 2001; Campbell and Howell, 1972; Magnussen et al., 2001; Pritchard, 1961; Troxler, 1804).

One final troubling point for most theories of binocular rivalry, including those implicating high-level mechanisms, is the fractionation of the rivalry percept. Particularly for large patterns containing a high density of visual structure, perception does not consist of uniform alternation between the two monocular targets, but instead develops into a dynamic spatial mosaic of left- and right-eye dominance. This piecemeal percept illustrates that at some level, the resolution of interocular conflict during

rivalry must take place on a spatially localized level. Experiments using high spatial frequency grating patterns as rivalry targets have suggested that the fundamental size for a zone of unitary perception during this piecemeal rivalry is linked to representations in the primary visual cortex. In particular, the spatial scale of fractionation varies with eccentricity in a manner consistent with the human magnification factor⁸ in primary visual cortex (Blake, O'Shea, and Mueller, 1992).

Furthermore, a recent elegant study has quantified the dynamic properties of "waves" of perceptual dominance during rivalry, and suggested that they propagate with a constant speed over the cortical sheet, independent of eccentricity (Wilson, Blake, and Lee, 2001). This last result, providing strong evidence that some aspects of binocular rivalry resolution must refer back to representations in the topographic cortical areas, in addition offers a novel and useful paradigm to study the electrophysiological basis of piecemeal percepts during rivalry. While the suggestion that piecemeal rivalry reflects a perceptual investment in the early visual areas is difficult to refute, it is possible that other, higher-level factors might also contribute. For example, during normal vision, in contrast to rivalry or strabismus, zones of interocular conflict arising from binocular geometry are generally restricted in their spatial extent, particularly near the center of gaze. Vergence eye movements ensure that a properly fixated object and its immediate surroundings will lie within Panum's fusional area, whereas objects at larger eccentricities tend to contribute larger zones of monocular or interocular conflict.

While these observations do not explain the generation of piecemeal rivalry, they offer some expectation that the brain might tend toward disbelief of a global monocular solution. Organizational mechanisms might thus fractionate the percept based on several factors, including the approximate size of monocular zones common in normal vision. It may be revealing that under some conditions, such fractionation can indeed work in a cooperative manner (e.g., Alais and Blake, 1999) with other elements of perceptual organization to form a unified percept. This is illustrated, for example, by old and new experiments in which principles of interocular grouping draw cooperatively from portions of the two eyes at once, in accordance with basic Gestalt principles (Diaz-Caneja, 1928; Kovács et al., 1996; Kulikowski, 1992; Leopold, 1997). Thus, mixed percepts in rivalry suggest that perception is at least constrained by feature representations in the early cortical areas, but that these constraints are subject to modification by global information. Recent results have argued that basic

sensory representations might similarly constrain higher-order aspects of perception during binocular rivalry (Suzuki and Grabowecky, 2002).

SUMMARY

The evidence presented in this chapter argues that the dominance and suppression during binocular rivalry stem from central, interpretive neural processes that have access to both eyes' views. Most psychophysical and nearly all electrophysiological experiments (but not all neuroimaging experiments) are in agreement that an unperceived stimulus penetrates well beyond the site of binocular combination, and thereby makes a significant mark on cortical neurons at many processing stages. In considering why central mechanisms might choose to entirely discard one eye's image from perception, we argue that interocular conflict is a common feature of natural binocular vision, and that in most cases it is settled by adopting one eye's information. From these points, we conclude that our percept during rivalry derives from principles of normal binocular vision. Given the processing of both eyes' patterns, but the visibility of only one pattern, we suggest that monocular perception during rivalry is in its very nature illusory. It is a thinly cast veil over a binocular sampling of the world, perhaps serving to protect our ultimate percept from the chaotic mixing of incompatible images.

NOTES

1. *Perceptual organization* is a concept introduced by Gestalt psychologists (Wertheimer, 1923) to describe the active, interpretive elements of vision, such as grouping, motion correspondence, and figure/ground organization. Neural mechanisms underlying perceptual organization pose a great challenge for modern brain scientists, as they are thought to involve integrated processing among diverse brain areas.
2. *Adaptational aftereffects* are perceptual distortions following prolonged viewing of visual patterns. Adaptation, sometimes referred to as the "psychophysicist's electrode" is thought to isolate and temporarily diminish the contribution of specific subpopulation of neurons normally contributing to perception. While their physiological basis remains poorly understood, most are known to have a cortical origin.
3. *Interocular transfer* (IOT) refers to the presence of an aftereffect measured in an eye contralateral to that in which monocular adaptation was performed. In the motion aftereffect, for example, IOT accounts for roughly half the full aftereffect magnitude (Mather et al., 1998). The magnitude of IOT has often been used to gauge the relative contribution of monocular vs. binocular neurons.

4. During binocular vision, a point in three-dimensional space may or may not fall on corresponding regions of the two retinæ. The set of all points for which this is the case is defined as the *horopter*, which is a function of eye position and, in particular, vergence. For a given fixation point, there exists a region of 3-D space surrounding the horopter in which binocular fusion is possible. This is commonly referred to as Panum's fusional area after the nineteenth-century German scientist (Panum, 1858), although its existence has been described since the time of Alhazen in the eleventh century (Howard and Rogers, 2002). Information impinging the retina from objects outside this region produces retinal projections that cannot be binocularly combined.
5. *Cyclopean vision* refers to the fact that our binocular view in the world subjectively appears to emerge from a single eye located halfway between the actual eyes (Howard and Rogers, 2002; Julesz, 1971).
6. *Utrocular discrimination* refers to a subject's identification of the eye through which a target pattern is shown. In general, humans are extremely poor or incapable of performing such a discrimination (von Helmholtz, 1925).
7. *Absolute disparity* refers to the horizontal difference in the location of a point striking each retina with respect to the two foveae. *Relative disparity* refers to the distance between absolute disparities of two features in three-dimensional space. Unlike absolute disparity, perception of relative disparity is robust to uniform distance changes and vergence movements, and is therefore thought to serve as the basis for human stereo judgments (Thomas et al., 2002).
8. The cortical *magnification factor* refers to the transformation by which visual space is mapped onto the visual cortex. In the primary visual cortex, there is a large overrepresentation of the central portion of visual field.

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