BRAIN MECHANISMS OF VISUAL AWARENESS

Using Perceptual Ambiguity to Investigate the Neural Basis of Image Segmentation and Grouping

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INTRODUCTION

“I cannot see how it would be possible to refute a system of even the most extreme subjective idealism, which would consider life as a dream.”

Hermann von Helmholtz (1821-94), taken from Hobson (1988)

VISUAL PERCEPTION

The ability of humans to reflect upon their own internal representation of the world is arguably the most profound cognitive discontinuity in the animal kingdom. One can only speculate that when a member of our lineage first contemplated his or her own subjective perception thousands of years ago (or perhaps millions) it was in response to an apparent incongruity in the environment—an optical illusion, or a scene that spontaneously changed in appearance. Our perception is so inherently a part of us that only in its *fallibility* did it become a concept.

It is precisely the fallibility of perception that is the topic of the present dissertation. By investigating conditions in which we are *unable* to arrive at an accurate and unique depiction of the world, it is possible to learn how we perceive our environment under normal conditions. In this study I focus on vision, and pose the question "How is the resolution of perceptual ambiguity reflected in the activity of individual neurons in the visual system?" The phenomenon of *binocular rivalry*, which is an optical trick that can be used to artificially destabilize perception, is employed to address this question in both physiological experiments in monkeys and psychophysical experiments in humans. In this dissertation I hope to demonstrate that by examining the visual system as it struggles to make sense of the world one can learn much about the fundamental organizing principles governing normal perception.

The Study of Perception

The modern study of perception is but a few centuries old, with its deepest identifiable roots reaching into 17th century British empiricist philosophy. Not until the early 19th century, with the birth of positivism, was perception considered to be a candidate for objective scientific investigation (Copleston 1974; Kandel, Schwartz et al. 1991). Over the next century, with the emergence of experimental psychology, scientists for the first time began to pursue the specific relationship between a sensory stimulus and its evoked subjective experience. Pioneering individuals such as Maxwell, Weber, Fechner, and Helmholtz, elaborated numerous quantitative methods and principles addressing this relationship, many of which are still invaluable in modern psychophysics (Warren and Warren 1968; Schiffman 1982).

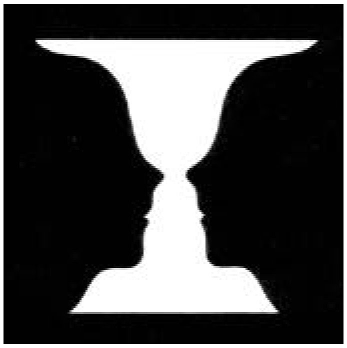

Figure 1 Rubin's celebrated Face vs. Vase stimulus, in which the central white goblet and flanking black silhouettes compete for perceptual dominance

In the first decades of the present century, a new school of psychology emerged and profoundly changed the way in which perception was conceived. The founders of this school included Wertheimer, Koffka, and Kohler, who adopted the name *Gestalt*, meaning roughly "shape" or "configuration", to describe their new psychology. The school's primary emphasis was on the higher order configurational properties of patterns, that cannot be derived from infinitely breaking them down into more and more primitive features. Perception, the gestaltists argued, is not the inevitable combination of elemental sensory events, such that the whole of perception is the sum of its parts. Instead, the *configuration* of these parts plays a crucial role in our interpretation of shape and motion. Rather than simply reporting what is in the visual world, perception sculpts a sensory pattern into a meaningful representation according to a set of fundamental organizing principles. In the Gestalt school these principles were elaborated for many aspects of vision, such as the perceptual synthesis of a visual pattern from its parts, as well as audition, such as the grouping together of successive musical notes into a melody (Koffka 1935).

The fallibility of visual perception was central to the thinking of the Gestalt school. Following the lead of Rubin (Rubin 1958), the gestaltists outlined a set of rules designating which areas within a two-dimensional pattern will be seen as figure and which will be seen as ground (see, for example, Rubin's Face vs. Vase, Figure 1). For many stimuli these assignments are ambiguous, and are thus of interest in the current study since they provoke the visual system to continually search for unique perceptual solutions. Although the Gestalt school was short-lived, formally dissolving by the middle of this century, during its brief existence it unveiled principles of our perceptual organization that remain central to our thinking, and for which underlying physiological mechanisms are still sought to this day.

With the advent of electrophysiological methods in the middle of this century, it became possible to objectively measure the responses of individual neurons (Hartline 1938; Kuffler 1953; Hubel and Wiesel 1959; Werner and Mountcastle 1963) and eventually to correlate these responses with the behavioral responses of an animal (e.g. Evarts (1966); Goldberg and Wurtz (1972)). This approach allowed scientists for the first time to measure the activity of individual neurons directly and quantitatively, and to compare it with simultaneous psychophysical measurements.

The difficulty in studying perception neurophysiologically stems from the fact that a perceptual experience is nearly always coupled with a sensory event, so it is often unclear whether one is measuring a neural correlate of perception or a programmed response of the sensory processing machinery. Some have argued that visual perception precisely *is* the processing of sensory information to more and more complex levels. Barlow (Barlow 1972), for example, suggested, “Perception corresponds to the activity of a small selection from the very numerous high-level neurons, each of which corresponds to a pattern of external events of the order of complexity of the events symbolized by a word.” Many physiological experiments, demonstrating that single neurons in higher visual centers respond *extremely* selectively to stimuli such as faces and complex objects indicate there must be very high specialization in the activity of some cells in the visual system (Gross, Roche-Miranda et al. 1972; Perrett, Rolls et al. 1979; Logothetis and Pauls 1995; Sheinberg and Logothetis 1997; for a review see Logothetis and Sheinberg (1996)); however, the extreme view that our perception of a given object or concept relies upon the activity of a single neuron or small group of neurons is probably inaccurate. The multifarious nature of perception all but guarantees that any simple metaphor will be insufficient. Nonetheless some metaphors are better than others. Central to many physiological studies, for example, is the notion that neurons acting as *stimulus detectors* dictate our perception (e.g. Britten, Shadlen et al. (1992)). One of the aims of this dissertation is to argue that although the concept of a detector is appropriate and useful for describing our capacity to process sensory input, it is severely limited in its ability to provide a framework for thinking about how we perceive. Perception can be best studied only if it is first distilled away from sensory mechanisms and viewed in isolation.

This introductory chapter outlines a diversity of approaches that have been employed in the study of perception in humans (psychophysics, neuroimaging, and clinical neuropsychology), as well as in animals (electrophysiology). Its common thread is the notion that perception can best be studied only if it is first disconnected from concomitant sensory events. The reviewed experiments can be divided into three general classes:

- visual perception in the absence of sensory input
- deficits in perception despite adequate sensory input
- changes in perception despite a constant sensory input

Experiments from each of these categories address the question, “How does the activity of neurons in the cortical visual areas, which analyze the sensory input, relate to the subjective perception of a visual stimulus?”. The diversity of experimental methods used to address and expand this question is a testament to its inherent philosophical appeal. It also suggests that perception is intractable by any single experimental paradigm, and only in combining results from different disciplines might a suitable framework for the neural basis of perception emerge.

Perceptual Deficits Following Brain Damage

A large part of our understanding about the functional organization of the visual system derives from studying human patients afflicted with damage to the striate and extrastriate cortical visual areas. It is obvious from this literature that "understanding" the visual world involves numerous sensory, perceptual, and semantic processing stages. Lesions to different cortical areas can affect perception in entirely different ways, causing in some cases difficulties in recognition alone, in others the inability to put elementary features together into a whole representation, and in some the inability to maintain the *awareness* of a stimulus for more than a few seconds. In this section I give a brief overview of visual and perceptual deficits resulting from cortical lesions, with an emphasis on damage to the early prestriate areas.

Visual Agnosias

Visual agnosias constitute a broad category of ailments in recognition that result from damage to cortical tissue. They are extremely rare disorders, and a recent review of all the cases reported in British and French journals since the turn of the century cited only 99 patients total (Farah 1990). The term "agnosia" was introduced by Freud (Freud 1891), and referred to those brain-lesioned patients who had lost their ability to recognize common objects. Lissauer (Lissauer 1890) divided the visual agnosias into two general categories of deficits which he termed *apperceptive* and *associative*. Farah (Farah 1990) makes the distinction in the following way:

> …*apperceptive agnosias are those in which recognition fails because of an impairment in visual perception , which is nonetheless above the level of an elementary sensory deficit such as a visual field defect. Patients do not see objects normally, and hence cannot recognize them. In contrast, associative agnosias are those in which perception seems*

> *adequate to allow recognition, and yet recognition cannot take place. It is said to involve the oft-quoted phrase of Teuber (1968), a "normal perception stripped of its meaning."*

Associative agnosias generally arise after bilateral damage to the temporal lobes. Afflicted patients, despite often losing their ability to read, recognize faces, and name common objects, often retain the ability to copy a picture by hand, or identify two shapes as being the same. Thus despite the enormous difficulty for these patients in recognizing and understanding their visual environment, their basic perceptual capacities are often unimpaired (Teuber 1968).

The apperceptive agnosias consist of a heterogeneous group of recognition deficits and are, in their nature, more relevant to the present discussion. These deficits typically result from damage to the posterior brain areas and, like the associative disorders, exhibit preserved elementary visual functions, such as acuity and color discrimination. However, unlike the previous group, apperceptive agnosias are likely to affect recognition only indirectly, as their primary influence is a disruption of perceptual organization, and for this reason, they have been considered by some to be "pseudo-agnosias" (Warrington 1985). Traditionally, the two groups have been distinguished by the patients' ability to copy and draw figures. Associative agnosics are usually competent at these exercises, despite their lack of recognition, whereas apperceptive agnosics tend to be greatly impaired (Campion 1987).

Apperceptive Agnosias

Unlike the associative agnosics, patients with apperceptive agnosia are generally *unable* to perform tasks that involve perceptually synthesizing a whole pattern from its parts, such as drawing or shape-matching. In this sense, their deficits affect their spatial understanding of a pattern, and their vision is perturbed at an earlier stage of processing than the associative agnosics, which is also reflected in the more posterior cortical lesions. Within the category of apperceptive agnosias there is also a taxonomy which has poorly-defined boundaries, owing largely to the small number of samples. Here I follow the taxonomy of Farah (Farah 1990).

At the most basic level, the *apperceptive agnosics proper* (Farah's designation for one subset of the more general category) are impaired in their perception of shapes. Although these patients often have good elementary visual functions and general cognitive ability, they can appear to be wholly blind to a casual observer (Efron 1968; Farah 1990). Their difficulties lie not in recognition per se, but in the construction of a meaningful representation of a whole pattern. Says Farah "In apperceptive agnosia, only a very local contour is perceived. It is so local that patients cannot trace across a break in a line, trace dotted lines, or avoid 'derailment' onto irrelevant slashes drawn across a figure." Two figures that generate difficulties for patients are shown in Figure 2 (Landis, Graves et al. 1982). Patients attempting to read the top drawing are completely confounded by the line drawn through the word. Evidently, the mechanisms that the patients have developed in order to compensate for their visual deficits, such as tracing lines with their finger or head movements, are rendered inadequate with such a stimulus. Their inability to separate the relevant word from the irrelevant slash clearly reflects a deficit in visual segmentation. This is made even more salient by the observation that when the diagonal line is of a different color, the patients regain the ability to read the word.

Figure 2 Examples of stimuli that pose a difficulty for apperceptive agnosics, from Landis (1982).

The lower drawing is equally remarkable, as the mere presence of two small discontinuities within the letters forced at least one patient to consistently perceive the pattern as "7415" rather than "THIS". In his piece-by-piece analysis of the drawing, he was unable to bridge the small gaps in the letters "T" and "H" to recognize their overall shape. It is interesting to reflect that the Gestalt theorists might have predicted the existence of perceptual deficits such as these. It is perfectly fitting with Gestalt theory that a patient who can perceive individual components of an object but who fails to combine them into a whole configuration would be unable to perceive its shape.

Another class of apperceptive agnosics are said to have a deficit in their simultaneous perception of two stimuli, and are therefore termed *simultanagnosics* (Wolpert 1924). These patients again divide into two group, based on the location of brain lesion as well as on the nature of the deficits. Dorsal simultanagnosics, whose lesions are often located in the dorsal striate and occipitoparietal areas, have difficulty in perceiving more than a single object at once (Luria 1959; Tyler 1968; Rizzo and Hurtig 1987). Despite an adequate ability to comprehend shape, subjects cannot see more than *one* shape, and are often completely unaware of major constituents in a visual scene, especially when the scene is cluttered with several objects. While apperceptive agnosias proper may reflect impairments in perceptual grouping, dorsal simultanagnosia is generally believed to result from deficits in spatial attention. Once attention becomes locked onto a single element of a scene it cannot become disengaged, and perception is limited to the attentional focus (Posner, Walker et al. 1984). Ventral simultanagnosia resembles its dorsal counterpart in many respects, although anatomically its lesions are found in the more ventral striate and prestriate areas. Again, there is difficulty in the understanding of a stimulus when it is presented among many. And, as in dorsal simultanagnosia, the limitations are governed not by the size of the stimulus, but by the number present. Despite the differing neuropathology, simultanagnosia is often considered to be a single ailment, but more thoughtful testing reveals that with dorsal lesions only one stimulus can be *seen* at all, while with the ventral lesions, the patient can see all the stimuli present, but can only *recognize* one—perception remains intact but recognition is fragmented (Farah 1990).

The apperceptive agnosias, in which there is a selective impairment in only a *subset* of perception’s building block’s, suggest that there are multiple dissociable stages of perception, distinct from sensation, that actively require the early cortical areas. By studying how perception is compromised following specific cortical lesions, many investigators are beginning to gain a greater understanding of the organization of perception in the human brain. In the final chapter I return to the topic of apperceptive agnosias in the context of developing a framework for thinking of binocular rivalry, the focus of the present dissertation.

Blindsight

A final category of lesions that yields information regarding the neural substrates for perception derives from damage to the striate cortex. Until the early 1970's patients suffering from lesions to this area were assumed to be completely blind in the afflicted part of the visual field, and only after careful scrutiny with forced choice experiments was it discovered that "cortically blind" individuals retained sufficient visual capacities to respond correctly to stimuli when tested visually (Poeppel, Held et al. 1973; Weiskrantz, Warrington et al. 1974). Remarkably, these patients, who insist that they can see no visual stimulus, can consistently perform significantly above chance in the detection and discrimination of motion and flicker (Blythe, Bromley et al. 1986), orientation (Weiskrantz, Warrington et al. 1974), and wavelength (Stoerig and Cower 1989). The mechanisms underlying this *blindsight* remain controversial (Farah 1994). While some investigators attribute the phenomenon to small pieces of intact visual cortex within the lesioned area (Fendrich, Wessinger et al. 1992), others postulate a variety of alternative routes by which retinal information can be processed sufficiently to account for this performance (Stoerig and Cowey 1989).

Residual perceptual abilities following V1 lesions has also been demonstrated in monkeys (Cowey and Weiskrantz 1963). This animal model of blindsight is not, however, unequivocal, as other studies in which the striate cortex was lesioned in monkeys have found no such residual visual capacity (Merigan, Nealey et al. 1993). Cooling of area V1 (and hence strongly depressing neuronal activity there) completely eliminates responses to visual stimuli in V3, V3a and V4 in a topographic manner (Girard, Salin et al. 1991; Girard, Salin et al. 1991), which suggests that activity in these areas is unlikely to be responsible for any residual ability to discriminate shapes. Nonetheless, studies have shown that monkeys with striate lesions not only perform remarkably well on forced choice tasks in the afflicted field, but, when given the choice, they categorize these trials as blank trials (i.e. one in which no stimulus was presented at all) (Cowey and Stoerig 1995). This is directly analogous to reports of human blindsight patients who are successful at discriminations despite insisting that no stimulus was presented, suggesting that striate lesions in monkeys provide an adequate animal model in which to study the phenomenon.

Regardless of the whether it is mediated through subcortical structures or residual tissue in V1, blindsight provides us with an important piece of information about visual perception—that a great deal of information about a stimulus can be processed in the absence of subjective awareness. It, along with similar phenomena, such as *covert recognition*, in which a patient who cannot visually understand spatial relationships can use vision to guide hand movements (Farah 1994), underscores the notion that not only are sensation and perception dissociable, but that the perceptual processing of a stimulus is itself complex, with subjective awareness being only one of its facets.

Visual Perception in Dreaming

The subjective experience of dreaming is familiar to nearly everyone, and constitutes one of the strongest arguments that the brain's perceptual apparatus can act autonomously. Two remarkable aspects of dreaming are 1) the coherent and often bizarre narrative guiding a sequence of dreamed events, and 2) the vividness in visual imagery, audition, and other perceptual experience. Freud, in his nineteenth century psychoanalytic dream theory, postulated a framework for the understanding the narrative content of dreams. Dreams, according to him, represent a disguised rendition of forbidden wishes and instinctual desires (Mccarley and Hobson 1977). In this context, dreams are replete with symbols and metaphors that, when scrutinized, can reveal much about the dreamer's psychological constitution. Freud's interpretations of dream symbolism changed the field of psychology and remained a stronghold of psychoanalysis for decades after its introduction. Yet, despite its popularity, the theory offered little insight into how the brain internally generates such a perceptually realistic representation of the world. Some have even argued that Freud's psychoanalytic theory, by nature of its unchanging reign over psychology, *forestalled* scientific research into the neurobiological basis of dreaming (Hobson 1988).

Neural Activity in the Visual System during Sleep

In the middle of this century, interest in the physiology of dream perception was catalyzed by the discovery of rapid eye movements (REM) and their relationship to dreaming (Aserinsky and Kleitman 1953; Dement and Kleitman 1957). Periods of increased ocular motility, it was shown, correlated with episodes of vivid dreaming, as well as *activation* of the cortex. "Activation", in this context, refers to a desynchronization of brain activity as measured by an electroencephalogram (EEG) characteristic of the waking state, with the majority of the gross electrical activity of the brain being of low amplitude and residing in the gamma-frequency range (>20 Hz). This is in contrast to the brain's activity throughout much of sleep, where large amplitude delta- (1 to 4 Hz) and theta-range (4 to 8 Hz) oscillations abound (Steriade and Hobson 1976; Steriade and McCarley 1990). Subjects awakened during REM sleep had a significantly higher frequency of visual imagery in their dreams than those awakened during non-REM (NREM) sleep. This studies were important because they demonstrated for the first time a physiological correlate of dreaming. The brain, it appeared, could act as a state system, and it could only support perception within certain physiological states. This concept was not entirely new, as phenomena such as the "alpha block" had been described previously [1]. The activation of cortex coincident with

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[1] "Alpha block" refers to the well-known diminution of 8-13 Hz oscillations in the occipital cortex upon the opening of one's eyes. These oscillations, known as "alpha rhythms" permeate the occipital cortex in subjects who are awake but relaxed with their eyes closed. They represent large, synchronized waves of cortical activation, and can be eliminated not only by opening one's eyes, but by visual imagery, heavy concentration, or various other exercises . They were first

dreaming prompted several investigators to examine the activity of *individual neurons* during sleep and REM episodes.

Hubel (Hubel 1959), in the dawn of modern electrophysiology, recorded the activity of single neurons in area 17 of unrestrained cats during sleeping and waking states. Contrary to the expectations of many, he found that the brain does not shut down during sleep, but that some cells actually *increase* their spontaneous activity. He and others (Evarts 1963; Livingstone and Hubel 1981) went on to demonstrate that across cells the overall spontaneous firing rate in the visual cortex did not change very much between sleeping and waking states, but that action potentials occurred in bursts during sleep, and were found with more regular intervals after arousal. A similar pattern was observed in the lateral geniculate nucleus (Livingstone and Hubel 1981). Evarts (Evarts 1963) found similar effects in the motor cortex of unrestrained monkeys. He recorded from pyramidal tract (PT) cortical neurons that he identified by antidromic stimulation and found that their pattern of activity was consistently different during periods of waking, sleeping, and REM sleep. During waking, cells fired steadily with phasic increases in activity as the animal made movements. When the animal fell asleep, the cortical activity lapsed into the same type of burstiness that was observed in the visual cortex, with a slight decrease in the overall firing rate. During REM sleep the burstiness was also present, but in these cases each individual burst was stronger, lasted longer, and occurred more infrequently. The similarity of the activity changes in primary sensory and motor areas suggested that the change in neuronal firing during sleep is a generalized cortical phenomenon.

Neural responsiveness to evoked visual stimuli is also demonstrably different during sleeping and waking. Cortical as well as thalamic visual responses are generally weak in sleep as compared to the waking state. Neurons in striate cortex, for example, were found to be more responsive to either excitatory or inhibitory stimuli during waking, although the

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described in the late 1920’s by Hans Berger (1873-1941), a key figure in the invention of the electroencephalogram Hobson (1988). The Dreaming Brain. New York, Basic Books, Inc..

changes in response were generally quantitative and not qualitative (Evarts 1963; Livingstone and Hubel 1981). In the inferotemporal cortex (IT), on the other hand, the animal's level of consciousness, as measured by EEG, was found to have a profound influence on the neuronal responses. Gross et al. (Gross, Roche-Miranda et al. 1972) examined the responses of IT cortical neurons to complex visual patterns in monkeys under barbiturate anesthesia. They noted that cells responding vigorously to stimuli during periods of "low voltage, fast and asynchronous EEG" (corresponding to the brain's *active* state) would often respond little or not at all to the same stimuli during "high voltage, slow and synchronous EEG" (corresponding to slow-wave sleep).

The above physiological studies suggest that although much of the visual system responds to visual stimuli in a *grossly* similar way during sleep as waking, the level of consciousness does affect the way the sensory input is processed in the thalamus and cortex. Clearly, there is reduced perception of sensory inputs during sleep. If one could attain a better understanding of this difference in neural responsiveness that results in the profound perceptual suppression of the external world during sleep, one might better understand the way in which perception is normally derived from a sensory stimulus.

Pontogeniculoccipital Waves and Dreaming

The existence of pontogeniculooccipital (PGO) waves during REM sleep adds yet another level of complication to the role of cortical neurons during sleep and dreaming (Steriade and McCarley 1990). PGO waves are electrical signals that are generated in the pontine brainstem and propagate to relay cells in the lateral geniculate nucleus (LGN), to other thalamic nuclei, and to the striate cortex. Their time course consists of a tonic activation, which is roughly temporally coincident with each REM phase in the sleep cycle (and hence the activation of cortex), as well as a series of individual phasic components. Two observations regarding PGO waves suggest that they may have significance for perception. The first is that phasic PGO waves in the cat are often coincident with specific saccadic movements during REM sleep (Jouvet 1962). The second is the discovery that specific eye movements in REM sleep can be correlated with specific perceptual events, such as changes in gaze direction, during dream imagery (Dement and Kleitman 1957). These discoveries, considered together, inevitably suggest that PGO waves are physiological correlates of dream perception (Steriade and McCarley 1990). Furthermore, given the fact that PGO waves propagate to the same structures as the visual information striking the retina, one can speculate that they carry information that will be interpreted visually, perhaps reporting information regarding the movement of the two eyes as it relates to perception in a dream.

This presents a scenario that is highly counterintuitive: that a brainstem center, in a seemingly *random* series of bursts, simultaneously issues eye movements and signals to the visual cortex that *direct* visual perception during a dream. Based on this notion, Hobson and McCarley (Hobson and McCarley 1977) proposed a physiologically rooted model of dreaming that is an alternative to Freud's psychoanalytic theory. This model, given the title "activation-synthesis", describes a dream sequence in the following way. The pontine brainstem nuclei are nonspecific state generators, activating, through PGO waves, the primary sensory and motor areas. Phasic impulses into these areas then generate the perception of movement, which is subsequently incorporated into the dream itself. Says Hobson (Hobson 1988) of activation synthesis:

> *This new model is brain-based: the strangeness of dreams is attributed to the distinctive physiological features of REM-sleep generation by which disparate and chaotic internal data must be integrated in the absence both of the structure of external space-time data and of the internal chemical controls necessary for thought, attention, and insight.*

According to activation-synthesis, scene perception (and hence the entire dream narrative) continually evolves around random activity reaching the LGN, striate cortex, and cortical association areas. What is not known is whether activity in these areas during dreaming resembles in any way that during normal visual stimulation--such experiments are, for obvious reasons, difficult if not impossible. Recent PET imaging studies in humans during REM sleep suggests a strong involvement of the limbic areas, notably the amygdala, but provides little information about the early visual cortex (Maquet, Peters et al. 1996). A better understanding of the activity in the earlier areas during dreams might provide clues as to how a vivid visual scene can be spontaneously generated by the brain when the eyes are closed.

Visual Imagery

Our ability during the waking state to willfully envision a familiar face or object illustrates yet another paradigm by which investigators have examined the role of the early visual areas in perception. Visual input is generally eliminated during mental imagery, just as in dreaming, so any visual experience is necessarily internally generated. Imagery offers the added benefit over dream studies of a more convenient and controllable experimental paradigm, in which subjects can be instructed to imagine specific objects or scenes in a specific locus in the visual field. The disadvantage of the mental imagery paradigm is that the relationship between imagery and normal perception remains unclear. Some investigators have challenged the notion that mental imagery is even *related* to visual perception, claiming that the depictive properties of imagery are *epiphenomenal*, and based on representations that are purely propositional, much like those underlying language (Kosslyn and Ochsner 1994). However, the major debate in the field of visual imagery is not whether it exists as a depictive process, but whether or not it necessarily engages the same areas involved in normal visual processing, most notably the early, topographic striate and prestriate cortical areas (Roland and Gulyas 1994; Kosslyn, Thompson et al. 1995). Human lesion studies, as well as imaging data, are divided on this issue.

Neuropsychology

The similar manner in which brain lesions affect mental imagery and visual perception in many visual agnosic patients provides evidence that the two processes are related. Many agnosic patients have been shown to exhibit similar and parallel deficits in perception and imagery, and in some cases these deficits are confined to a single aspect of an image such as its color or spatial structure (Levine, Warach et al. 1985). In one case study, the unilateral removal of an occipital lobe in treatment for chronic epilepsy resulted in the patient's field of mental imagery being reduced in much the same way as their actual visual field (Farah, Soso et al. 1992). These results suggest that not only are perception and imagery related, but that they normally exploit the same neural structures.

However, the existence of patients with other types of lesions, in which visual deficits are confined to either perception or imagery, but not both, calls this conclusion into question. For some agnosics, mental imagery alone is eliminated (Basso, Bisiach et al. 1980) or impaired (Guariglia, Padovani et al. 1993) with a complete sparing of visual perception. In other patients imagery is unaffected despite a severe perceptual deficit (Riddoch and Humphreys 1987; Jankowiak, Kinsbourne et al. 1990). In one particularly intriguing case (Behrmann, Moscovitch et al. 1994), an agnosic patient (CK) was able to circumvent his perceptual shortcomings by exploiting visual imagery. Following a motor vehicle accident CK lost his ability to recognize many familiar objects and line drawings. Computerized tomography revealed no focal lesions, although magnetic resonance imaging suggested a bilateral thinning of the occipital lobes. Despite near perfect face recognition, CK had a severe deficit in the recognition of letters, line drawings and three dimensional objects, although he was able to identify all the objects with tactile presentation. He was able to draw from memory quite well (which is often used as a measure of imagery ability), and several other tests demonstrated that he was at least average with respect to mental imagery. When instructed to perform spatial mental manipulations during imagery, he could recognize patterns that were intractable visually. For example, when presented with the instructions—

“Imagine the letter B. Rotate it 90 degrees to the left. Put a triangle directly below it having the same width and pointing down. Remove the horizontal line.” -- he had no trouble in recognizing the newly formed shape as being a heart, although he could not recognize his own drawings of a heart. This double dissociation between imagery and visual perception, revealed through human lesion studies, demonstrates that although the two phenomena are likely to be related, there is not complete overlap in the neural structures they engage.

Neuroimaging

Conflicting results also emerge from studies in which the brains of human subjects are scanned as they perform mental imagery. Most notably, positron emission tomography (PET) studies from the laboratories of Kosslyn (Kosslyn, Alpert et al. 1993; Kosslyn, Thompson et al. 1995) and Roland (Roland and Gulyás 1995) have provided conflicting results regarding the involvement of the earliest cortical areas during mental imagery. Kosslyn et al. have shown that not only is striate cortex active during imagery, but that parts of it are *more* active during imagery than during normal perception. Moreover, the pattern of activity in the early topographic areas depends crucially on the spatial nature of the pattern being envisaged. When subjects were asked to imagine tiny letters the majority of activation in striate cortex was posterior and medial, while the imagining of large letters resulted in a more anterior focus of activation. These general findings have been corroborated by other groups (Goldenberg, Müllbacher et al. 1995), and the mechanism is generally thought to involve retroactivation of the early cortical areas by back projections from the temporal visual association areas to V2 and V1 (Kosslyn and Ochsner 1994).

In contrast, Roland and colleagues report, using a generally similar paradigm, that V1 is seldom if ever active during visual imagery (Roland and Gulyás 1995). In their studies there is a consistent activation of the parieto-occipital and temporo-occipital cortical areas, but seldom of the posterior occipital lobe corresponding to V1. Roland and Gulyas suggest that this restricted pattern of activity may arise because the imagining of a visual stimulus no longer requires a topographic representation (Roland and Gulyas 1994). Regarding the first cortical processing stages they assert, “These early areas are more computational than representational, and if the brain already possesses a computed representation then why do the job over again?” They make the bold suggestion that the differences between their results and Kosslyn’s are rooted in “differences in methods and stimulus paradigms”. However, they are quick to point out that despite the discrepancies there are a number of consistencies common to the two studies. For example, in both cases the “areas that are remote from the early visual areas, and that are located in the parieto-occipital and temporo-occipital regions of regions of the brain are consistently active in visual imagery.” Secondly, “multiple cortical fields having distinct localizations in these parieto-occipital and temporo-occipital areas are active, whether one single pattern or several patterns are imagined.” Although the degree to which the early areas are engaged remains unclear, all the evidence suggests that at least some prestriate cortical areas are active during imagery. In fact, there is some evidence that the degree to which the visual system, including the early areas, is active during imagery is directly correlated with the vividness of imagery as rated by the subject (Sakai and Miyashita 1994).

Eidetic Imagery

Eidetic imagery, the ability to visualize and scrutinize the memory of a complicated picture for minutes after it is removed, is perhaps the most extreme form of visual imagery, although it is a relatively rare talent (for a comprehensive review see Haber (1979)).The majority of reports of eidetic imagery have been from school age children who are asked to examine a complicated visual scene for a number of seconds, and then describe it after it is taken away. Between 2-15% of children and a significantly smaller percentage of adults, termed eidetics, are endowed with this ability to describe a “remembered” image in remarkable detail, not because they simply recall which objects were present, but because the image still persists visually. For eidetics, a recalled image tends to be perceived more fully when the subject makes no attempt to memorize the sample, but just scans it. Remarkably, while “perusing” a remembered image, an eidetic subject can even be surprised to discover *new* elements that had previously escaped his or her attention. There appears to be a sharp discontinuity in children who possess this ability and those who do not, and the incidence of eidetics falls nearly to zero for adults (Haber 1979).

Eidetic imagery is potentially useful in revealing the mechanisms underlying normal visual perception. The maintained perception of a visual scene in the absence of input is reminiscent of visual experience during dreaming and hallucinations, and again illustrates the dissociation that can be made between visual input and subjective perception. As with most of the perceptual phenomena discussed in this chapter, the involvement of the early cortical areas during eidetic imagery is largely unknown, although its phenomenology has invited speculation (Wolfe 1988). It is not, for example, retinal, or more accurately, retinotopic. Unlike afterimages[1], eidetic images do *not* move when a subject redirects his or her gaze, and subjects can even move their eyes about “within” an eidetic image to focus on a particular feature or search for a hidden object (Pollen and Trachtenberg 1972). This “nontopographic” quality has been used to rule out potential mechanisms involoving the lateral geniculate nucleus, as well as the earliest cortical processing stages (Wolfe 1988). One peculiarity of this phenomenon, however, which may be relevant to binocular rivalry, is the fact that eidetic imagery appears to be primarily a *monocular* phenomenon. When subjects view a sample image through one eye, they are generally not able to close the viewing eye, open the other, and continue to see the persisting eidetic image (Haber and Haber 1988). This has been interpreted as a lack of interocular transfer (Wolfe 1988), suggesting that eidetic imagery involves the adaptation of monocular cortical cells, similar to the aftereffects of color (e.g. the McCollough effect (McCollough 1965)), although it is complicated by the fact that the persistence of eidetic images is often interrupted by closing one’s eyes, such as in blinks. One remarkable recount of an eidetic subject adds a further layer of complexity to this issue (Stromeyer and Psotka 1970). In this case, a subject was able to monocularly view a single half image of a Julesz-type (Julesz 1960) random dot stereogram, and then recognize the embedded stereo-defined target when viewing the other half image through the other eye up to 24 hours later. This result strongly argues for a monocular mechanism, but given that even eidetics are generally unable to do this, and that only a single subject with this ability has ever been reported, one must be cautious in one's interpretation (Wolfe 1988).

Finally, bistable perception can be supported by eidetic images. Herwig and Jaensch and also Kluver found that binocular rivalry could ensue between an eidetic image of a color patch and a real patch of a different color (Stromeyer and Psotka 1970). Others have found that a bistable stimulus, notably the Necker cube (Necker 1832), continued to undergo reversals in its perceived configuration during an eidetic episode (Haber 1979). Imagery, like dreaming and visual hallucinations, provides an excellent example of how the brain can generate visual perception, relying on the memory of past visual experience but no immediate sensory input. The current dispute over the involvement of the early visual areas is likely to be clarified in the coming years, and this might provide more information regarding the fundamental organization of perception in the brain.

Multistable Perception

It is easy to demonstrate using stimuli such as those in Figure 3 that perception is not simply a recapitulation of the real world, but an active, constructive process. The left panel appears to most naïve observer to be nothing more than random clusters of black splotches. The stimulus on the right (from Patrick Cavanagh, personal communication) takes the appearance of three parallel bars with different lengths and with slightly different protrusions. In each case, a small amount of information can drastically change the way the image is perceived. The blotches in the left image form the shape of a Dalmatian dog facing

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[1] Afterimages are visual patterns that can be seen following prolonged or intense exposure to a visual stimulus. They are the result of adaptation of cells in the retina and thus will appear to move when the eyes move.

Figure 3 Two stimuli whose appearance depends up prior knowledge and expectations of the visual system. The left stimulus appears at first to be a field of black splotches on a white background. The stimulus on the right appears to be three more or less horizontally oriented shapes in a vertical row. Perception is profoundly altered upon the realization that the stimulus on the left is a Dalmatian dog (facing away, bent over for a drink) and the right is a block letter E.

away, with its head down, while the bars on the right constitute the shaded portion of a block letter "E". For these and similar stimuli, once the embedded figure is recognized it becomes virtually impossible upon subsequent viewing *not* to see it. This is because the visual system has adopted a new set of expectations which dictate what we see, just as the Gestaltists emphasized.

In a similar vein, pictures and geometric figures that spontaneously change their appearance have been employed by scientists and artists alike to explore perception. Perceptual ambiguity stimulates vision to become dynamic, exploring different visual solutions based on previously shaped expectations. If there are multiple feasible solutions, perception will alternate relentlessly between the them, a phenomenon often described as *multistable* perception (*bistable* for only two alternatives).

Ambiguous Figures

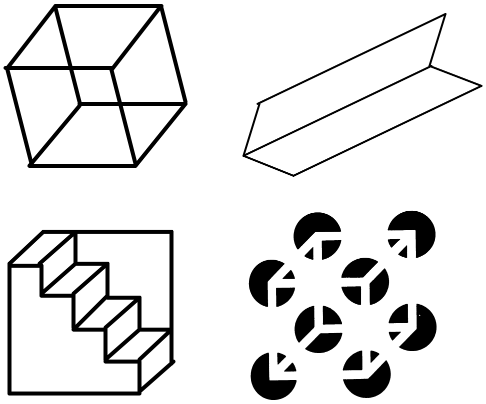

Figure 5 Examples of drawings that appear to change in depth. In each of these cases, the two dimensional lines comprising the drawing give rise to two equally valid geometrical interpretation. Perception, faced with this dilemma, alternates between the two. Starting in the upper left and moving clockwise, Necker's cube, folded card, subjective Necker's cube (Bradley and Petry 1977), and Schroeder's stairs.

Perhaps the most familiar stimulus associated with bistable perception is the line drawing of a cubic crystal described by Louis Albert Necker in 1832 (Necker 1832), shown in the upper left panel of Figure 5. This falls into the category of multistable stimuli known as "depth reversals", and it is shown along with three other examples. Perceptual bistability in these instances is likely to be due to the fact that vision begins with a two-dimensional surface (the retina). Although a straight line in the world casts a unique line onto the retina, a straight line on the retina may be the projection of any of an infinite number of curves viewed by an accidental vantage point. In normal vision, such ambiguity is generally eliminated by exploiting redundant cues, such as color, motion, shading, and stereopsis, to accurately resolve the three dimensional pattern. Even in the Necker cube, where individual line segments could offer infinite solutions on their own, perception is confined to only two solutions (at most three, the third being a completely flat pattern), testifying to the great effort on the part of the visual system to disambiguate its input as much as possible.

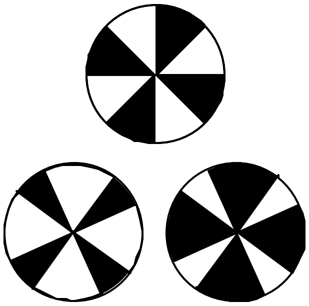

Figure 4 A demonstration of *relative size* as a determining factor in the assignment of figure and ground in ambiguous figures. The narrower wedges tend to be seen as figure, and the wider arms as background. Adapted from Koffka (1935)

This idea that perception conforms to predefined expectations about the world was one of the true insights of the Gestalt school in the beginning of this century. *Pragnanz*, literally "best figure", was the term given to this concept, whereby the most parsimonious interpretation of a stimulus was automatically adopted. Normally, object boundaries are defined simultaneously and redundantly by changes in luminance, texture, color, etc. Purposefully minimizing this redundancy by isolating only one of these can, on occasion, produce a figure in which the pragnanz does not converge onto any single solution, and perception therefore becomes ambiguous. Edgar Rubin (Rubin 1958) demonstrated this possibility with his renowned *face vs. vase* stimulus, shown in Figure 1, where the assignments to be made between figure and ground are unclear and thus perception becomes unstable. Koffka later extended Rubin's concepts in his *Principles of Gestalt Psychology* (Koffka 1935), outlining the rules governing which portion of a pattern is more often seen as figure and which more as ground. Properties such as relative size, closure, and symmetry were among those dictating the pragnanz of an ambiguous pattern. Figure 4, adapted from this work, demonstrates this principle. In the upper circle, where the black and white wedges are the same size, the dynamic figure/ground assignments are roughly equal over time. In the lower figures, however, the *smaller wedges*, whether black or white, tend to be seen as the figure, illustrating the principle that surfaces with larger area tend to be seen as background.

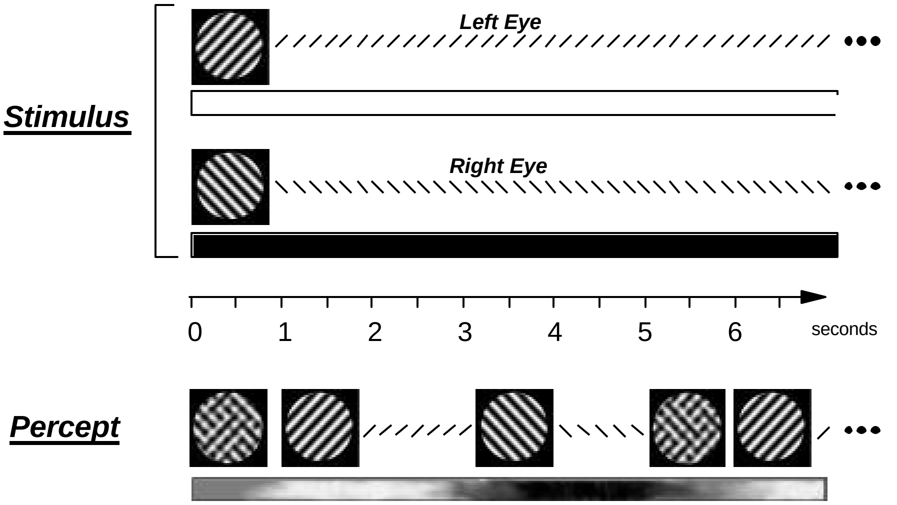

Figure 7 Binocular Rivalry. Two nonmatching patterns, presented separately and simultaneously to the two eyes, will not be perceptually combined into a third pattern except for very briefly. Instead, perception *select*s between the two patterns at each point in time, such that one or the other is entirely visible. Dominance of the two patterns alternates every few seconds.

Figure 6 The work of M.C. Escher. These two wood cuts illustrate how ambiguous borders can yield a dynamic stimulus. In each example, a white, detailed shape is seen as the figure on the left, which gradually is overtaken by the increasingly detailed black stimuli on the right.. Taken from (Bool, Kist et al. 1992).

The individual who is perhaps best known for employing perceptually ambiguous figures, and thus popularizing the fallibility of perception, is the Dutch graphic artist Maurits Escher. His long career began while the Gestalt school was being formed, and he was undoubtedly influenced by the work emerging from Rubin and Koffka (Teuber 1974). Two examples of his works are depicted in Figure 6. Escher was interested in, among other things, the concept of *plane filling* in art, and constantly emphasizes through his work the notion that a figure cannot exist in isolation, without its background (Bool, Kist et al. 1992).

Binocular rivalry

The focus of the present work is the phenomenon of binocular rivalry, which is formally a bistable perceptual phenomenon. During rivalry[1] binocular conflict leads to spontaneous changes in perception. Whenever stimuli in the two eyes are so different in nature that they cannot be perceptually fused into a single representation, perception oscillates between the

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[1] In the present dissertation there are references to several “types” of rivalry -- binocular, monocular and, more generally, perceptual. Unless otherwise specified, “rivalry” will refer specifically to *binocular* rivalry.

two monocular alternatives, seemingly unsatisfied with either result. The study of rivalry predates Gestalt psychology and even positivism, and its history and phenomenology are discussed more thoroughly in Chapter 2.

Neural Correlates of Perception

A number of physiological experiments have aimed at uncovering the functional organization of the central nervous system as it relates specifically to perception. These studies, which generally involve measuring the responses to stimuli and correlating them with the perception or inferred perception of an animal, reinforce the idea that the visual cortex is intimately involved in our perception of a stimulus. However, most studies have been unable to dissociate the sensory and perceptual components of neural firing and, just as in the results from the imaging studies and human lesions, the involvement of the early areas in perception remains unclear.

Single Unit Studies

One can divide studies seeking neural correlates of perception into two categories. In the first, neural responses are measured as an animal is shown a stimulus that is known to produce a well known perceptual effect or illusion, and those neurons responding to such stimuli are considered to be more closely allied with perception than others. Examples include neural responses to illusory contours (von der Heydt, Peterhans et al. 1984), coherent plaids (Movshon, Adelson et al. 1984), and brightness induction (Rossi, Rittenhouse et al. 1996), as well as correlates of adaptational aftereffects (Barlow and Hill 1963; Movshon and Lennie 1979), and other perceptual phenomena. Such studies generally rely on previous human psychophysical data to dictate what “would be perceived” by the animal, since the animal is often anesthetized and paralyzed during the experiment. Other studies in behaving animals, usually monkeys, compare cell activity directly with the simultaneous report of an animal making a perceptual discrimination. These experiments are more powerful in that specific instances of neural responsiveness can be correlated with individual behavioral responses. Such studies have investigated, for example, the neural sensitivity to motion stimuli (Salzman, Britten et al. 1990; Britten, Shadlen et al. 1992) and the neural basis of depth perception in random dot stereograms (Poggio, Motter et al. 1985). In such studies, neuronal and perceptual thresholds are often compared to make inferences about how neural activity underlies our perceptual capacity.

All the above studies, although extremely informative about the organization of the visual system, do little to address which cells are most closely allied with the *perception* of a stimulus per se. Many visual illusions, for example, are likely to be explained by relatively low-level inhibitory and/or adaptational processes among neurons involved in *sensory* processing. Although these effects do govern our perception of a stimulus, their neural correlates are not of the type that we seek in the current investigation. They are more akin to the perception of retinal afterimages, which derive from the fatigue of cells in the retina but nonetheless have a profound impact on perception. Furthermore, the presence of these correlates in *anesthetized* animals suggests that although they may account for a variety of visual illusions, their activity is not synonymous with subjective perception. Similarly, studies in the alert animal in which the psychophysical discrimination threshold is compared with that of an individual neuron also measure perception-related activity only indirectly. In this case, the *limits* of neural detection are compared to the *limits* of perception, viewing neurons as "stimulus detectors". Although it is possible that this approach may provide insights as to how brain activity underlies perception, it is by no means guaranteed. If the perceptual and neural thresholds both represent sensory limits, just as the sensitivity to a faint flash is dictated by the absorbance of rods and cones in the retina (see, for example, Hecht, Schlaer et al. (1942)) it may not be possible to generalize this activity to the workings of the perceptual system. Even when it is shown that the perception and neuronal responsiveness co-vary from trial to trial (e.g. Shadlen, Britten et al. (1996)), it is still possible that this variability derives from noise in the generalized sensory transduction.

Lesion Studies

A few studies have investigated the specific action of the early visual system on perception by making distinct lesions and then measuring the perceptual capabilities of a monkey afterwards. Schiller et al. (Schiller, Logothetis et al. 1990), for example, selectively ablated both the magnocellular are parvocellular layers of LGN in monkeys and subsequently tested them with a variety of perceptual tasks. It was found that while some of the perceptual abilities were much more strongly affected by one type of lesion than another, either channel could transmit sufficient information to support the perception of most stimuli. Lesions in the striate and prestriate cortical areas of monkeys are more relevant to the present investigation, and have the potential to reveal much about the functional organization of perception. In general, animals with well defined ablations to these regions retain their visual abilities to an extraordinary degree (Merigan, Nealey et al. 1993; Pasternak, Tompkins et al. 1995; Merigan 1996). Their detection thresholds and contrast sensitivity are, in general, only slightly diminished. However, assays specifically involving perceptual grouping required to perform a shape discrimination revealed that the ability to perceptually organize elements into a pattern was severely disrupted in these animals. This combination of perceptual deficits with intact basic visual capacities is very similar to the condition of those apperceptive agnosic patients discussed earlier and mentioned again in final chapter, suggesting that lesions of the early areas, V2 and V4 in particular, may serve as good animal models for the agnosic disorders. Unfortunately the utility of these studies is limited by the ability of monkeys to communicate their subjective perception in the context of a psychophysical task, and must therefore be done at the most cursory levels. With improved techniques and perceptual assays, lesion studies could provide a great deal of information regarding the role of different cortical areas in the subjective perception of a stimulus.

Neural Correlate of Visual Awareness

So what exactly is it that one seeks when trying to uncover perceptual mechanisms in the brain? What does one look for in a neural correlate of a subjective visual experience? Certainly there are a number of *gedanken* experiments that would provide much information if they were feasible. For example, if one could measure how single neurons in the brain were activated during a *dreamed* visual scene, one might begin to fathom how the brain "generates" perception, as there is no contamination from external visual stimulation. Likewise, if small numbers of cells, or individual neural circuits, could be "knocked out" or temporarily depressed while an animal performed a perceptual task, one could potentially learn a great deal about how the wiring of the brain underlies our perception. This sort of reverse engineering could provide an animal model for perceptual disorders such as the apperceptive agnosias.

In the present study I describe the measurement of neuronal correlates of subjective visual perception. We employed visually bistable stimuli to ask how the activity of neurons in the early areas relates to spontaneous, subjective changes in appearance. Given that most bistable stimuli, such as Rubin's *face vs. vase*, or Necker's cube, are relatively inflexible and thus make poor candidates for an electrophysiological study, we employed the more general phenomenon of binocular rivalry, mentioned above and elaborated in the next chapter. Its generality lies in the fact that nearly any monocular stimulus that can activate a cell will periodically become perceptually suppressed if it is simultaneously presented with a sufficiently different stimulus in the other eye. Such subjective changes are spontaneous and internally generated, and can therefore be used to examine how neural activity in the early visual cortex is related specifically to the perception of a stimulus.

A RIVALRY BETWEEN THE TWO EYES

> I glued a round patch of blue taffeta of about an inch in diameter onto one side of a sheet of cardboard, and on the opposite side, another patch of yellow taffeta of the same size, so that the two were exactly back to back. I placed the cardboard against my nose in a vertical plane and perpendicular to my face. Through my right eye I saw only the blue patch and not the yellow, and vice versa for my left eye. Thus each of the two patches formed separate images; blue in my right eye, yellow in my left eye. However I was only aware of one patch…That single patch which I saw sometimes appeared blue and sometimes yellow, apparently according to the rays of light from one or the other patches striking my eyes with more energy. Also, sometimes the patch appeared partly blue and yellow…May we not now conclude that at any instant my mind only receives the impressions of half the total amount of light reflected by the two patches…? (DuTour Discussion d’une question d’optique (1760), translation by O'Shea (1983))

The above quote represents the first recognized recount of the phenomenon of binocular rivalry. Even in this short passage the essence of rivalry is captured. Two different patterns are presented to the visual system, one through each eye, and yet singleness of vision is maintained. The subjective pattern that occupies perception is not a superposition of the two alternatives, but a selection between them. Neighboring spatial locations within the percept can make different selections, resulting in a mosaic of the two monocular views. And finally, perception is unstable, continually switching between alternative states.

Since the time of DuTour rivalry has been described in the context of numerous metaphors, ranging from ethereal shifts in attention to the mechanistic workings of an autonomous oscillator. One of the aims of the present study is to develop a framework for thinking of rivalry as a *perceptual* dilemma for the visual system. Vision is characterized by processes, such as grouping and image segmentation, that organize extracted features from two dimensional retinal patterns into representations of shapes and three dimensional objects. These operations are so inherently a part of our own perception that they are difficult to study objectively. By employing rivalry, I shall argue, one gains the ability to perturb these processes and examine them in isolation as they struggle to make sense of an artificial and paradoxical sensory input. Although these concepts are not entirely new, they do represent a departure from the last thirty years or so of research, in which rivalry has been considered a phenomenon specific to binocular vision. In the present chapter I briefly review the evolution of thought pertaining to rivalry since it was first described. I then turn to a number of psychophysical experiments from the last few decades that have shaped the way in which rivalry is generally conceived.

Historical Notes

In the last two centuries rivalry has been studied primarily in the context of psychophysics, less often biophysics, and at times metaphysics. It is, by definition, no less of a bistable perceptual entity than any of the ambiguous figures, but it was largely ignored by the Gestaltists and gradually came to be viewed as a problem peculiar to binocular vision.

Rivalry and attention

In the nineteenth century much debate focused on whether attentional shifts could explain rivalry. DuTour, in his original formulation, had considered that attention dictated perception during rivalry, a view that was later embraced by Helmholtz, who became the premier proponent of attention-based rivalry. Helmholtz states *(Warren and Warren 1968)*:

> *… there are some very curious and interesting phenomena seen when two pictures are put before the two eyes at the same time which cannot be combined so as to present the appearance of a single object… In spite, however, of what former observers have said to the contrary, I maintain that it is possible for the observer at any moment to control this rivalry by voluntary direction of his attention…hence, retinal (binocular) rivalry is not a trial of strength between two sensations, but depends upon our fixing or failing to fix the*

> *attention… Indeed there is scarcely any phenomenon so well fitted for the study of the causes which are capable of determining the attention…If, on the other hand we leave the mind at liberty without a fixed intention to observe a definite object, that alternation between two pictures ensues which is called retinal rivalry. In that case, we find that, as a rule, bright and strongly marked objects in one field of vision prevail over those which are darker and less distinct in the other either completely or at least for a time.*

As implied, the view that rivalry is subject to voluntary control was not held by all investigators. In fact, it is curious that Helmholtz felt so strongly that one can so freely manipulate their perception during rivalry, as it has been subsequently shown that although there is some limited control over the alternation process, such as raising or lowering its rate, it is clear that such control is limited.

Hering (Hering 1893) in particular rejected the notion that rivalry is related to attention. He was perhaps the first to explain the perceptual changes as a natural physiological consequence of having different contours in the same region of visual space in the two eyes. In his view, the dynamics of rivalry were governed not by how “interesting” the stimuli were, as Helmholtz thought, but by their physical *structure.* This idea has persisted until today and, although the debate between attentional and structural theories of rivalry remains, the vast majority of recent papers favor structural explanations of rivalry alternation, independent of attention (Levelt 1965; O'Shea 1983; Blake 1989), but see (Ooi and He 1995; Ooi and He 1996).

More recent studies do, however, provide unequivocal evidence that attention can *influence* rivalry. Subjects can, for example, learn to increase or retard the overall alternation rate, or to bias perception toward one or the other of the stimuli. Meredith and Meredith (Meredith and Meredith 1962), for example, found nearly a threefold difference in alternation rate when the subjects were instructed to consciously speed up the process as opposed to when they were told to slow it down. Other studies provide similar results, and demonstrate that the control over rivalry emanates from a central rather than peripheral process (Lack 1969; Walker 1978).

A Psychoanalytic Tool?

Beginning in the middle part of this century, a number of studies considered whether perception during rivalry could be used to reveal meaningful psychological predispositions. Articles with titles such as "Binocular Rivalry and the Study of Identification in Asthmatic and Nonasthmatic Boys" (Purcell and Clifford 1966) and "Binocular Resolution and Perception of Race in South Africa" (Pettigrew, Allport et al. 1958) illustrate the detour taken in rivalry research during this period. In general, these and other studies found a weakly positive influence of the semantic or emotional content of a scene in which of two stimuli was perceived (see Walker (1978) for a review of this literature). This effect is not altogether surprising given that attention can influence which stimulus dominates during rivalry. Nonetheless it does appear to be confined to the semantic content of *images*, as the semantic content of words does not appear to either influence the balance of dominance and suppression (Blake 1988), nor prime subsequent perception when flashed in the suppressed eye (Zimba and Blake 1983).

Studies of rivalry between faces suggest some organizational aspects pertaining to high order scene content are preattentive. It is known that during rivalry an upright face will generally prevail when paired against an inverted face (Engel 1956). In a study by Hastorf and Myro (Hastorf and Myro 1959) subjects were dichoptically presented upright and inverted faces for periods of 100 and 200 milliseconds and asked to report whether they saw no face, two faces or a single face, and, if it was a single face, whether it was upright or inverted. Under these conditions the upright faces were still reported with roughly twice the frequency of the inverted faces, suggesting that rivalry dominance may be influenced by higher order stimulus content without necessarily being mediated by attention. This view is also supported by results from a more recent study in which it was shown that the famous "Dalmatian Dog" stimulus (Figure 3) predominated during rivalry more than similar stimuli containing no figure. Remarkably, this effect was seen even before subjects were aware that any figure was embedded, again arguing that preattentive mechanisms can bias perception (Yu and Blake 1992).

Finally, a few groups have demonstrated a link between alternation rate during rivalry and overall intelligence (Spearman 1927; Crain 1961). As Crain states:

> *The hypothesis is this: that level of intellectual functioning and rate of binocular rivalry are related, higher intelligence being associated with higher rate of rivalry and lower intelligence being associated with lower rate of rivalry.*

He demonstrates that this hypothesis is correct by testing numerous subjects first in a variety of intelligence tests and then asking them to report their alternations during rivalry. Those performing better on virtually all of the tests tended to have faster rivalry alternations than those performing poorly. These results are deemed unconvincing and irrelevant by the present author, who happens to have a relatively low alternation rate.

The Levelt Restoration

Levelt, in his seminal dissertation On Binocular Rivalry, (Levelt 1965) made perhaps the single most significant contribution to the field since rivalry was first described (Blake 1989). In his work he made a thorough review of the previous rivalry literature, clarifying points of confusion between rivalry and similar phenomena, and established a framework for studying rivalry that has persisted until today. Levelt rejected Helmholtz's attentional theories, and favored instead the view of Hering and Breese (Breese 1899; Breese 1909), that the structure of the monocular stimuli was the determinant of the alternation dynamics. He says of attentional rivalry theories:

> *The next question immediately becomes: 'what determines attention', and so we come back again to stimulus factors. Attention theory is only a theoretical escape mechanism…the* deus ex machina *which explains each apparent irregularity in the phenomena.*

Levelt viewed binocular rivalry as an interaction between binocular brightness averaging and a contour mechanism which was not in itself inherently binocular. He also described for the first time the characteristic dynamics of binocular rivalry. The process of perceptual alternation, he recognized, was random, where the duration of a given phase of dominance could not be predicted even with knowledge of all previous phases; however, the distribution formed by these phases is deterministic and reproducible, forming a skewed shape that he modeled using a gamma function. He considered the dynamics of rivalry to result from a stochastic process in which a certain number of events ("excitation spikes") were required for a perceptual change to result. Small eye movements, he claimed, were good candidates for these events, although it has subsequently been shown that normal rivalry can be experienced even with stabilized images or paralyzed extraocular muscles. (Blake, Fox et al. 1971; Lack 1978). Nonetheless, Levelt's formulation of the rivalry's basic dynamics still hold true. In his thesis, he also elaborated the rules governing how long, on average, a stimulus is perceived during rivalry. *Stimulus strength* he defines operationally as the ability of a given stimulus to suppress another in the contralateral eye. He then goes on to outline the rules governing the perceptual balance between two stimuli competing for dominance given their absolute and relative strengths. In keeping with Hering, the structure of the stimulus was considered to be the only important factor in determining its potency during rivalry.

Since Levelt, rivalry has generally been viewed as a problem specific to binocular vision, setting in when binocular fusion is impossible. However, Levelt himself showed that *monocular rivalry* a condition which he evoked using the phenomenon of metacontrast, could generate very similar perceptual conditions to binocular rivalry. He demonstrated that some salient features of binocular rivalry, such as the perceptual conjunction of a contour with its background, could be mimicked by successive monocular presentation instead of continuous dichoptic presentation. He claims:

> *That a stimulus can 'take its background along' can also be shown in monocular experiments. Binocular rivalry can be simulated, by presenting two different stimuli in rapid succession to the same eye.*

Levelt's discovery of this monocular rivalry effect, which he points out is strikingly similar in appearance to binocular rivalry, is not (to the knowledge of the writer) recognized anywhere in subsequent rivalry literature. Monocular rivalry, in a different form, was described several years later (Campbell and Howell 1972), which I shall return to in a later chapter.

What is Perceived During Rivalry

Subtleties in what is perceived during binocular rivalry can reveal much about potential mechanisms, but are unfortunately difficult to assay. Rivalry is in its very nature unstable, consisting of fleeting subjective changes that cannot be measured directly, only indirectly through the judgments of a subject in the context of a specific experimental paradigm. To add another complication, subjects' proficiency with perceptual tasks changes over time. During the first exposure to a bistable stimulus the naïve subject may not understand at all what he or she is supposed to be seeing. However, after several "practice" sessions, and being perhaps influenced by instructions from the experimenter, the same person is often able to experience profound and reliable perceptual bistability. In some cases, it is hard even to define what a naïve subject is. Finally, even for experienced subjects, the rate of alternation, the unitariness of the rivalry percept, and the ability to see rivalry in "difficult" stimuli widely varies. As a result, there is arguably no direct, objective way to measure and generalize what is perceived during binocular rivalry. Yet, this does not mean that its phenomenology cannot be studied indirectly. In this section I outline many experiments that give insight into what is common in the subjective perceptual experience of many subjects during binocular rivalry.

Spatial Nature

Rivalry is an inherently spatial phenomenon. Its very existence owes to the fact that we have two retinae, but only one representation of visual space. Perhaps a lizard or similar creature whose two eyes can independently scan the environment is able to simultaneously represent each monocular view even when they differ substantially. However, primates, who have front mounted eyes, generally rely on binocular agreement when both eyes are open. If this agreement is violated, and conflicting stimuli fall on corresponding parts of the retinae, singleness of vision is enforced by eliminating one of the conflicting pair. Only in rare instances (e.g. with very low contrasts or short presentations) are conflicting monocular patterns perceptually fused into a third pattern (Wolfe 1983; Liu, Tyler et al. 1992). Rivalry can be provoked by a conflict in any stimulus dimension as long as two patterns are spatially overlapping. It will occur between differing colors, textures, directions of motion, and even afterimages (Blake, Fox et al. 1971; Wade 1973; Wade 1977; Wolfe 1983).

Whether two monocular stimuli are fused or begin to alternate depends upon their similarity. In general, binocular fusion is robust to stimulus mismatches over a limited range, but gives way to rivalry if the differences exceed a threshold (although hysteresis can sometimes maintain fusion well beyond this threshold). Two monocular drifting gratings will begin to rival when their directional disparities exceed 30 angular degrees, and stationary gratings when their orientation difference exceeds 15 degrees (Blake 1989). These values are similar in value to both the half widths of the psychophysical orientation channels, as well as the physiological tuning curves of orientation-tuned neurons in macaque striate cortex (De Valois, Yund et al. 1982). It is also interesting to note that these represent the same limits of perceptual fusion that occur in *monocular* rivalry, between pairs of monocularly superimposed contours (Campbell and Howell 1972), discussed in a later chapter.

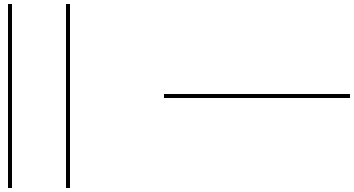

Figure 8 Demonstration of the spread of suppression after Kaufman (1963). If the two half-images above are fused (two vertical lines vs. one horizontal line) suppression of the horizontal line is not restricted to the areas of intersection, but often includes the entire portion between the vertical lines.

When rivalry does occur, it can take one of two forms. Perception can either alternate between complete, coherent representations of the competing stimuli, or it can take on a piecemeal appearance. In the latter case, the visible stimulus takes the form of a mosaic pattern, consisting of interleaved regions of right and left eye dominance. Completeness in perception is, as a general rule, governed primarily by the size of the rivaling stimuli (Blake, O'Shea et al. 1992), although recent evidence suggests that is an oversimplification, and that a more complex interaction between the size and the spatial structure of a stimulus (i.e. spatial frequency content) determines its unitary dominance (O'Shea, Sims et al. 1996).

Rivalry is spatially confined to the region of disagreement—if, in one part of the visual field two contours are in binocular conflict, they will compete while simultaneously a pair of matching contours elsewhere will be perceptually fused. However, the spatial confines of rivalry do extend beyond the immediate point of conflict, a phenomenon which has often been referred to as the “spread of suppression” (Kaufman 1963) or sometimes the “spread of exclusive visibility” (O'Shea, Sims et al. 1996). In general, a pair of rivaling contours, say dichoptic orthogonal lines that cross each other at their center point, will alternate dominance not only at their intersection, but in a region extending roughly a half a degree around that point, depending on the exact stimulus and eccentricity (Kaufman 1963; Fukuda and Blake 1992). As mentioned above, this spread of exclusive visibility is not peculiar to binocular rivalry, but is also seen under certain *monocular* conditions (Levelt 1965; Sindermann and Luddeke 1972). Finally, the exclusive visibility of a rivalry target increases with its retinal eccentricity in a way that mirrors the human cortical magnification factor, suggesting that the rivalry mechanism employs the early, topographic visual areas (Blake, O'Shea et al. 1992). These points will be discussed more thoroughly in later chapters.

Limits of Rivalry

One of the most remarkable aspects of rivalry is the ability of a very weak stimulus to completely suppress a much stronger one. Blake (Blake 1977), for example, found that “a pattern at its own contrast threshold can suppress temporarily a contralateral pattern, regardless of the contrast of the latter”. The contrast threshold for rivalry is almost identical in value to that of detection over the entire range of spatial frequencies and stimulus eccentricities. In fact, although a threshold-level stimulus rises only infrequently to dominance over a strong one, when it does, it will stay dominant, on average, just as long as a much higher contrast stimulus would.

Although the rivalry process operates under many stimulus conditions, it does possess spatial and temporal limits. When two dichoptic grating patterns are *both* near their contrast threshold, for example, they can appear superimposed, resulting in perception of a plaid pattern. Although investigators are divided on whether such a pattern is truly indistinguishable from a binocular plaid (mainly because of the perception of luster), it is clear that rivalry itself is no longer present with such stimuli (Blake, Yang et al. 1991; Liu, Tyler et al. 1992). In a similar vein, when the presentation time of a conflicting pair of orthogonal gratings is less than 150 msec, neither stimulus is perceived on its own, but again perceptual fusion of the two patterns results. A flickering pattern can be maintained in such a fused state when each presentation is less than 150 msec, and each blank interval is more than 150 msec, for both real images and afterimages (Wade 1973; Wolfe 1983; Wolfe 1983).

If, however, the presentation time increases above this value and/or the blanking interval dips below it, fusion once again gives way to normal binocular rivalry.

Temporal Dynamics

As in all bistable phenomena, rivalry is characterized by continual changes in what is perceived. The temporal dynamics of these changes can reveal much about the nature of rivalry, and, as discussed later, about its relationship to other bistable percepts (Walker 1975). At its most elementary level, the rivalry process can be considered to be stochastic—a given phase of dominance endures for an amount of time that does not depend at all on the previous pattern of alternation**.** Yet, as Levelt first noted, despite this sequential independence, the distribution of dominance durations is nonrandom, and, when normalized to the mean dominance time, forms a characteristic shape for most subjects and nearly all stimulus conditions. Similar temporal dynamics are seen for rivalry between conflicting contours (Fox and Herrmann 1967; Levelt 1967), chromatic stimuli (Walker 1975), and even afterimages that are immobilized on the retina (Blake, Fox et al. 1971).

Despite its randomness, the mean dominance of each stimulus can be manipulated during rivalry. As mentioned above, attention can alter the balance of left and right eye dominance (Lack 1978). But, by far the most potent determinants of this balance are the structural properties of the stimuli placed in the two eyes. Levelt (Levelt 1965; Levelt 1966) clarified the relationship between stimulus strength and mean dominance in the form of four propositions, rephrased here:

- The fractional dominance of a stimulus increases with its strength.
- The mean dominance of a stimulus does not increase with its strength.
- The overall alternation rate increases with an increase in the strength of one stimulus.

- The overall alternation rate increases with an increase in the strength of both of the stimuli

Strength, in this context, is dictated by properties of a stimulus such as contrast, spatial frequency content, wavelength, and speed. The first and second of these propositions, when considered together, reveal a peculiar property of rivalry: the strength of a monocular stimulus primarily influences how long on average its *competitor* is perceived. As discussed below, this observation poses difficulties for many simple rivalry models. It is also interesting to note that adaptation to previously viewed stimuli can bias the alternation process. If, for example, the orientation-specific contrast threshold of a grating is raised due to adaptation, its potency in subsequent rivalry will be decreased (Blake, Westendorf et al. 1980), and the alternation process will respect its apparent, rather than real, contrast .

Finally, when a pair of rivalrous stimuli is presented, perception can be profoundly biased by a brief stimulus presented immediately beforehand. For example, if one eye views a vertical grating pattern for several hundred milliseconds, after which a horizontal pattern is added to the corresponding region of the contralateral eye, the newly added pattern will nearly always dominate perception during rivalry (Wolfe 1984). This phenomenon, known as “flash suppression” has recently been shown to be phenomenologically similar to spontaneous rivalry suppression (Baldwin, Loop et al. 1996), and provides a useful paradigm by which perception during rivalry can be deterministically controlled. The temporal conditions governing this influence have been studied and cited in support of eye-dominance models of rivalry, and I shall return to flash suppression in later chapters.

What is Not Perceived During Rivalry

Most modern theories of rivalry have attributed its singleness of vision to a *suppressive* process in which the representation of the unwanted stimulus is eliminated at an early stage of processing, generally through inhibition of monocular neurons (Blake 1989; Lehky and Blake 1991). In this view, information from one of the eyes meets a barricade beyond which it cannot pass, and thus never reaches higher conscious centers. A few have considered the possibility that suppression is not a monocular process, but that it acts upon groups of binocular neurons sensitive to specific stimulus features (Grossberg 1987), and some have suggested that the concept of suppression is unnecessary in a theory of rivalry (Crovitz and Lockhead 1967). The following section outlines different psychophysical approaches that have been taken to discover the extent to which information entering the suppressed eye is processed by the visual system.

Nonselectivity of Suppression

A number of experiments have shown that during binocular rivalry a test probe, bearing no resemblance to either rivaling stimulus, becomes more difficult to detect when shown to the eye in which a rivaling stimulus has vanished. In such an experiment, an observer is engaged in binocular rivalry and reports the progression of dominance and suppression of the two stimuli. Meanwhile, faint spots of light are occasionally flashed in each eye, to which the observer is required to press a button indicating whether the spot was perceived. The ability to notice these flashes is then evaluated as to how strong the flash was and whether or not the rivalry stimulus in the flashed eye was dominant or suppressed. This provides a measure of monocular sensitivity during dominance and suppression (Wales and Fox 1970; Blake and Overton 1979; Cogan 1982; Smith, Levi et al. 1982). Similar approaches have used recognition thresholds (Fox and McIntyre 1967; Fox and Check 1972) and reaction times (Fox and Check 1968; O'Shea and Crassini 1981; Westendorf and Blake 1988) during dominance and suppression to measure this sensitivity.

The general result of these studies is that virtually all thresholds are elevated during rivalry's suppression phase, and that this suppression is almost entirely nonselective. Fox and Check (Fox and Check 1968), for example, demonstrated that the detection of a moving target could be completely abolished during rivalry initiated by static grating patterns, and similar experiments have shown that suppression is not orientation selective (O'Shea and Crassini

1981). Suppression is all or none, and remains at a constant depth throughout its tenure (Fox and Check 1972). Blake, in his 1989 review (Blake 1989) uses these facts to make the case for "eye competition" in his model of rivalry:

> *What is critical is that these inhibitory connections, when activated, operate nonselectively on the entire group of monocular neurons innervated by a given eye, not just on a subset of those monocular neurons tuned to a particular feature. This nonselectivity property is included to account for the psychophysical finding that suppression operates on all information presented to a suppressed eye not just on those features composing the originally suppressed target.*

Yet even within the context of eye competition there are a few exceptions to the nonselectivity of suppression. Smith et al., for example, found that during suppression the sensitivity to monochromatic test probes is more severely diminished for short wavelengths than for higher wavelengths (Smith, Levi et al. 1982). They suggest, based on this result, that perception during the dominance phase of rivalry is mediated by the chromatic channel, and that during suppression the luminance channel takes over. This is supported by the observation that perception of a test probe's color disappears during suppression even when the probe is detected, while the color is perceived normally when seen during a dominance phase. Other studies have similarly found differences in chromatic processing during rivalry, prompting some to label rivalry as tritanopic[1] (Hollins and Leung 1978; Rogers and Hollins 1982).

A second exception to the rule of "blanket rivalry suppression" centers on the observation that within a given region of space rivalry and binocular fusion can occur simultaneously. Julesz and Miller (Julesz and Miller 1975) demonstrated that when rivalrous masking noise

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[1] "Tritanopic" describes the decreased sensitivity to short (blue) wavelengths, usually in color blind patients.

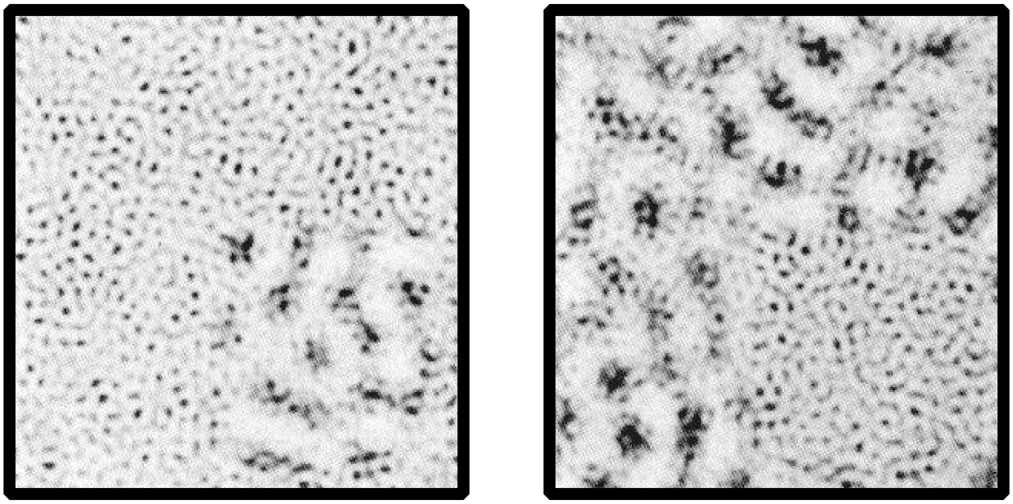

Figure 9 Stimulus of Frisby and Mayhew (1979). Binocular combination of the two half-images above results in the stable fusion of the high spatial frequency texture pattern, while the low spatial frequency pattern fades in and out of visibility. The discontinuity in texture in the lower right corner becomes imperceptible.

was added to a random dot stereogram the noise could rival while the dots were stably fused, as long as their frequency bands were at least two octaves apart. Figure 9 shows a similar arrangement, taken from Frisby and Mayhew (Frisby and Mayhew 1979), in which binocular combination of the two stimuli yields a unification of the high frequencies that is roughly stable, while the superimposed low frequency pattern tends to drift in and out of perception. The notion of simultaneous rivalry and fusion has recently been challenged, however, by those who suggest that although rivalry and stereopsis may be simultaneous in neighboring regions of an image, they are never both temporally *and* spatially coincident (Blake, Yang et al. 1991).

Potency of an Unperceived Stimulus

Numerous studies have aimed at discovering the degree to which a perceptually suppressed stimulus permeates the visual system. Information never reaches conscious perception, but is it still represented in the activity of cells in different cortical areas? This question is, of course, central to the electrophysiological studies presented as part of the current dissertation. But it is interesting to note that numerous psychophysical studies have addressed exactly this question. “Psychoanatomic techniques”, as they were originally called (Julesz 1971), use psychophysical methods, along with what is known about the basic organization of the visual system, to make inferences about the relative order of different aspects of visual processing. In the case of rivalry, many of these experiments were aimed at identifying the site of suppression, or the point at which information about the nondominant stimulus is blocked. One category of particularly clever experiments has explored the degree to which a suppressed stimuli can generate adaptational aftereffects[1]. Given that these illusions are the result of cortical adaptation, the efficacy of a stimulus in generating them gives a measure of the degree to which it is processed by cortical cells. The strength of simple aftereffects, such as the waterfall illusion (Wohlgemuth 1911), contrast threshold elevation (Blakemore and Campbell 1969), spatial frequency shift (Blakemore and Sutton 1969), the tilt aftereffect (Gibson and Radner 1937), is known to be directly proportional to the duration of adaptation. It is assessed quantitatively by either measuring the degree to which perception is affected, or the length of time the aftereffect persists. Several investigators, starting with Fox and colleagues (Blake and Fox 1974; Blake and Fox 1974; Lehmkuhle and Fox 1975), and later other groups (Wade and Wenderoth 1978; Blake and Overton 1979; Wade and De Weert 1986) tested whether during rivalry a *suppressed* stimulus was able to adapt the appropriate cells in the visual system sufficiently to cause aftereffects, or if information about the suppressed stimulus was blocked before it reached these cells. For the simple aftereffects, the results are unequivocal[2]: a stimulus will contribute fully to an adaptational aftereffect whether or not it is perceptible. Suppression does not prevent information from fatiguing those cortical neurons that comprise the psychophysical channels for orientation, direction of motion, etc., suggesting that if there is a “site” of suppression it

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[1] Adaptational aftereffects are visual illusions that can be elicited by gazing for several seconds at one stimulus (the adapting stimulus) and then quickly looking at a second pattern (the test stimulus), which appears be changed. Prolonged adaptation to a single orientation, direction of motion, color, or spatial frequency can generate such attribute-specific illusions, resulting from the fatigue of narrowly-tuned psychophysical channels.

[2] with the exception of a single study Lehky, S. R. and R. R. Blake (1989). “Binocular Rivalry Affects Strength of Contrast Adaptation.” Investigative Ophthalmology and Visual Science Supplement **30**: 253.

must lie beyond the very initial stages. This notion is bolstered by the subsequent observation that the interocular transfer[1] of aftereffects is also preserved (O'Shea and Crassini 1981).

How does one reconcile the idea that suppression cannot precede binocular adaptation with the notion from the previous section that rivalry unilaterally suppresses information entering the nondominant eye? It is impossible. Results from the adaptation experiments are a thorn in the side of those who believe that rivalry suppression acts by the absolute inhibition of a monocular pathway. Blake, who has been a major proponent of this view of rivalry, categorizes the aftereffect results (many of which are his own work) as an “unresolved issue”, and a “weakness in the theory that must be remedied” (Blake 1989).

More recent psychoanatomical experiments have suggested that the representation of a suppressed stimulus is in fact diminished as it reaches the prestriate visual areas. Some higher order aftereffects that are thought to result from neural activity in these areas, such as the tilt of subjective contours (Van der Zwan and Wenderoth 1994) and a number of complex motion effects (Wiesenfelder and Blake 1990) are not as strong when the adapting stimulus is unperceived. In a similar vein, a stimulus that, by its presence, would normally “spend” a stored motion aftereffect ceases to do so when it is perceptually suppressed during rivalry (Wiesenfelder and Blake 1992). These results suggest that although a suppressed stimulus is represented in the firing of cortical neurons in striate cortex, its representation is diminished at higher visual areas—those responsible for such high-order aftereffects.

Finally, a variety of experiments have examined other subtle ways in which a suppressed stimulus may or may not contribute to perception, offering mixed results. Westendorf (Westendorf 1989) found that a suppressed stimulus does not contributed to dichoptic masking, which is taken as evidence for suppression to act nonselectively over an entire

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[1] Interocular transfer refers to the condition in which one eye is adapted and the other eye is tested. If the unadapted eye demonstrates the aftereffect one can infer that *binocular* neurons are responsible. Most simple aftereffects demonstrate roughly 70% interocular transfer.

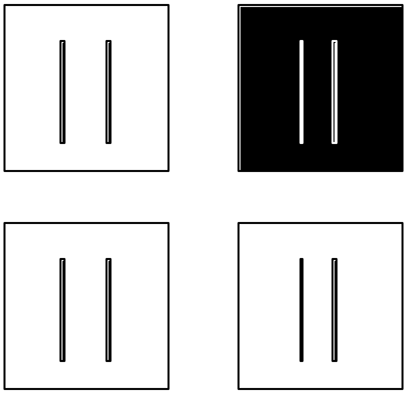

Figure 10 Stereo can be observed even when images are of opposite polarity, and hence undergo rivalry.

monocular channel. Wiesenfelder and Blake (Wiesenfelder and Blake 1991) found that apparent motion was weakened but not eliminated when the first of two frames was unperceived because of suppression. This contradicts an earlier study (Ramachandran 1975) where it was found that suppression blocked the perception of motion entirely in such a stimulus. Finally, a recent study (Schall, Nawrot et al. 1993) found that a visual cue presented to a suppressed eye during rivalry was ineffective in orienting visual attention correctly to a subsequently viewed target. Hence, psychophysical studies of rivalry send mixed messages regarding the degree to which an unperceived stimulus is processed by the visual system. On the one hand, its potency to adapt psychophysical channels is relatively high, as most aftereffects are unaffected by suppression. On the other hand, a suppressed stimulus cannot be recalled, or utilized meaningfully to perform a task--as if it were never shown.

Rivalry and Stereopsis

Rivalry and stereopsis have always been strange bedfellows. On the one hand, it has been known since Helmholtz (Helmholtz 1925) that stereopsis can occur simultaneously with vigorous rivalry. According to Hering "Binocular depth perception…is *only* possible through retinal rivalry and the victory of contours" (italics mine) (Hering 1864). On the other hand, the degree to which rivalry and stereopsis can be spatially and temporally coincident has prompted a great deal of debate (Blake and O'Shea 1988; Wolfe 1988; Blake, Yang et al. 1991). Some investigators maintain that it is impossible for rivalry and stereopsis to coexist peacefully because rivalry represents the default outcome of binocular vision only when stereoscopic fusion is impossible (Blake 1989). Others suggest that rivalry and stereopsis can occur in parallel, simultaneously drawing on different groups of neurons for stereoscopic

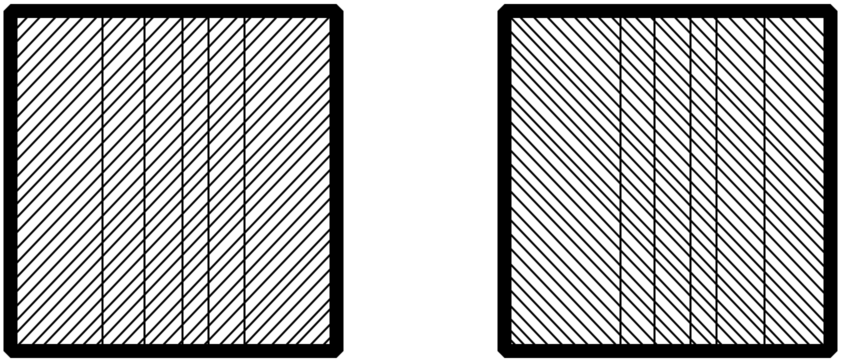

Figure 11 Demonstration of the coexistence of stereopsis and binocular rivalry. If the above stimuli are cross-fused there is clear perception of depth in the vertical lines despite vigorous rivalry.

matches and nonrivalrous mismatches (Julesz and Miller 1975; Wolfe 1986). The relationship between the two phenomena is important to clarify because it could give insights into the functional organization of perception in the visual system. It is thought that the perception of stereopsis relies on the activity of neurons in the earliest cortical areas, where information from the two eyes is combined. This is supported by the existence of cells in all early cortical areas that are specifically tuned for binocular disparity[1] (see next chapter). Also consistent with this notion is decreased interocular transfer of adaptational aftereffects for stereoblind humans (Movshon, Chambers et al. 1972), as well as the reduced number of binocularly responsive neurons in the early cortical visual areas of stereoblind monkeys (Crawford, Smith et al. 1984).

Yet, in spite of the general disagreement regarding rivalry and stereopsis, when the data are viewed objectively they lend themselves to some generalizations. The first is that the simultaneous perception of stereopsis is indeed possible during conditions of binocular rivalry, as most investigations have found that the two phenomena can coexist to some extent (Helmholtz 1925; Triesman 1962; Kaufman 1964; Ogle and Wakefield 1967; Julesz

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[1] Binocular disparity refers to the slight shift in position of the two retinal projections, with respect to the position of the foveae, of a point in 3-D space. Horizontal disparities are the natural consequence of the parallax generated by having slightly different viewpoints afforded to each eye in normal vision. The polarity and size of these relative shifts provide information about the distance to an object in space relative to the plane of fixation. With binocular viewing stereopsis can be experienced even in nonsense stimuli, when horizontal disparities are added to each monocular view.

and Miller 1975; Frisby and Mayhew 1979; Levy and Lawson 1982; Wolfe 1986; Blake, Yang et al. 1991). Figure 11 shows an example of a typical stimulus in which stereopsis and rivalry coexist (taken from (Ogle and Wakefield 1967)). The second generalization is that stereoscopic judgments are impaired or degraded during concurrent binocular rivalry. This is reported in many of studies to a greater or lesser degree (Frisby and Mayhew 1979; Levy and Lawson 1982; Blake, Yang et al. 1991) with only a rare exceptions where the stereoscopic thresholds remain unchanged during rivalry (Ogle and Wakefield 1967). Many of the differences of opinion in interpreting the data appear to stem from initial differences in the authors' null hypotheses. For example, Figure 10 (adapted from Blake, Yang et al. (1991)) illustrates another example of the coexistence of rivalry and stereopsis. Whereas this type of reverse-contrast image has been used to make the point that rivalry and stereopsis can coexist (Helmholtz 1925; Levy and Lawson 1982), Blake et al. compare this figure to that beneath it to make the point that stereopsis is significantly degraded during rivalry. As Blake et al. summarize, "if rivalry and stereopsis coexist in the complemented stereogram, it is certainly an uneasy coexistence".

One concept that is present in several reports is that stereopsis and rivalry themselves compete for perceptual dominance. Ogle and Wakefield (Ogle and Wakefield 1967) for example, reported that stereoscopic images tended to suppress rivalry itself in favor of stereoscopic fusion. Blake, Yang, et al showed that when rivalrous noise is added to a stereogram, depth perception becomes unstable and is often overtaken by rivalry, again suggesting a competition. The present author similarly conducted informal investigations of stereopsis and rivalry using random dot stereograms (Julesz 1960) superimposed on rivalrous grating patterns. Never did the rivalrous stimulus preclude the facile discrimination of depth; however, when attention was directed towards the rivalry alternations the perception of stereopsis tended to disappear.

A final point about rivalry and stereopsis involves perception while viewing two surfaces at different depth planes. Under these conditions simple geometry will demonstrate that there are two unmatched portions of the monocular images resulting from the differential occlusion of the rear plane for the two eyes. The left eye will see a strip of the back plane that the right cannot and vice versa. Formally, any mismatch of this sort should be a condition for binocular rivalry; however, during normal viewing no rivalry is perceived. In a remarkable demonstration, Shimojo and Nakayama (Shimojo and Nakayama 1990; Shimojo and Nakayama 1994) have shown that when nonmatching flanking regions are added to a half image in a stereogram the perception or suppression of each depends on whether its placement is "ecologically valid", and not on low-level binocular correspondence. They argue that successful grouping in this case necessarily involves the utilization of eye-of-origin information, which implicates the earliest stages of cortical processing. An alternative interpretation, and that favored by the author, is that suppression of ecologically invalid regions is the consequence of segmentation and grouping mechanisms well beyond the point of binocular combination, in those areas subserving the perceptual representation of the stimulus.

Models of Rivalry

Numerous models have been formulated to account for the phenomenology binocular rivalry, and their elaboration would be well beyond the scope of the present dissertation. Many of the early models involved selective attention (Helmholtz 1909) but the majority of recent models consider the rivalry mechanism as an autonomous oscillator that may be *influenced* by attention, but does not depend on it. Modern rivalry models are divided roughly equally between those that attempt to account for its temporal dynamics (Fox and Rasche 1969; Sugie 1982; Matsuoka 1984; Mueller 1990; Lehky and Blake 1991), and those that describe its relationship to the rest of binocular vision (stereopsis, binocular fusion, etc.) (Sperling 1970; Julesz and Miller 1975; Wolfe 1986; Grossberg 1987; Blake 1989). Many consider suppression to be the result of targeted inhibition of neurons carrying monocular information (Fox and Rasche 1969; Matsuoka 1984; Blake 1989; Lehky and Blake 1991), while a few consider rivalry to involve competition between stimulus features at a more central representation (Walker 1978; Grossberg 1987).

The concept of reciprocal inhibition is central in many of the above models. Its appeal lies in its ability to account for two of the most salient aspects of rivalry. The first is differential suppression—only one stimulus is perceived while the other is suppressed. The second is alternation—a neural reciprocal inhibition circuit could easily act as an autonomous oscillator if inhibition could be "timed" by an adaptational process. There are also several fundamental problems with reciprocal inhibition schemes as they relate to the dynamics of rivalry (Lehky 1988). First, as mentioned in a previous section, the durations of successive phases during rivalry are completely uncorrelated. Were rivalry to involve reciprocal inhibition between groups of adapting neurons one would expect that a given dominance duration would reflect how long that stimulus had previously been recovering from adaptation (Walker 1978). Second, as seen earlier, the strength of a monocular stimulus during rivalry does not dictate its own dominance duration, but rather its suppression duration, which also presents difficulties for simple reciprocal inhibition schemes (Fox and Rasche 1969). Finally, the depth of suppression in rivalry is roughly constant throughout a given phase (Fox and Check 1968), where an adapting mechanism might predict that suppression would weaken as a phase progressed. Some or all of these difficulties have been addressed in many of the above models (see especially Lehky (1988)) but there is as yet no realistic rivalry model that adequately circumvents each of these problems.

Evoked Potentials During Rivalry

Several investigators have attempted to correlate EEG evoked potential activity with perception during binocular rivalry. The notion that multistable perception will be reflected in the gross activity changes of populations of cortical neurons in the cortex is a very old one. Unfortunately, there are a number of drawbacks to using EEG to measure spontaneous perceptual changes. The first is that it is a very gross measure of activity, and its relationship to cortical activity is poorly understood. The second is the requirement to incorporate *evoking stimuli* into the rivalry stimulus. For the EEG measurement to be effective it needs to measure the response to a visual transient averaged over many trials. Thus, studies have either relied on numerous short presentations (Martin 1970), flickering stimuli (Lansing 1964; Riggs and Whittle 1967; Lawwill and Biersdorf 1968), contrast reversing stimuli (Cobb, Morton et al. 1967), or superimposed flashed probes (Donchin and Cohen 1970). The addition of such transients is generally detrimental to the rivalry percept itself. Lansing (Lansing 1964), in the first of these studies, reported that the spontaneous changes in dominance and suppression during rivalry were clearly reflected in the amplitude of evoked responses on the EEG signal. Most subsequent investigators, have, however, failed to reproduce this result using similar paradigms (Cobb, Morton et al. 1967; Riggs and Whittle 1967; Donchin and Cohen 1970; Martin 1970) although some maintain differences during dominance and suppression can be observed (Lawwill and Biersdorf 1968).

The evolution of thought pertaining to rivalry is one of extremes. From its beginning it has vacillated between psychic and mechanistic explanations. Notably absent is a rigorous investigation into rivalry as a problem of perceptual organization. In the current investigation we develop the idea that binocular rivalry has been largely misinterpreted in its modern history as a phenomenon specific to binocular vision, and that it is more accurately described as a perceptual dilemma for the visual system that is largely independent of dichoptic presentation. In this context, rivalry represents an extremely useful tool for investigating perception both psychophysically and physiologically. Before describing our own experiments, I first review the relevant physiological studies pertaining to binocular vision and rivalry.

RIVALRY AND THE PHYSIOLOGY OF BINOCULAR VISION

Despite the intensive history of research directed toward binocular rivalry in the fields of perceptual psychology and psychophysics, neurophysiological experiments in animals have provided little information regarding its basis, with a few exceptions. This difference is undoubtedly attributable to reliance on the subjective report of an observer , a measure which is easy to obtain from humans but considerably more difficult from laboratory animals. Numerous experiments have presented rivalrous *stimuli* to the visual system, most often while recording from the thalamus or striate cortex of anesthetized animals, usually to examine how signals from the two eyes interact to influence the firing of individual neurons. In this section I review much of the work that has been done regarding the physiology of interocular interactions during fusion, stereopsis, and binocular mismatch.

Lateral Geniculate Nucleus

Binocular Interactions

The earliest point in the visual system in which the signals coming from the two eyes can possibly interact is the dorsal lateral geniculate nucleus (dLGN). Several investigators have previously suggested that inhibition in this structure is likely to mediate perceptual suppression during rivalry. Singer (1977), for example, states that “binocular rivalry is likely to be one of the psychophysical correlates for transmission in such a bistable gate [in the dLGN]. Reciprocal inhibition between afferents from the two eyes always causes one eye to be dominant over the other.” Numerous studies have found that there are many interocular suppressive interactions in the dLGN of both cat (Sanderson, Darion-Smith et al. 1969; Singer 1970; Rodieck and Dreher 1979; Pape and Eysel 1986; Guido, Tumosa et al. 1989; Moore, Spear et al. 1992; Tong, Guido et al. 1992; Sengpiel, Blakemore et al. 1995) and monkey (Marrocco and McClurkin 1979; Rodieck and Dreher 1979). The majority of these interactions do not depend much on the parameters of the stimulus in the nondominant[1] eye, weakening the case for their involvement in binocular rivalry, which requires interocular conflict.

A few studies have indeed found that interocular inhibition in dLGN was contingent upon a stimulus mismatch. Varela and Singer (Varela and Singer 1987), for example found that inhibition was strongest between dichoptic gratings that differed in their orientation and direction of movement. They attributed this orientation-selective inhibition to cortical feedback, as it was destroyed when the cortex was ablated. Although some investigators have failed to find orientation-specific inhibitory effects in the dLGN (Moore, Spear et al. 1992; Sengpiel, Blakemore et al. 1995), there is growing evidence that spatial-frequency selective interocular inhibition does exist (Guido, Lu et al. 1992; Moore, Spear et al. 1992; Tong, Guido et al. 1992). It is poorly understood why such suppressive interactions should exist at all, let alone those specifically selective for a stimulus mismatch. Given that each of these studies was carried out in anesthetized cats, it is difficult draw any general conclusions regarding their relationship to binocular rivalry. Finally, other thalamic structures, such as the lateral pulvinar, also demonstrate complex binocular interactions in single unit recordings (Benevento and Miller 1981), the significance of which is again unknown.

Binocular Rivalry

A recent study in awake animals strongly suggests the absence of any subcortical suppression in the geniculostriate stream during rivalry. Lehky and Maunsell (Lehky and Maunsell 1996) investigated the hypothesis that the alternate transmission of retinal information through ipsilateral and contralateral dLGN layers governs perception during rivalry (Blakemore,

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[1] *Dominant* and *nondominant*, in reference to physiological studies takes on a different meaning than the same terms applied to perception. A physiologically dominant eye is with reference to a neuron or recording site—the eye in which stimulation produces more activity is dominant. A perceptually dominant eye, on the other hand, is with reference to what is seen. There are numerous ways in which one eye can be dominant over another in perception. Rivalry dominance, in which the nondominant stimulus entirely disappears, differs from other forms of ocular dominance (Coren 1974), and has been shown to be fundamentally distinct from the dominance of one eye during strabismic suppression (Smith et al., 1985) .

Iversen et al. 1972; Singer 1977; Lehky 1988; Lehky and Blake 1991) by recording from this structure in awake monkeys as they continually viewed rivalrous stimuli. Monkeys were trained to fixate for extended periods as they were dichoptically presented orthogonal drifting gratings in the two eyes. Individual spike trains were then extensively analyzed in the frequency domain for modulation that would correspond to rivalry alternations, which are known to occur in monkeys (Myerson, Miezen et al. 1981), and found "no evidence for a neural correlate of binocular rivalry in the LGN of awake monkey". In fact, they found no binocular interactions of any sort, not even the type described above. This result places the perceptual rivalry mechanism squarely on the shoulders of the cortex, but does not eliminate the possibility of a mechanism based on reciprocal inhibition between monocular neurons, as the two eyes remain largely segregated in the input layers of striate cortex.

Striate Cortex

Models of binocular vision generally begin at the point where information is combined from the two eyes in primary visual cortex (Poggio and Poggio 1984; Grossberg 1987; Anderson and Nakayama 1994). It is here that *monocular* cells (those activated through only through one eye) converge onto *binocular cells* (those activated through either eye), and this combination is thought to govern binocular summation, stereopsis, and, by some, binocular rivalry.

Binocular Interactions

That the striate cortex was the first site of binocular confluence has been known since Minkowski (Minkowski 1913) demonstrated that focal lesions in cat's area 17 resulted in degeneration in all layers of LGN. Numerous investigators have subsequently evaluated the binocular nature of cells in the striate cortex of cats (Hubel and Wiesel 1962; Barlow, Blakemore et al. 1967; Blakemore, Fiorentini et al. 1972; Ohzawa and Freeman 1986; Ohzawa and Freeman 1986) and monkeys (Hubel and Wiesel 1962; Poggio and Fisher

1977). In cats most striate cells are binocular, and the influence of the ipsilateral and contralateral eyes varies along a continuum, with a slight bias toward contralateral (Hubel and Wiesel 1962). The functional organization of binocularity is subtle, where neighboring cells often have preferences for different eyes. In the monkey, the segregation is much more pronounced (Hubel and Wiesel 1962) , suggesting that binocular information in the visual system of the cat converges earlier than in the monkey, perhaps accounting also for the abundance of thalamic interocular interactions. Moreover, the percentage of binocular neurons in striate and prestriate cortex is dependent on visual experience, as monkeys raised in a visually disruptive environment, with prisms preventing normal binocular combination, lose not only their ability to see stereopsis, but retain a permanently decreased fraction of binocularly driven neurons in V1 and V2 (Crawford, Smith et al. 1984).

Much of the physiology of binocular vision has been devoted to possible physiological mechanisms of stereopsis. Barlow, Blakemore, et al. (Barlow, Blakemore et al. 1967) considered the fact that the binocular parallax associated with stereopsis produces a horizontal disparity on the two retinae, and searched for cells in cat striate cortex responsive to such positional differences. In this sense, they viewed horizontal positional disparity as a “trigger feature” by which a neuron could signal the presence of an object a certain distance away. They found that many cells were indeed tuned to a narrow range of horizontal disparities. In contrast, Hubel and Wiesel found only a few cells in striate cortex of the cat with this property (Hubel and Wiesel 1973), and none in the monkey (Hubel and Wiesel 1970). They found, however, that many cells in monkey area 18 (V2) did respond to such stimuli and, based on this result proposed that stereoscopic vision may be mediated by extrastriate cortex. These findings were all conducted with anesthetized animals whose extraocular muscles were paralyzed.

Experiments in the behaving monkey paint a different picture of disparity selectivity in monkey striate cortex. In contrast to the earlier studies, Poggio and Fischer (Poggio and Fischer 1977) found that *most* neurons are sensitive to specific horizontal disparity. With the monkey fully awake and fixating a spot on a computer screen, they presented bars in depth and classified cells according to whether they were maximally responsive to crossed or uncrossed disparities (corresponding to in front of and behind the plane of fixation, respectively), and how broadly tuned they were for this attribute. They found that 84% of the cells they tested from areas 17 and 18 were "sensitive to the location of a stimulus in depth", reviving the notion that cells as early as striate cortex could act as feature detectors for stereopsis. Moreover, they found that, in the context of disparity testing, almost no cells (4 out of 199) could be considered entirely "monocular", or only influenced by one eye. In addition, the disparity responses of many neurons (30%) could be elicited with even dynamic random-dot stereograms, suggesting that striate neurons may be involved in the representation of global, rather than simply local, stereopsis.

Freeman and colleagues (Ohzawa and Freeman 1986; Ohzawa and Freeman 1986) have examined the possibility that disparity selectivity is the natural result of differences in receptive field structure in the two eyes. In reference to previous studies, they insist that by making the assumption that cells are "depth detectors" one automatically biases the interpretation of the results, and suggest instead an alternative model in which differences in receptive field structure encode depth information for different spatial scales (Freeman and Ohzawa 1990).

Binocular Rivalry

Beyond the investigation into depth perception, little is known about how neurons in the striate cortex respond when presented with a binocular mismatch. It has been reported that a cell responding to an oriented grating presented to one eye is only minimally influenced by simultaneous presentation of an orthogonal grating to the other—a rivalry condition (Freeman, Ohzawa et al. 1987). Nonetheless, recent results, including those presented here, suggest that this is not the case. Three studies have specifically examined the activity of neurons in primary visual cortex in an attempt to uncover mechanisms of binocular rivalry.

In the first study, Sengpiel et al. found that about half of the cells in anesthetized cats showed a significant depression of their response to their preferred stimulus when a rivaling stimulus was placed in the other eye (Sengpiel and Blakemore 1994; Sengpiel, Blakemore et al. 1995). Although monocular cells in layer 4 resembled LGN cells in that they exhibited only modest inhibitory interactions that were independent of the other eye's stimulus, many binocular striate cells showed more a dramatic suppression. For these cells, there was generally a facilitation in their response when the orientations in the two eyes were congruent, and a depression when the orientation mismatch exceeded 15-20 degrees. Moreover, this orientation selective suppression was contingent upon the neuron having been previously exposed to its preferred orientation. This last point, they suggest, demonstrates that these effects may be related to the perceptual suppression experienced during binocular rivalry. This relies on the phenomenon of "flash-suppression", mentioned briefly in the last chapter, where exposure to a monocular stimulus prior to rivalry onset biases subsequent perception to the other stimulus. (Wolfe 1984). Although these results are auspicious, they are by no means conclusive, considering that only four cells were tested in this manner. Moreover, when strabismic cats were tested in the same paradigm they found that any stimulus placed in the contralateral eye, rivalrous or congruent, showed the same suppression, with a similar dependence on previous monocular exposure. Yet, although the conclusions that can be drawn from these results are unclear, this study does clarify that the activity of binocular neurons in the striate cortex critically depends upon the degree to which two monocular inputs match.

A second relevant study in which striate activity is monitored during rivalry is very recent and follows the publication of many of the results presented in this dissertation. This experiment used multiple chronically implanted wire electrodes in awake, squinting cats to measure striate activity during rivalry (Fries, Roelfsema et al. 1996). Perception was inferred by the animals' bias resulting from their squint, which was initially confirmed by measuring optokinetic nystagmus (OKN) during motion rivalry (Peter Koenig, personal communication). They report that in primary and secondary visual cortex the synchronization between simultaneously recorded neurons encoding a stimulus is higher when that stimulus is dominant during rivalry than when it is suppressed. Differences in such synchronization were observed mostly in the gamma frequency range and did not necessarily correlate with changes in the mean activity of either unit. Although it is tempting to speculate that the perception of a single stimulus during rivalry arises from the unique synchronization of the neural machinery representing that stimulus, the results are, on their own, inconclusive. First, the cats do not report specific instances of perception, but are assumed to remain in a perceptual state for extended periods based on their squint. It would add a great deal of credibility to the study if cats were continually monitored, with OKN as an objective indicator, or even if a paradigm such as that used by Sengpiel and Blakemore (Wolfe 1984; Sengpiel and Blakemore 1994) were employed to provide instances of unambiguous perception. Second, and more importantly, it has been shown that suppression due to strabismus and amblyopia is not the same as perceptual suppression during binocular rivalry (Smith, Levi et al. 1985; Holopigian, Blake et al. 1988), which makes the interpretation of these results even more difficult. Nonetheless, the results do warrant further investigation, as the notion of a macroscopic organizing principle, such as a subset of cells firing in synchrony, governing the representation of a stimulus either in rivalry or in normal vision would be a welcome addition to any theory of perceptual organization (von der Malsburg and Buhmann 1992).

The third relevant study comes from behaving monkeys in the laboratory of Allman. It is very similar in design to some of the experiments in this dissertation, and was conducted concurrently for two years (Dobbins, Jeo et al. 1994; Dobbins, Jeo et al. 1995). Briefly, cells were recorded in macaque areas V1, V2, and V4 as the monkey reported his perceptions during rivalry, as in the present study. It was found that there was little to no change in the mean activity of neurons in accordance with to the monkey's reported perception, but that the variability in firing increased during periods of binocular rivalry, with a tendency for neurons to fire in bursts of spikes. These results differ from those of the present work, and are, in the opinion of the author, likely to be due to an unreliable perceptual report from the monkey during the rivalry periods.

Extrastriate Cortex

Binocular Interactions

Although it is rare to find purely monocular cells beyond striate cortex, many neurons in all prestriate areas are biased in their responses toward a stimulus presented to one eye or the other. There is also a continued sensitivity to binocular disparity as one progresses to higher cortical areas, possibly mediating stereopsis. Zeki (Zeki 1978) systematically studied binocular properties of neurons in cortical areas V2, V3,V3a and V4 and found that the majority responded roughly equally to stimuli placed in the two eyes. There was, however, in each of the areas a significant fraction of neurons favoring one eye over the other, including some that were strictly monocular. Disparity-sensitive neurons have also been identified in each of these areas (Burkhalter and Van Essen 1986; Felleman and Van Essen 1987; Poggio, Gonzalez et al. 1989). Maunsell and Van Essen (Maunsell and Van Essen 1983) found that most cells in the middle temporal cortical area (MT) were largely binocular, although often influenced more by one eye than the other. Pure monocular cells were rare. Most MT cells were sensitive to binocular disparities, but there did not seem to have a significant preference for horizontal disparities over vertical, drawing question to their role in stereopsis. Finally, little is known about the binocular properties of neurons in the inferotemporal (IT) cortex. An early study reported that roughly half of the neurons in IT had a distinct preference of one eye over the other, split roughly equally between the ipsilateral and contralateral eyes (Gross, Roche-Miranda et al. 1972).

Binocular Rivalry

A single previous study examined the activity of extrastriate cells during binocular rivalry. Logothetis and Schall (Logothetis and Schall 1989; Logothetis and Schall 1989) taught monkeys to report the direction of motion of a drifting grating stimulus by making a saccade at the end the trial. The monkeys were conditioned using optokinetic nystagmus (OKN) as an objective indicator of their perception to honestly report their perceived direction of motion during rivalry. Individual neurons were monitored in the middle temporal (MT) area and the medial superior temporal sulcus (MST) as the they performed the task. During rivalry, a significant number of cells (roughly a quarter) demonstrated activity that consistently correlated with the subjective state of the animal. Of these perception-related cells, half showed increased activity when the monkey reported seeing the cell's preferred direction, and half when the preferred direction was phenomenally suppressed. This study underscores the fact that the visual cortex is involved in perception, although it leaves open the possibility that the modulations seen in these areas are the natural consequences of a gating of information at an earlier processing stage. Area MT is known to receive direct projections from the striate cortex (Zeki 1971), and would thus register the effects of an early blockade of information there.

In order to examine the functional organization of perception in the brain during rivalry it is necessary to know more about the activity in the earliest cortical areas during the perceptual changes. Will monocular cells in V1 show the strongest perception-related changes? Are cells anywhere in the visual system capable of completely shutting down even when their preferred stimulus is present? Is rivalry manifested similarly in the dorsal and ventral processing streams? Is there a site of rivalry suppression? It is with these questions in mind that we begin exploration into the physiology of binocular rivalry.

METHODS

EXPERIMENTAL DESIGN AND ANIMAL TRAINING

Implicit in the previous chapters is the notion that rivalry would be a useful paradigm for studying the physiological underpinnings of perception. Its utility draws from its generality—nearly any type of visual stimulus can participate, from small oriented contours to colored patches to faces. Hence one is able to tailor a stimulus to the preferences of an individual neuron, which guarantees that nearly any visually responsive cell can be tested for its activity during rivalry. In this manner, individual neurons can be subject to the *perceptual suppression* of a stimulus to which they normally respond, and their role in perception can be studied. By investigating how cell activity relates to subjective perception during binocular rivalry we hope to better understand the functional organization of perception in the brain.

Behavioral Training

In executing this study, we needed two simultaneous measurements—one biological (brain activity) and one psychological (subjective perception). In experimental animals, the measurement of brain activity can be performed with much more precision, but the psychological assay becomes exceedingly difficult. Behaving monkeys provide the rare opportunity to measure both aspects of perception simultaneously. In the present study, monkeys were trained to report which of a pair of conflicting stimuli was seen during binocular rivalry as the activity of single neurons was monitored in their visual cortex.

Initial Training

Four macaque monkeys (macaca mulatta) were used in this study. Three of them (RAY-1, RUR-1, 90004, in this study referred to as monkeys A, B, and C, respectively) were successfully trained to report their perception during binocular rivalry and one (90013, monkey D) was examined only in the context of a fixation task. Each monkey began its training by learning to make the transition from its cage to a primate chair, and then to sit patiently and comfortably for extended periods of time. A pair of levers was mounted on the front panel of the chair that the monkey could easily reach, and it received a juice reward in exchange for simply pulling the levers. Eventually, it was taught to pull the left lever when an LED turned green and the right lever when it turned red. At the end of this brief shaping period, usually lasting 1-2 weeks, each monkey was able to perform a simple color discrimination for a reward.

Monkeys A, B, and C, were, in addition, taught to perform a simple orientation discrimination task, in which they responded to a grating pattern shown on a computer screen by pressing the right lever if it was rightward tilted (rotated less than 90 degrees clockwise from vertical) and the left lever if it was leftward tilted. The discrimination was always well above threshold, as rotations within 5 degrees of vertical or horizontal were never used. The monkey then learned to perform multiple successive orientation discriminations separated by random intervals, initially receiving a reward after each correct response. Two of the monkeys (A and B) were simply required to respond to *transitions*, while monkey C was taught to hold the lever down throughout the entire interval in which the stimulus was perceived. Once proficient at this task, each monkey learned to operate on a variable reward schedule, where a correct response had associated with it a probability of reward, rather than a certainty. This allowed us to eliminate the need for immediate positive feedback for correct responses, as such feedback is impossible during real binocular rivalry. Note, however, that the monkey still received feedback for *incorrect* responses, where the entire observation period would immediately abort. The variable ratio in this schedule was systematically increased until the monkey received reward only at the end of multiple successful responses, at which point he was given a large bolus of juice.

Next, the presentation sequence was changed in two basic ways to create a sort of rivalry emulation, preparing the animals for the subjective experience of real binocular rivalry. First, “mixed” periods were introduced, in which the stimulus consisted of a combination or mosaic of right and left orientations. For this stimulus, neither lever was pressed. Second, the abrupt reversals in orientation were replaced by gradual ones, where the contrast of one of the orientations was gradually lowered as the contrast of the other increased. The monkey was required to wait until the new orientation was faded in roughly 75% before responding. These innovations were designed to familiarize the monkey with the notion that there may be periods of ambiguity in the rivalry discrimination, and that he should wait for this ambiguity to resolve into a unified orientation before responding. Once the monkeys could respond consistently and correctly to the rivalry emulation, the initial training was considered complete.

Headpost and Eye Coil Surgery

The monkeys weighed 6-9 kg at the time of surgery were at all times cared for in accordance with the National Institutes of Health Guide, and the guidelines of the Animal Protocol Review Committee of the Baylor College of Medicine. Each animal underwent an aseptic surgery for the placement of the head restraint post and the scleral search eye-coil (Robinson 1963). The monkey was given antibiotics (Tribrissen 30 mg/kg) and analgesics (Tylenol 10 mg/kg) orally one day before the operation. Food was withheld overnight but the monkey had water ad libitum until 3 hours before the surgery. Fifteen minutes before the preanesthetic, the monkey was injected with atropine (0.05 mg/kg IM) to avoid congestion during surgery. It was then restrained with an intramuscular dose of ketamine (10 mg/kg). An intravenous catheter was placed aseptically in the saphenous vein and flushed with heparinized saline (two units/ml). The catheter was fixed to the surrounding tissue and secured with a dry dressing. Induction of surgical anesthesia was accomplished with Pentobarbital (8 mg/kg). The larynx was sprayed with Cetacaine and the monkey was intubated. The animal was placed on the surgical table, and the incision sites and surrounding areas were scrubbed with Betadine and Nolvasan.

Somatic responses were always tested, particularly during surgical manipulations. Before making incisions or placing the animal in the stereotaxic head holder (for the attachment of the head post) the sites of incision and the pressure points were infiltrated with local anesthetic (lidocaine). Throughout the surgical procedure the animal received administrations of 5% dextrose in lactated Ringer's solution, at a rate of 15 ml/kg/hr. Heart rate, blood pressure and respiration were monitored constantly and recorded every 15 minutes. Body temperature was kept between 35.0 and 37.0 degrees Celsius using a heating pad. Maintenance of anesthesia was accomplished with isoflurane (1.2 to 1.5 % with 0.8 L/min oxygen). At the end of the surgical procedure the animal was extubated, and allowed to sleep. In this ``sleep'' period the animal received 5% dextrose in lactated Ringer's solution, at a rate of 20-40 ml/kg/hr. Only when the monkey was completely able to stand was it returned to its home cage. Postoperatively, the monkey was administered an opioid analgesic (Buprenorphine hydrochloride 0.02 mg/kg, IM) every 6 hours for 2 days, and Tylenol (10 mg/kg) and antibiotics (Tribrissen 30 mg/kg) for 3-5 days.

Fixation Control

Prior to surgery, training was accomplished without head restraint or control over gaze position. For that reason, no fixation point appeared on the screen, and trials were initiated only with a tone. Following the headpost and eye coil surgery a fixation point was always present during all tasks, and fixation of a small spot was continuously required and measured with the scleral search coil technique (Robinson 1963). This technique provided vertical and horizontal positions of the monkeys' center of gaze to within less than 1 minute of arc, allowing strict online behavioral control, as well as accurate off-line analysis (see following chapter). Aside from infrequent blinks, the monkey was not allowed to direct his center of gaze outside of an imaginary box (generally less than 1.0 degrees on a side) centered on this fixation point as long as it was present. Due to the long fixation periods required during the behavioral paradigms, monkeys were allowed to make brief excursions outside the window for blinks, as long as they returned within 120 msec—longer excursions resulted in an abort.

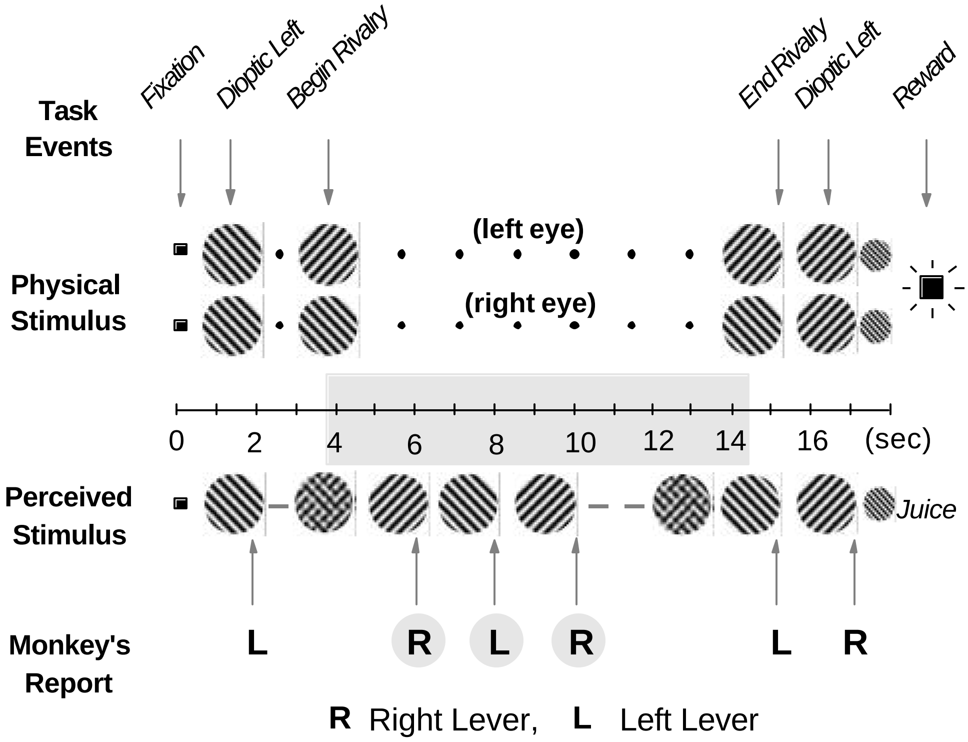

Figure 12 Binocular rivalry task . While the monkey fixated a small spot a series of nonrivalrous and rivalrous stimuli was presented. Nonrivalrous stimuli were either dioptic (same in each eye) or monocular (not shown). The monkey was required to press either the left or right lever according to which orientation was presented. During rivalrous periods (shaded region) the monkey continued to respond to subjective orientation changes.

Rivalry Task

During physiological sessions the rivalry task took the following form, illustrated in Figure 12. A tone was followed by the appearance of a small blue spot (9´ on a side) which the monkey was required to fixate. Since the task consisted of extended viewing periods during which the monkey made multiple lever responses, it is important to clarify the terminology used throughout the remainder of this description. *Observation period* will refer to the interval from the onset of fixation to the time that the monkey is rewarded (or aborts the trial with a stray eye movement or incorrect response). *Trial* refers to either the presentation of a nonrivalrous stimulus (and the monkey appropriately responds or doesn’t respond) or the monkey's response to a perceptual change during binocular rivalry. A *phase* refers to the time between perceptual transitions, during which perception is dominated by a single pattern.

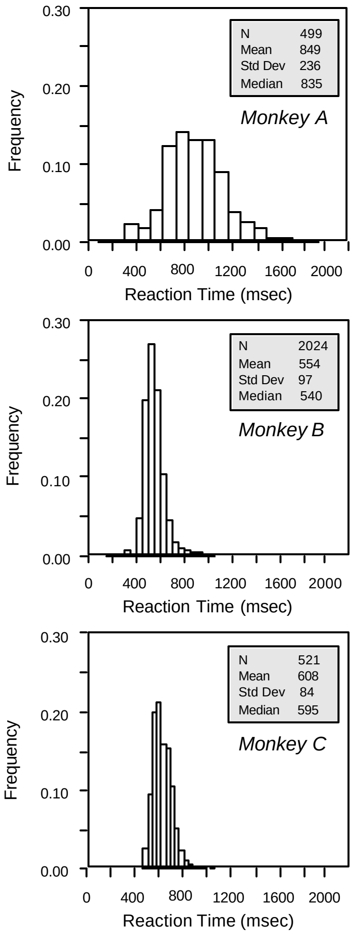

Figure 13 Reaction time distributions for three monkeys during nonrivalry trials.

Observation periods lasted between 10 and 25 seconds. While fixating, the monkey would observe a sequence of rivalrous and nonrivalrous stimuli. Nonrivalry stimuli were smoothly faded between leftward and rightward orientations, with phase durations and fade times drawn from a uniform distribution and lasting 3000±2000 msec and 400±200, respectively. For each of these presentations, the monkey pressed the appropriate lever in the manner described above, with an error rate that was consistently below 5%. The reaction time distributions for monkeys A, B, and C are shown for these nonrivalry trials in Figure 13. The reaction times of monkeys B and C, from whom most of the data in this study was collected, were distributed in a unimodal fashion, with a standard deviation of less than 100 msec. Given that during nonrivalrous trials the transitions were not always abrupt but sometimes gradual, it was important for us to specify the effects of fading time on the monkey's reaction times. These results are shown in Figure 14, where the means and standard deviations of the reaction times are plotted for different fading times for Monkey C. The dark black line corresponds to the increasing reaction times associated with increasing fading durations. If there were no influence of the fading on the reaction time, it would remain at its base value, shown by the horizontal gray line (0%). If, on the other hand, the stimulus had to fade in completely before the monkey could begin to respond, each millisecond of fading would add a millisecond to the reaction time, represented by the gray, diagonal line labeled 100%. The effect of fading on the monkey's data lay roughly half way between these extremes (43%). The relatively constant slope of the reaction times with increased fading indicates that only when the grating was faded in roughly half way, regardless of the fading rate, could the monkey respond normally. This allowed us to compensate for fading during subsequent data analysis.

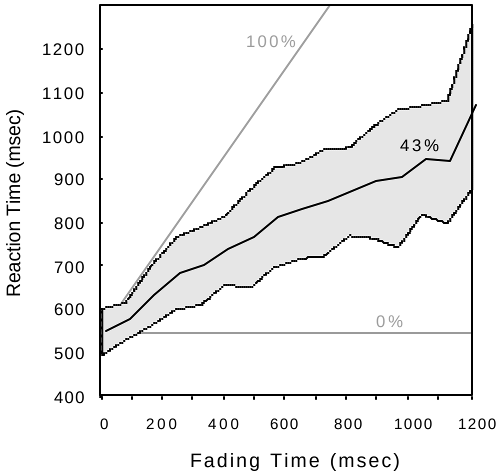

Figure 14 Effect of fading time on monkey's reaction time during binocular rivalry. The black line corresponds to the mean reaction time for a given fading time. The gray horizontal line represents the expected result if the fading had no effect on reaction times, and the diagonal line the result if each millisecond of fading added a millisecond onto the reaction time.

Rivalrous periods lasting between 5 and 15 seconds were introduced into the observation period among the nonrivalrous presentations. During these epochs the monkey continued to respond to perceived changes in orientation, even though the physical stimulus remained constant. Each rivalry period ended with a catch trial, described below. In all cases, prolonged excursions from the behavioral fixation window or an improper response to a nonrivalry trial would result in the abortion of the observation period.

Behavioral Controls

Binocular rivalry, being an inherently "private" event for monkeys as well as humans, does not provide the experimenter with an objective measure to know when the monkey is telling the truth. This makes it impossible to provide positive or negative feedback based on the correctness (or honesty) of the monkey's response. For this reason it was necessary to employ several behavioral controls. This drew from two basic strategies, the first involving the introduction *catch-trials* into the rivalry observation periods, and the second involving the temporal statistics of the perceptual alternations.

Catch Trials

Catch trials were of several different varieties, but in general consisted of fading in a nonrivalrous stimulus shortly after a response during rivalry. For example, if the monkey reported seeing the leftward tilted grating, that grating would fade away leaving only the rightward grating, which would require an immediate right-lever response. Catch trials were generally monocular, but sometimes dioptic (same orientation in each eye). In some cases, the gratings *opposite* that last reported would fade in, and the monkey was specifically required *not* to report a change. Finally, in some instances the catch trials consisted of mixtures of both orientation, to which the monkey was required to let both levers free. These controls were an effective means of monitoring the monkey's "honesty" on-line, and lapses in performance would return the animal to a strictly nonrivalrous regimen. Performance in rivalry would invariably improve subsequent to "remedial training" in the rivalry emulation. In this way there was a delicate equilibrium in the monkey's training that required constant behavioral monitoring and appropriate action.

Alternation Phase Distribution

The second set of controls employed rivalry's well-known alternation statistics. Prior studies have shown that even though the durations of successive phases are sequentially independent random variables, and that mean durations vary both with subject and with stimulus type. The distribution formed by these durations is, however, remarkably predictable when each is considered as a fraction of the overall mean, and is well

$$f(t) = \frac{l^r}{\Gamma} t^{r-1} e^{-lt}$$

approximated by a gamma function:

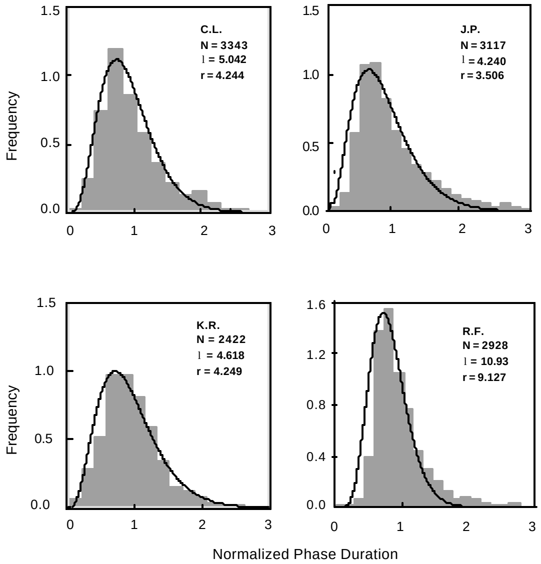

Figure 15 Distribution of phase durations during binocular rivalry for four human subjects. Each of the durations is normalized to the mean duration for the subject. The black lines represent the best fitting gamma function for each distribution . The number of phases N, as well as gamma function parameters r and λ are listed in the upper right of each panel

where t is a phase duration, $\Gamma=(r - 1)!$, and r and λ are the free parameters, which show considerable inter-subject similarity for both humans and monkeys (Levelt 1966; Fox and Herrmann 1967; Blake, Fox et al. 1971; Walker 1975; Myerson, Miezen et al. 1981; Leopold and Logothetis 1995).

The gamma distribution has been commonly interpreted as representing the waiting time for the r^{th} event when a single event is a Poisson process of waiting time λ. As such, it directly suggests a variety of possible processes that may underlie a perceptual change during rivalry. One is a threshold process, in which the threshold can be reached by the convergence of a number of independent excitations. These could be, for instance, excitatory post-synaptic potentials needed to eventually overcome the hyperpolarization caused by inhibition. Interestingly, it has been shown that fluctuations in excitatory input can indeed account for the random variations in successive suppression durations (Sugie 1982). Earlier studies have also shown that the source of such excitation events is likely not to be peripheral (Blake, Fox et al. 1971), but rather resides in the central visual system. Alternatively, however, the relative phase distribution may simply be considered a Poisson distribution with a refractory period convolved with a gaussian ``filter'', that in this case might be the reaction times of the monkey.

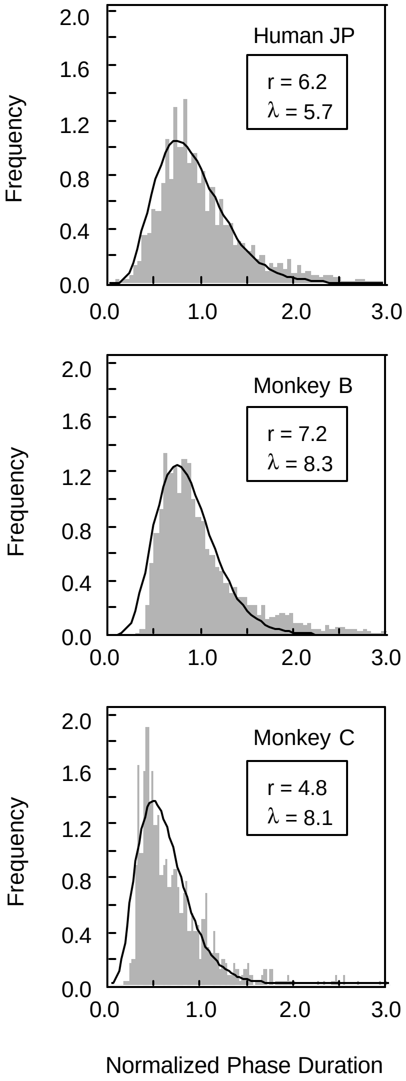

Figure 16 Gamma distributions for Monkeys B and C, as well as one human JP, reporting under identical stimulus conditions to the monkeys.

In addition to any possible information regarding rivalry's underlying mechanism, the gamma distribution offers a "signature" of binocular rivalry which is useful for the experiments in the present dissertation. Of special interest is the fact that the general shape of the phase distribution, as well as the parameters of the best fitting gamma function, are similar for both humans and the two monkeys evaluated in the study. For the monkeys the phases were collected during the neurophysiological recordings, when conditions were a compromise between optimal psychophysical and physiological testing. In analyzing the monkey data each phase duration was normalized to the mean duration obtained while a particular rivalry stimulus pair was used, rather than to the overall mean for all sessions. This normalization guaranteed that biases in the parameters of the physical stimulus, such as contrast and spatial frequency, that can influence the mean phase duration, did not affect the shape of the distribution. Figure 16 shows the distributions obtained from two of the monkeys below that obtained from one human subject under identical stimulus conditions (actually sitting in the monkey's place). Note that the relationship of the mean to the standard deviation excludes the possibility of an exponential ``holding-time'' distribution such as a Poisson, where the mean is equal to the sigma. The data were again well approximated by a gamma distribution. Most interestingly, the data do show significant departures from the expected values of a normal distribution having the same mean and standard deviation. In addition, the distribution of relative intervals between successive *random* lever-presses in human experiments (first three panels in Figure 17) also deviates significantly from a gamma distribution (Kolmogorov-Smirnov one sample test) at the $p < 0.005$ level. This is in contrast to the distribution of phase times from a human subject reporting the spontaneous depth reversals of the Necker cube (lower right panel in Figure 17), which is very similar to the distributions obtained during rivalry. The similarity in the parameters of the theoretical distribution describing the monkey and human rivalry data provides additional evidence for the reliability of the monkey's performance, for it is highly improbable that the time periods between the animal's reports would show a gamma distribution were the monkey not accurately reporting rivalry.

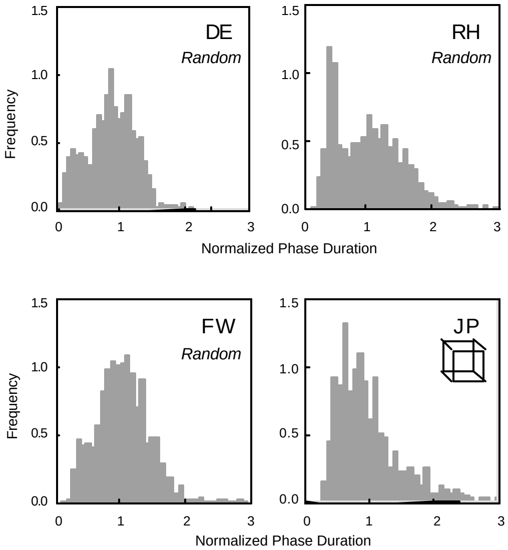

Figure 17 Distribution of phases for three subjects instructed to press two levers at random intervals, and one responding to subjective reversals of the Necker cube (lower right).

Effects of Interocular Contrast Differences

Even stronger evidence as to the reliability of the monkeys' reports comes from changes in the mean phase durations in response to manipulating the interocular contrast (Figure 18). During rivalrous stimulation, increasing the stimulus strength in one eye increases the visibility of that stimulus, not by increasing its own duration of mean dominance, but by decreasing the mean period for which it remains suppressed. The data obtained from the monkey show the same relationship between stimulus strength and eye dominance as do the human data in the present and other studies. Specifically, as the contrast of the stimulus in one of the eyes is lowered, the main influence is an increase in the dominance of the other eye’s stimulus.

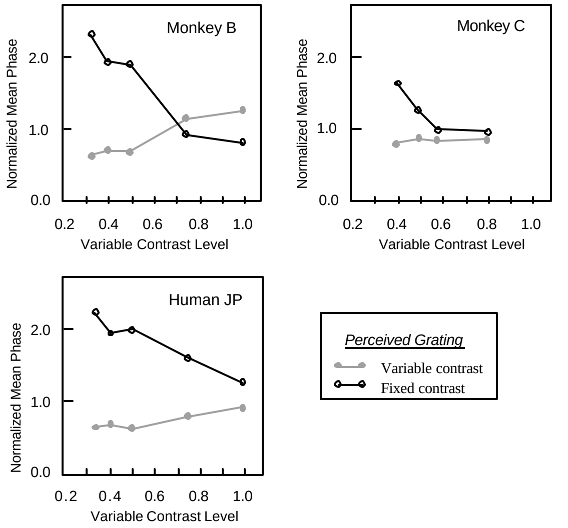

Figure 18 Effects of manipulating the interocular contrast difference for two monkeys and one human subject.. The gray lines (closed circles) represents the average duration that the variable-contrast grating appeared dominant for different contrast levels. The black lines (open circles) show the same for the grating whose contrast was not manipulated.

For the subjects in Figure 18, there are differences in the mean duration of the two stimuli even when the contrasts in the two eyes are equal (rightmost points), due to behavioral eye dominance. Human individuals are known to differ in behavioral dominance when viewing rivalrous stimuli, and such dominance cannot be predicted by other measures of eye dominance, such as acuity, preferred eye for sighting, or handedness (Washburn, Faison et al. 1934; Enoksson 1961; Coren 1974). Not surprisingly, our data show that monkeys, too, may differ in rivalry eye dominance. Most importantly, however, the monotonic dependence of phase duration on contrast provides another important behavioral control over the monkey’s psychophysical performance, as no random tapping of the levers could possibly yield this type of consistency, nor is it likely that the animal (or the human subject) systematically adjusts its behavior for different interocular contrasts.

Extracellular Electrophysiology

Visual Stimulus Presentation

The visual stimuli were generated with an image processing system (MV200 Datacube, Inc.), and were presented on a display monitor (BARCO CDID 7651) placed at 97 cm distance

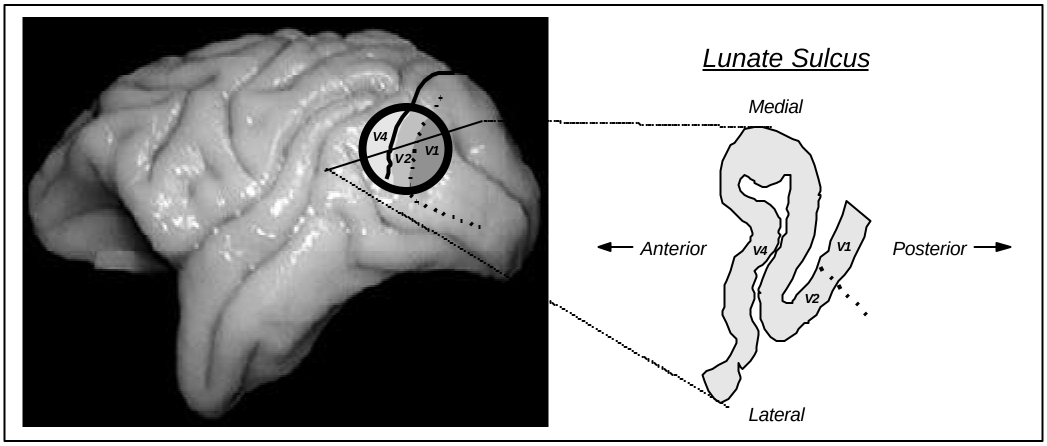

Figure 19 Approximate placement of V1/V2/V4 open chamber with respect to the monkey's brain. Each chamber (black circle) was 18mm in diameter and implanted over the lunate sulcus (solid black line). This positioning allowed access to foveal representations of areas V1 and V2 on the surface of the brain, as well as area V4 in the lunate sulcus.

from the subject. Stereoscopic presentations were accomplished using a liquid crystal polarizer (Tektronix SGS 610), that allowed alternate transmission of images with circularly-opposite polarization at the rate of 120Hz (60Hz for each eye). Stereo glasses, which transmitted only the properly-polarized light to each eye, were used for separating the time-interleaved images. The extinction ratios (on image/off image) of red, green, and blue (P22 phosphors Rxy=0.609,0.347, Gxy=0.286,0.587, Bxy=0.148,0.076) of the monitor-modulator system were (14/1, 10/1, 8/1) and (20/1, 15/1, 10/1), for the left and right eye respectively, allowing presentation of high contrast stimuli (up to 80%) with no discernible crosstalk. Polarity changes were triggered by a stereo-signal synchronized to the vertical retrace of the monitor. To create a stereoscopic display, parts of the Datacube memory corresponding to the right eye and left eye image, respectively, were displayed in alternation synchronized to the vertical retrace of the system.

Chamber Placement and Recording Techniques

Six 18mm chambers were implanted on six hemispheres of four monkeys. Figure 19 shows the approximate chamber location over the lunate sulcus. Figure 20 depicts each of the individual chambers, along with the stereotaxic position of their centers (below). The light gray lines correspond to the best approximation of the sulci as seen through the dura at the time of implantation. Each chamber was positioned such that foveal representations of areas V1, V2, and V4 could be accessed. The horizontal meridian, representing the boundary between area V1 and V2, was estimated for each chamber, based on the progression of receptive fields during exploratory plotting, as well as the clustering of monocularly driven cells (black rectangles), and is shown by the dotted black lines. During the rivalry task, cells were recorded primarily from the foveal areas near this border (from V1 and V2) as well as foveal regions on the anterior bank of the lunate sulcus (V4). Recording of single unit activity was done using Platinum-Iridium electrodes of 1-3 Megohms impedance. Surface sites (primarily areas V1 and V2) were accessed by piercing the dura each day with the tip of the electrode itself. After several weeks, when the dura became impenetrable, a guide tube apparatus was inserted on a daily basis which allowed continued recordings from the fundus and anterior bank of the lunate sulcus for many weeks. Action potentials were amplified (Bak Electronics, Model 1A-B), filtered, and routed to an audio-monitor (Grass AM-8), and to a time-amplitude window discriminator (Bak Model DIS-1). The output of the window discriminator was used to trigger the real-time clock interface of a PDP11/83 computer.

Fixation Plotting

In addition to the rivalry task, each cell was tested extensively while the monkey performed a simple fixation task. During such testing the monkey would fixate a small spot for 10-20 seconds, responding at the end of several seconds to a change in its color. During these periods each neuron was evaluated for several physiologic properties. First, the extents of its receptive field was plotted with a computer controlled bar stimulus, and the width and height of the optimally oriented bar were used to determine the orientation, spatial frequency and size of a test grating. Once the cell's "preferred" grating was created, the cell was tested for its responses to different orientations, ocular configurations, and a variety of other attributes. A single observation periods consisted of 4 to 8 presentations in which one stimulus dimension varied at a time, holding all other properties constant at the optimal value for the cell.

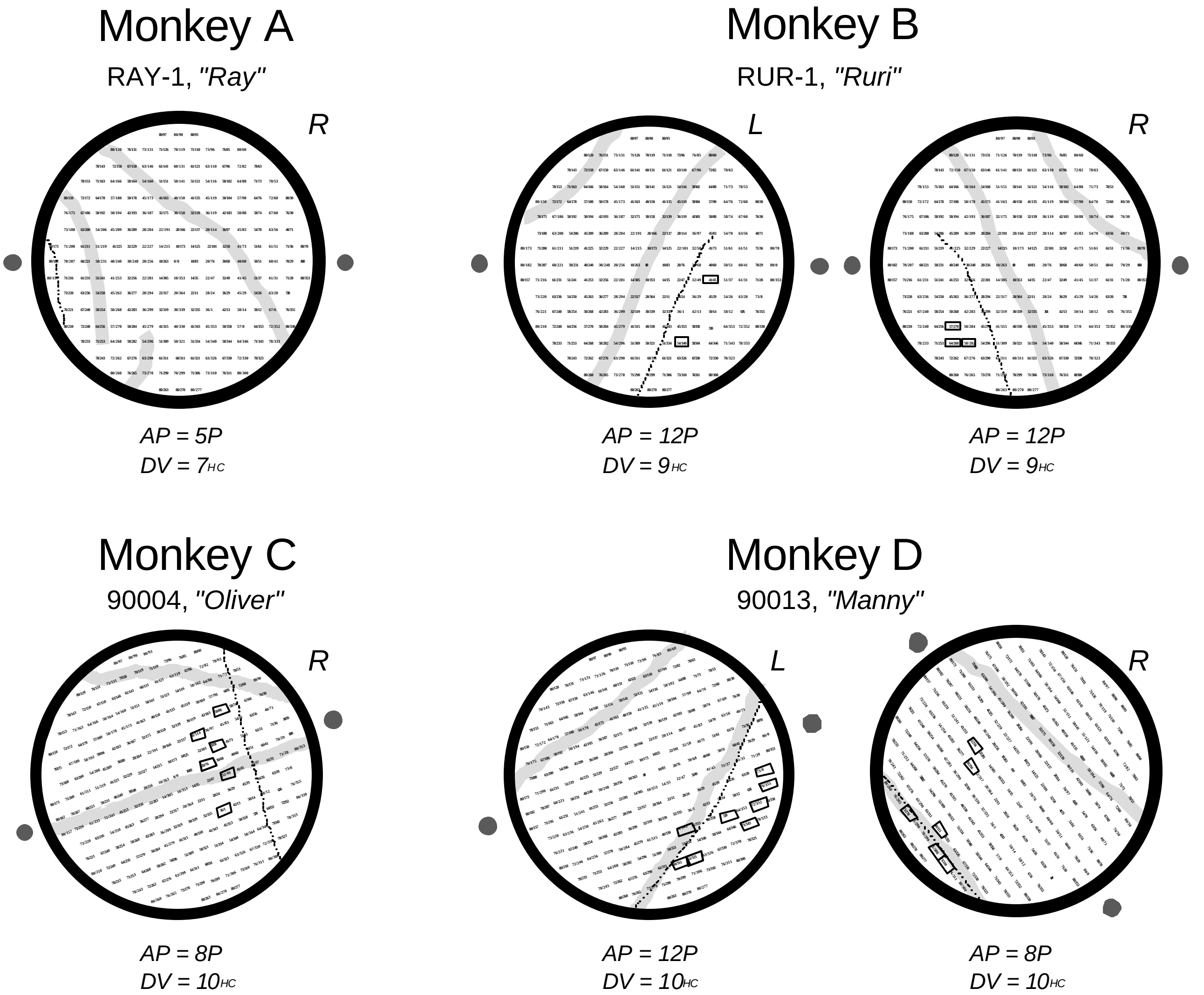

Figure 20 Chamber placement on the six hemispheres used in this study. Chambers are oriented with left being posterior for right hemisphere chambers (*R*) and right being posterior for left hemisphere chambers (*L*). The faint gray lines designate the best estimation of visible sulci sketched during the surgical procedure. Sites enclosed by rectangles represent those where neurons were isolated that could be activated only through one of the eyes. The black dotted lines correspond to the best estimate of the V1/V2 boundary based on the progression of receptive field positions as well as the clustering of monocular sites. The stereotaxic Horsley-Clark coordinates of the center of the chamber, as recorded during implantation, are written below each of the chambers.

The grating pattern that best activated the cell, along with a similar stimulus rotated 90°, formed the dichoptic pair used during subsequent rivalry testing. In addition, monkeys C and D were shown rivalry during fixation in the *flash suppression* paradigm. This consisted of exposing the monkey to a monocular stimulus for 1500 msec, and subsequently flashing the opposite oriented stimulus into the contralateral eye for 1500 msec while the first stimulus remained present. It is known from psychophysical studies that this paradigm can disambiguate perception during rivalry in humans (Wolfe 1984), and it has been employed in both anesthetized cats (Sengpiel and Blakemore 1994) and behaving monkeys (Sheinberg and Logothetis 1997), who consistently report seeing the newly added stimulus.

RESULTS

In the history of science the collector of specimens preceded the zoologist and followed the exponents of natural theology and magic. He had ceased to study animals in the spirit of the authors of the bestiaries, for whom the ant was incarnate industry, the panther an emblem, surprisingly enough, of Christ, the polecat a shocking example of uninhibited lasciviousness. But, except in a rudimentary way, he was not yet a physiologist, ecologist, or student of animal behavior. His primary concern was to make a census, to catch, kill, stuff, and describe as many kinds of beasts as he could lay his hands on. Like the earth of a hundred years ago, our mind still has its darkest Africas, its unmapped Borneos and Amazonian basins. In relation to the fauna of these regions we are not yet zoologists, we are mere naturalists and collectors of specimens. That fact is unfortunate; but we have to accept it, we have to make the best of it. However lowly, the work of the collector must be done, before we can proceed to higher scientific tasks of classification, analysis, experiment, and theory-making.

Aldous Huxley, from “Heaven and Hell” (1954)

SINGLE UNIT RESPONSES DURING BINOCULAR RIVALRY

The large number of visual cortical areas that have been described over the past decades are diverse both in their hypothesized roles in vision, as well as the criteria used to consider them a "unique area". The common characteristic of each is the existence of neurons that respond to the presence of a visual stimulus[1] (Felleman and Van Essen 1991). Nonetheless, as discussed in the first chapter, there are many situations when the brain can generate visual perception in the absence of sensory input. This raises the question, "does *internally generated* perception rely on the same areas and/or neurons as *externally generated* perception?". Cell activity in the visual areas is often considered to "represent" a stimulus, but does it represent only a sensory pattern, or can it represent a subjective experience? What is the role of the well-described visual areas in perception?

It is clear that the visual system, despite having the obvious first approximation of a serial sensory processing machine, is anything but strictly serial. The existence of massive projections "backwards" in the stream of visual processing, as well as the fact that all visual areas that have been studied have multiple connections to many other cortical areas at many levels, underscore this notion, and the role of projections other than the massive forward projections is almost completely unknown. Almost certainly, such diverse inputs provide the substrate for the modulatory influence of different behaviors (e.g. the focusing of attention), collectively termed "extraretinal effects" (Haenny, Maunsell et al. 1988; Maunsell, Sclar et al. 1991; Motter 1994; Assad and Maunsell 1995; Connor, Gallant et al. 1996; Treue and Maunsell 1996). But it is possible that such inputs could also be responsible for activating topographic visual areas during an *internally* generated visual percept, such as during dreaming and imagery. Yet single unit studies have so far provided little evidence that the topographic areas are even directly involved in perception. The

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[1] In some cases, a visual area can be classified as such by simply receiving input from another visual area, but in general this statement is true.

present paradigm involving binocular rivalry in the alert monkey presents the opportunity to study the relationship between the firing of a cell, and an internally generated, subjective change.

Neuronal Activity during Binocular Rivalry

A total of 429 cells were recorded from 4 monkeys in this study. Of these, 157 were fully tested for orientation tuning, binocular preferences, and activity changes during binocular rivalry. In addition, 93 cells were completely tested using the “flash suppression” paradigm, described below. Nearly all the neurons selected for the binocular rivalry task had foveal receptive fields, 74 of which came from the border of V1 and V2 posterior to the lunate

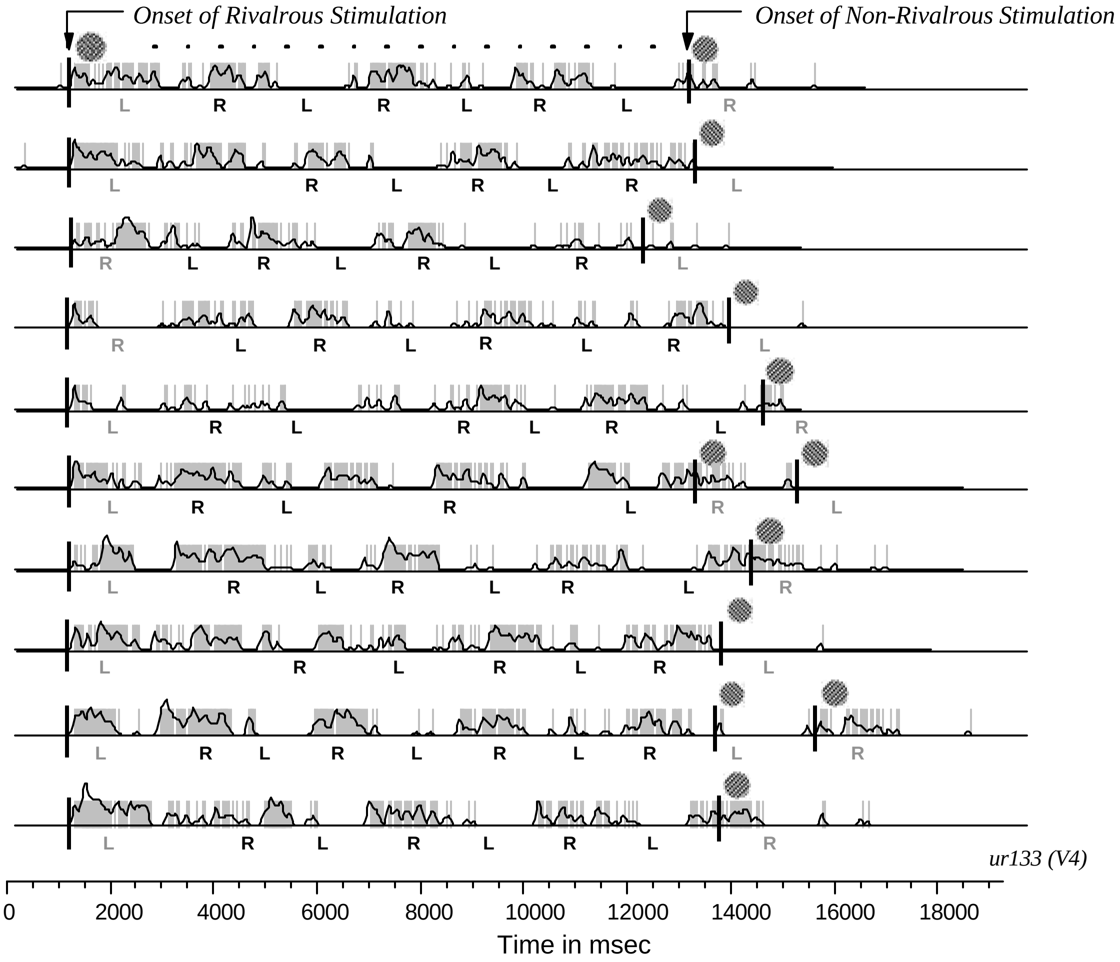

Figure 21 Activity of a cell in area V4 during binocular rivalry task.. Each horizontal trace represents a single observation period, where the vertical gray lines represent individual action potentials from the onset of a rivalry period throughout its duration of 10 to 15 seconds. Vertical black lines correspond the physical presentation of the grating pattern, either rivalrous (on the left) or nonrivalrous (on the right). The grating next to the bar on the right signifies the orientation of the nonrivalrous stimulus immediately following the rivalry period. The monkey’s reported perceptual transitions are indicated during the rivalry and nonrivalry periods below the horizontal traces, where L and R correspond to transitions to the left and right tilted gratings, respectively. Responses designated with black letters represent spontaneous alternations.

sulcus, and the remainder (83) came from the fundus and posterior bank of the lunate sulcus, most likely V4. During the rivalry task cells in each of these areas showed a diversity of responses in comparison with the perceptual changes experienced by the monkey. Many of the neurons modulated their firing in accordance with which of the two stimuli the monkey was perceiving during rivalry. The most common pattern of modulation was a brief increase in firing shortly before the monkey pressed the lever indicating that he saw the preferred orientation, although other patterns were observed as well.

Figure 21 shows the firing of a cell from area V4[1] as the monkey performed the binocular rivalry task. Under passive fixation conditions this neuron gave its largest responses to a grating tilted 45° to the right, and fired relatively little for the orthogonal orientation. It gave roughly equal responses to binocular stimulation and monocular stimuli presented to either eye. Each of the horizontal traces corresponds to a single observation period through time as the monkey fixated and reported his perceptual transitions. The gray vertical lines represent individual action potentials, and the spike density function, which is calculated from the action potentials and is an estimation of the probability of spike generation at each point in time, is shown as the black curve. The thick, black vertical lines correspond to the presentation of a physical stimulus, either rivalrous (on the left) or nonrivalrous (on the right). During rivalry the neuron fired variably, with periods of high activity and periods of relative quiescence. This variability in firing was highly correlated with the animal's changing percepts, which are shown by the letters L and R beneath each trace, corresponding to the monkey's pressing the left and right levers, respectively. Perception of the rightward grating (the cell's preferred orientation), was often accompanied by an increase in firing, while perception of the leftward grating was generally reported during epochs of low cell activity.

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[1] Cells were classified as being from area V4 based on initial observations of the position of the lunate sulcus during the surgery, the stereotaxic position of the chamber, recording depth, receptive field size and position, and receptive field properties.

This can be seen more easily by examining the mean cell responses around the time of the monkey's subjective transitions. The lower panels in Figure 22 show data from the same cell as in the previous figure, but with each of the spike trains (rows of small black dots) aligned to the monkey's lever responses, and makes it clear that the mean activity as a function of time is considerably higher when the cell's preferred stimulus rises to dominance than when it is suppressed. The vertical black line corresponds to this alignment point, where the computer registered the monkey's actual lever response, indicating that he sees the cell's preferred (left plot) or nonpreferred (right plot) orientations. The gray shaded area corresponds to the activity of the cell 1000 msec before to 1000 msec after this event,

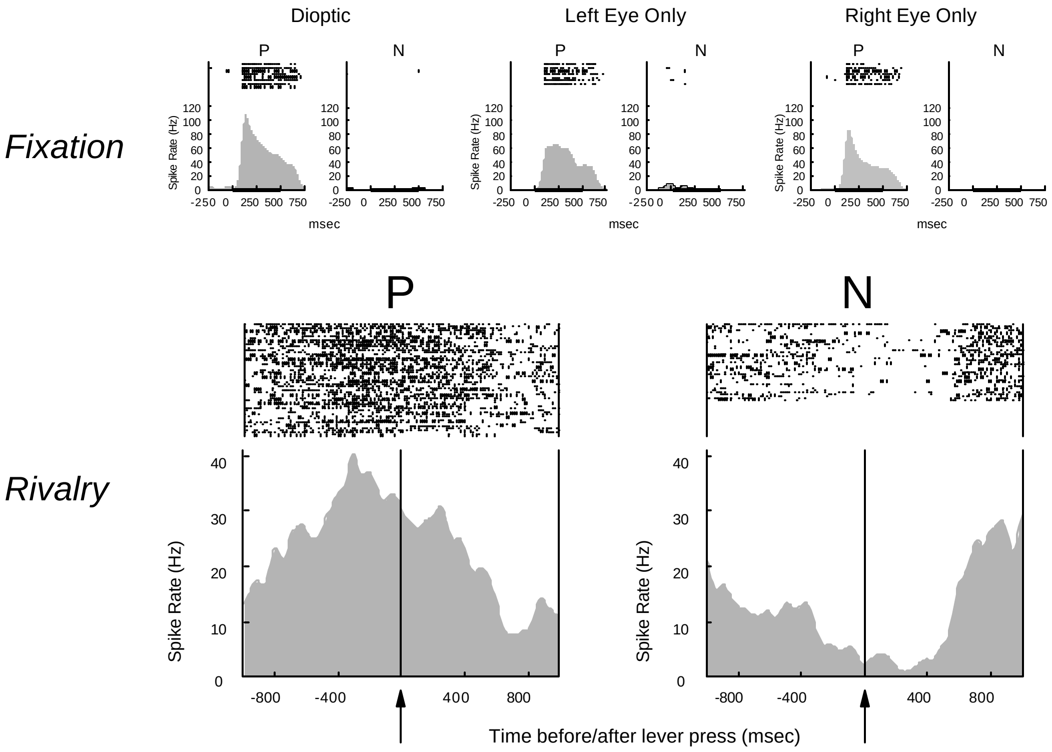


Figure 22 Responses of V4 cell from Figure 21 under nonrivalrous fixation conditions and during binocular rivalry. In these plots as well as those in later figures small black dots correspond to spike trains, where each dot represents and individual action potential. Each trial is represented by a single horizontal row of dots. The gray shaded areas correspond to average instantaneous firing rate of the cell around the times of the perceptual transitions. The upper plots show the post stimulus time histograms (PSTH's) during dioptic and monocular conditions for the preferred (P) and nonpreferred (N) orientations. The bottom panels show the activity around the time of the perceptual transitions during rivalry (see text).

averaged over many trials. This continuous measure of the instantaneous spike rate was calculated by using the spike times to compute each individual trial's spike density function, which represents a probability density estimation for firing a single spike at each point in time. A variable-width kernel size, after Parzen (1962), was used in this process to maximize the amount information retained despite changes in the mean activity. In this and the following figures this measure of the instantaneous spike rate is approximately equivalent to that generated by a smoothed histogram of spike timing events. The upper panels show the post stimulus time histograms immediately following the presentation of the preferred (P) and nonpreferred (N) gratings under dioptic and monocular conditions, demonstrating that this cell is both highly tuned and equally driven by the two eyes.

Figure 23 shows several more examples of cells recorded during binocular rivalry. For each, the activity is shown during both nonrivalry trials (top) and rivalry trials (bottom) for leftward and rightward orientations. For this figure, only the rivalry trials are aligned to the monkey's lever responses, while the nonrivalry trials are aligned to the onset of the stimulus itself. The top two cells, both from area V4, were typical of cells found in all the areas recorded. Each strongly preferred one orientation over the other during both the nonrivalry trials and passive fixation (not shown). However, during rivalry neither displayed activity changes in accordance with the perceptual dominance and suppression of the preferred orientation. In contrast, the two cells in the bottom half of this figure, one from V1 and one from V4, consistently did reflect the monkey's perceptual choice in their firing, generating more spikes when the preferred stimulus was seen than the nonpreferred. This type of response was especially prevalent in area V4.

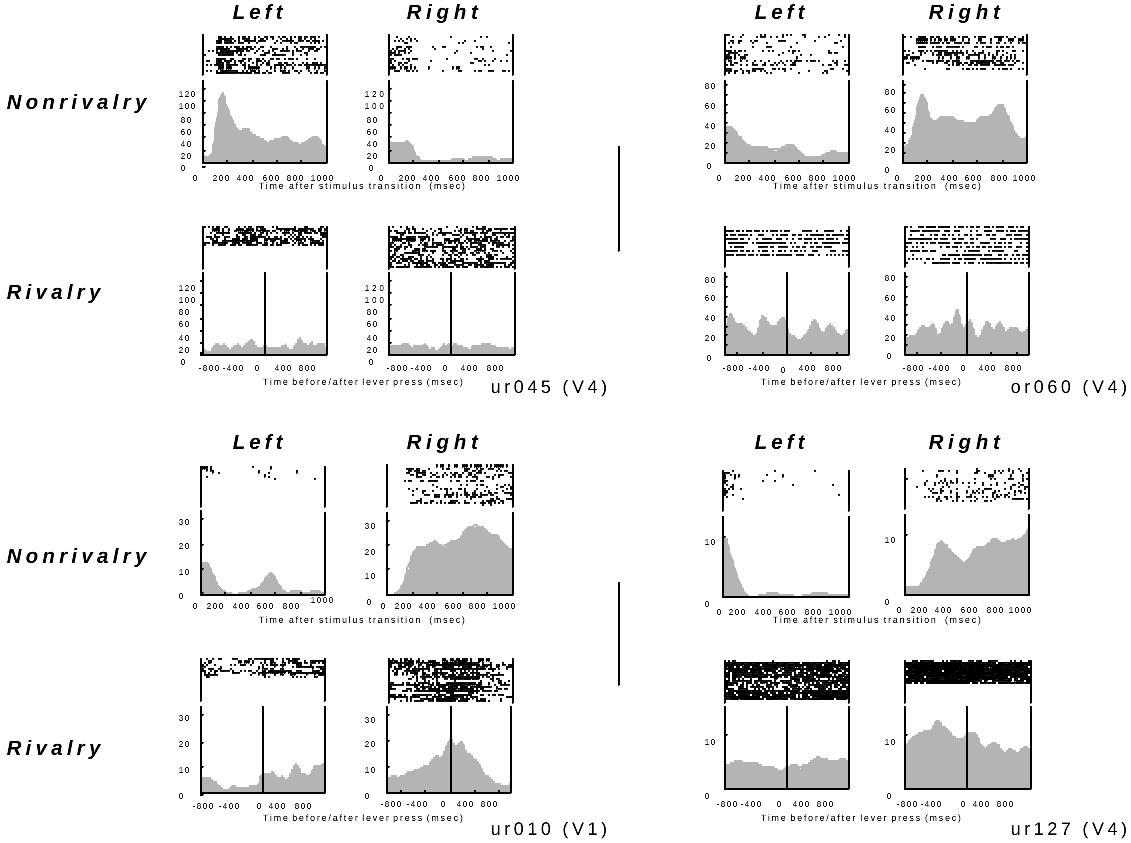


Figure 23 Four cells demonstrating the variety of response types during rivalry. In each case, the cell's firing is evaluated under nonrivalrous stimulation for its responses to leftward and rightward orientations in the upper panels. This corresponds to the dioptic presentations during the rivalry task itself and provides a measure of the difference in sensory response to the two orientations. The lower panels in each quadrant correspond to the cell activity around the time of the perceptual responses of the monkey.

Figure 24 shows the average responses of 12 such V4 cells during transitions to their preferred and nonpreferred orientations during rivalry. In this plot, the response profile for each neuron is divided by its mean firing rate to normalize for differences in overall rate, and the mean and standard error (gray shaded area) of these normalized traces are plotted. Note that the activity increases associated with the preferred orientation are, on average, short-lived, with an increase beginning roughly a second before the monkey strikes the lever, peaking at several hundred milliseconds before, and then declining again to near baseline shortly after the monkey makes his response. In contrast, for the nonpreferred orientation

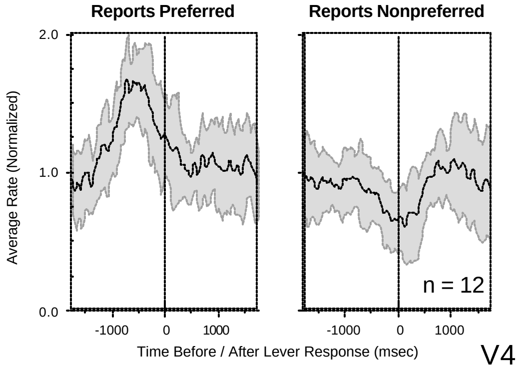


Figure 24 Average of 12 V4 cells in the binocular rivalry task during instances the monkey reports seeing the preferred (left) and nonpreferred orientations (right). The plots were generated by averaging the response profiles from cells displaying this profile, where each was first normalized by dividing by the cell's overall mean firing rate. The gray shaded area corresponds to the standard error of the two mean profiles as a function of time.

there is relatively little change in activity prior to 500 msec before the lever press, but just as the lever is pressed there is a dip in firing. A subset of cells, almost exclusively from area V4, modulated their activity during rivalry in the opposite manner as during nonrivalry. An example is shown in Figure 25.

For a number of cells from monkey C the local field potential was measured simultaneously with single cell activity during the rivalry task, using electrodes of relatively low impedance (≤ 1.0 MOhm). The analog signal was sampled and saved at 30 kHz, individual spikes were extracted from the signal and matched with those collected from the window discriminator. The temporal course of the local field potential was then examined around the time of the lever responses in the same fashion as the instantaneous spike activity. Preliminary results from one recording site in area V4 are shown in Figure 26, in which the local field potential and the instantaneous rates are shown during the nonrivalry conditions (upper panels) and the rivalry conditions (lower panels). Note that the isolated cell at this site had a higher instantaneous spike rate following the presentation of the rightward orientation over the leftward (gray shaded area in upper panel).

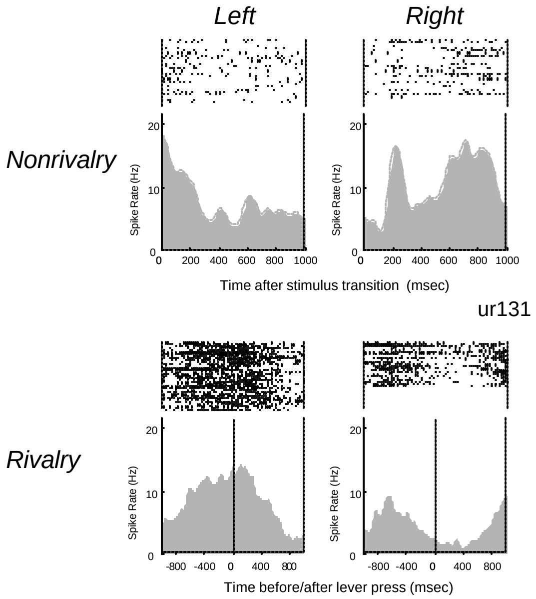


Figure 25 Cell whose firing rate increases when the monkey reports a transition to the *nonpreferred* stimulus.

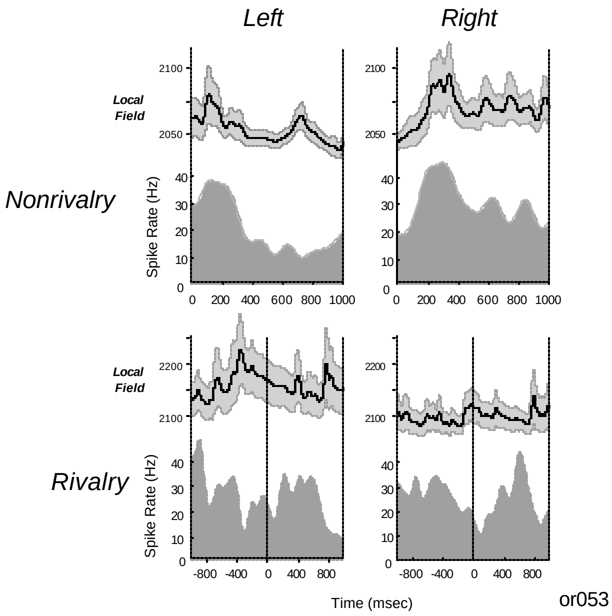


Figure 26 Local field activity and instantaneous spike rate measured for a site in V4 during the binocular rivalry task. For each of the four panels, the instantaneous rate is shown by the dark gray shading, using the same conventions as in previous figures. In addition, the mean local field potential averaged over many trials is shown by the dark black line, where the scale refers to A/D points and the light gray regions corresponds to the standard error.

The local field at that site gave similar responses when the new orientation was shown (thick black lines in the upper panels). During rivalry, however, there was no demonstrable relationship between the individual cell's activity and the monkey's perceived grating, while the local field showed a notable increase in activity shortly before the monkey reported seeing the left (nonpreferred) orientation. The thick black lines correspond to the mean local field potential where the units are in A/D points, and the light gray region represents the standard error over all traces.

Because the dispersion in eye positions, even during controlled fixation, is often larger than the receptive fields of neurons in the earliest visual cortical areas, we considered it important to fully investigate the effects of small eye movements on our data. We were not overly concerned that the eye movements were creating artifactual modulatory activity for at least three reasons. First, modulations caused by small eye movements should, in theory, cancel out when averaged over many trials. Second, for many modulating cells, especially those in V4, receptive fields were considerably larger than the amplitude of the eye movements. Third, a strong majority of modulating cells displayed increased firing specifically when the cell's *preferred* stimulus was perceived. It is, of course, impossible that the monkey could systematically adjust his eye movements based upon the preferences of the cell being monitored. Nonetheless we were interested in examining the patterns of eye movements during rivalry and nonrivalry as they

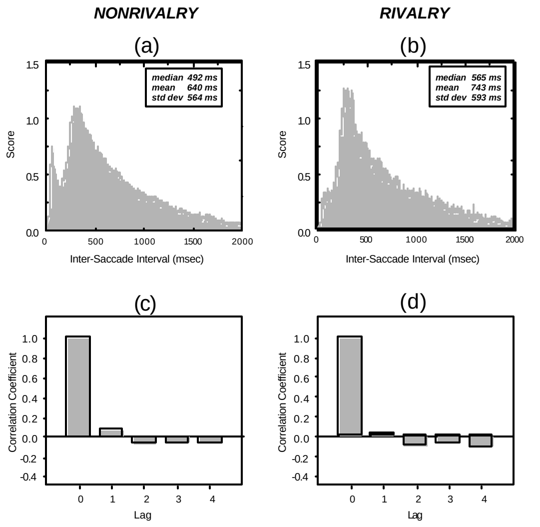


Figure 28 Distributions of intersaccadic intervals during nonrivalry (a) and rivalry (b). Autocorrelation of successive intervals during nonrivalry (c) and rivalry (d).

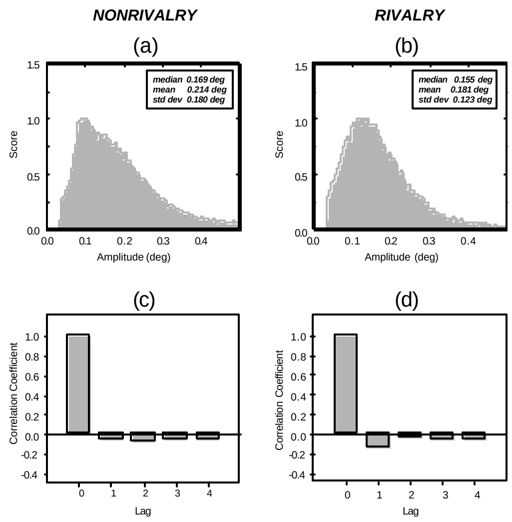


Figure 27 Distributions of saccade amplitudes during nonrivalry (a) and rivalry (b). Autocorrelation of successive amplitudes during nonrivalry (c) and rivalry (d).

may be related to the patterns of dominance and suppression, as well as the activity of the cell. We used the methods outlined in the Appendix to parse each of the observation periods into saccade events and epochs of fixational stability.

Fixational Patterns during Rivalry and Nonrivalry

The patterns of both fixation and microsaccades were examined during rivalry and nonrivalry to determine whether there were any systematic differences between the two conditions. Generally speaking, the patterns were quite similar. Figure 27 shows the distribution of saccade amplitudes, as well as the autocorrelation of successive amplitudes during nonrivalry and rivalry. The distributions are slightly different, but the median amplitude is roughly the same in the two conditions, and neither autocorrelation reveals any significant sequential dependence between successive amplitudes. Likewise, Figure 28 shows how the intersaccadic intervals are distributed during rivalry and nonrivalry, as well as the sequential dependence of these times. Again the differences between the two distributions is subtle.

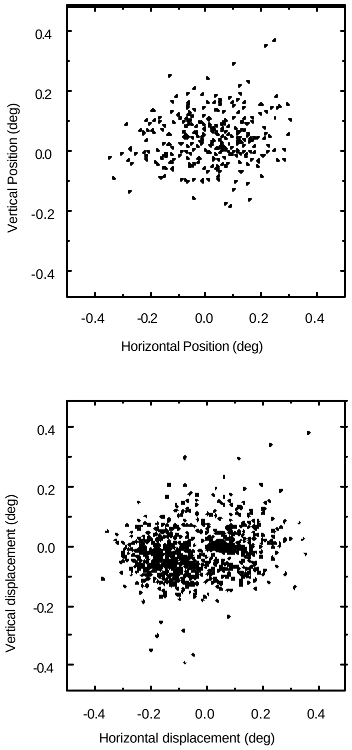


Figure 29 Typical pattern of eye movements observed during rivalry, collected from monkey B during one session. The upper panel represents the end destination of corrective saccades specifically during the perception of one of the grating stimuli during rivalry. The bottom panel shows the amplitudes and directions of saccades during rivalry when each of the saccades are considered to arise from the origin.

The “spike” at 200 msec on the nonrivalry distribution most likely an artifact from positional corrections during the smooth fading between the two orientations during the rivalry emulation. The autocorrelation does not reveal any obvious relationship between successive microsaccade intervals.

Given that saccades identified as “corrective” were prevalent in our data, and that corrective saccades are small positional adjustments to direct gaze toward a visual target, we were interested to see whether the pattern of corrective saccades during rivalry and nonrivalry could reconstruct which oriented stimulus the animal was perceiving. If, say, a rightward stimulus was being presented (or *perceived* in rivalry) the destinations of the corrective saccades may reflect the rightward oriented bars of the grating itself. The upper panel in Figure 29 shows a typical pattern of corrective saccade end positions when a particular stimulus was reported dominant during rivalry. The data were collected in a single session. Although there were no rigorous statistical tests applied to these patterns, for most cells there were no obvious stimulus-related patterns in the end saccade positions either in rivalry or nonrivalry (not shown). Rather, there was a normal elliptical cloud of end-fixation positions centered around the fixation point. We then considered whether the *direction* of saccades could provide a similar measure of the perceived stimulus. If the animal systematically made jumps in gaze from bar to bar, it is possible that the directions of the saccades could be, on average, perpendicular to the grating’s orientation. The lower panel on Figure 29 shows this data for one session during rivalry. In this figure, each saccade is considered to start from the origin, and each plotted point is the end of a vector whose angle and length signify the direction and amplitude of the saccade, respectively. Only saccades classified as *real* (i.e. those that fit all the criteria and were not corrective) were considered in this plot. As with the corrective end-positions, only rarely did patterns emerge that convincingly reflected the stimuli either in rivalry or nonrivalry. During rivalry, the pattern observed in the lower panel, with two densities on the horizontal meridian on either side of the fixation spot, was frequently seen, regardless of the orientations of the competing gratings. This is likely to be attributable to small vergence movements stemming from the binocular mismatch.

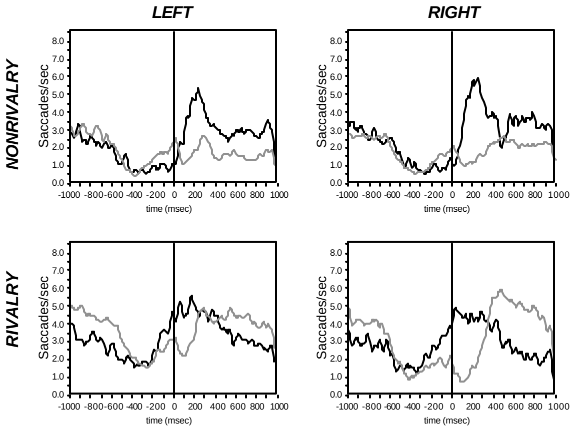


Figure 30 Frequency of saccades before and after the monkey presses each of the levers during rivalry and nonrivalry. The gray curves represent Monkey B and the black curves represent Monkey C.

We then examined the patterns of microsaccades throughout the course of a rivalry trial itself. Figure 30 shows the frequency of saccades relative to the times the monkey pressed each of the levers during both rivalry and nonrivalry trials for all of the rivalry sessions together for two monkeys. As in the cell plots, the times are centered around the lever presses of the monkey, and the curves represent how the frequency of saccades changes as a function of time. There are clear differences in the saccade frequency profiles between rivalry and nonrivalry, as well as between the two animals, however, only relatively small differences between pressing the right and left levers. In each case there seems to be a relatively decreased frequency of saccades several hundred milliseconds before the lever response (during the time of the maximal modulation of cell responses, see Figure 24), followed by a rapid increase in frequency either when the lever is pressed or shortly afterwards. The significance of these patterns is unknown, and it is also unknown whether humans display the same fixational patterns during rivalry.

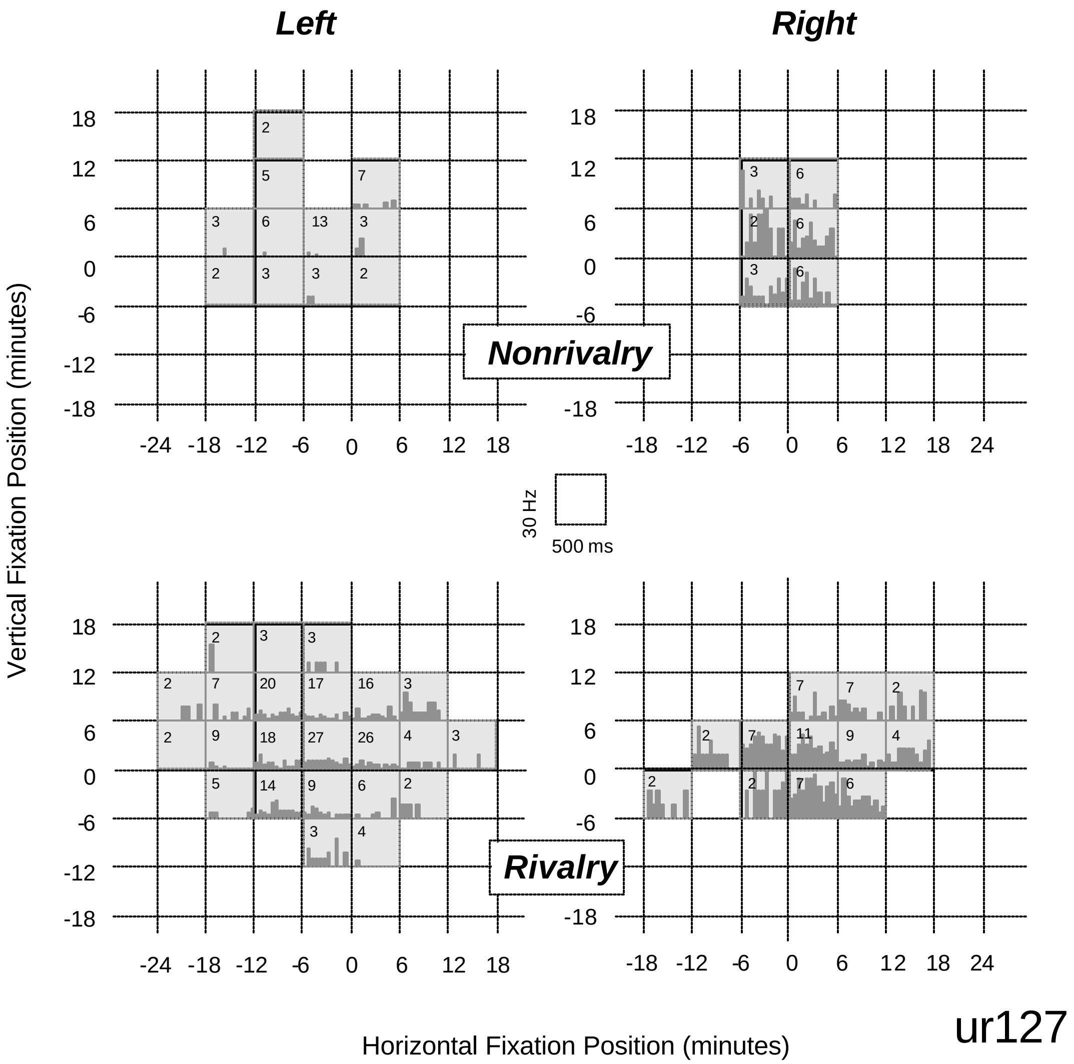


Figure 31 Cell activity during periods of fixation as a function of fixation position for a cell in area V4. Each of the shaded histograms corresponds to the activity of the cell from the onset of fixation to 500 msec into the fixation periods. The upper panels demonstrate the post-fixational activity during extended viewing of nonrivalrous (monocular and dioptic) gratings. The bottom panels show the activity during rivalry for all fixation periods initiated between 800 and 200 seconds before a lever press. Gray squares correspond to those eye positions for which there were at least two stable fixation positions. The number of periods used in generating each histogram are shown in the upper left of each square. The fixation spot consisted of a 9 minute square centered on the point at which the dark black lines cross.

Cell Activity during Stable Fixations in Rivalry

Physiological responses were reexamined by considering only activity in the stable fixation periods extracted using the methods described in the Appendix. This allowed us to examine very accurately the activity of each cell with precise knowledge of the direction of gaze.

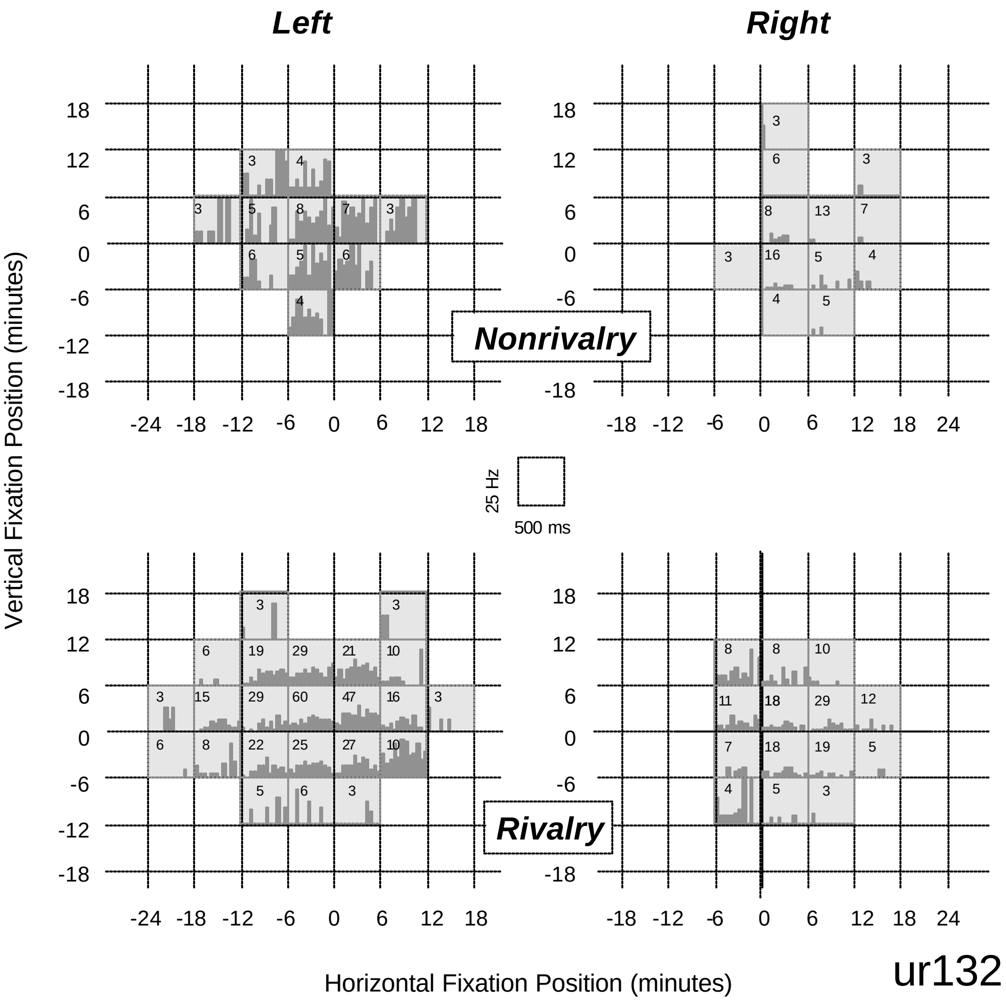


Figure 32 Another perception-related V4 cell shown in the same format as the previous figure

Within a fixation period the standard deviation of the eye position was very small and comprised of two physiological components, drift and tremor. The tremor was negligibly small, calculated to be 0.003 degrees (about 11" of arc) for our data. The drift was more significant, but still very small, generally between 0-8´ per second. Each of these values agrees well with those measured in humans (Carpenter 1988). Given this stability, each single fixation could reasonably be considered to be confined to a single point in visual space.

The activity during fixations was compared during rivalry and nonrivalry for arbitrarily small regions of visual space, from the beginning of each fixation period onward. Figure 31 and Figure 32 show two examples of V4 cell activity during nonrivalry and rivalry as a function of fixation position. Each square represents a spatial bin of 6´ (0.1 °) on a side. Within each bin is shown the average activity of a the cell during the first 500 msec of fixations within that region of space. Fixations less than 500 msec were also included, and their length was taken into account in computing the average activity. In each figure, the upper panels represent cell activity during nonrivalry, and the lower panels during rivalry. Numbers in the upper left corner represent the total number of fixations within the given bin during that condition. In order to isolate those epochs in which the modulations were most likely, only fixation periods initiated between 800 and 200 msec before the lever press were considered for the rivalry trials. The nonrivalry plots used

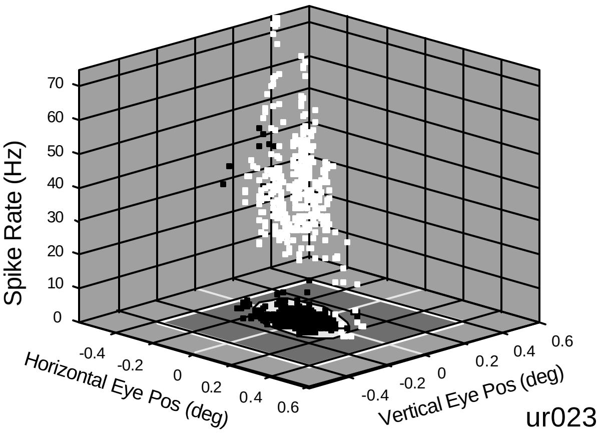


Figure 33 Activity of modulating V2 cell during binocular rivalry. Activity of the cell is plotted during rivalry for horizontal and vertical eye positions. The ellipse in the center represents a mapping of eye positions which optimally activated the cell during nonrivalrous testing. Each point represents the average firing rate of the cell during an epoch in which the monkey perceives the preferred (white) or nonpreferred (black) orientations. The dark shaded square represents the monkey's behavioral fixation requirements.

fixations made whenever the stimulus was physically present. The resolution of 6 minutes in this plot was very fine considering that the miniature square fixation point that the monkey acquired at the beginning of each trial was 9 minutes across.

It is clear that for both cells the activity during those fixation periods initiated before the monkey reported the preferred orientation was significantly greater than that preceding the nonpreferred orientations. The activity pattern in the right and left plots during rivalry resembles that during the nonrivalry condition in which only the preferred or nonpreferred stimuli were shown. In other words, when the nonpreferred stimulus was reported, the activity of each cell was significantly diminished despite the maintained physical presence of the preferred stimulus.

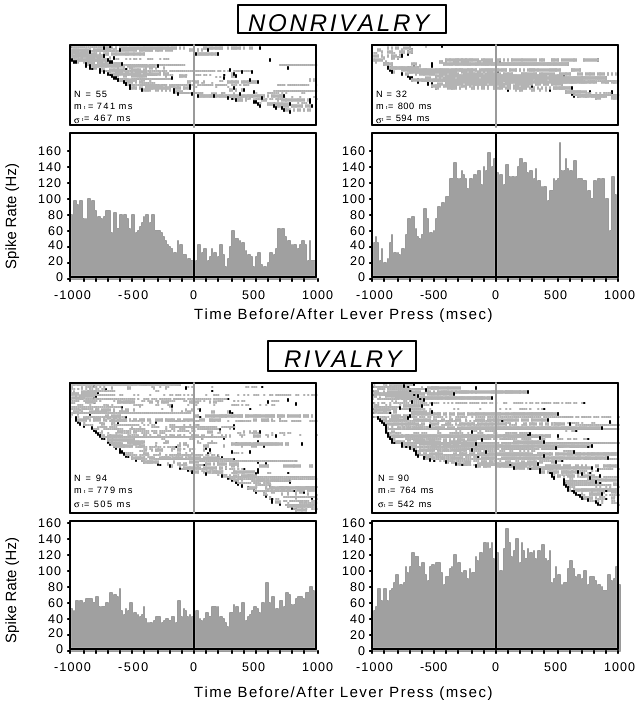


Figure 34 Activity of V1 cell during nonrivalry and rivalry trials considering only fixation periods where the center of gaze is within a region 0.2 degrees on a side, centered on the fixation point. Each of the spike trains (rows of gray ticks) is considered only from between the onset and offset (black ticks), and each is positioned according to when it occurred with respect to the lever press. The spike trains are sorted based upon the time of their onset.. The number of fixation periods (n), as well as the mean (m_t) and standard deviation (σ_t) of the fixation period lengths are given for each of the conditions.

Figure 33 shows another representation of the effects of eye position and perceptual state on cell activity, this from a strongly modulating neuron from area V2. Each dot represents the average spike rate over an epoch of 200 msec, where white dots represent instances the monkey reported seeing the cell's preferred orientation and the black dots instances of seeing the nonpreferred orientation. The horizontal and vertical eye positions are shown as the position with respect to the bottom axes. Notice that when the monkey reports that the preferred stimulus is phenomenally dominant the cell fires strongly, and when the nonpreferred stimulus is dominant the cell shuts down entirely, even though both the stimulus and the eye positions are identical in the two cases.

Finally, neuronal activity around the time of the lever press was examined for both rivalry and nonrivalry, using only complete fixation periods. This is plotted for a cell isolated from the superficial layers of striate cortex in Figure 34. This cell had a preference for rightward oriented contours, and fired roughly equally to monocular presentations in either eye. The plots show activity restricted to a window 12´ (0.2°) across, centered on the fixation point. The number of fixation periods (n), as well as the mean (m_t) and standard deviation (σ_t) of the fixation period lengths are shown. The rows of gray ticks correspond to spike trains during individual epochs of stable fixation, with the dark black ticks representing the beginning and end of these periods. Fixation periods are sorted from earliest (top) to latest (bottom). The gray spike histograms, derived from the raster plots above, reveal that during fixation periods confined to this small region there is considerably more activity when the monkey's perceived orientation matches that normally preferred by the cell, either during nonrivalry or rivalry. For this cell, restricting the analysis window to 0.2 degrees significantly enhanced the measured modulation, suggesting that for small receptive fields subtle changes in eye position *dilute* perception-related activity changes.

Flash Suppression

The paradigm of flash suppression was used to evaluate 93 cells during passive fixation. This method, in which a stimulus is presented to one eye (satiation stimulus) and after a period of time a second, rivalrous stimulus is added to the other eye, has been shown to result in the unambiguous perception of the newly added stimulus in both humans (Wolfe 1984) and monkeys (Sheinberg and Logothetis 1997). We were interested to see how cells in the early areas would respond during such a sequence. It also allowed us to test one

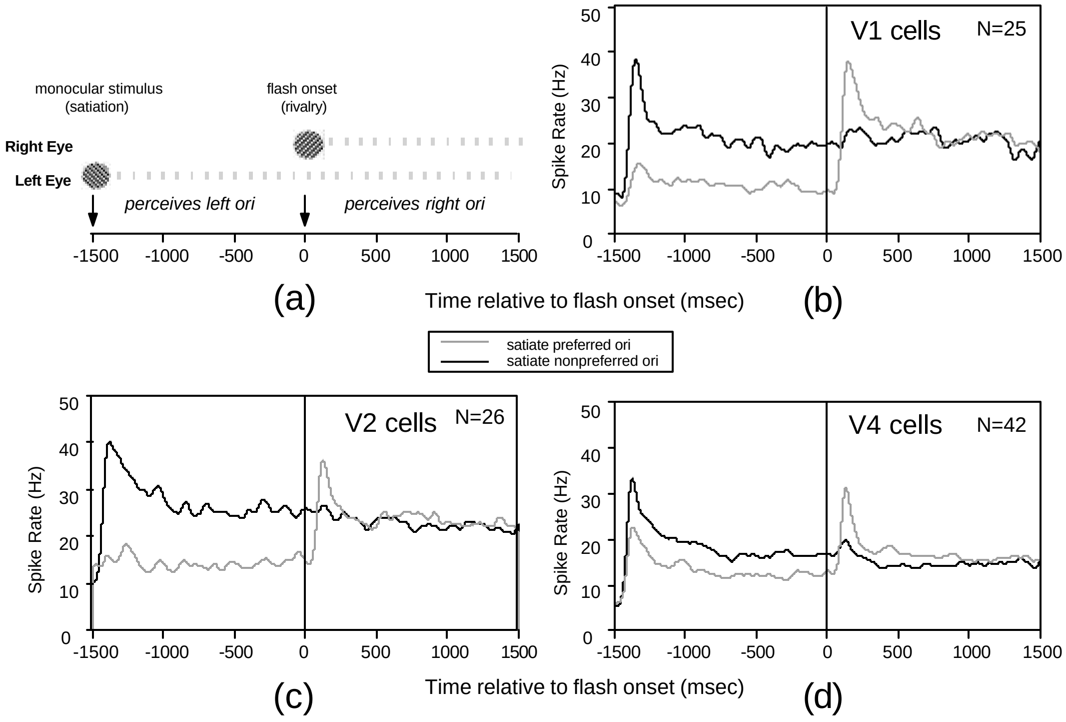


Figure 35 Flash onset. (a) Paradigm. One eye views a monocular stimulus (satiation stimulus) for 1500 msec while the other eye views only a blank field. After this period, a second stimulus is quickly placed in the eye opposite the first, result in the perception of the newly added stimulus. In (b)-(d) the black lines correspond to those trials in which the neuron's preferred orientation was the satiating stimulus, and the gray lines show those trials in which the nonpreferred stimulus was the satiating stimulus. The curves represent the overall mean instantaneous spike rate for the two conditions in each area from 1500 msec before the rivalry (start of satiation) to 1500 msec afterwards.

monkey who was unable to learn the binocular rivalry task (Monkey D).

A typical flash suppression trial is outlined in Figure 35a. Here, a leftward tilted (satiating) grating is shown to the left eye for 1500 msec, at which point a rightward tilted (rivaling) grating is suddenly added to the right eye. When the new stimulus is added, the stimuli in the two eyes are in conflict and, given sufficient time, normal binocular rivalry alternations will ensue. However, for the first second(s) after the flash itself perception is nearly always dominated by the newly added stimulus. Cells in the early visual areas exhibited a wide variety of responses during flash suppression. The average response of all the cells tested in each area is shown in Figure 35b-d. In these plots, the black lines correspond to those trials in which the monocular satiation stimulus was the preferred orientation of the cell and the nonpreferred orientation was added to the other eye after 1500 msec. The gray lines correspond to a nonpreferred orientation for the satiation stimulus, and the preferred stimulus added second. Note that for each of the areas, the *average* activity is roughly what one might expect based on the orientation preferences of the cells. The addition of the nonpreferred stimulus had relatively little effect when the preferred stimulus was already being shown, and the addition of the preferred stimulus caused a normal response in the cell when it was satiated with the nonpreferred stimulus. Each area did, however, show a slightly higher sustained activity after the preferred stimulus was flashed compared to when the nonpreferred was flashed, the largest effect being in V4 (Figure 35d).

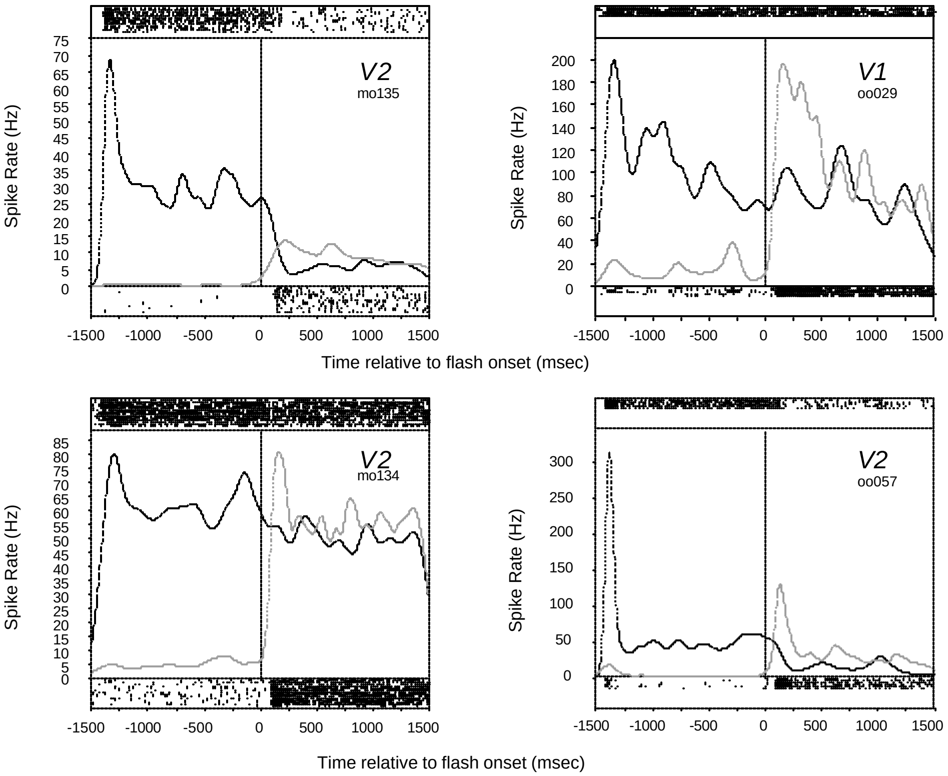


Figure 36 The responses of four neurons in the earliest cortical visual areas during the flash onset paradigm. The conventions are the same as in Figure 35, where the gray curves correspond to satiation with the nonpreferred orientation and the black curves with the preferred orientation

The mean flash suppression activity does not adequately convey the diversity of responses seen during the flash suppression paradigm in each of the areas studied. Figure 36 and Figure 37 show the responses of a number of individual cells during flash suppression. The conventions are the same as in Figure 35, except each panel now corresponds to a single cell. Note that in some cases flash suppression of the nonpreferred stimulus (black lines) has relatively little influence on the cell's firing for the preferred stimulus, while in other cases it drastically depresses the cell's firing. A fraction of cells even fired maximally during rivalrous stimulation relative to either orientation alone (not shown).

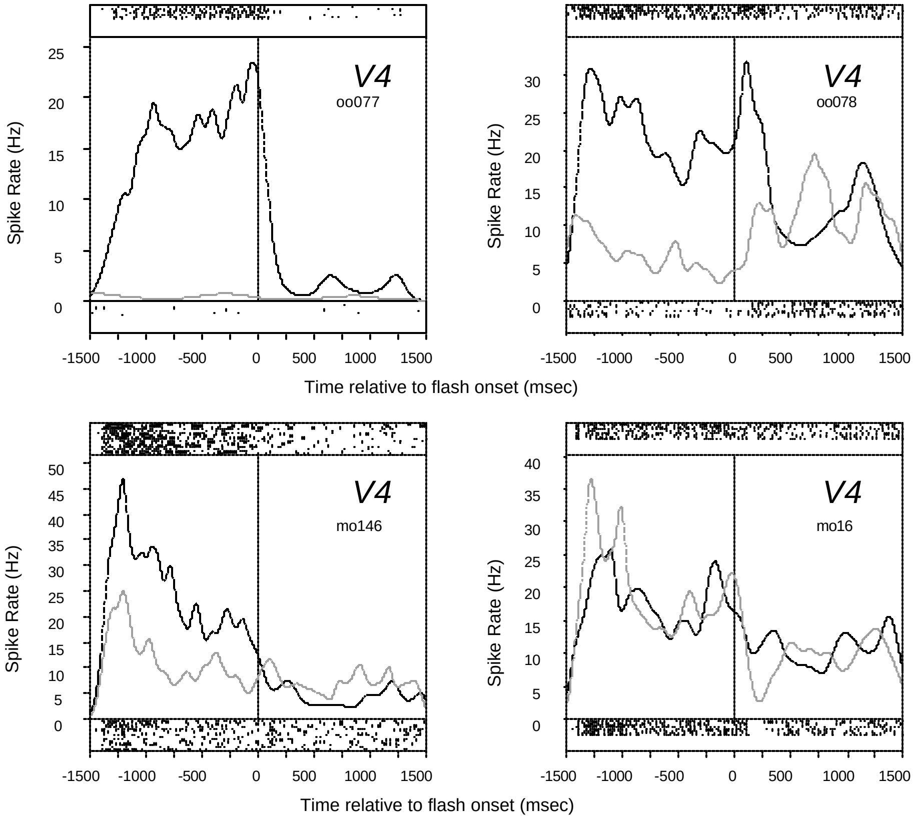


Figure 37 The activity of four V4 neurons during flash suppression paradigm. Response profiles were diverse among cells within V4, ranging from strong interocular suppression upon addition of the nonpreferred stimulus to no effect at all. A few cells even fired most strongly when nonmatching stimuli were present.

Population Analysis

A summary of the modulatory activity of cells during the rivalry task is shown in Figure 38. Each square plotted in this figure represents a single neuron from either V1 (open), V2 (black) or V4 (gray). The coordinates of each point on the x and y axes correspond to the *modulation index* (MI) of the cell during nonrivalry and rivalry, respectively. Modulation indexes were defined as the standard Michelson contrast $MI = \frac{\bar{r}_p - \bar{r}_n}{\bar{r}_p + \bar{r}_n}$, where $\bar{r}_p$ is the mean rate of the preferred orientation and $\bar{r}_n$ is the mean rate of the nonpreferred orientation. Rivalry and nonrivalry modulation indexes, MI_R and MI_N, were calculated based only on the activity during stable fixation periods. In addition, only fixations within a square zone 30´ (0.5º) across, centered on the fixation point, were considered in the analysis. Given the observation from the trial plots that during rivalry modulatory activity tends to be maximum shortly before the lever press (see Figure 22 to Figure 24), MI_R was calculated based on those fixation periods whose *onset* occurred between 800 msec before and 200 msec before the time of the lever press. The nonrivalry index, MI_N , was calculated based on fixations initiated during the first 500 msec in which the nonrivalrous stimulus was physically present. These requirements were quite rigorous, and only cells that were completely tested for orientation preference and selectivity, binocular preferences, and had at least four stable fixations within this region during this time window for each condition (N = 116) were included in this analysis.

During nonrivalry, the modulation index considered the activity difference elicited by the different stimulus conditions (preferred and nonpreferred presented alone). This value, roughly indicating the degree to which the preferred stimulus elicited a greater response than the nonpreferred, is plotted on the abscissa. On the ordinate is plotted a similar measure, but in this case the means are derived from stable fixation periods during those times the monkey *perceived* either the preferred or nonpreferred stimulus. In other words, the Michelson contrast is used to gain a measure of the modulatory activity of the cell based on the monkey’s perception. Figure 38 plots the MI for the rivalry condition against that for the nonrivalry condition. In interpreting this plot, it is perhaps helpful to consider the

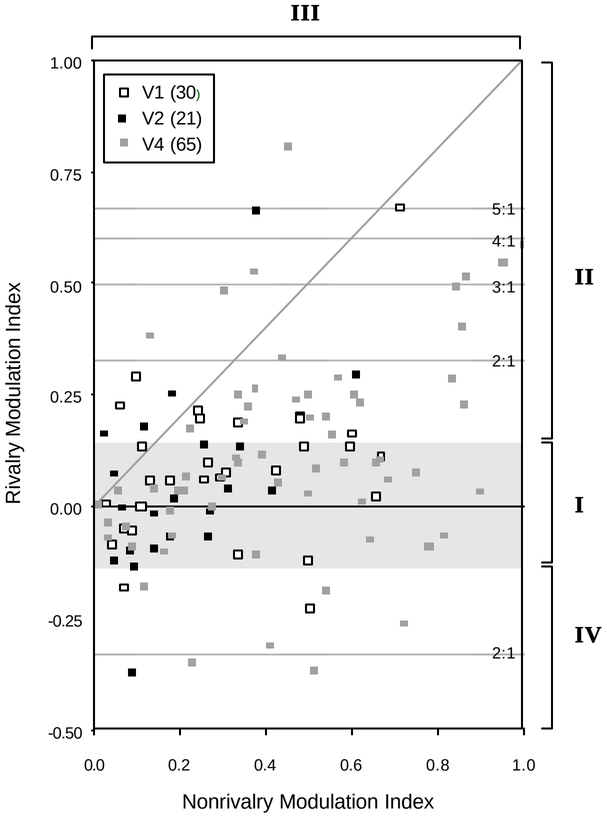


Figure 38 Perception-related modulation index computed during binocular rivalry versus a similar index calculated during the nonrivalry trials. See text for details.

extremes. Were a cell completely unrelated to the monkey's perception and maintained a constant level of firing, its rivalry MI would be zero, and it would lie as a point on the abscissa. On the other hand, if the activity of a cell was always dictated by the monkey's perception, during both nonrivalry and rivalry, the modulation indexes would be the same in the two conditions, and the square would lie on the diagonal line in the upper half of the plot. The horizontal dotted lines correspond to those values of the MI in which the cell's mean firing rate is an integer multiple higher in one perceptual condition over the other (i.e. 3:1 in the upper half of the plot corresponds to a three times higher mean rate when the monkey perceives a change to the preferred orientation relative to the nonpreferred).

The plot can therefore be divided into four regions, I, II, III and IV. Region I (shaded area) corresponds to all those cells for which the activity during rivalry was roughly equal (< 25% difference in mean rate), whether the preferred or nonpreferred stimulus was being perceived. A total of 68/116 cells (58.6%) fell into this category, including 20/30 (66.7%) from V1, 15/21 (71.4%) from V2, and 34/65 (52.3%) from V4. Region II represents the majority of modulating cells, and corresponds to activity changes during rivalry that approached, but did not reach, the level of activity changes during nonrivalry. A total of 29 cells (25.0%), including 7 V1 cells (23.3%), 1 V2 cell (4.8%) and 21 V4 cells (32.3%), fell into this category of perception-related activity. Region III, above the diagonal line, corresponded to those cells whose activity changes were actually more pronounced during rivalry than nonrivalry. Ten cells total (8.6%) showed this type of enhancement during rivalry, including 2 V1 cells (6.7%), 4 V2 cells (19.0%) and 4 V4 cells (6.2%). Finally, region IV corresponds to rivalry modulations that were of the opposite polarity than the nonrivalry case, where

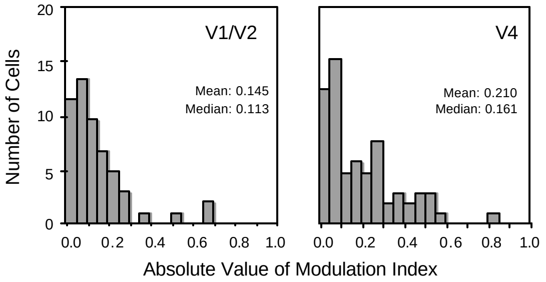


Figure 39 Histograms of the modulation indices for cells at the V1/V2 boundary and in V4. The absolute value of the rivalry modulation index measures the magnitude of activity differences the two perceptual states.

perception of the preferred stimulus resulted in a decreased activity relative to perception of the nonpreferred stimulus. A total of 11 cells behaved in this manner, including 2 V1 cells (6.7%), 1 V2 cell (4.8%), and 6 V4 cells (9.2%). Figure 39 compares the distribution of modulation indexes from cells in areas V1 and V2 with those from cells in area V4. The mean modulation index for cells in V4 was 0.20, corresponding to a 33% difference in mean rates between the two perceptual conditions, whereas in the earlier areas the mean index was 0.15, corresponding to a corresponding to a 24% difference.

The modulatory activity of each of these neurons was then evaluated as a function of its monocularity, that is, the degree to which it was selectively activated by a stimulus placed in one eye over the other. This is shown in Figure 40. In this case an index of ocular preference, $OI = \left| \frac{\bar{r}_L - \bar{r}_R}{\bar{r}_L + \bar{r}_R} \right|$, was computed, where $\bar{r}_L$ and $\bar{r}_R$ correspond to the mean firing rates with the stimulus presented in only the left or only the right eye, respectively. Small values of *OI* thus correspond to cells in which there was no significant preference for activation through either eye (*binocular* cells), and larger values represent cells that are more and more biased toward one eye, with a maximal value of 1.0 for purely *monocular* cells. The horizontal dotted lines represent the same modulation index values as in the previous figure, and the gray, vertical line shows the value of the

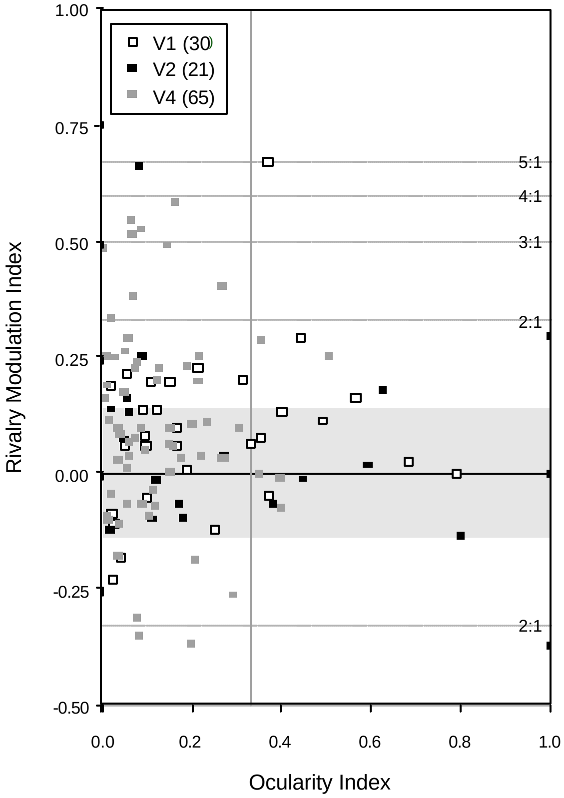


Figure 40 Rivalry modulation index for 116 cells as a function of the cell's ocular preferences. The ocularity index represents the degree to which a cell is biased to being activated by one eye more than the other during monocular presentation.

ocularity index corresponding to exactly twice the response in one eye versus the other. Note that with few exceptions the strongest modulating neurons arise from area V4 and do not strongly favor either eye.

Summary of Results

The presence of neurons in the topographic visual areas whose activity reflects the spontaneous subjective changes experienced during binocular rivalry demonstrates that the sensory processing of a retinal pattern and its perceptual representation are neither one and the same, nor are they entirely separable. A number of cells in all areas tested responded entirely based on the physical stimulus, as if they were devoted only to scrutinizing the retinal pattern. Other cells in the same regions continually changed their mode of firing to match the *perception* of the monkey at each point in time. Many cells fell into an intermediate range, where their activity was modulated according to the perceptual changes, but only subtly, and there seemed to be a continuum in the degree to which perception was represented.

Given that the representation of many cells is complex, consisting of both a sensory and perceptual component, the notion of neurons as *stimulus detectors* becomes an unacceptable metaphor for considering brain mechanisms of perception. The ability of a neuron to detect or discriminate a stimulus does not elucidate that neuron’s role in perception, but rather its role in the *limits of sensation*, whether one examines cells in area MT or in the retina. Ironically, those neurons whose activity is the most closely allied with perception are likely to be relatively *poor* stimulus detectors compared to those devoted to the scrutiny of the retinal pattern.

The relative abundance of perception-related neurons in area V4 as compared to the earlier areas suggests that despite the presence of both perception-related and sensory-driven activity in each of the areas, there is a distinct trend towards increased perceptual representation as one climbs the classically defined visual hierarchy (Felleman and Van Essen 1991). This is consistent with the previous finding that area MT, which resides in a comparable hierarchical level to V4, contains roughly the same fraction of neurons reflecting perception during rivalry (Logothetis and Schall 1989), as well as during perceptual bistability in a structure from motion stimulus (Chang, Bradley et al. 1996). It is also consistent with recent results from our laboratory, in which a very high fraction of cells in the inferotemporal cortex (IT) were found whose activity directly reflects the monkey's perception during rivalry (Sheinberg and Logothetis 1997). In this study it was again noted that individual neurons often had clear contributions of both the physical and perceived stimulus combined in their responses.

Given the diversity of activity among cells in all areas during rivalry, simultaneous recordings from multiple cells would be of great interest. It is possible, for example, that the perception of a stimulus depends upon the correlated firing between cells (von der Malsburg and Buhmann 1992; Singer and Gray 1995), or precise spatiotemporal firing patterns (Abeles, Bergman et al. 1993; Abeles, Bergman et al. 1995). A recent study by deCharms and Merzenich (deCharms and Merzenich 1996), for example, found that the sustained perception of an auditory tone was much more highly correlated with the sustained *synchrony* between pairs of cells in auditory cortex than with their instantaneous firing rates, which showed only transient changes. Given that the majority of V4 cells tested during rivalry gave a *short-lived* increase as the preferred stimulus rose to dominance, falling back to baseline as the phase persisted (see Figure 24), it is possible that the sustained visual perception of the preferred orientation is also better reflected in the coordinated activity of multiple cells. The observation that the local field activity can reflect perception in cases where individual cell responses do not further suggests that perception-related changes can in some cases be better measured by the coordinated firing and macroscopic activity than by the activity of a single neuron in the recording field. Recent studies have shown that the spontaneous macroscopic activity in the cortex of both anesthetized cats and alert monkeys show large fluctuations in activity that are unrelated to any sensory input (Arieli, Shoham et al. 1995; Arieli, Donchin et al. 1996). If the balance between rivalrous states reflects a competition between alternative macroscopic activity patterns, and these patterns can be affected by such random activity, it is possible that the stochastic nature of the perceptual alternations during rivalry and other bistable phenomena reflects the randomness of these fluctuations themselves. If this is the case, the coordinated activity among many cells may in some cases prove to be a better "physiological unit" of perceptual activity in the brain than the firing of any single neuron alone. If, for example, perceptual bistability in ambiguous figures, reflects the random waves of on-going cortical activity, it is likely that a neural understanding of figure and ground can only be understood by examining the brain at this higher level. Certainly, this notion fits with the Gestalt ideas that elemental sensory events cannot be understood without knowledge of higher order configurational properties.

The basis of a correlative approach to studying perception, relies on finding the *best* representation of a perceptual entity an a biological measurement. Even though it is possible that the perceptual apparatus engages the exact same neurons as the sensory processing apparatus, it may do so in an entirely different manner. While sensory representation in the cortex may be primarily feedforward and hierarchical, perceptual representation might involve the formation of specific but distributed patterns of activity that are inaccessible using standard single unit recordings. In this sense, the metaphor of a "state system" might be found to be preferable to that of "stimulus detection" as the neural basis of perception. Activity states may be more dynamic in the earlier topographic areas, where sensory receptive fields are constantly repositioned with respect to a stimulus, than in the higher areas such as inferotemporal cortex, where sensory responses are robust to eye movements. It may be precisely the coordination of these differing macroscopic activity patterns that is, for example, responsible for the one's stable perceptual representation of an object as it sweeps across the retina with every change in fixation position.

RIVALRY BETWEEN SPARSE SURFACES

This remainder of this dissertation is aimed at clarifying the nature of the competition and perceptual suppression underlying binocular rivalry in hopes of providing insight into segmentation and grouping principles in vision. The experiments described in this and the next chapter were designed with a specific purpose in mind—to arrive at a paradigm by which one could establish with certainty whether rivalry represents a competition between the eyes or between central representations of conflicting stimuli. Although in the past decades singleness of vision during rivalry has been generally attributed to the suppression of an entire monocular channel in the framework of eye competition, with a few exceptions (Crovitz and Lockhead 1967; Walker 1978; Grossberg 1987), there remains the possibility that rivalry occurs between stimulus *representations*, after information from the two eyes is combined. Certainly, the physiological results presented in the previous chapter support this possibility, as the neurons that correlate most strongly with perception during rivalry are found well beyond the site of binocular combination. In the this and the next chapter I present the results from experiments employing two novel stimulus paradigms that argue that rivalry does indeed represent a competition between extracted stimulus representations. In this chapter I ask if two surfaces devoid of local interocular conflict can compete for perceptual dominance, and if rivalry can occur between two stimuli that are each partially represented in each eye. In the next chapter, I ask whether a stimulus can persist in its perceptual dominance during rivalry even while it is periodically rerouted between the two eyes.

Rivalry Between Sparse, Uniform Fields

Introduction

As mentioned earlier, numerous studies have shown how perceptual suppression “spreads” in contour rivalry (Kaufman 1963; Hochberg 1964; Blake, O'Shea et al. 1992; Fukuda and Blake 1992; O'Shea, Sims et al. 1996). These studies share the notion that binocular rivalry does not simply occur between two contours, but that dominance and suppression include regions of the “background” surrounding the contour conflict. It is also known that when a contour is presented in one eye while a blank field (or Ganzfeld) is shown to the other, the contour is always perceived. This latter condition is generally considered to be one of stable fusion (Blake and Boothroyd 1985), and as long as two monocular stimuli are presented in different spatial locations they should be simultaneously perceived, even if shown to different eyes. But what happens when stimuli in different eyes begin to encroach upon each other’s suppression zones? Will they be perceived simultaneously and continuously as if they were separated by several degrees? Or will perception be unable to support both stimuli and become unstable, even though there is no direct spatial conflict.? Questions such as these were the original motivation for the present experiment.

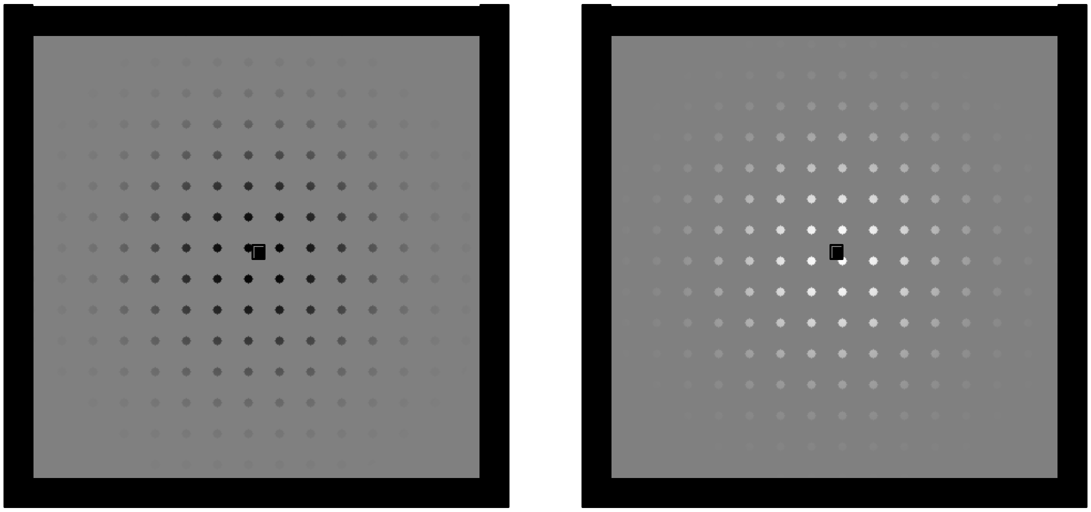


Figure 41 Example of stimuli used in the uniform dot field experiments. The stimulus on the left was presented to one eye while the stimulus on the right was shown to the other. Subjects were required to fixate a small central spot in the center.   The overall spatial extent of the stimulus was approximately 10 degrees.

Rather than presenting two single monocular elements, in this experiment arrays of small dots were presented to each eye, all black in one eye and white in the other. The size and spacing of the dots was varied from presentation to presentation.   Each array was spatially displaced with respect to a central fixation point, such that each dot in the left eye was offset horizontally and vertically from its nearest neighbor in the right eye (see Figure 42). The background was gray, with a gamma-corrected luminance of approximately 50 cd/m^2. Each stimulus element represented a step from gray to white (>100 cd/m^2) or black (< 1 cd/m^2) in the highest contrast regions. Dots ranged in size from 12´ (0.2°) to 30´ (0.5°) in diameter, and their minimum interocular distance, shown in Figure 42, was varied from 12´ (0.2°) to 75´ (1.25°). Edge effects during binocular viewing were minimized by multiplying a large element array with a 2-D gaussian envelope, such that the contrast was highest in the center of each surface and faded away gradually with increasing eccentricity. The standard deviation of this gaussian was 1.25°, providing a rivalry field that exceeded 7°. The fraction of time in which there was complete dominance of either color was measured as the MID was varied for each observer. A typical dichoptic pair is shown in Figure 41, in which rivalry can be seen if the images are binocularly fused.

Subjects

Five subjects (DL, CA, SS, JB, and ER) were used in this experiment, ranging in ages from 21 to 28. Subjects dichoptically viewed rivaling stimuli through a mirror stereoscope. The stimuli were generated by a Silicon Graphics computer (Indigo/Elan, 72 frames/second), and displayed on a 21” Sony monitor located 60 cm from the eyes of the subject. Great care was taken in adjusting the mirrors of the stereoscope to ensure correct binocular alignment of the displays for each observer. The luminance contrast between the patch and the background, together with a small (0.2º x 0.2º) fixation spot, were used to aid proper convergence. Subjects were required to fixate the central point, but eye position was not explicitly measured. The subjects initiated the onset of each period, and were instructed to take a break whenever necessary. Each of the subjects viewed each of the conditions for 4 1-minute periods, reporting with a computer mouse instances in which either of the competing patterns disappeared from view. In this experiment subjects were specifically instructed that they should hold the mouse button down only if there was *complete* dominance of either the black or white dots, and upon seeing a single dot of unlike color the button should be released.

Results and Discussion

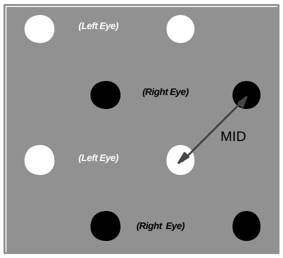


Figure 42 Minimum interocular distance (MID)., defined as the distance between the center points of the nearest interocular neighboring dots.

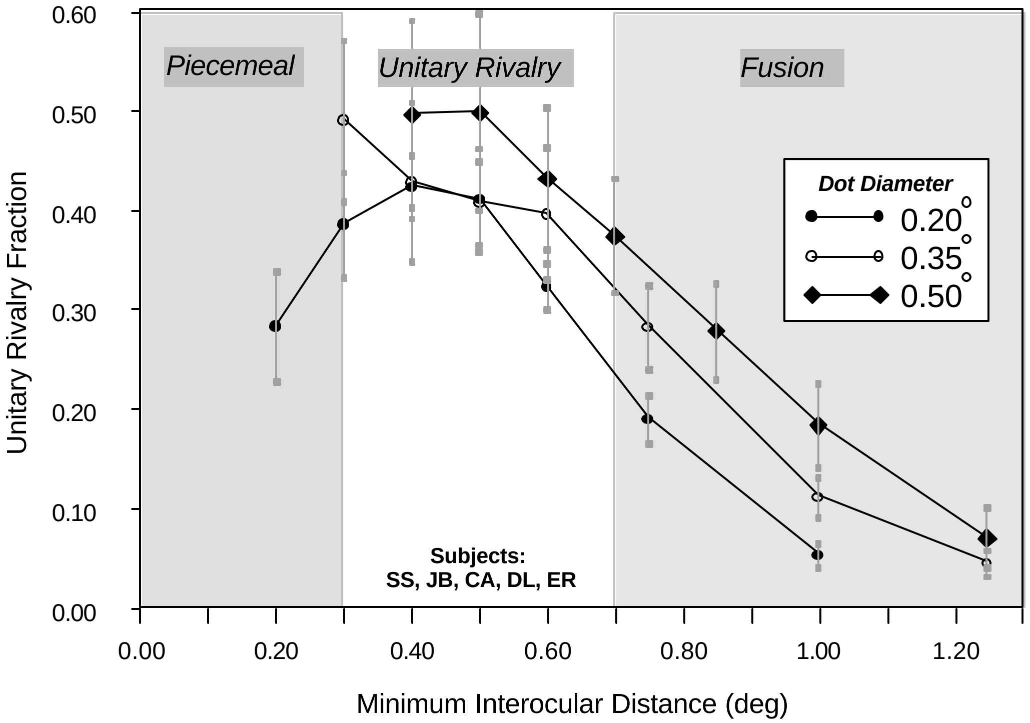


Figure 43 Results from uniform dot stimulus in the uniform dot experiment. Each curve represents the unitary rivalry fraction as a function of MID for a given dot diameter. Average unitary fractions are shown for five subjects, with the gray vertical bars signifying the standard error. See text for details.

Figure 43 shows the effect on the unitariness of rivalry of varying the MID and dot size. Each curve represents the mean data for dots of a given size, and the gray, vertical bars correspond to the standard error for five subjects. Unitary perception of either all black or all white dots was maximal when the MID was between 0.3 and 0.7 degrees. At larger spatial intervals, there was a tendency for all of the dots to be perceived at the same time (stable fusion), fitting with the expectation that the “suppressive zones” surrounding the dots in one eye no longer encroached on those from the dots in the other. For MIDs smaller than 0.3° subjects reported that unitary rivalry was often replaced by a piecemeal appearance, where there was ample perceptual suppression, but in some domains the suppressed dots were black and in others they were white. One subject described this stimulus as having a “shimmering” appearance, perhaps resulting from dichoptic luster. It is perhaps not surprising that this distance of 0.3° is very close to Kaufman’s (1963) estimation of 15 minutes of arc for the spread of suppression away from a monocular contour. It is interesting to note, however, that this decrease in unitary rivalry was perceived only for the *smallest* dots when they became very dense, and did not seem to be exclusively due to the proximity of their contours. For example, when the 0.2° diameter dots were spaced with a MID of 0.2° their borders of the nearest interocular neighbor dots were just touching and unitary perception decreased. However, for the 0.5° dots, the unitary perception was at a maximal when their spacing was such that their edges just touched, at 0.5°. It is possible that this is due not to any specific local interactions but to the larger dots' ability to better represent a unified, coherent surface. It seemed in this way that there was a trade off between minimizing local interactions in the competing stimuli and maximizing the surface representation of each.

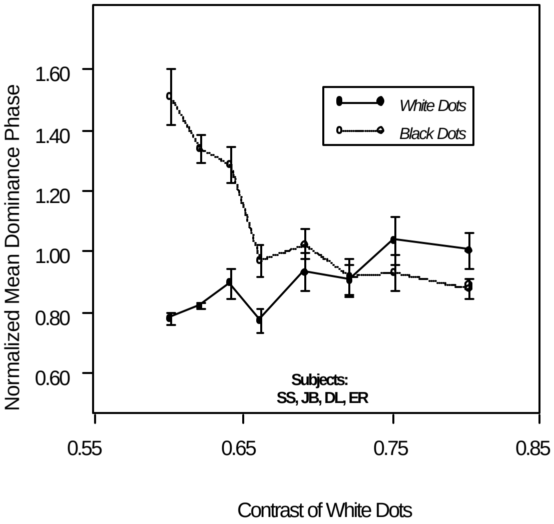


Figure 44 Effect of manipulating the intensity of the white dots on the dominance and suppression of the two surfaces. The solid lines (filled circles) indicates the mean dominance phase for perception of the white dot surface, and the dotted line (open circles) to the perception of the black dot surface. The mean dominance durations are normalized to the overall mean for each subject, and the vertical bars designate the standard error for these normalized curves for four subjects.

The most striking finding in this experiment was the strength and extent of the unitary rivalry that occurred for intermediate MIDs in the absence of interocular conflict. When the MID fell within the range of 0.3° to 0.7° degrees there was profound, completely unitary rivalry between the two patterns more than 40% of the time, where subjects reported that perception each single dot of a given color had perceptually vanished throughout the stimulus. This is a considerably higher unitary dominance fraction for a stimulus exceeding 7° than would be expected based on those studies measuring dominance with conflicting contours, where stimuli tend to fragment with significantly smaller angular extents (Blake, O'Shea et al. 1992; O'Shea, Sims et al. 1996).

Figure 44 shows the effect of manipulating the intensity of the white dots on the relative balance of perception between the white and black surfaces. The 0.2º dot diameter and 0.5º MID were used. As the contrast of the white dots was lowered, there was a predictable increase in the mean dominance time for the perception of the black dots, with relatively little influence on the white. This patterns is the same as that described in the previous chapter when the contrast of the gratings was manipulated. In this case, the effect of changing the intensity of the dots cannot be attributed to mechanisms involving local competition since the dots are spatially disparate, but is likely to reflect a manipulation of either the perceptual salience or coherence of the competing surface representations.

Rivalry Between Sparse, Mixed Fields

Introduction

Given the results of the first experiment, and the notion that the representation of a surface could be an important prerequisite for unitary rivalry between sparse patterns, we next investigated the hypothesis that the surface completion could be attained by *interocular* grouping of similar elements. In this experiment, the competing surfaces were composed of all black dots and all white dots, but in this case half of each competing surface was shown to each eye, such that half the dots in each eye were black and the other half white. We were interested whether or not, for any range of MID, rivalry would ensue between all the white dots and all the black dots, which would require the construction of the two surfaces through interocular grouping.

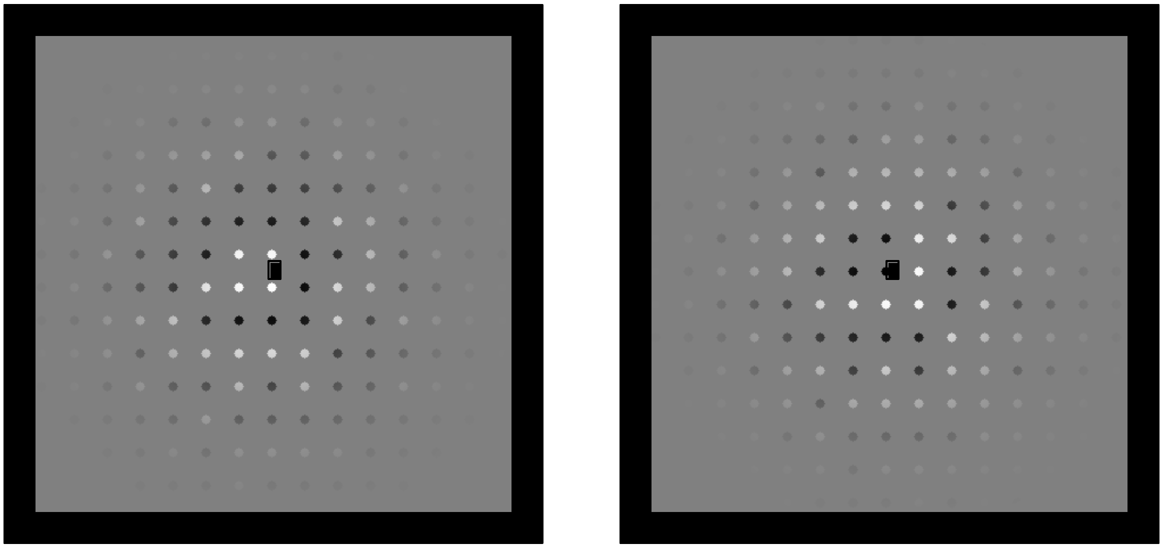


Figure 45 Mixed dot stimuli used in Experiment 2. The stimuli were similar to the dot stimuli in Experiment 1, except the white and black dots were randomly divided between the two eyes. Each point in "binocular space" was well-represented by both white dots and black dots, which can be seen to rival when the two half -images are fused.

Stimuli and Methods

Three subjects were used in this experiment (DL, JL, and NL) ranging in age from 25 to 46. Their task was the same as in the uniform dot experiment. Stimuli were constructed by starting with the dot arrays used in the previous experiment and interchanging half of the dots in each eye with its nearest, opposite-colored neighbor, such that when both eyes were considered, each region of visual space was adequately represented by both black and white. The dots were still horizontally and vertically offset between the two eyes with respect to the fixation point, as shown in Figure 45

Each of the subjects viewed each of the conditions for two 1-minute periods, reporting with a computer mouse instances in which either of the competing patterns was dominant. Pilot experiments suggested that only very rarely would each single dot of a given color completely disappear, but that there were often periods in which the perceived pattern was *nearly* complete, with one or two dots lingering of the opposite color. For this reason, unlike in the first experiment, subjects were instructed to report instances in which perception was "clearly dominated" by one or the other color. They were told that for this condition to be reported there must be greater than 85-90% unity in dot color. They were not specifically trained to identify this percentage, and their subjective variability could be a potential source of error, but all subjects were experienced and clearly understood the instructions. In addition, it was emphasized that dominance entailed the complete perceptual suppression of individual dots, not merely a "heightened visibility" one color over the other.

Results and Discussion

Under these conditions, subjects reported many instances of clear perceptual dominance of

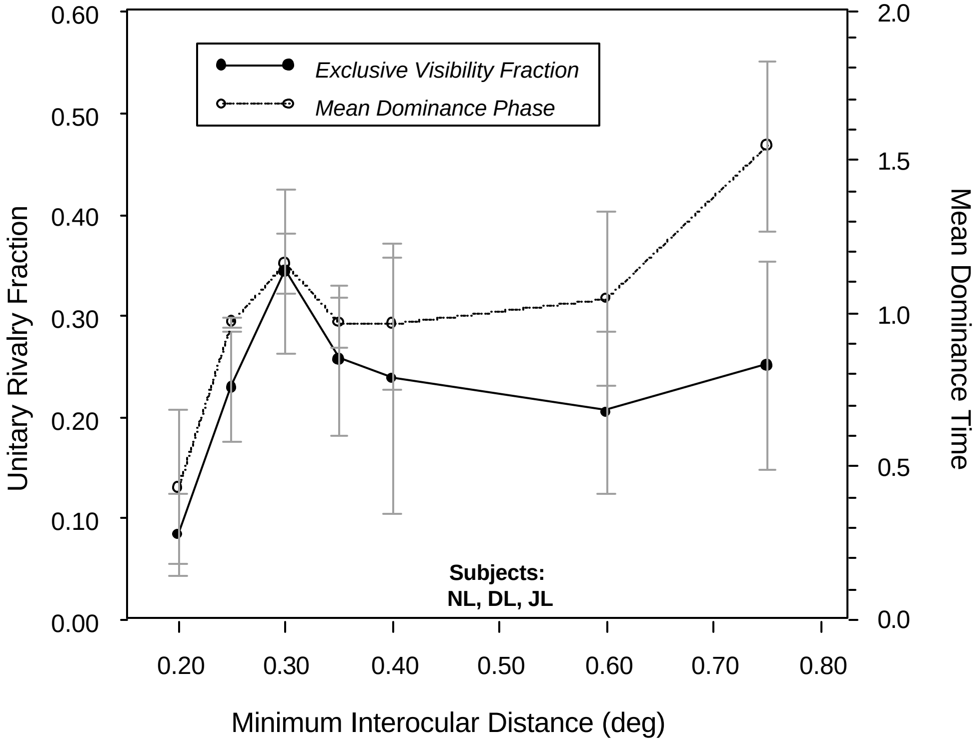


Figure 46 Data from three subjects in the mixed dot experiment. The solid black line (filled circles) corresponds to the unitary rivalry fraction as a function of MID for the mixed stimuli (leftmost axis). The dotted lines (open circles) represent the mean dominance phase durations (rightmost axis).

one color over the other. Such percepts could only arise through *interocular grouping* of like dots to form two central representations of competing surfaces. It was often reported that one of the surfaces would ``congeal'', becoming suddenly dominant, followed by an abrupt transition to the other color, followed again by the stimulus lapsing into a "mixed" state. The fraction of unitary rivalry, as well as the mean dominance time of a unitary phase, are shown in Figure 46 as a function of interocular spacing for dots 0.2° in diameter. Note again that for MIDs below 0.3° there was a significant decrease in unitary rivalry. For two of the three subjects, unitary perception fell to below 5% when the MID had a value of 0.75°, while it remained high for the third. The peak value of 35% is well above the value expected if individual dots drew independently from the two eyes. The mean dominance time (dotted line) increased with larger and larger dot spacings.

These results provide further evidence that perception during rivalry is not governed solely by a discrepancy in local contour information, but is dictated to a large degree by higher level grouping properties. That this grouping can be accomplished by combining information from the two eyes, and that the grouped representations can then compete for perceptual dominance argues strongly against theories attributing rivalry to the complete dominance and suppression of a monocular channel. This observation has been noted a handful of times

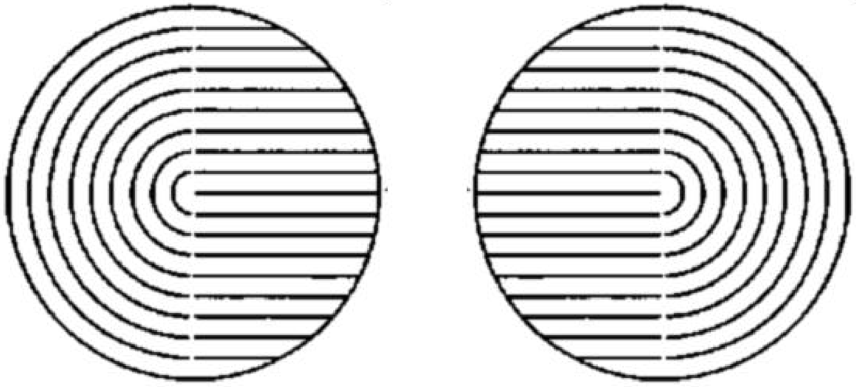


Figure 47 Stimulus of Diaz-Caneja (1928). When the two half-images are stereoscopically combined, there is seldom perception of either half image alone. Rather, perception is most often dominated by concentric circles or parallel lines.

before in different contexts. Caneja (Diaz-Caneja 1928), for example, demonstrated that when the two half-images in Figure 47 are interocularly presented perception is most often dominated by either all circles or all lines, and only rarely either monocular view. This early experiment demonstrated that high level Gestalt principles could direct perception during the dichoptic presentation of unlike images. Similar interocular grouping effects have been observed during rivalry by Whittle et al. (Whittle, Bloor et al. 1968) for contour segments belonging to the same line, as well as for (Kulikowski 1992) for colored patches. In each case, a high-level grouping principle takes precedence over eye dominance during rivalry. Likewise when the two images in Figure 9 (Frisby and Mayhew 1979) are stereoscopically combined the texture discontinuity in the bottom right corner disappears from perception, and rivalry ensues between the superimposed textures of different frequencies. The disappearance and reappearance of the low spatial frequency texture occurs uniformly across the entire image, ignoring the monocular discontinuity. A very recent study along the same lines by Kovacs et al. demonstrated that even images divided between the two eyes and then spatially filtered could be perceived in unison (Kovács, Papathomas et al. 1996) during binocular rivalry.

General Discussion

The ability to experience robust rivalry under conditions where there is little or no local interocular conflict suggests that rivalry can involve a competition between two large surfaces even when there is only minimal local competition. The fact that these surfaces can be formed even by interocular grouping argues that this surface representation is central and largely independent of monocular alliances between neighboring surface elements.

A notable result from the experiment with uniform dots is that rivalry can remain unitary for a very high fraction of time for a large field even when there is no explicit interocular conflict. Not only was the unitary dominance fraction much higher than if the individual dot elements acted independently, but, given the size of the stimulus (effective diameter > 7º) it is significantly higher than unitary rivalry between high spatial frequency grating patterns (Blake, O'Shea et al. 1992). O’Shea et al. recently reported that in rivalry between two grating patterns the fraction unitary dominance involved a trade-off between spatial frequency and stimulus size. For lower spatial frequencies, larger diameter stimuli can be seen to rival in unison. (O'Shea, Sims et al. 1996). The present results suggest that this facilitation of unitary rivalry may be the result of *minimizing* the degree to which nonmatching contours in the two eyes interact. With both sparse surfaces, as well as low spatial frequency sinusoidal gratings, there is a low degree of interocular contour conflict, and the unitary rivalry fraction is high. This observation contradicts the traditional notion that rivalry *requires* local conflict to be initiated (Hering 1864; Kaufman 1963; Levelt 1965). For the sparse surfaces, the degree of unitary rivalry fell to nearly zero for the large stimulus when the dots were spaced too closely. In this case the local interactions predominated again and neither surface easily rose to dominance.

One explanation that could account for these results is the notion that the size of a “zone of exclusive visibility” is dictated by the degree to which the early cortical areas are activated by the competing stimuli. In this sense, stimuli that are highly scrutinized by contour extracting mechanisms in the primary visual cortex, such as high spatial frequency gratings, lines, dense patterns, etc., might be more fragmented than stimuli that bypass this analysis, such as low spatial frequency gratings and sparsely defined surfaces. It is known, for example, that the unitary dominance of two competing images is significantly influenced by spatial filtering (Fahle 1982), and that unitary dominance between two stimuli is often improved when their high spatial frequency components are removed (Sheinberg and Logothetis 1997).

The temporal dynamics of the rivalry were not examined in this study beyond evaluating the mean dominance time and unitary rivalry fraction. Subjectively (to the author) the alternation dynamics appeared during the monocular grouping of dots similar to those normally associated with more traditional stimuli such as gratings. The interocularly grouped stimuli, on the other hand, had notably different dynamics, with fleeting moments of dominance that were almost always followed by an abrupt transition to the other color, and then a regression back to a mixed pattern. These dynamics could reflect the difficulty of the perceptual synthesis caused by the interocular surface presentation and warrant further investigation.

The perceptual grouping of the dots to form surfaces that compete during rivalry, whether done intra- or interocularly, suggests that the perceptual mechanisms involved in the dominance and suppression of competing patterns during rivalry may be related to fundamental mechanisms of image segmentation and grouping. In this sense, rivalry may be considered a useful tool for investigating these mechanisms. For example, by delineating the structural properties of a stimulus that allow it to engage in unitary rivalry one might learn about how these properties play a role normal perceptual organization. In the mixed dot experiment, for example, grouping processes were clearly able to override monocular alliances between neighboring stimulus elements, at least for some of the time.

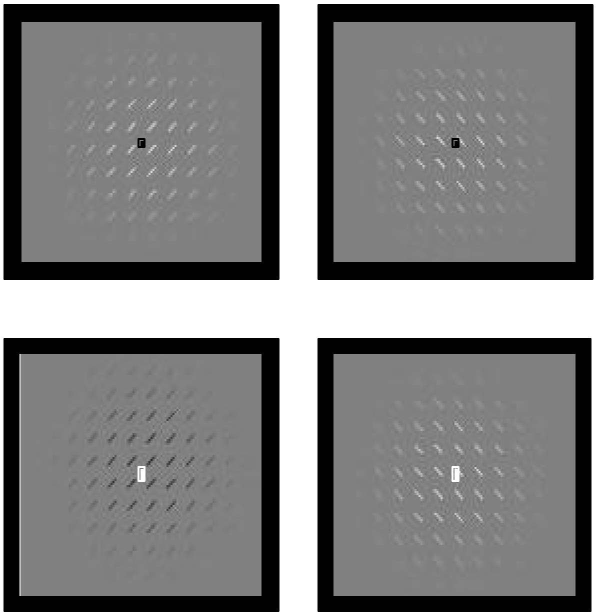


Figure 48 Line segment arrays used in Experiment 1. Each eye contained an array of similarly oriented line segments. Individual segments were 18´ (0.3º) in length and 1.2´ (0.02º) in width, and oriented 45º clockwise or counterclockwise. The MID spacing was varied from trial to trial. The entire stimulus was approximately 5 degrees on a side.

The stimuli in Figure 48 demonstrate that the grouping responsible for two complete surface representations during rivalry is considerably stronger if it is based on a first order stimulus attribute, such as luminance, rather than a higher order attribute, such as orientation. The upper panels show a rivalry pair in which line segments are similarly oriented within each eye, but are perpendicular between the two. Again, the specific interocular conflicts are minimized by spatially offsetting each of the elements between the two eyes. Note that when grouping relies on orientation, as in the top panel, the fraction of time that either stimulus is wholly dominant is very small. However, if luminance differences are added is added, as in the lower panels, unitary rivalry is resurrected. It therefore appears that perceptual rivalry is much more coherent when the elements are grouped by luminance rather than form.

Figure 49 Drawing from M.C. Escher illustrating perceptual bistability. Note that the simultaneous perceptual dominance of all white or all black figures, despite their differences in shape and texture. Taken from (Bool, Kist et al. 1992).

Interestingly, this property appears to be common among bistable percepts, and is not unique to binocular rivalry. An example of this is shown in Figure 49, which shows a drawing by M.C. Escher. In this figure, one can see spontaneous perceptual changes, where all the black figures are dominant together, and then all the white figures are dominant together. Unlike many similar drawings, however, there is no obvious way to group similarly colored elements based on their spatial structure, and this illustrates that, like rivalry between sparse surfaces, grouping in ambiguous figures also draws primarily from first order stimulus attributes, such as color (in this case black vs. white).

PERSISTENCE OF A PERCEPTUAL REPRESENTATION: RIVALRY DURING INTEROCULAR STIMULUS EXCHANGES

Introduction

In the previous section I described an experiment that demonstrated that information from the two eyes could be combined, based on simple grouping principles, into two patterns that could subsequently rival for perceptual dominance. This was taken as evidence that rivalry involves competition between central stimulus representations rather than between monocular pathways. The experiment in this chapter further investigates this possibility by testing whether normal rivalry can develop between two stimuli even if they are not continually bound to separate eyes.

The temporal conditions required to initiate rivalry are potentially revealing about its underlying mechanism. In an earlier chapter I mentioned that when dichoptic, orthogonal grating patterns are presented for less than 150 msec, rivalry does not have time to initiate and one sees an "abnormal fusion" between the two orientations--a crossed pattern. A flickering rivalry pattern can maintain such a fused appearance indefinitely when each presentation is less than 150 msec and each blanking interval is more than 150 msec (Wolfe 1983). Rivalry is, however, quite robust to many changes in the conflicting stimuli. It can, for example, be elicited between two stimuli that are never simultaneously presented. If a stimulus consists of two alternating frames, where the first has a horizontal grating in the left eye and nothing in the right, and the second has nothing in the left eye and vertical grating in the right, rivalry will ensue between the two orientations when the two frames are shown repeatedly with a frequency between 3 and 20 Hz (O'Shea and Crassini 1984). At lower flicker frequencies, perception is dominated by each of the two stimuli appearing in succession, mirroring the physical presentation—i.e. there is no persistence. A similar range of flicker values can support rivalry when two stimuli are shown simultaneously to the two eyes, as long as the on/off balance is outside the range of abnormal fusion. Normal rivalry can even persist when the frame rate dips below 1.5 Hz, or >300 msec on and off times, where individual dominance phases span several blank intervals.

Given this propensity for rivalry to “ignore” the brief disappearance of a stimulus while continuing to generate slow, smooth perceptual changes, we decided to investigate the possibility that rivalry could survive even more dramatic temporal perturbations. Specifically, we asked whether normal perceptual rivalry could ensue between two conflicting patterns even if they are continually exchanged between the two eyes several times per second. Under these conditions, if rivalry specifically involves competition between monocular channels, a given ``eye-dominance'' phase would be characterized by the periodic perception of each stimulus in succession, as it is placed into the dominant eye. If, on the other hand, if rivalry represents a more general conflict resolution scheme, one that does not depend on the eyes through which the conflicting stimuli arise, such a stimulus could result in slow, gradual alternations, just as in normal binocular rivalry.

Stimuli and Methods

Observers viewed a pair of orthogonally oriented gratings patches tilted 45º clockwise in one eye and 45º counterclockwise in the other. Gratings were 3º x 3º squares with a spatial frequency of 2.5 cycles per degree and a space average luminance of 20.4 cd/m^2. Gratings were achromatic and had a contrast of 0.25, unless otherwise stated. The background luminance was 1.5 cd/ m^2. The contrast between the grating and the background, along with a small 0.2º x 0.2º fixation point were used to aid proper convergence. Observers were seated in a dark room and viewed the stimulus display through a mirror stereoscope. The stimuli were generated by a Silicon Graphics computer (Indigo/Elan, 72 frames/second), and displayed on a 21” Sony monitor located 60 cm from the eyes of the subject. The subjects controlled the rate of testing and were instructed to take a break whenever

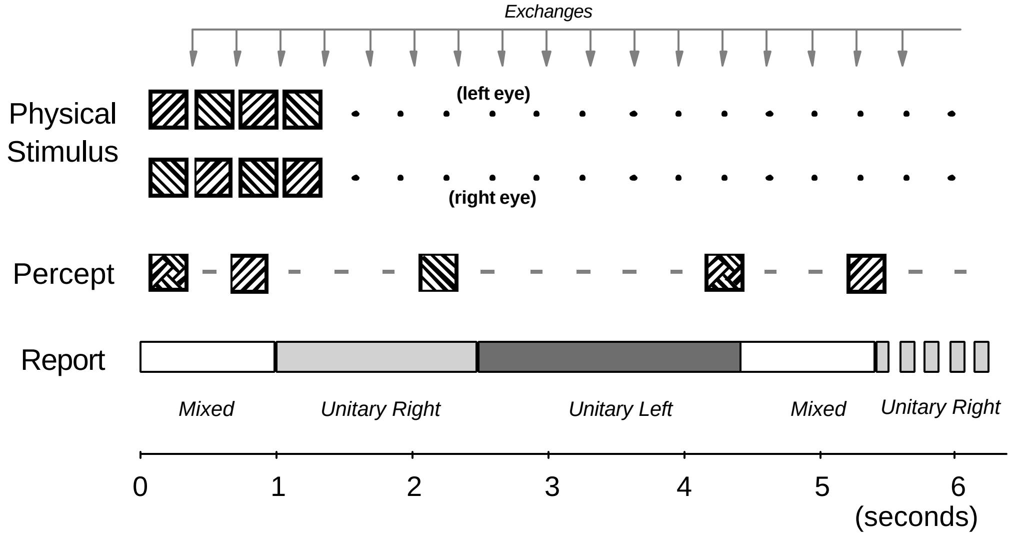


Figure 50 The stimulus consisted of a pair of orthogonally oriented gratings tilted 45 degrees from vertical, clockwise in one eye and counterclockwise in the other. Subjects viewed the stimulus under two conditions, referred to as the "switching" and "nonswitching" conditions. In the switching condition, illustrated here, the grating patterns were exchanged between the two eyes each 333 msec so that each eye's view was continually flipping between orthogonal orientations. In addition, the stimuli were flickered at a frequency of 18 Hz (not shown here). This was done to minimize the perception of transients caused by the physical stimulus exchanges. The subjects were required to report which of the two orientations was seen (or neither) as a function of time. The bottom bar represents the time course of their holding down one of two buttons indicating which of the two orientations they were perceiving. Note that their perception of a single orientation persists despite numerous physical orientation reversals of each monocular pattern. The nonreversal control conditions (not shown here) consisted of a the same stimulus except the flickering gratings remained continually bound to separate eyes.

necessary. Great care was taken in adjusting the mirrors of the stereoscope to ensure correct binocular alignment of the displays for each observer.

Figure 50 illustrates the time course for the experimental (reversal) condition. In the nonreversal control condition (not shown), the rivalrous stimuli remained bound to the two eyes throughout the duration of the 120 sec trial. In the experimental condition, the two gratings were exchanged between the eyes each 333 msec, resulting in periodic reversals in the orientation of each monocular view. In both conditions, the stimuli were continually flickered on and off with a frequency of 18 Hz (flashes of 27.7 msec that were separated by intervals of 27.7 msec). This was added to minimize the perception of any transients resulting from the physical stimulus exchanges.

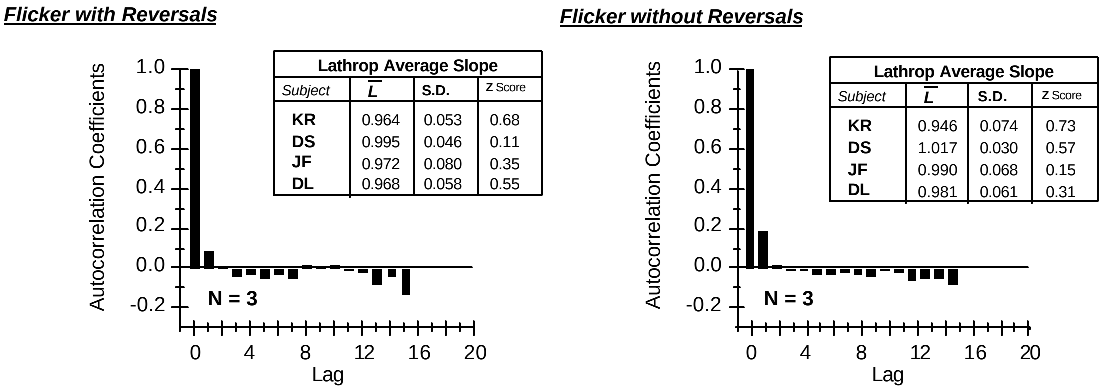
Six subjects were used in this study, ranging in age from 21 to 45. Each of the subjects had normal or corrected to normal vision, and was able to see depth in a simple random dot stereogram. Observers participated in 9 sessions of 13 trials, with each lasting 130 seconds, and three sessions devoted to each stimulus condition. A session started with a few minutes of practice trials and continued for 75-80 min, with 5-10 min rest every 20 min. The subjects reported exclusive perceptual dominance of each stimulus orientation by holding down buttons on a computer mouse. The subject was instructed to press neither button during periods of piecemeal rivalry. Data analysis was restricted to the last 120 sec of each trial.

Results

In both the reversal and nonreversal conditions, all six subjects reported normal rivalry with phases of complete dominance of a stimulus persisting for up to several seconds. The mean dominance times during the reversal and nonreversal conditions are shown for each of the subjects in Table 1. The overall mean for the reversal condition was greater than two seconds, spanning six physical exchanges of the gratings. To establish whether the perceptual rivalry experienced in the reversal trial is the same as that experienced with conventional stimuli we investigated the temporal dynamics of the perceptual alternations. Specifically we examined (1) the extent to which rivalry phases are sequentially independent by performing an autocorrelation analysis of successive durations and calculating a test for sequential dependence; (2) the distribution of alternation phases; and (3) the influence of the contrast of one stimulus on the mean dominance of the other.

Subject	*Nonreversal*	*Reversal*
DL	*2994*	*2346*
KR	*3212*	*1925*
NL	*2577*	*1954*
JF	*2324*	*2373*
DS	*2205*	*1824*
mean	*2662*	*2088*

Table 1 Mean dominance times for six subjects used in this study under the reversal and nonreversal condition, as indicated by the manual button presses.



Flicker with Reversals

Subject	$\bar{L}$	S.D.	Z Score
KR	0.964	0.053	0.68
DS	0.995	0.046	0.11
JF	0.972	0.080	0.35
DL	0.968	0.058	0.55

Flicker without Reversals

Subject	$\bar{L}$	S.D.	Z Score
KR	0.946	0.074	0.73
DS	1.017	0.030	0.57
JF	0.990	0.068	0.15
DL	0.981	0.061	0.31

Figure 51 Temporal dynamics of rivalry under different stimulus conditions. Autocorrelation coefficients for sequences of rivalry phases, averaged for three different subjects for reversal experiment left and nonreversal (control) experiment right.

The product-moment correlation coefficients that were calculated for the durations of dominance and suppression through lag 15 are shown in Figure 51. Data from three subjects are shown for rivalry recorded in non-reversal and reversal trials. Note that, even for the shortest lag, the durations of rivalry are stochastically independent in both experiments, just as reported for conventional rivalry. Absence of sequential dependence was also shown using the Lathrop statistic L (Lathrop 1966), a measure of the mean absolute slope of successive durations for each subject, shown in Table 1 with their respective Z-scores. The value of L is given by the formula:

$$L_j = \sqrt{\frac{\sum_{i=1}^{n-1} \left| x_{(i+1)j} - x_{ij} \right|}{(N-1)s}}$$

where Lj equals the value of the statistic for the jth sequence (here all phases recorded from a subject); xij, x(i+1)j are successive responses in the jth sequence; and σ equals the standard deviation of the phases within the jth sequence. The theoretical Lj value distribution has a mean L = 1.0 and a $sL = \frac{1}{2}\sqrt{N}$. A correlation between successive phases yields Lj values that are lower, and an anticorrelation yields Lj values that are greater

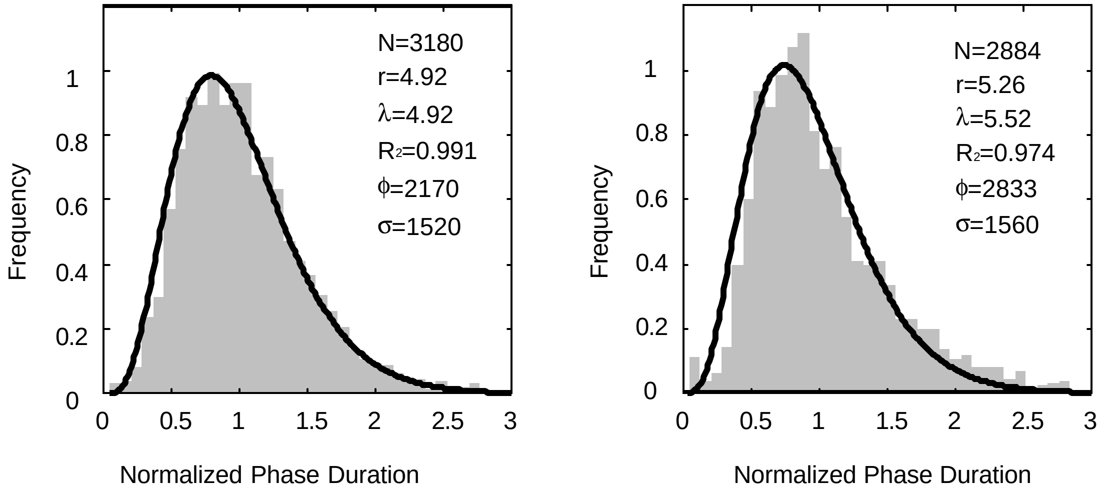


Figure 52 Distribution of dominance durations in rivalry in the reversal (left) and nonreversal (right) conditions. The frequency histograms show the relative phase durations, that is, phase durations expressed as a fraction of their mean. The smooth, thick, black lines illustrate the approximation of the histogram with a gamma distribution function. The parameters of the theoretical distribution describing the data obtained during either condition are very similar. Each distribution represents the mean of three subjects. N denotes the number of phases from all subjects; R^2 is the coefficient of determination, that is, the square of the correlation coefficient between the experimental data and the corresponding gamma function (R^2 equals the ratio of the explained sum of squares of the frequency variable to the total sum of squares of this variable); ϕ denotes the mean phase duration in msec across all subjects; and σ the standard deviation of the phases.

than 1.0. Note that none of the obtained values in either of the paradigms differs significantly (Z-Scores) from the expected value of mean L (1.0 for random sequences).

The distribution of relative phase durations (durations expressed as a function of their mean) during standard binocular rivalry is typically approximated by a gamma density function, the parameters of which show consistent intersubject similarity (Fox and Herrmann 1967; Levelt 1967; Walker 1975). The distribution of relative phases for the non-reversal and reversal conditions are shown in Figure 52. In agreement with previous studies both distributions were found to be unimodal, asymmetric with a fast growth and long tail, and both were approximated well with gamma distributions with very similar parameters (thick black lines).

Finally, the effects of the strength of one stimulus on the mean dominance and suppression of each stimulus were examined. Levelt (1965) showed that the strength of a stimulus in

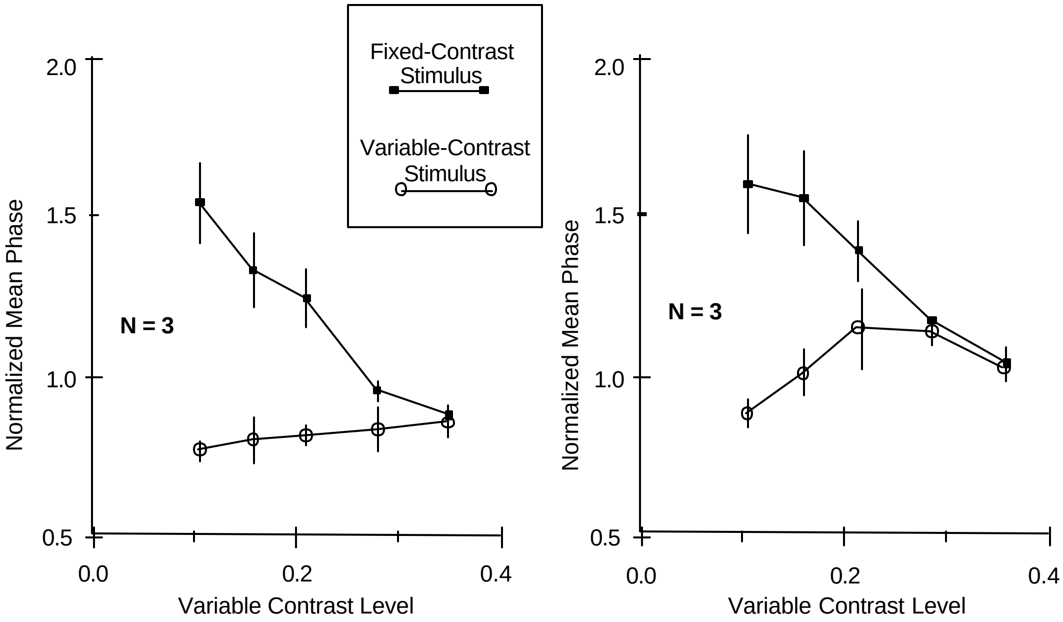


Figure 53 Effect of variation of interstimulus contrast differences on the mean dominance phase. Fixed contrast was set to 0.35. On the abscissa is plotted the varied contrast of one stimulus, when the stimulus is constantly switched between the eyes (left) or remains continually in the same eye (right). The ordinate shows the normalized mean dominance duration of the stimulus whose contrast is varied systematically (diamonds), and of the stimulus that has a fixed contrast (squares). Data area averaged from three subjects. The bars show the standard error of the mean. Note that, in both conditions, decreasing the strength (here contrast) of one stimulus primarily results in a monotonic increase in the mean dominance time of the fixed-contrast stimulus.

one eye primarily influences the dominance of the stimulus in the other. This has been shown to be true for many types of rivalry in both humans and monkeys (Levelt 1966; Fox and Herrmann 1967; Blake 1977; Leopold and Logothetis 1995; Logothetis and Leopold 1995; Sheinberg and Logothetis 1997). A similar pattern for both the reversal and nonreversal trials is shown in Figure 53. Note that in the reversal trials the contrast of one orientation primarily affects the mean dominance time of the other orientation, even though each eye sequentially sees both the fixed- and variable-contrast stimuli. Hence it is the strength of the competing *stimuli,* independent of the strength presented to either eye, that governs the effect.

As a final test, we investigated whether further distinguishing the competing stimuli by the addition of a second attribute would enhance the periods of exclusive visibility. To this

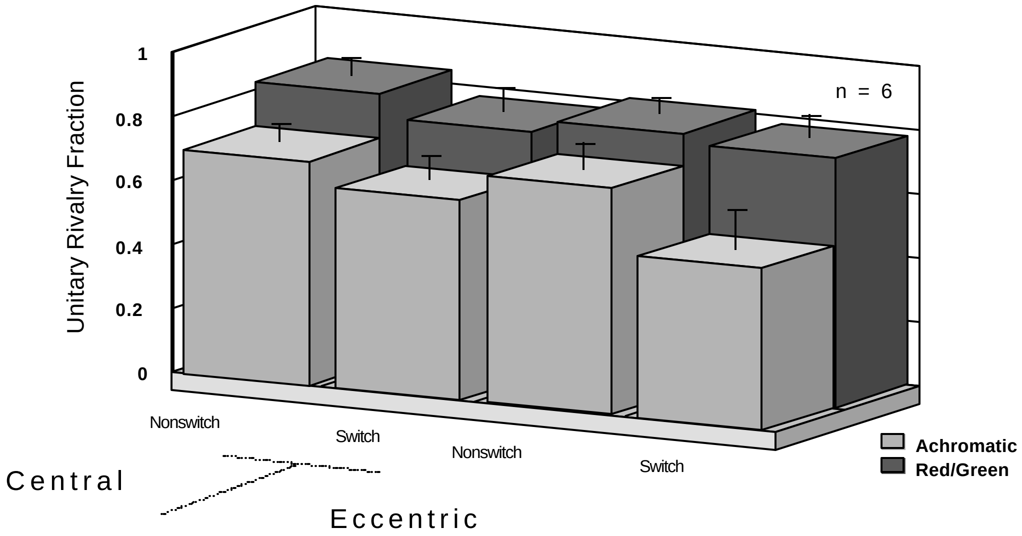


Figure 54 Effects of eccentricity and the addition of color to the quality of rivalry during the reversal and nonreversal paradigms. The front row of bars represent the achromatic gratings that were used in this study and the back row. The unitary rivalry fraction, or fraction of time that either of the orientations was completely dominant, is shown for the reversal (switch) condition and nonreversal (nonswitch) conditions for both central and eccentric (?? Degrees) presentation. The back row of bars corresponds to the same conditions when one of the orientations was given a slight greenish tint and the other a slight reddish tint.

end, a greenish hue was added to the leftward grating and a reddish hue to the rightward grating. Six subjects reported their unitary perception of either grating in the switch and nonswitch conditions for both foveal and eccentric presentations, and the unitary dominance is plotted in Figure 54. Note that in all cases the addition of different colors to the two gratings aids in the perception of unitary rivalry.

Discussion

Conflicting stimuli can rival for perceptual dominance despite being completely dissociated from the two eyes. Were rivalry based on eye competition, a given dominance phase would be equivalent to the closure of one eye, and one would perceive each of the conflicting stimuli in rapid succession. This can be easily demonstrated by closing one eye during any of the above experiments. However, since these physical changes of the monocular view are rarely if ever visible, and the perceptual alternations are instead slow and stochastic, we conclude that rivalry is a central process, where binocular representations compete for dominance well beyond the site of binocular convergence.

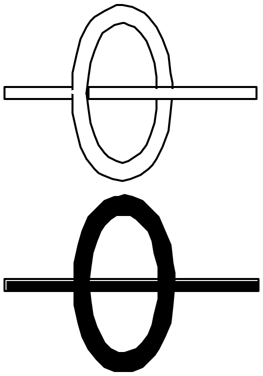


Figure 55 Satiation stimulus of Carlson (1953). Staring at the top stimulus for several seconds influences the subsequent perception of the bottom one, which is ambiguous.

The main result reported here at first seems to contradict a previous result reported by Blake, Westendorf et al. (1980), in which they present rivaling stimuli, wait until one of the stimuli is wholly perceived, and then switch the stimuli between the eyes a single time. In their study, the newly perceived stimulus is always that which was previously suppressed, which they attribute to its being rerouted into the currently dominant eye. This is taken as evidence that it is the eye itself that is dominant during rivalry. Our results do not fit this model of rivalry, and offer an alternative explanation to these previous results. Specifically, we suggest that if rivalry dominance is allowed to fully develop, as in the case of Blake et al., any perturbation in the system, such as exchanging the stimuli, which requires the reinitiation of rivalry is likely to favor the representation that was previously suppressed. This viewpoint is also consistent with the reversal of ocular dominance observed by Wolfe (Wolfe 1984), who found that when a monocular stimulus was viewed for several seconds, a nonmatching stimulus added to the other eye was immediately perceived during rivalry. Informal observations from our laboratory demonstrate that this preview need not be monocular to generate a reversal of dominance during subsequent rivalry, but dioptic stimuli worked nearly as well. We suggest then that this effect is mediated, not by reversal of ocular dominance, but rather by the *satiation* of stimulus features, akin to that observed in other, monocular stimuli (see, for example, Figure 55, taken from Carlson (1953)).

With the present stimulus one does not observe a reversal in dominance when the stimuli are exchanged, but smooth changes that are not synchronized to the physical reversals. This is likely to be a result of the relatively short exchange interval chosen (333 msec). It is known that suppression is not immediate, but requires time to initiate. Several studies have shown that this time is around 300 msec, similar to the exchange interval used in the present study (Wolfe 1983; O'Shea and Crassini 1984). This suggests that dichoptic rivalry never has the opportunity to fully develop in register with the early cortical areas, and is therefore continually *in limbo*. It is perhaps because of this instability that the two competing stimuli can freely alternate in perception, which cannot find a foothold in the activity within the early areas. It is interesting to note that the temporal requirements for stereopsis to occur between successive monocular stimuli is also roughly 300 msec (Dodwell and Engel 1963; Engel 1970).

The statistics of the temporal dynamics in the reversal condition are identical to those of standard dichoptic rivalry and are similarly influenced by changing the strength of one of the stimuli. In standard dichoptic rivalry, the strength of one eye’s stimulus primarily influences the mean dominance time of the stimulus in the other eye. This has classically been exemplified by manipulating the interocular contrast differences, as in the nonreversal condition here, and has been used to argue in favor of an eye-competition mechanism (Fox and Rasche 1969; Blake 1989; Mueller and Blake 1989). However, in the reversal paradigm the identical pattern was obtained for contrast differences between the stimuli, even though each eye successively viewed both contrast values. Once again, these results together provide strong evidence that the mechanisms responsible for normal binocular rivalry involve competition between central representations of a stimulus, rather than between monocular channels.

When unique colors were associated with conflicting stimuli the quality of the unitary rivalry was significantly enhanced, which agrees with the hypothesis put forth in the previous chapter that first order stimulus attributes such as color are less likely to be disrupted by early cortical processing than second order features such as oriented line elements, and can therefore *guide* the perceptual system in constructing a global representation. When one of the grating orientations is tagged with a red hue and the other with a green hue, subsequent rivalry is considerably more unitary. In this case, the associated color may even serve to “reunite” pieces of the individual rivaling stimuli after they have been fragmented by early cortical processing, as suggested previously. When conflicting natural image pairs were examined under the switch paradigm, various degrees of success were exhibited. One factor that impeded their ability to form effective rivalry pairs was apparent motion correspondence between sequentially presented images. For example, if one image has a prominent feature in the lower left and the second in the upper right, successively swapping the stimuli will often produce the illusion of motion between the two tokens. This leads to another possible interpretation of the increased effectiveness of rivalry with the red and green stimuli. Specifically, in the ``reversal'' trials with the achromatic stimuli perception can in principle be the oscillatory apparent rotation-motion of a single grating, which is a third possible stimulus interpretation. The addition of an orientation-specific color may eliminate any perception of apparent motion, and this explain the enhancement in stability of each single orientation.

The reversal interval was a critical variable in determining the efficacy of rivalry. For high reversals there was perceptual fusion of the competing patterns. For low reversals there was a high correlation of the perceptual transitions with the physical stimulus exchanges, as observed by Blake et al. (Blake, Westendorf et al. 1980). Most subjects had optimal rivalry for intervals between 222 and 444 with a peak at 333 msec. The experimental system, in its limited temporal resolution, did not allow more precision with these variables. The temporal dynamics of the stimulus exchanges, such as the interval, regularity, abruptness, etc., are potentially revealing about not only binocular rivalry, but about the time course of perception in general, and are currently under investigation by our laboratory.

THE EFFECT OF MINIMIZING ATTENTION DIRECTED TOWARD BINOCULAR RIVALRY

Introduction

As alluded to in the second chapter, one of the first explanations of the rivalry phenomenon was put forth by Helmholtz, (Helmholtz 1925) who felt that shifts in attention were responsible for the perceptual alternations during binocular rivalry. According to him, not only did attention dictate rivalry, but *volitional* attention could be used to control it. He claimed, for example, that the perceptual alternations could be stopped by ``mere mental means''. Since the time of Helmholtz it has become clear that conscious control over rivalry does not allow the subject to decide which rivaling stimulus he sees at each point in time, nor does it affect the depth of rivalry suppression (Lack 1973). Volitional attention can, however, be used to affect the time course of the alternation process, primarily by increasing or decreasing the rate of alternation, yet the limits of this conscious control are limited (Meredith and Meredith 1962; Lack 1978).

In addition, we have seen in previous chapters that rivalry has peculiar dynamics, in which the phase durations of perceptual dominance and suppression form a characteristic distribution, and the balance between the two stimuli can be manipulated by changing basic attributes of the competing stimuli. We were interested in clarifying the role of attention in rivalry by asking whether these characteristic dynamics are a reflection of the rivalry alternation mechanism itself, or if they are a consequence of the attention and/or decision making process involved in reporting rivalry. To the knowledge of the author, all previous psychophysical experiments investigating the dynamics of binocular rivalry have been under conditions where the subject was actively reporting his or her perceived stimulus. Hence it has been impossible to disambiguate contributions of the perceptual rivalry mechanism from those of attention and decision making. In order to circumvent this problem we have exploited the well known coincidence between the direction of the slow phase of optokinetic nystagmus (OKN) and the perceived direction of motion during stimulation with patterns drifting in opposite directions in each eye. Specifically, during binocular rivalry, as opposite moving rivalrous stimuli alternate in their visibility, the OKN changes according to the perceived direction of motion (Enoksson 1963; Enoksson 1968). Hence, by analyzing the eye movement trace of a subject undergoing motion rivalry, it is possible to extract the phases during which each of the rivaling stimuli is perceptually dominant, thus providing an *objective indicator* of the subject's perception.

Given that attention is known to influence the rate of the perceptual alternations experienced during binocular rivalry, might it also affect the stochastic nature of rivalry and the perceptual balance resulting from stimulus manipulations? Would relative dominance phases show their usual gamma-like distribution if neither of the rivaling stimuli is actively attended by the subject? These questions could provide important information not only in the psychophysical study of rivalry, but also in designing paradigms for physiological experiments. If OKN can be used as an objective indicator of rivalry even under conditions where the attentional state of an animal is ill-defined, as in a simple fixation task, much time could be saved in training animals to report their perceived changes during rivalry.

In these experiments, the alternation process is examined in human subjects using OKN as subjects concentrate their attention on concomitant tasks, thus directing it away from the rivalry itself. Phases of dominance and suppression are extracted from the eye trace, rather than reported by the subject. First, in a pilot study, the reliability of the extraction process is assessed by comparing individual *extracted* dominance phases with *reported* dominance phases. Then, in the actual experiments, the phase statistics based on the eye trace are compared under different attentional conditions, while the subjects performed one of two difficult concurrent tasks.

Stimuli and Methods

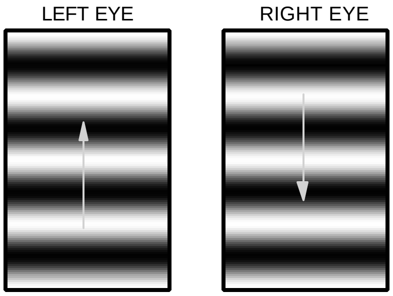


Figure 56 Rivalry motion stimulus used to generate OKN in these experiments. Sinusoidally modulated grating patterns drifted upward in the left eye and downward in the right. For all experiments, the gratings had a spatial frequency of 0.5 deg^{-1}, a contrast of 33%, and a speed of 8.0 deg/sec.

All experiments were conducted in a dark, designated human psychophysics room. Subjects were seated and viewed a computer screen from 68.6 cm through a mirror stereoscope, with their head placed on a chin rest. The visual stimuli were generated by means of a PC-based graphics card (Number Nine Computer, SGT board), and displayed on a Hitachi 20s color monitor (P22 phosphors), with Red (x=0.625, y=0.349, Y=66.3 cd/m^2), Green (x=0.281, y=0.609, Y=220 cd/m^2), Blue (x=0.142, y=0.061, Y=29.4 cd/m^2) chromaticity coordinates, and white balanced at 9370K. The display system was hosted by a 386 PC computer (Missing Byte), which controlled the timing of the stimulus presentation and the data collection through a real-time clock (DT2819 Data Translation, Inc.) and a analog/digital interface (DT2811 Data Translation, Inc.)

Subjects viewed the monitor through a mirror stereoscope, where the two fields of view were separated by a black septum. The stimulus consisted of sinusoidal , rectangular (6.1° x 10.5°) drifting gratings, bordered by a white frame, 0.26° in width. The stimuli were optimized in terms of their spatial and temporal frequencies as well as their contrasts to generate both effective rivalry and consistent OKN. After initial testing with different combinations of these parameters, both subjects settled on a contrast of 0.33, a spatial frequency of 0.5 cycles/deg, and a temporal frequency of 4.0 cycles/sec, resulting in a grating speed of 8.0 deg/sec. These parameters yielded primarily unitary rivalry and drove the OKN well. In general, the contrast of the gratings in the two eyes was fixed at 0.33. During the variable contrast experiments the contrast of one of the gratings was always

0.33, while the contrast of the other was varied between 0.23 and 0.33. On half the trials the variable grating was shown to the right eye and on the other half to the left. During nonrivalry trials, the gratings in the two eyes were perfectly fused, drifting in the same direction. At random intervals between 1 and 8 seconds, the direction of motion of the fused gratings would reverse. During the rivalry trials, the gratings moved in opposite directions in the two eyes, with the left eye's grating moving upward and the right eye's grating moving downward.

Two subjects (JF and EH, females aged 22 and 26 yr, respectively) participated in these experiments, each of whom had normal or corrected-to-normal vision and could pass a basic stereo vision test. The use of subjects was approved by the Baylor Affiliates Review Board for Human Subject Research. Vertical eye displacement was measured using an electrooculogram (EOG-5, Micromedical Technologies, Inc.). A pair of differential electrodes (ARBO H59P Ag/AgCl Disposable Monitoring Electrodes) were placed above and below the subject's right eye, with a ground on the forehead. The EOG device was preprogrammed to amplify the differential signal by a factor of 10,000. The signal was AC coupled with a 10 second time constant and low pass filtered with a cutoff frequency of 40 Hz. The analog eye position output was recorded on the computer via the analog-to-digital board, and samples were collected every three milliseconds in response to an output pulse from the real-time clock. Trains of eye position values were recorded in a buffer and dumped to the disk at the end of each observation period. Rough calibration was done at the beginning of each session; however, since the primary concern was only the polarity of the OKN, the calibration was only approximate. The quality and amplitude of the OKN was assessed at the beginning of each session using the nonrivalrous test stimulus.

During the pilot sessions, each of the subjects was tested with nonrivalrous gratings. The gratings reversed their directions every few seconds, and the subjects reported the perceived direction by pressing one of two buttons. These sessions served two functions: to accustom

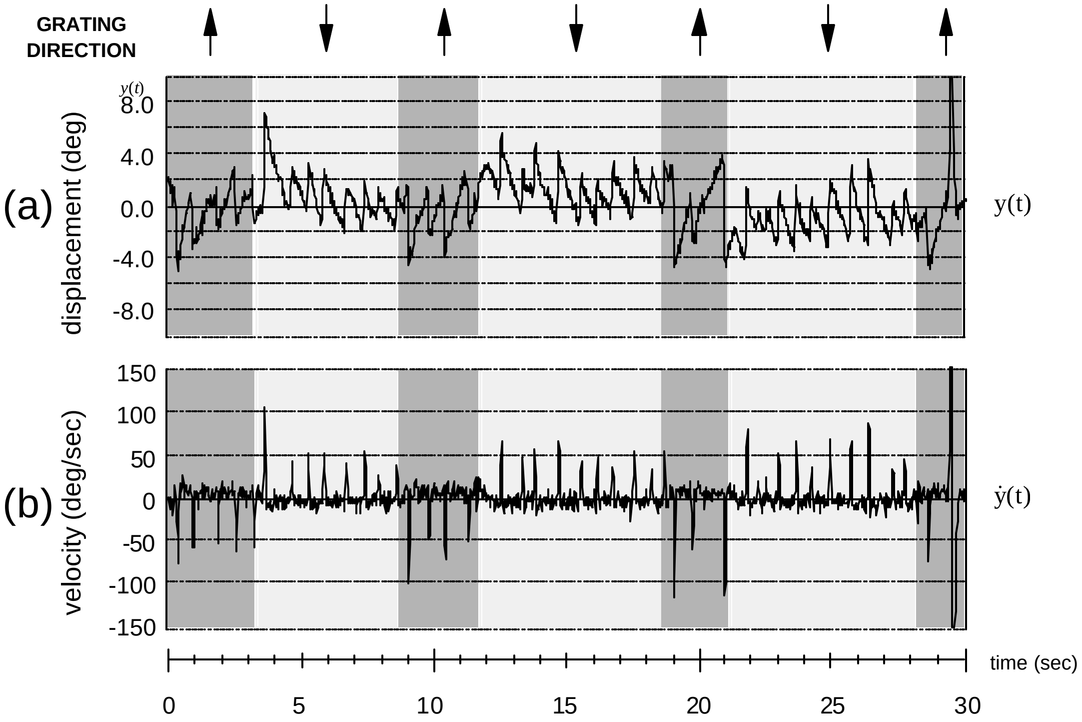


Figure 57 Optokinetic nystagmus (OKN) of a subject during nonrivalrous trials, as measured by an electrooculogram (EOG). Throughout the observation period, the grating stimulus is always congruent, moving in the same direction in each eye. This direction was reversed for both eyes at random intervals between 1 and 8 seconds. The light gray regions correspond to periods in which the gratings were moving downward, and the dark gray regions periods of upward motion. The polarity of the OKN reflects the motion of the grating in each of the phases. (a) Vertical eye displacement $y(t)$. As the gratings drift upward, the eyes follow the upward motion gradually (slow phase of OKN) , and then periodically saccades back to the original position (fast phase). The direction of the slow phase indicates the direction of the drifting gratings. The large, upward deflection at the end of the observation period is the result of a blink. During full analysis of the EOG trace blinks were automatically spliced out of the traces by a computer using an algorithm that identified blinks on the basis of peak displacement, biphasic velocity, and duration. (b). Vertical eye velocity $\dot{y}(t)$. Differentiation of the displacement signal further emphasized the difference between the upward and downward OKN. The downward velocity spikes correspond to downward saccades, identifying regions of upward grating drift, and vice versa.

the subjects to the testing procedure, and to generate an unambiguous control correlating the polarity of the OKN with the direction of motion of the stimulus.

During the actual experiments, the gratings were rivalrous, moving upward in one eye and downward in the other, where the eye-direction assignments were randomized. Each observation period began with a tone, followed by the rivalrous stimuli appearing in the center of the screen. Subjects were instructed to maintain their gaze in the central region of the rectangular grating throughout the 30-60 second observation period. Each subject generated strong OKN under these conditions, and the EOG trace was measured and collected as the subject performed the assigned task. For each of the experiments described below, subjects were tested with both the fixed- and variable-contrast paradigms. Both subjects were fully tested for the attended condition and yielded similar results. Only JF was fully tested for the unattended conditions, and it is her data that appears below.

In Experiment 1 subjects actively reported the perceived direction of the stimulus, indicating their choices by pressing one of two buttons in on a box in front of them. Neither button was pressed during ambiguous or mixed periods. This data was collected in order to reaffirm that OKN polarity reflects perception during rivalry, as well as to generate OKN

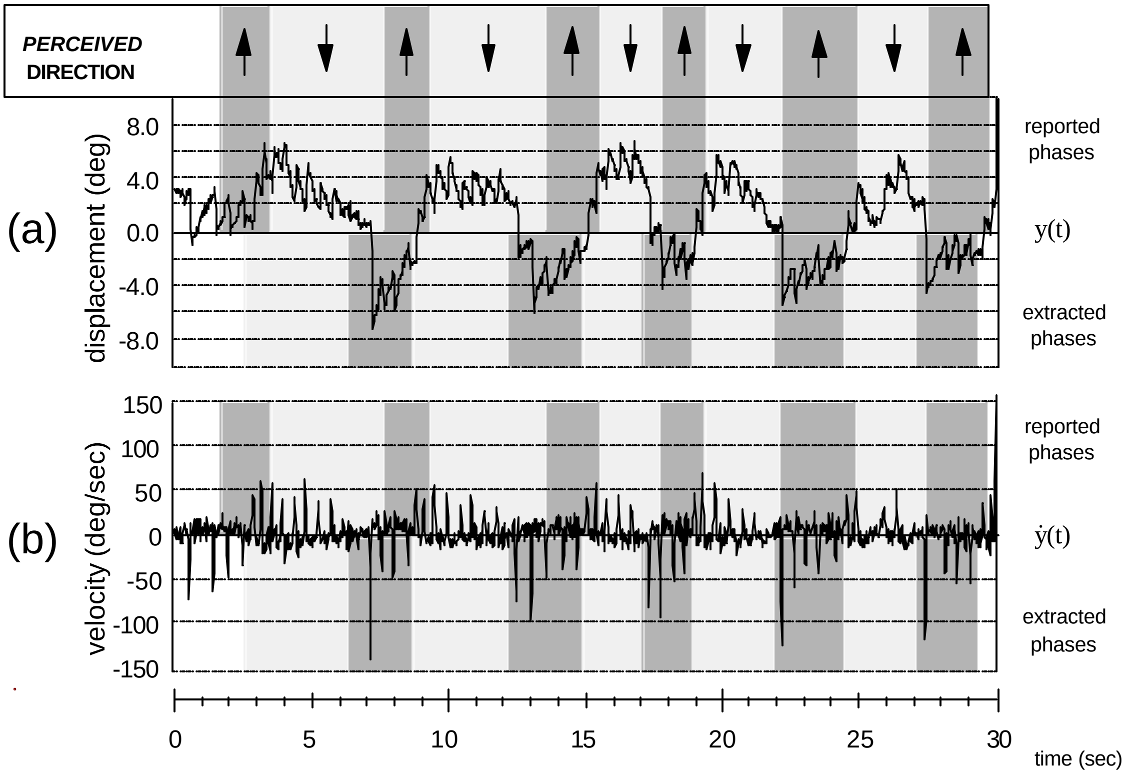


Figure 58 Optokinetic nystagmus (OKN) of a subject during binocular motion rivalry. The subject viewed stereoscopically presented dichoptic gratings, moving upward in one eye and downward in the other. The polarity of the OKN reflected the subject's *perceived* direction of motion. The shading in the upper half of each figure represents phases in which the subject reported perceiving upward (dark gray) or downward (light gray) motion. The shading in the lower half corresponds to the upward and downward OPN phases, as extracted by one of the analysts. (a) Vertical eye displacement $y(t)$. Note that the slow phase of the OKN follows the perceived direction of motion during binocular rivalry. (b) Vertical eye velocity $\dot{y}(t)$. The velocity trace facilitates parcelation of the signal into distinct phases. Note that the OKN phases reliably match the subject's perceptual phases.

data in the normal, attended condition that could be later compared with similar data during the attention task.

In Experiment 2 subjects continued to gaze toward the central region of the rivalrous moving gratings as their eye position was monitored. However, in this case, they were required to complete a difficult auditory counting task during rivalry. During each observation period, a series of low, medium, and high pitched tones were played (see Figure 59). Each tone was 150 msec in duration, and the interval between tones was 600 msec ± 50%. Subjects listened carefully to the auditory stimulus, counting the tones of a specified pitch, while gazing blankly at the rivalry pattern. After the tenth tone of a specified pitch, subjects were required to press a button, the failure of which would count the observation period as being incorrect and exclude it from analysis. This task demanded considerable concentration, and each subject required approximately 30 minutes of practice in order to perform the task with greater than 90% accuracy.

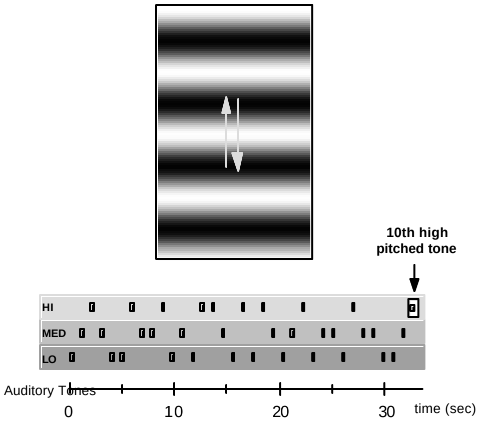


Figure 59 Counting Task. Subjects were required to concentrate on a sequence of auditory tones played by the computer while gazing at the central rivalry stimulus, which was identical to that in Experiment 1. Low. Medium and high pitched tones lasting 150 msec were played at intervals randomized between 300 and 900 msec. The subject was instructed to press a button after the tenth tone of one of three pitches specified beforehand. As the subjects performed the psychophysical task their OKN was continually recorded.

In Experiment 3 a concurrent visual task was performed as the subject gazed at the moving rivalry stimulus. In this case, the concomitant task involved attending to a series of short, binocular presentations of stimuli in the region of the screen surrounding the central grating. Stimuli were small red or yellow filled circles (diameter 0.44 deg) placed in a rectangular array around the surrounding frame. Dots ranged in distance from 4.4 degrees to 8.5 degrees from the center of the rivalry grating (see Figure 60). Approximately every three seconds, this stimulus was flashed for a presentation time of 125 msec, and the subject reported whether or not the color of one of the stimuli was different from all the rest by pressing one of two buttons. Half the time there was an odd-colored stimulus, and half the time it was absent. When present, its was randomized with each presentation. This ``multiple'' task required constant visual attention from the subject, who again required numerous practice observation periods to reach 90% reliability

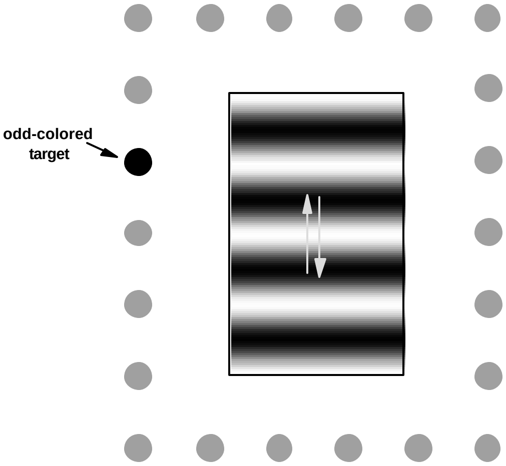


Figure 60 Multiple pop-out task. Peripheral “pop-out” stimulus consisted of brief presentation of small red or yellow filled circles surrounding the central rivalrous gratings. After each presentation , subjects were required to report whether all stimuli flashed in the periphery were of the same color, or if one was colored differently from the rest. Again, the OKN of the subjects was recorded during all observation periods.

Eye position information was sampled and saved every three milliseconds from the digital output of the analog-to-digital board connected to the EOG. Figure 57 illustrates the eye movements during a typical observation period of nonrivalrous, dioptic stimulation. In addition to the 40Hz cutoff frequency of the EOG device, the signals were convolved with a gaussian kernel with a standard deviation of 25 msec. In the resulting displacement signal $y(t)$ the slow and fast phases of OKN are easy to distinguish, as are changes in the polarity of the signal (fast up, slow down, and vice-versa). Nonetheless, to facilitate the identification of distinct phases of upward and downward OKN, the time derivative $\dot{y}(t)$ was calculated from the filtered signal to yield a continuous representation of the eye's vertical velocity (lower trace). Peaks in this trace represent saccades, where upward peaks are upward saccades, and downward peaks are downward saccades. Because the slow phase of nystagmus follows the perceived motion, periods containing upward saccades represent epochs of perceived downward motion, and those containing downward velocity peaks represent periods of upward perceived motion.

In order to extract phases from the OKN signal, two experimenters (DL and JF) independently analyzed the OKN phases generated during each individual observation period in the study. Each analyst extracted the phases of clear upward and downward OKN from every observation period trace. Decisions about current OKN phase were based primarily on the velocity trace (see Figure 52), where a series of peaks (saccades) in the same direction constituted a discrete phase. The filtered raw trace was also available on the screen as a second reference, and sometimes resolved phase transitions that the velocity trace alone could not. The extraction process consisted of systematically scanning through each observation period on the screen, and manually demarcating (using buttons of a mouse) periods of upward and downward dominance, as well as ambiguous periods, where there was no clear indication of the perceived direction. Ambiguous phases could represent either perceptually ambiguous periods, periods where the signal clarity was diminished, or a period where the OKN had stopped for other reasons.

Strict criteria were followed in analyzing the data, and only clear transitions were marked. Although there was a subjective element in the exact placement of each transition line, the uncertainty was generally less than 500 msec. Periods marked ``ambiguous'', comprising between 22% and 49% of the total testing time, were eliminated entirely from subsequent analysis. In all cases, the first analyzed phase started from the first transition, rather than from the beginning of the observation period. In addition, phases truncated by the end of the observation period were not included in the analysis. An exception to this rule occurred when phases exceeded 10 seconds before the observation period ended, which was sometimes the case during the interocular contrast experiments. Elimination of these long phases would result in a systematic and often severe underestimation of the mean phase of the lingering stimulus. To compensate for this possibility, stimuli that remained dominant for longer than 10 seconds before the end of the observation period are included in the analysis.

Results

Experiment 1: Attended Rivalry

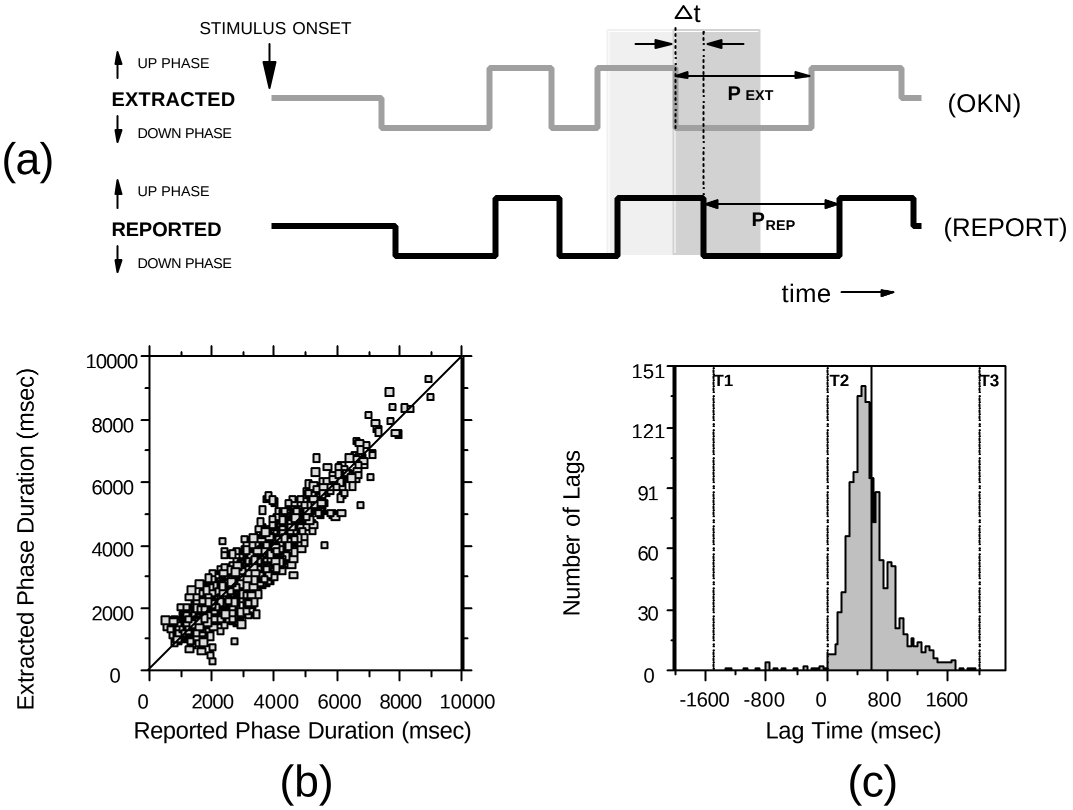


Figure 61 Comparison of reported and extracted dominance phase data. (a) For the observation periods during which the subjects reported their perceived direction of motion, there were two means of evaluation dominance phases. The gray lines represent phases of upward and downward perceptual dominance determined from the OKN (i.e. P_{EXT}). The black lines correspond to the subjective report of upward and downward motion derived from the subjec2w button press (P_{REP}). The lag L between the two traces corresponds to the subjects manual reaction time to the perceived change. In all cases, greater than 90% of extracted phases could be paired with a corresponding reported phase. All unmatched phases were discarded. (b) Extracted vs. reported phase durations. In all cases, the correlation coefficient R was at least 0.95 (c) Distribution of lag times between the extracted and reported transitions. Negative values indicate that the reported transition occurred before the extracted transitions, and positive values that the extracted transitions occurred first. Line T1 and T3 correspond to the maximum positive and negative delays allowed for a reported transition to match with an extracted transition. Note that the entire distribution falls well within these limits. The line marked T2 marks instances where the reported transition occurs simultaneously with the extracted transition.

Analyst	N	R	L	%
JCF	1558	0.95	552	95.1
DAL	1426	0.95	575	90.7

Table 2: Comparison between extracted and reported transitions: number of phases (N), correlation coefficient ®, mean lag (L), and percentage of matched phases (%) for each of the two analysts.

The motivation for the attended experiment was to assess the reliability with which rivalry phases could be extracted from the eye movements alone. A high correlation between the polarity of the OKN signal and the perceived direction of motion has previously been established in both humans (Fox, Todd et al. 1975) and monkeys (Logothetis and Schall 1990). A similar approach to the former study was used here, where individual phases of upward and downward OKN extracted from the EOG traces were compared with the subjective report of upward and downward perceptual dominance during the same observation period. At no time did the analysts consult the button responses of the subject to aid in determining phase transitions. Each extracted phase was compared to the subject's reported direction of motion at that time. Figure 61a illustrates a comparison between pairs of extracted and reported phases during the same observation period. For a given reported phase to "match" an extracted phase, the following criteria were required to hold. First, the direction of the OKN had to match the subject's reported direction of motion. Second, the reported transition had to occur no later than 2000 msec after the transition in the extracted trace. This corresponds to the darkly shaded region. Finally, a reported transition was not permitted to occur more than 1500 msec before a matching extracted transition (the lightly shaded region). These constraints were intentionally "loose" so that the method of analysis would not artificially constrain the maximum extent of the calculated latencies between the OKN and the subjective report. Using these criteria, it was possible to clearly match >90 % of all extracted phases with corresponding reported phases Table 2.

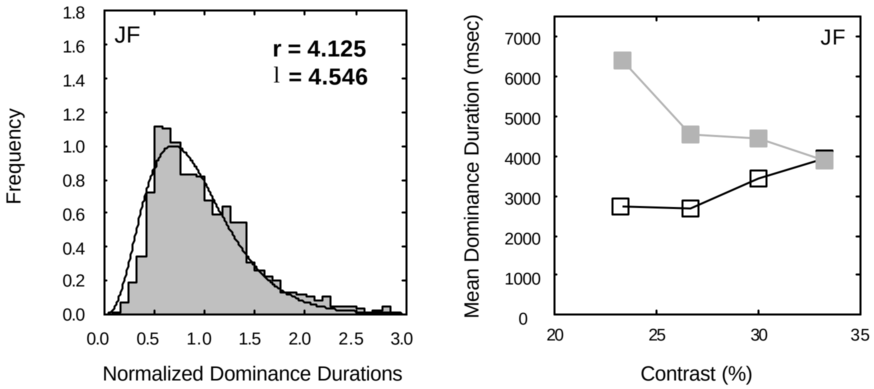


Figure 62 Rivalry phase statistics during experiment 1, the attended condition. Table 2 lists distribution parameters for two independent analysis. (a) Distribution of phase times. Each phase time is expressed as a fraction of the mean for the distribution . A gamma function is fit to the bin values of the frequency histogram, and the values of the parameters r and l closely resemble values previously reported din the literature for rivalry between a variety of stimuli. (b) Effect of interocular contrast upon the mean dominance time for each grating. The contrast of the grating in one of the eyes was fixed, while the contrast in the other eye's grating was varied Lowering the contrast of one of the grating had relatively little effect on the mean dominance time of that grating (black line with open squares). However, the mean dominance time of the fixed grating was significantly increased with the lower contrasts (gray line with filled squares).

Figure 61b shows the correlation between all matched extracted and reported phase durations for one subject (N = 1558). The strong correlation between the two measures demonstrates a high degree of reliability in the method, with a correlation coefficient of 0.95 for each analyst. Figure 61c further illustrates the reliability of the extracted phases by plotting a histogram of the *lags* between the extracted OKN transitions and the reported phase changes. In this figure, negative values indicate that the reported transition preceded the extracted transition, and positive values that the reported transition followed the extracted transition. This distribution is composed nearly entirely of positive lags, where the

Analyst	t	%t	r	λ	N	R^2
JCF	2998	78	4.13	4.55	1639	0.973
DAL	2889	72	3.81	4.13	1572	0.970

Table 3 Attended condition. Mean dominance time (t), percent unambiguous OKN signal (%t), gamma parameters (r and λ), total number of dominance phases (N), and R^2 is the coefficient of determination for the fit of the gamma function to phase distribution data

button was pressed after the change in OKN, with a mean of 550-575 msec. This resembles a standard reaction time distribution, suggesting that the initiation of the OKN transition roughly reflects the time of the perceptual transition. Table 2 summarizes the reliability of the extraction process during rivalry for two independent analysts, including the total number of phases extracted (N), the correlation coefficient (R), the median of the reaction time distribution (L) in milliseconds, as well as the percentage of reported phases that matched an extracted phase.

Tests of the temporal dynamics of based on the extracted phases in Experiment 1 are shown in Figure 62. This was the control condition and, given the high correlation between the extracted and reported phases, it was not surprising that the statistics matched very well those reported for standard rivalry in numerous previous experiments. The left panel shows the distribution of phases and, as can be seen in Table 3, the gamma function fits the distribution very well ($R^2 > 0.97$) and the parameters of the gamma function, r and λ, are in agreement with values reported in previous studies of binocular rivalry. The right panel shows the results of altering the contrast of one of the gratings from trial to trial while keeping the other fixed. In each observation period, the contrast of one of the rivaling gratings was fixed at 0.33, while the contrast of the second grating was varied between 0.23 and 0.33. The curves represent the mean time that the stimulus in each eye remained dominant as the contrast in one of the eyes was varied. The black curve (open squares) corresponds to the mean durations that the variable contrast stimulus was dominant, and the grey curve (filled squares) represents the mean dominance of the fixed contrast stimulus. On the abscissa are the contrast values of the variable gratings. Notice that as the contrast is lowered, the mean duration of phenomenal dominance decreases minimally for the variable contrast stimulus, while the dominance time increases greatly in the unchanged eye. These results, as expected, are also consistent with previously reported findings, where changes in the strength of one of a pair of rivalry stimuli primarily affect the mean duration

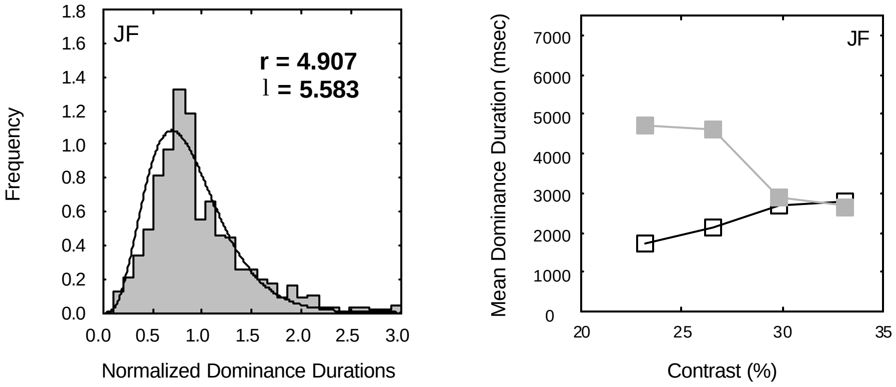


Figure 63 Rivalry phase statistics during the concurrent counting task. (a) Distribution of phase times for constant contrast stimuli in Experiment 2. The normalized distribution was again fit with a gamma function, whose parameters are listed in Table 4. The auditory task did not have a significant effect the overall distribution of dominance times (b). Results of Experiment 2b, effect of changing the contrast of one of the gratings during the counting task .

of the unchanged stimulus (Fox and Rasche 1969; Blake 1977; Bossink, Stalmeier et al. 1993)

Experiment 2: Rivalry During Concurring Counting Task

The counting task had little or no effect on the binocular rivalry alternation. Reversals in optokinetic nystagmus continued to occur at irregular intervals, just as was observed in Experiment 1. The gain of the OKN signal was slightly lower in this condition than the attended trials which resulted in a slightly higher fraction of extracted ambiguous periods. In addition, the overall alternation rate was slightly higher during this task. However, the statistics of the phases durations derived from the OKN signal very closely matched the results of Experiment 1. Figure 63a shows their distribution and Table 4 shows their

Analyst	t	%t	r	λ	N	R^2
JCF	2414	51	4.91	5.58	1151	0.947
DAL	2363	53	4.43	4.85	1212	0.965

Table 4 Rivalry statistics during counting task.. Conventions as in Table 2.

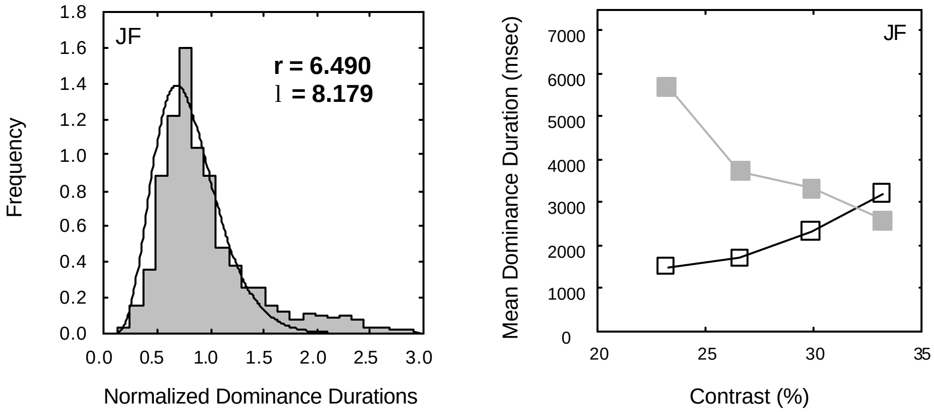


Figure 64 Rivalry phase statistics during the concurrent pop-out task. (a) Distribution of phase times for constant contrast stimuli in Experiment 3. The normalized distribution was again fit with a gamma function, whose parameters are listed in Table 4. The concurrent visual task has little effect on the overall shape of the distribution of phase times. The values r and λ are slightly are slightly higher than in the attended rivalry condition, however they are still within the range of parameters observed in study of binocular rivalry. (b). Results of Experiment 3b. Changing the contrast of one of the gratings during the pop-out task yielded results nearly identical to the condition where the subject actively attended to the direction of motion.

associated statistics. As in the first experiment, the distribution was modeled very well with a gamma function with the expected parameters. When the contrast of the stimulus was predictably changed (Figure 63b), the results were again very similar to the attended condition. A decrease in the contrast of one of the stimuli increased the mean dominance time of the other.

Experiment 3: Rivalry During Concurring Pop-out Task

The pop-out task required the subject to respond to multiple short stimulus presentations surrounding the rivalry stimulus. This also had minimal effect on the dynamics of the binocular rivalry alternations, again with the exception of a slight rate increase. The gamma function approximating the distribution in this experiment had slightly higher parameters

Analyst	t	%t	r	λ	N	R^2
JCF	2143	72	6.49	8.18	2425	0.960
DAL	2550	55	7.53	10.9	1681	0.915

Table 5 Rivalry statistics during pop-out task. Conventions as in Table 2.

than in the other two experiments, however they were still within the range of parameters previously reported for normal rivalry. It is unknown whether the change in the shape of the distribution is of any significance. The effect of changes in interocular contrast (Figure 64, Table 5) again closely resembled the fully attended condition. Decreasing the contrast of one of the gratings primarily resulted in an increase in the mean dominance time of the unaffected stimulus. Hence, despite the attentional requirement of the peripheral visual task, the same characteristic pattern was observed as in the fully attended condition.

Discussion

A number of studies have demonstrated that the conscious control over rivalry is significantly less than over other bistable perceptual phenomena, such as figure reversal (Washburn and Gillette 1933; George 1936). One consistently observed effect of attention on rivalry is ability to control the rate of alternation. Meredith and Meredith (Meredith and Meredith 1962), for example, found a nearly threefold difference in alternation rate when the subjects were instructed to consciously speed up the alternation rate, as opposed to when they were told to slow it down. The experiments presented here examine the influence of attention both on rivalry's alternation rate, and on its statistical profile of dominance and suppression. In short, there was no indication from any of the experiments presented here that the characteristic dynamics of binocular rivalry, measured by two classic tests, are dependent upon, or even significantly influenced by, the attention paid to the rivaling stimulus. In our experiments, attending to the rivalrous stimuli yielded a small (21%) decrease in alternation rate. It should be noted that in these experiments the subjects were not instructed to either speed up or slow down the course of rivalry.

That optokinetic nystagmus can be used to study rivalry perception is a consequence of the more general phenomenon that the pursuit system usually respects the perceived, rather than physical stimulus. In addition to rivalry, pursuit can be found to follow stimuli such as during anorthoscopic perception, where a moving shape is seen only through a narrow slit, (Steinbach 1976), or stationary points of light that are intermittently flickered to create the illusion of visual motion (Kowler 1990). Interestingly, not all perceived motion can be pursued, however. Motion aftereffects, and motion induced by moving the surround, for example, do not activate pursuit (Mack, Fendrich et al. 1979; Kowler 1990). Beyond serving simply as a useful tool by acting as an objective indicator during binocular rivalry, OKN, and pursuit in general, may reveal much about perceptual mechanisms.

The data presented here suggest that the amount of attention directed towards a stimulus does not affect the fundamental dynamics of rivalry. Does this imply that rivalry is in its very nature preattentive? Most descriptions of rivalry in the binocular vision literature would suggest that rivalry is clearly preattentive, involving the blockade of information from one eye before even it is combined with that from the other. Although the results presented here invite the interpretation that rivalry is largely independent of attention, there exists the possibility that attention in this task was not sufficiently challenged to eliminate the phenomenon. It was noted, for example, that the gain of OKN was diminished during the concurrent tasks as compared to the attended condition. Perhaps if attention were completely eliminated, to the point where a subject could not even maintain his or her gaze, the OKN would fall to zero, and rivalry would cease to occur. In this context, it would be interesting to further examine the conditions under which OKN undergoes spontaneous reversals during rivalry, with respect to the nature of the stimuli, the attentional load, and even the level of consciousness of a laboratory animal.

DISCUSSION

SOCRATES: *Well then, my friend, here is a hypothesis: take vision first. The color white is nothing distinct in itself either outside your eyes or in your eyes—in fact you may not locate it anywhere. If you did it would have a position and it would be stable—in other words it would not be undergoing the process of generation.*

THEAETETUS: *What do you mean exactly?*

SOCRATES: *If we follow the theory we mentioned just now, and assume that nothing is a single, non-relative entity, then we will find that black, white, and so on are adapted, and that what we call a color is neither the thing which does the meeting, nor the thing which is met, but something generated in between, which is peculiar to the individual perceiver.*

Theaetetus, Plato (427-347 BC)

BINOCULAR RIVALRY IN THE CONTEXT OF MULTISTABLE PERCEPTION

The results from previous chapters suggest that there is more than a superficial relationship between binocular rivalry and other visual phenomena involving spontaneous perceptual changes. In the present chapter I provide more evidence supporting this notion. First, I discuss the results of the above studies and those from other laboratories that argue that rivalry represents an example of a general mechanism for resolving perception ambiguity in vision. Next I discuss several concrete examples of the similar phenomenology of rivalry and ambiguous figures.

What is Rivaling during Binocular Rivalry?

Previously I described two experiments in which normal rivalry alternations are shown to occur without rivaling stimuli being continuously dichoptically bound. In neither case was perception dominated by a monocular view, but was integrated between the two eyes, spatially in one case and temporally in the other, to generate a percept that was guided by perceptual grouping and obeyed fundamental Gestalt principles. I also mentioned previous experiments in which similar effects were observed with different types of stimuli (Diaz-Caneja 1928; Whittle, Bloor et al. 1968; Kulikowski 1992; Kovács, Papathomas et al. 1996). These results demonstrate that rivalry does not represent a true competition between the eyes per se, as in none of the cases is perception generally dominated by a monocular view, but is integrated either spatially or temporally between the two eyes.

There are two extreme views of dichoptic presentation during rivalry. The first view is that rivalry represents a competition between the two eyes, and therefore it is only active during dichoptic presentation when two stimuli cannot be binocularly fused. This has been the generally accepted view for the past 25 years (for a review, see Blake (1989)). Another possible explanation is that rivalry is a conflict between any two stimulus *representations* and that dichoptic presentation is merely a convenience for presenting exactly two nonmatching stimuli. The psychophysical and physiological results in this dissertation argue strongly in favor of the latter extreme view over the former, with the caveat that it is perhaps overstated. Dichoptic presentation is likely to be more than just a convenience for presentation—it can be easily shown that it greatly facilitates vigorous perceptual alternations that are much more difficult to elicit under any monocular presentation paradigm. Nonetheless, the existence of monocular alternation phenomena that closely resemble perception during binocular rivalry provides strong evidence that rivalry does not always pertain to an interocular conflict.

Monocular Rivalry

One of the strongest arguments that the perceptual alternation process during rivalry can be divorced from dichoptic presentation is the existence of monocular rivalry. This phenomenon, originally described by Campbell and Howell (Campbell and Howell 1972; Campbell, Gilinsky et al. 1973), would more appropriately be termed “nondichoptic” rivalry or “perceptual rivalry” since it can occur either monocularly or dioptically. They described the phenomenon in the following way:

> *If two gratings with sinusoidal luminance profiles are projected upon a white screen and if they are at right angles to each other, the appearance of the gratings continuously changes. If the gratings are of different color the effect is seen even more dramatically. Say the gratings are red and green, and their intensities are matched so that where they cross yellow is perceived, one observes that sometimes the red gratings is seen on its own and at other times the green grating is observed. There are periods when both gratings appear together, but there are never periods when both disappear.*

Numerous subsequent studies have confirmed and extended these findings, demonstrating that the perceptual alternations are not the result of a trivial mechanism, such as one involving afterimages or small eye movements (Sachin Ahuja, personal communication; Georgeson 1984).

Monocular and binocular rivalry share several properties. First, each allows a small mismatch in orientation or spatial frequency before perceptual alternations are initiated. In the nondichoptic condition, grating patterns will begin to rival when they are 15-20 angular degrees different in orientation or 1 octave different in frequency (Campbell and Howell 1972). These values are quite similar to those known to initiate binocular rivalry (Blake 1989), and resemble the bandwidths of their respective psychophysical channels (Campbell and Kulikowski 1966; Campbell and Robson 1968). Finally, although not much is known about the dynamics of the alternations during monocular rivalry, it was recently demonstrated that the predominance and alternation rate off superimposed contours are largely influenced by their respective contrasts within the pattern (Sachin Ahuja, personal communication). This property again emphasizes, as do the results from the switch paradigm, that the perceptual balance between two stimuli during rivalry depends on the strengths of their central representations, and not specifically differences in interocular strength.

Spread of Suppression

One argument that has been made in the past for eye dominance during rivalry has been based on the observation that suppression is not confined to the exact point of interocular contour conflict, but appears to "spread" away from this point (Asher 1953). Hochberg (Hochberg 1964) termed this region the "contralateral suppressive field'', which was subsequently measured to spread maximally across 15 minute of arc (Kaufman 1963). When two interocularly presented contours cross each other, say two black bars on a white background, this spread appears as a "halo" around the dominant contour. It was thought that if rivalry involved a perceptual competition between stimulus features, rather than between eyes, such a halo would not be observed.

Subsequent experiments, however, have shown that this line of reasoning, although sensible, is likely to be wrong. At least two studies have demonstrated that such a halo can occur without dichoptic presentation at all. Levelt (Levelt 1965) after demonstrating that one perceives a halo when attempting to dichoptically combine two reverse-polarity boundary edges found that a virtually identical percept could be elicited during suppression caused by monocular metacontrast masking. Sindermann and Luddeke (Sindermann and Luddeke 1972) presented even more striking evidence that the spread of suppression is not governed by eye suppression, but by feature suppression. They examined monocular rivalry between afterimages after horizontal and vertical bright bars on a black background were successively presented to the same eye for 40 seconds each. The authors describe the rivalry in the following way:

> *After successive monocular presentation of a horizontal and a vertical bar on a black background with the fixation point in the center of each bar, the negative afterimage might be expected to be a dark cross representing the negative of a mixture of the two images. What is perceived in the after-image, however, is a dynamic image alternating between complete or partial dominance and suppression of one or the other of the two bars.*

What was remarkable however was the similarity of the percept between the rivaling monocular afterimages, and the perception during dichoptic presentation.

> *A striking phenomenological similarity was demonstrated between binocular contour rivalry and a monocular phenomenon. Even the halos in the vicinity of a dominant*

> *contour were present in the monocular analogue. They seem to have the same dimensions as in binocular rivalry and were influenced by varying conditions in an identical manner.*

These results demonstrate that the "spread of suppression" is also likely to represent a more general phenomenon that could be related to the fundamental mechanisms of image segmentation. This effect could, for example, suggest that, as the Gestalt psychologists observed, there can be no figure without a background, and that for a perceptual entity to rise to dominance, the foreground and background work together as a "fundamental unit of perceptual organization".

Phenomenology of Rivalry and Ambiguous Figures

Binocular rivalry and ambiguous figures have more than just a superficial similarity. Much work has been done to investigate the phenomenology of each and, although there has been little cross-referencing between the two phenomena with a few exceptions (e.g. Walker (1975)) they have many common features. In this section I discuss two general ways in which ambiguous images resemble binocular rivalry. The first involves the dynamics of the perceptual alternations, and the second the perceptual thresholds for a test probe stimulus.

Temporal Dynamics

Despite the numerous studies directed towards understanding the phenomenology of multistable perception, little had been described about the temporal dynamics of the alternation process, regarding either ambiguous figures or binocular rivalry, until the mid-60's. Levelt, in his landmark dissertation entitled On Binocular Rivalry (1965) was the first to examine the statistics of the alternation process, focusing on phases of uninterrupted perceptual dominance. Rivalry alternation is a stochastic process (Fox and Herrmann 1967) but, as seen in previous chapters, its phase durations have a well defined mean/standard deviation relationship and thus form a characteristic, repeatable distribution even for subjects with different mean rates. In Levelt's original formulation, he envisioned this distribution to arise from the summation of a small number of independent events, such as ``small flicks in eye movements'', which has been subsequently shown to be unlikely (Lack 1978). As shown in the present dissertation, these dynamics seem to be resilient to vastly different stimulus conditions (e.g. switch rivalry) and attentional conditions (e.g. OKN attention task), and are thus likely to represent the workings of a central perceptual mechanism.

This view is bolstered by observations that an alternation profile similar to that seen in rivalry is shared by several ambiguous figures, including the Necker cube and several other reversible images. Because of rivalry's history as a phenomenon specific to binocular vision, studies examining the dynamics of multistable percepts have made no mention of rivalry. For example, Borsellino et al., (Borsellino, De Marco et al. 1972) investigated the alternation pattern of depth reversals and found that sequential phases durations were independent and that their distribution could be modeled well with a two parameter gamma function, just as Levelt had found earlier for rivalry. Yet no mention was made of the similarity until Walker (Walker 1975) who states, based upon the similar dynamics "a parallel may exist between binocular rivalry and the perceptual reversal of ambiguous figures". Yet despite this recognition, even recent papers in which the dynamics of ambiguous figures has been considered there is no mention of the similarity

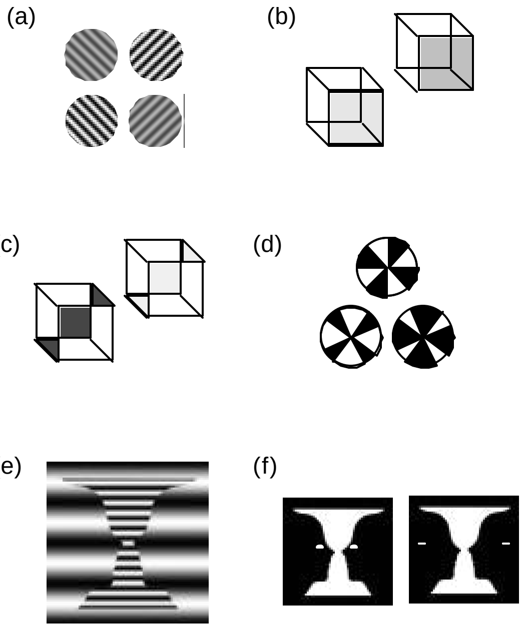


Figure 65 Examples of how bistable stimuli can be biased by stabilizing one or the other configuration. (a) Interocular contrast differences during binocular rivalry; (b) and (c) shading Necker's cube; (d) changing relative areas of figure and ground; (e) changing spatial frequency content between figure and ground; (f) adding high-order stabilizing element.

to binocular rivalry (Kawamoto and Anderson 1985; Ditzinger and Haken 1989).

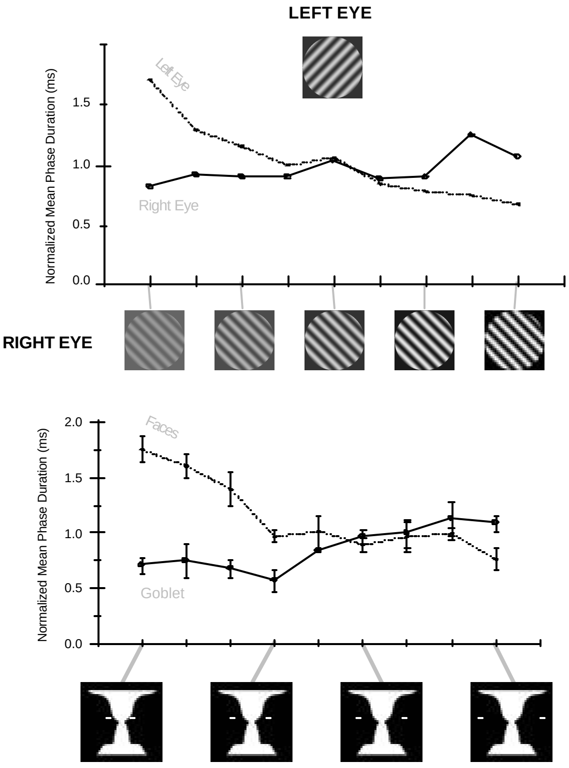


Figure 66 Two examples of differentially stabilizing one perceptual configuration in a bistable stimulus. In the upper panel, the contrast of one of a pair of rivaling gratings is varied. In the lower panel, the position of the eye on the face is varied. In each case, the mean dominance of one of the stimuli is greatly affected, while the other is not affected much at all.

Figure 65 shows several examples of how bistable stimuli can be manipulated to bias one or the other perceptual configuration. A small experiment involving example (f) is shown in Figure 66, where the addition of a eye to Rubin's face vs. vase stimulus either stabilizes or destabilizes the face configuration depending on its position. The upper panel shows the standard rivalry paradigm of manipulating the contrast of a stimulus in one eye while keeping the other constant. Where the contrasts are the same the two lines cross, indicating that the mean dominance duration is equal. In the bottom panel, a similar curve emerges when the position of an eye, added to the face vs. vase stimulus, is varied with respect to the front of the face (my apologies to Rubin). Here again, the lines cross, indicating that at some value of eye position, the balance is exactly the same between seeing the faces and seeing the vase. In each case, as the critical variable is changed, the contrast of the grating in the right eye in the upper panel and the position of the eye in the lower, there is a notable stabilization in the one of the perceptual configurations and relatively little effect on the other. In the lower example, the manipulation is no longer of a low order, such as contrast or brightness, but relies on a higher order configurational change in the stimulus that undoubtedly draws on our predefined expectations of how a face should appear.

All these studies together demonstrate that the temporal dynamics of the alternation process is indeed very similar, if not identical, for ambiguous figures and binocular rivalry. Although, to the knowledge of the author, a rigorous statistical analysis has never been done regarding the alternation process during monocular rivalry, it is likely that it would have a similar profile. What is unknown, however, is the significance of these findings. Why are dominance durations in multistable phenomena stochastic, but consistently form distributions that are modeled extremely well by a two parameter gamma distribution? And why does the mean dominance of one stimulus, but not the other, change when the strength of one is systematically varied? The answers to these questions are unknown and could be potentially very important in contributing to the understanding of perceptual instability.

Sensitivity during Suppression

Another piece of evidence in favor of a common underlying mechanism compares the visual sensitivity to test probes during rivalry and while viewing ambiguous figures. It has long been established that during rivalry it is harder to detect a test probe stimulus when it is flashed upon the suppressed stimulus ("in the suppressed eye") than when it is flashed upon the dominant stimulus ("in the dominant eye"). Specifically, suppression elevates detection (Wales and Fox 1970; Fox and Check 1972; Blake and Fox 1974; Blake and Overton 1979) and recognition (Fox and McIntyre 1967) thresholds in that eye, as well as the reaction times for detection (Fox and Check 1968). In addition, some studies have found that, compared to a nonrivalrous situation, stimulus thresholds actually decrease for the dominant eye: that is, it has a heightened sensitivity during rivalry dominance (Makous and Sanders 1978; Cogan 1982).

Intuitively, it is not surprising that test probe thresholds are elevated during rivalry given its nature. What is perhaps surprising, however, is the small amount by which they increase, significantly less than 1 log unit (Wales and Fox 1970). Given the relative ease in which rivalry can completely eliminate a stimulus from perception that is orders of magnitude above threshold, one might expect that detection thresholds in a suppressed eye would be considerably higher. However, in the context of rivalry belonging to the more general category of a genuine *perceptual conflict*, this number might not be surprising. Wales and Fox note at the end of their study:

> *At present, little is known about the mechanism that produces suppression, but it is interesting to note that the threshold elevation of 0.56 log units produced by suppression is of the order of magnitude of threshold elevation obtained in visual masking (see Kahneman, 1968, for review).*

Data from an additional set of experiments provides more evidence that this elevation is not due to monocular suppression. When a paradigm analogous to the rivalry test probe experiment was applied in a figure/ground context the results were remarkably similar. Wong and Weisstein (Wong and Weisstein 1982; Wong and Weisstein 1983), while investigating the effect of context on the detectability probe stimuli, discovered that a bistable stimulus could elicit a perceptual context effect—one in which basic visual sensitivity depended upon the current perceptual configuration. They used Rubin's face vs. vase stimulus to probe the sensitivity of subjects to a bar flashed on top the vase when it was seen as figure as compared to when it was seen as ground. They found that when the vase was seen as background the detectability of the probe, as well as the discriminability of its orientation, were impaired compared to when it was seen as figure. The same was true for probes placed on the adjacent faces. Remarkably, this difference in sensitivity is of approximately the same magnitude as in the rivalry test probe studies. Similar effects had been noted previously for the detection of a contour discontinuity (Weitzman 1963). This similarity between the "depth" of rivalry suppression and the effect of perceptual context is almost certainly more than a coincidence, and provides further evidence that rivalry and ambiguous figures share a common mechanism.

Suppression with monocular presentation is also observed during the phenomenon of crowding, in which a the spatial configuration of a group of stimuli can result in the perceptual suppression of a target member that would normally be easily visible (Bouma 1970; Toet and Levi 1992). Although crowding makes the discrimination of elementary features, such as orientation, impossible for the suppressed stimulus, the unperceived stimulus can still generate an orientation specific aftereffect (He, Cavanagh et al. 1996). This again parallels binocular rivalry, and suggests that perceptual suppression in paradigms that do not involve bistability may also be related to rivalry.

BINOCULAR RIVALRY AS A TEMPORARY, INDUCIBLE APPERCEPTIVE AGNOSIA

In this chapter I develop a metaphor for binocular rivalry based upon similarities in the phenomenology of rivalry and neuropsychological deficits associated with certain visual agnosias. The majority of previous models of rivalry have taken as their starting point its peculiar alternation dynamics (Matsuoka 1984; Lehky 1988; Mueller 1990), or relationship to binocular vision (Sperling 1970; Wolfe 1986; Blake 1989). These and other descriptions of rivalry have generally focused upon *suppression*, or what is not perceived during rivalry. In contrast, the following metaphor concentrates upon what *is* perceived during rivalry, comparing the perceptual experience with that of patients with lesions in early cortical visual areas. I include it as the last chapter in the dissertation because I believe the parallels between the two phenomena warrant further investigation and, in their combination, have the potential to reveal a great deal about the neural mechanisms underlying normal visual perception.

A Second Look at Apperceptive Agnosias

In order to construct the desired metaphor I must first elaborate more details about the phenomenology of apperceptive agnosias. The number of well-studied cases amounts to only a handful for each of the major subcategories of apperceptive agnosia, and the taxonomic boundaries are fuzzy (for an excellent review see Farah (1990)). In the present recount I will discuss features of apperceptive agnosia shared by many, but not all, of the patients, without much reference to their specific taxonomic classification.

Nature of the Lesions

One of the difficulties in studying structure-function relationships in apperceptive disorders stems from the character of the lesions themselves – namely their intersubject variability and their diffuse nature. In the majority of cases, cortical damage has resulted from anoxia, usually from carbon monoxide poisoning (Adler 1944; Efron 1968; Benson and Greenberg 1969; Campion 1987) or stroke (Luria 1959; Kinsbourne and Warrington 1962; Tyler 1968; Rizzo and Hurtig 1987). Inasmuch as lesions have be localized with EEG, CT, MRI, and histology, they have generally been restricted to the posterior cortical areas, in the occipital lobe and the surrounding regions, especially the superior association areas (Farah 1990). Anoxia resulting from prolonged vascular insufficiency is known to produce diffuse and widespread cortical damage, as well as numerous focal lesions within the same cortical tissue. Carbon monoxide poisoning has also been shown to produce a laminar necrosis which has the potential to interfere with horizontal cortical connections (Benson and Greenberg 1969).

General Visual Function

Patients with visual agnosias share, almost by definition, preservation of basic visual capacities. In most accounts of apperceptive agnosia visual acuity, brightness perception, and color perception remain relatively intact (Holmes and Horrax 1919; Adler 1944; Luria 1959; Kinsbourne and Warrington 1962; Tyler 1968; Benson and Greenberg 1969; Campion 1987; Rizzo and Hurtig 1987; Farah 1990) despite the impaired ability to negotiate their environment and interact in everyday situations. Some patients are able to orient themselves, manipulate objects, and lead independent lives (Campion 1987; Wilson and Davidoff 1993), while others will appear completely blind to an unbiased observer, constantly feeling about and stumbling over furniture, etc. (Luria, Pravdina-Vinarskaya et al. 1963). Most of the patients lie in between these two extremes (Holmes and Horrax 1919; Adler 1944; Tyler 1968; Benson and Greenberg 1969). Apperceptive agnosics generally have good insight into their own perceptual deficiencies and often find shortcuts to overcome them (Adler 1944; Kinsbourne and Warrington 1962; Wilson and Davidoff 1993).

As discussed in the opening chapter, it is unclear whether dreams and imagery engage the same machinery as normal visual perception. In several apperceptive agnosics deficiencies in these actions mimic their perceptual limitations. For example, one apperceptive agnosic lost all visual imagery in his dreams following his injury, describing his dreams as "occurring in a dark closet and consisting merely of threatening voices and cries" (Benson and Greenberg 1969). For another patient with deficits in visual imagery Alder remarks "The impairment follows the rule of the rest of her disturbance. She has no difficulty in visualizing colors, but the difficulty grows on visualization of objects with more than one dimension." (Adler 1944).

What Is Perceived

It is difficult to speak of what an apperceptive agnosic "sees" because of the inherent difficulty in communicating a bizarre subjective experience; however, the verbal descriptions of the abilities and disabilities of some patients through rigorous testing can begin to provide some clues. Farah (Farah 1990) generalizes these patients by saying

> *To sum up the abilities and impairments of these patients, there is a relative preservation of most 'elementary' dimensions of visual perception, with a striking impairment to recognize, copy, or match simple shapes as well as more complex objects.*

With many apperceptive agnosics tactile and proprioceptive sensations are preserved, and subjects adopt strategies of tracing contours with their fingers (Adler 1944; Farah 1990) or even motions of the head (Efron 1968). In some cases only very simple shapes are perceived correctly, and adding a single additional line element can disrupt the ability of the patient to correctly identify or copy the figure. Interestingly, lines are perceived better than curves, and a patient who can read straight-line numbers is often unable to read numbers comprised of curved elements (Adler 1944; Benson and Greenberg 1969; Farah 1990). For most patients, reading is completely disrupted, and when possible, accomplished only with great difficulty using a finger as a place holder (Holmes and Horrax 1919; Adler 1944; Luria 1959; Kinsbourne and Warrington 1962; Benson and Greenberg 1969; Farah 1990; Wilson and Davidoff 1993).

Simultaneous Perception

A trait shared by many apperceptive agnosias is a deficit in simultaneous perception, or the ability to perceive multiple things at once. Wolpert (Wolpert 1924) termed this ailment simultanagnosia, and its presence can be manifest at different degrees in different individuals. Tyler (Tyler 1968) states, "with this defect the patient can only see one thing at a time. This may be a 'whole' or a 'part' but upon 'seeing' this the patient recognizes little else." This singleness of vision is exemplified by the recount of one patient by Luria (Luria 1959):

> *If the patient is presented with a pattern of six dots arranged to form a rectangle, he can easily perceive and name it. But if the patient is then instructed to count the component dots, he experiences very considerable difficulty. The new task destroys immediate awareness of the configuration; it is now the separate elements which becomes the object of analysis.*

For some patients, however, the ailment is less severe and perception is fragmented, consisting of numerous locally perceived regions, where there is "an appreciable derangement of simultaneous visual synthesis". Under these conditions patients fail to perceive a complete pattern in unison, especially if it is complicated or cluttered. Instead they see bits and pieces of the pattern in no recognizable spatial arrangement. Often this results in the patient moving his head about, as if searching for the best vantage point or trying to deduce the identity of a pattern by seeing it from many different vantage points. (Campion 1987; Farah 1990). Writes Tyler (1968) of one patient:

> *A typical description of a picture of an American flag was as follows: 'I see a lot of lines. Now I see some stars. When I see things like this I see a lot of parts. It's like you have one part here and one part there and you put them together or see what they make'. …When the examiner asked her if it could be an American flag, she quickly recognized that what she saw could have been synthesized into a flag.*

This piecemeal perception is also characteristic of binocular rivalry between two stimuli that have multiple spatial components (e.g. large gratings with a high spatial frequency). In each case perception is broken and discontinuous, with multiple dynamic regions of visibility an suppression.

Short Presentations

Apperceptive disorders have often been associated with abnormal eye movements. In many cases, a patient can fixate a single light source with little difficulty, and can even maintain fixation when a stationary target perceptually fades away (Rizzo and Hurtig 1987). However, when attempting to scan an image or perform a cursory visual search, ocular movements become disorganized and ataxic (Holmes and Horrax 1919; Luria 1959; Luria, Pravdina-Vinarskaya et al. 1963; Benson and Greenberg 1969). For this reason, such disorders were originally considered to be rooted in oculomotor dysfunction, but subsequent studies using tachistoscopic presentation of stimuli clearly demonstrates that the perceptual deficit precedes any motor disorder, and is likely to be the cause of it. As stated by Kinsbourne and Warrington (Kinsbourne and Warrington 1962),

> *…the defect is already demonstrable before the scanning has time to begin, and in a setting in which scanning by eye movements is not usually required. At the very first*

> *glance, these patients perceived less than is normal, and there is therefore little information available to guide their eye movements*

Numerous studies have similarly examined simultaneous perception with short presentations (Luria 1959; Kinsbourne and Warrington 1962; Luria, Pravdina-Vinarskaya et al. 1963; Campion 1987), which is in some cases the only way to reveal a deficit in an otherwise recovered individual (Adler 1944).

A number of generalizations can be made from these studies regarding simultaneous perception. First, in apperceptive agnosia it is truly the number of elements in a pattern that governs perception, rather than the angular size of the pattern on the retina (Luria, Pravdina-Vinarskaya et al. 1963). Figure 67 shows a stimulus that reveals much about these patients' deficits (from Luria (1959)). When the two large, overlapping triangles are the same color and intensity, a subject will report seeing a six-pointed star. However, when the color of the two triangles is different, subjects consistently report seeing only one triangle or the other, but are never aware of both simultaneously. A similar dependency on a unified color of ink was found in interpreting a simple outline drawing of a human face. Second, if two simultaneously presented forms are identical, or combined into a single structure by drawing a line between them, their simultaneous perception is markedly facilitated (Luria 1959). This is perhaps related to their preserved ability to recognize textures comprised of numerous identical elements (Campion 1987), as well as the ability of the patient describing the American flag in the above example, who was able to simultaneously see several individual stars (Tyler 1968).

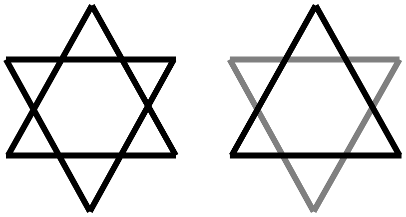


Figure 67 Stimulus posing difficulty for apperceptive agnosic patient.

Dynamics

One of the most striking similarities between simultanagnosia and binocular rivalry is the ability of a fixated, central stimulus to spontaneously disappear from view. Tyler, for example, described one patient who has a marked difficulty maintaining her perception of an object. She was able to perceive single objects, but whenever one was is viewed for more than 1-2 seconds it spontaneously disappeared. This had the unfortunate consequence that an object would often vanish just as she reached for it. Similar patients were described by Rizzo and Hurtig (Rizzo and Hurtig 1987), who investigated the ability of three individuals to maintain fixation during these periods of disappearance. They found that fixation was normal during these perceptual alternations:

> *The exact moment of reported target disappearance is associated with maintained and accurate fixation. Even though the subject complains that the light target has vanished, he is still looking right at it. He continues to look right at it of several seconds although he says he still cannot see it. Finally, when the target reappears to him, he is still on target.*

Farah (Farah 1990), in her recount of these spontaneous disappearances, speculates that they could be due to Troxler's effect, which also involves the spontaneous perceptual fading of stimuli with time. This is unlikely, however, given that Troxler's effect is known to occur primarily in the visual periphery (Levelt 1965; Blake, O'Shea et al. 1992) and in these patients stimuli fade from their center of gaze.

Binocular Rivalry as an Apperceptive Agnosia

Already it is clear that binocular rivalry and the apperceptive agnosias have much in common. Each is characterized by a competition for perceptual dominance between stimuli that are continually presented to the visual system. In fact, the explanations given for singleness of vision in apperceptive disorders often resemble those given for binocular rivalry. For example, Luria et al. (Luria, Pravdina-Vinarskaya et al. 1963) state:

> *it may be concluded that* simultanagnosia *and its related disturbance of oculomotor control arise from a process of inhibition in the occipital cortex which results in a restriction of excitation to a single point (Pavlov, 1955)*

In this description, competition is between spatial locations rather than monocular channels; however, it shares with models of rivalry the notion that perceptual unity results from the massive suppression of a subset of inputs.

Phenomenologically, binocular rivalry and apperceptive agnosia share numerous properties, which I list here. First, each can result in either the unified perception of a single stimulus or a fragmentary, piecemeal mosaic of individual component elements. Second, any *single element* that is perceived maintains its normal appearance with respect to color and fine detail. Third, the degree of fragmentation depends on the number of contour elements in a pattern. When the number of elements is low (in rivalry this could correspond to a low spatial frequency grating within a fixed angular size) the entire pattern will often be perceived. When the element density increases (high spatial frequency grating), perception tends to fragment into smaller and smaller unified regions. Fourth, piecemeal perception is dynamic, with different portions fading in and out of consciousness. Fifth, when the element density grows very high, and is seen to form a *texture*, unity of perception is regained, with a large textured pattern being perceived in unison in each case. And finally, in agnosias as well as in rivalry, a high contrast pattern can spontaneously disappear from the center of gaze, and then reappear as the subject continues to fixate. The time associated with such changes is on the same order in both cases.

In this section I will propose a framework for thinking of rivalry as an artificial apperceptive agnosia. First I will elaborate a simplistic model which explains how the two phenomena

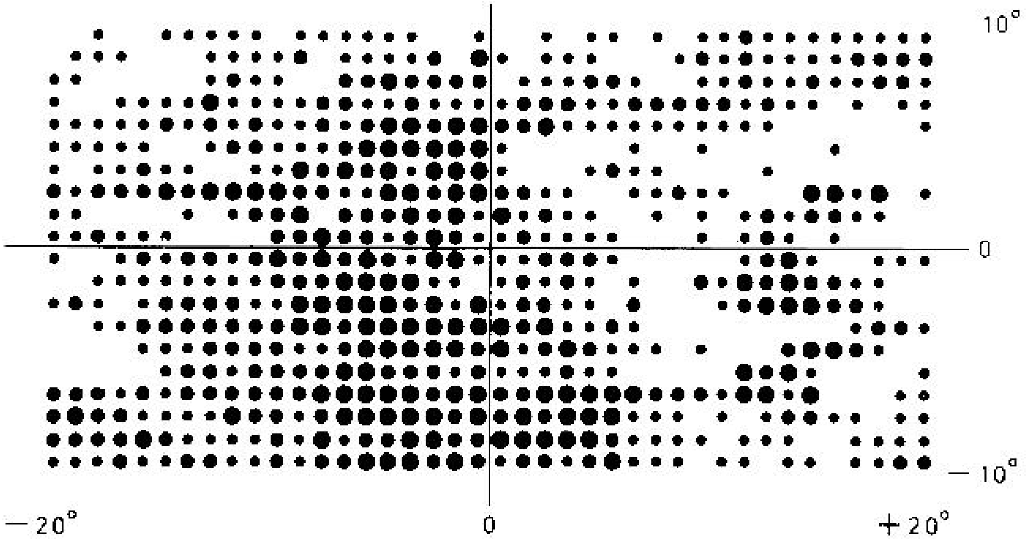


Figure 68 Mapping of the visual field of a patient with apperceptive agnosia. Each circle represents the sensitivity to brightness in a 1° by 1° square in the visual field (Campion and Latto 1985).

could share a common underlying mechanism. Next I will discuss how the physiological and psychophysical observations in this and other studies are consistent with this description of rivalry.

Framework

The framework that I shall introduce draws largely from a model of apperceptive agnosia proposed by Campion and Latto (Campion and Latto 1985; Campion 1987) in which the perceptual deficits are linked with the nature of the underlying lesions. Recall that the majority of patients with these deficits have experienced prolonged anoxia secondary to carbon monoxide intoxication, which is known to produce diffuse and multifocal lesions. In this model, which they call the masking hypothesis, they propose that following such lesions the visual field becomes “peppered with numerous minute scotomata”, and that these discontinuities in perception disrupt shape perception but leave acuity intact, in a manner similar to the “critical band masking” of Stromeyer and Julesz (Stromeyer and Julesz 1972). They tested this hypothesis in two ways. First, a patient with apperceptive agnosia was tested for perceived brightness with small stimuli across many portions of the visual field. One degree regions extending for 10 degrees above and below the fixation point and 20

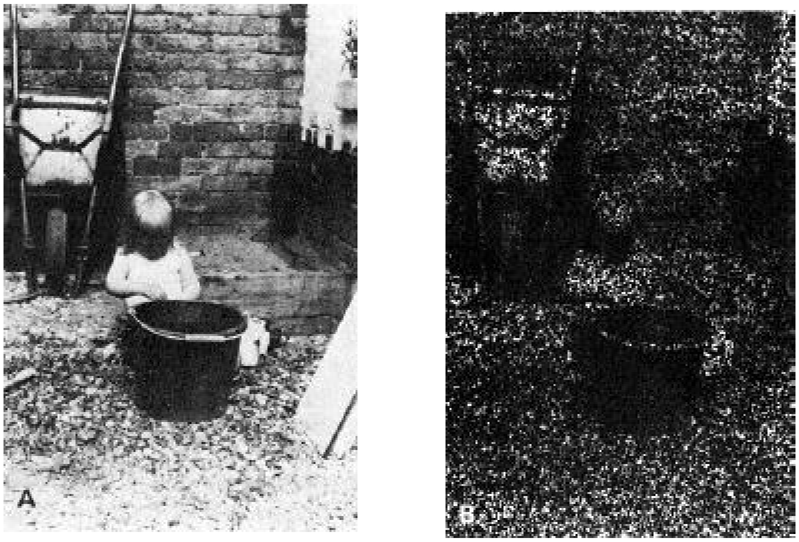


Figure 69 Addition of band-limited noise to the figure on the left produced an image that, when shown to naïve observers, mimicked the elicited reports similar to those often given by apperceptive agnosics (Campion and Latto 1985).

degrees to the left and right were tested monocularly with a spot of light, and subjects were asked to rate their percept on a scale of 1 to 4. Their results are in Figure 68, which show the visual field with the size of each square representing their rating. One can see clearly that, as predicted, there are many regions in which brightness perception is intact interspersed with those in which it is impaired. As a second test, they created a stimulus that would mimic the perception of a patient with such diffuse lesions, shown in Figure 69. The image on the right consists of the image on the left covered with a band-limited random dot mask, simulating what a patient with apperceptive agnosia might experience. They found that subjects viewing this image had a difficult time with recognition, and tended to make inferences from partial cues, much in the same fashion as their patients. Such a model implies that the perceptual difficulties experienced by patients with such an affliction result from difficulty piecing together information at the input stages of processing. In this context Campion states (Campion 1987):

> *Vision to such patients could be like trying to build up a picture of the world through scanning it by means of a tube with a very narrow angle of view, but in their case, they*

> *might have many different "tubes" of different sizes. Randomly spaced, and perhaps introducing their own "local" distortions such as poor brightness sensitivity or poor acuity.*

Carbon monoxide intoxication is known to cause, in addition to multifocal lesions, a laminar necrosis (Benson and Greenberg 1969), disrupting horizontal connections within the early cortex that may be crucial for early grouping mechanisms. The masking hypothesis, despite its simplicity, has been considered a good first approximation for this type of apperceptive agnosia (Humphreys and Riddoch 1987; Farah 1990).

In the present model of rivalry I consider the possibility that local contour conflicts, and

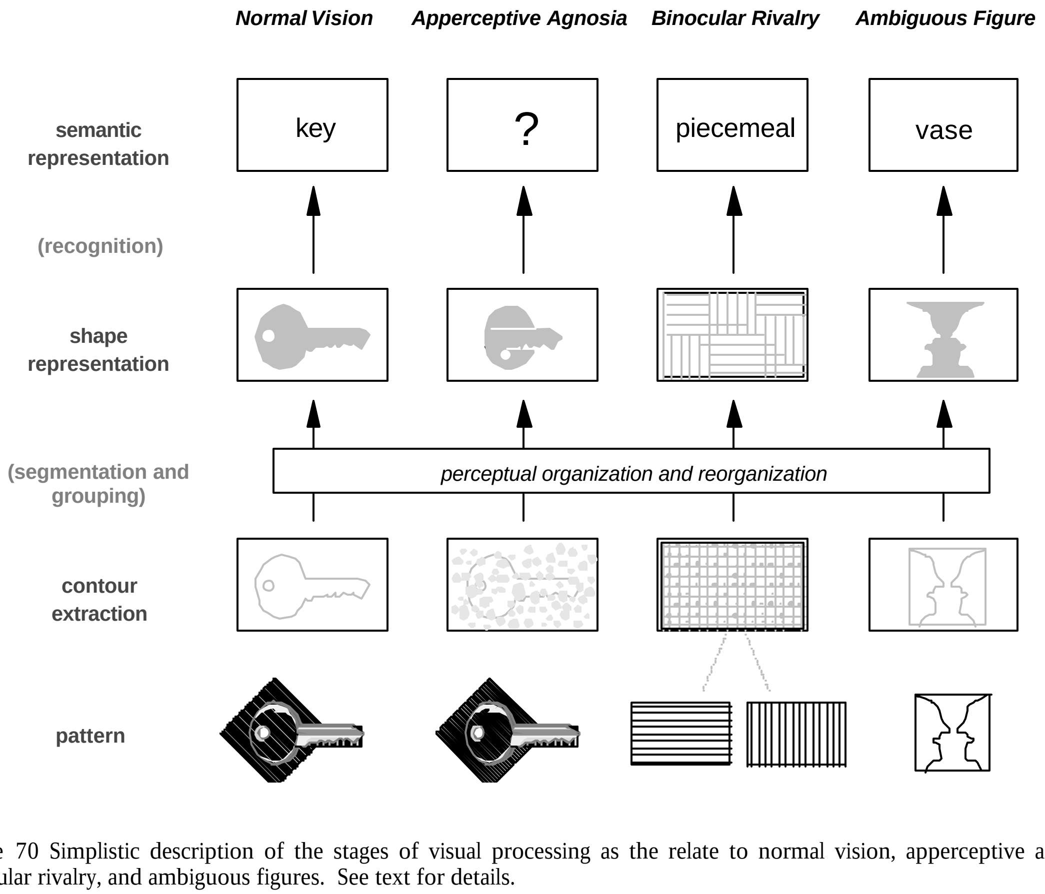


Figure 70 Simplistic description of the stages of visual processing as the relate to normal vision, apperceptive agnosia, binocular rivalry, and ambiguous figures. See text for details.

specifically interocular conflicts between stimuli competing for the same region of visual space, can mimic the neural damage associated with multifocal lesions in the earliest cortical areas, and thus lead to many of the same perceptual properties. The general scheme is shown in Figure 70. The stages are meant to represent abstract stages of perceptual representation that are by no means completely serial, but are shown serially for simplicity. The stage of orientation analysis corresponds roughly to the extraction of edges and contours normally associated with striate cortex, where many of the diffuse lesions are located in these patients. The stage of shape representation is not mapped to any specific area in the brain, and corresponds to the output of the initial perceptual organization of contours into figure and ground. Finally, the process of recognition follows shape representation, and it function has been the classical means of assaying perceptual deficits. The four columns correspond to these stages of processing as they apply to normal vision, apperceptive agnosias, binocular rivalry, and other multistable perception. In normal vision, the analysis of a pattern begins with the extraction of its contours, their perceptual grouping into a shape or shapes (including the separation of figure from ground), and the subsequent recognition of individual scene elements (see, for example Marr (1982)). In apperceptive agnosia, the extraction of contours is disrupted due to the numerous scotomata, as well as some of the initial grouping processes due to the laminar necrosis, and the perceptual grouping cannot successfully synthesize shapes and separate them from the background. Because shapes are never successfully represented the recognition of an object is impossible. This is essentially Campion and Latto's masking hypothesis.

In binocular rivalry, the interocular discrepancy between contours competing for the same point in visual space creates a physiological conflict, analogous to the scotomata, that similarly interferes with the extraction of contours, as well as their subsequent grouping across visual space. Given this conflict, the perceptual organization mechanism cannot support both patterns and, for simple stimuli, selects only one of the pair. When the stimuli contain many conflicting contours the number of "virtual scotomata" increases, and perception becomes fragmented into a mosaic drawing from each of the monocular views.

In either case, the conflict remains at the level of contour detection, prompting the perceptual organization mechanisms to continually test for parsimonious solutions. It is this stage of processing that is responsible for coordinated activity between unitary zones during rivalry, where "waves" of perceptual dominance across a large stimulus represent an effort to unify the percept. Such waves would be found nowhere in the cells responsible for the extraction of contours. Recognition, although never tested with large, contour rich stimuli during rivalry, is also likely to be impaired much in the same way as in apperceptive agnosias. Finally, in Rubin's face vs. vase, contours are extracted with no difficulty, but ambiguity sets in at the level of perceptual organization, resulting again in bistability.

Psychophysical Evidence

One of the best pieces of evidence that the masking hypothesis is not unreasonable for apperceptive agnosias, as well as rivalry, relates to an argument presented earlier, that unity in perception during rivalry is most likely to entail complete surface representations, and that contours tend to break up an image into small unitary zones. In rivalry, large images without many contours, containing primarily low spatial frequency information, can often be perceived in unison. This characteristic also appears to be present in apperceptive agnosias, in which the perception of color and other surface properties is often preserved, and the size of an object, per se, is not all that important. Consider the following recount of one apperceptive agnosic (Campion 1987):

> *In contrast to his very poor form perception, he could negotiate obstacles in the room, reach out to shake hands and manipulate objects or to reach for a cup of coffee… He could also comment on features of objects such as their color or whether they were shiny or not. He could also recognize the 'texture' of objects, although he found this difficult to describe.*

Clearly low spatial frequencies, including information such as the basic location of large objects in a room, can penetrate the lesioned tissue. It is possible that this information draws primarily from the representation of color and surface properties that do not rely on the scrutiny of precise orientation extraction in striate cortex, but can pass through V1 relatively easily. Even if surface representation requires some cells (such as those found in blobs, for example) to be intact in order to pass information through to higher visual areas, it is less likely than shape representation to be disrupted by damage to a subset of cells because it is less spatially precise. It is possible that the patients with a higher difficulty navigating and recognizing surfaces have more complete damage to these areas. Rivalry also exhibits the preserved perception of surface properties such as color and texture, and the high degree of unitary perception when local contours are minimized. This again could result from a relative lack of involvement of the orientation analyzers in V1 that tend to fragment perception in the face of “malfunction”. A recent study in which striate cortex was selectively lesioned in cats adds further support to this hypothesis. Pasternak et al. (Pasternak, Tompkins et al. 1995) found that such lesions specifically interfere with the analysis of high spatial frequency information, and that the perception of global motion is paradoxically improved in animals following striate lesions, presumably by “interfering with masking by high spatial frequencies”. Striate cortex, in its normal operation, can actually hinder the global perception of a stimulus.

Such a model also explains why the size of unitary zones of suppression increase with increasing stimulus eccentricity (Blake, O'Shea et al. 1992). Since the activity of cells in the hypercolumns in primary visual cortex dictate whether rivalry will be unitary or piecemeal, cells with larger receptive fields will allow, for a given spatial frequency, larger stimuli to rival in unison.

Physiological Evidence

The results from the present physiological investigation fit well with this view of binocular rivalry. Perception during rivalry relies upon the representation of a shape or pattern beyond the site of binocular combination. If two monocular images have many conflicting or nonmatching contours, the grouping process becomes unstable, the perception loses its footing, and an image breaks up into discrete zones of unitary perception. This view of rivalry makes several predictions about its underlying physiology. First, the activity of monocular neurons in V1 generally should not be affected by placing a rivalrous stimulus in the contralateral eye, but the orientation tuned neurons that receive *input* from monocular neurons should indeed be affected, sensing the interocular conflict. The binocular cells in V1 that do sense this conflict should maintain a constant, abnormal level of activity throughout the duration of interocular conflict, and their activity should *not* change in accordance with the perceived stimulus. Second, the activity of those neurons directly involved in the perceptual organization of contours into a shape, most likely binocular cells beyond V1, should indeed reflect the perceived orientation during rivalry.

The first prediction has been recently confirmed by the work of Sengpiel et al. (Sengpiel, Blakemore et al. 1995). It was found that monocular cells in V1 generally exhibited only modest inhibition when a stimulus was placed in the contralateral eye, which was independent of its orientation. Hence monocular neurons in V1 are not sensitive to interocular conflict. However, the majority of binocular neurons (25 out of 45) in V1 were significantly inhibited by the presence of a nonmatching stimulus in the contralateral eye, as would be predicted if these neurons were sensing a conflict in converging monocular neurons. An extension of this work by the same group (Sengpiel, Freeman et al. 1995) supports this view even more strongly. They found that similar orientations and spatial frequencies in the contralateral eye enhanced the activity of the cell, while suppression set in with increasing differences between the two eyes. What is striking is the similarity between the disparities in orientation and spatial frequency required for neuronal suppression and those values required to initiate binocular rivalry psychophysically in humans. An orientation disparity of, on average, 22 degrees was sufficient for neuronal suppression, which is compared psychophysical requirement 15-30 degrees to initiate rivalry in humans (Braddick 1979; Blake 1989). Likewise, a difference in spatial frequency of 0.5 octaves induced neuronal suppression for similarly oriented gratings, whereas the psychophysical rivalry threshold is roughly 0.4 degrees (Blakemore, Carpenter et al. 1970). These results fit perfectly with the notion that the earliest cortical areas govern whether or not there is a conflict to overcome, but are not directly involved in the perceptual solution. If oriented neurons in V1 receive conflicting information, their activity is altered, and the intra- and inter-areal interactions involved in perceptual grouping, and hence figure ground segregation, are disrupted. Interestingly, the minimal orientation and spatial frequency disparities required to initiate rivalry are similar in value to the half-widths of the psychophysical channels for these attributes in humans (Campbell and Kulikowski 1966; Campbell and Robson 1968), as well as their the half tuning-width for neurons in macaque striate neurons (De Valois, Albrecht et al. 1982; De Valois, Yund et al. 1982).

Both predictions are strongly supported by the data in the current physiological study. Perception-related activity was largely absent in cells in area V1, although many binocular cells were inhibited by rivalrous stimuli. Monocular cells were especially immune to perception-related activity, and were rarely even affected to a significant degree by the presence of a contralateral stimulus. The vast majority of neurons whose activity changed in accordance with the monkeys’ perception was located beyond the site of binocular convergence, with the highest concentration in area V4. This again is consistent with the idea that the perceptual conflict is resolved binocularly according to higher-order organizational principles in areas often associated with such roles (Merigan, Nealey et al. 1993; Merigan 1996). Clearly the activity of neurons in these areas still does not represent an all or none account in favor of the perceived stimulus during rivalry. Rather it appears that neurons in these areas carry information both about the physical stimulus present as well as the perceived stimulus. This fact explains again why a suppressed stimulus can create a potent adaptational aftereffects, and why the suppressed stimulus can have an influence on rivalry's dynamics. Recall that similar statements can be made for crowding (He, Cavanagh et al. 1996), which argues that perceptual suppression in general does not involve the activity of cells involved in contour extraction.

Some Notable Differences

Despite the numerous shared properties of binocular rivalry and apperceptive agnosia, several differences must also be addressed. Apperceptive agnosia, for example, does not have associated with it a strong oscillatory nature. Perception undergoes changes, such as the fading away of a stimulus, but there is no clear back-and-forth between solutions, as in a bistable perceptual phenomenon such as rivalry. This could be because the damage in apperceptive agnosia does not involve a direct spatial conflict where there are exactly two possible percepts as in rivalry. Rivalry presents a clear alternative to the visual system: which of two spatial patterns will occupy a given point in space? In apperceptive agnosias, the difficulties with simultaneous perception can occur with stimuli that are several degrees apart, and hence do not compete spatially.

Another difference between perception in the two cases is the ability of feedback from higher visual areas to affect segmentation. In previous chapters I describe the many ways that attention, as well as Gestalt-type grouping principles, can contribute to rivalry's effort to make sense of the conflicting input. Examples include Caneja's drawing in Figure 47 (Diaz-Caneja 1928). In contrast, it is thought that for patients suffering from apperceptive agnosia it is thought that the early visual system entirely loses its guidance from higher areas. Visual expectations play significantly less of a role in interpreting a shape, and patients often circumvent these difficulties by tracing with their fingers or moving their head. The pattern shown in Figure 3, for example was consistently read by one patient as “7415”, rather than “THIS” because of the two small discontinuities, one in the T and one in the H. Evidently, patients such as this, in their compensatory effort to make sense of such a pattern, cannot

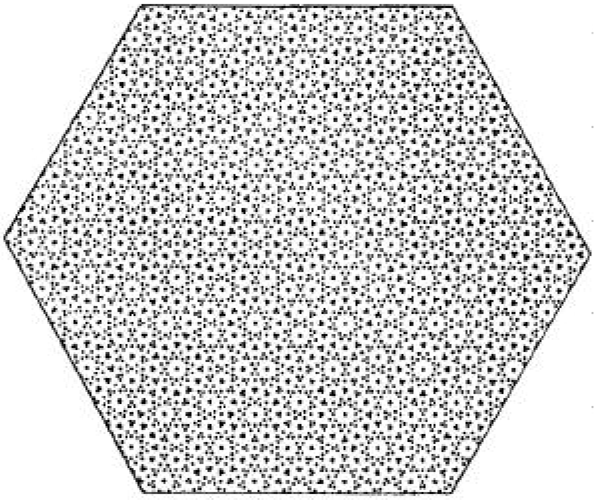


Figure 71 Dynamic stimulus taken from Marr (1982), illustrating the dynamic nature of the segmentation system searching for possible perceptual solutions.

bridge these gaps. This can only be attributed to the absence of guidance from higher visual areas in constructing a shape from a number of lines.

Are We Aware of Aberrant Neural Activity in V1?

Recently there has been much discussion regarding the relationship between the activity of neurons in V1 and the perception of a stimulus. Crick and Koch (Crick and Koch 1995) postulated, based on neuroanatomical arguments, that the activity of neurons in V1 provides an extension of the sensory representation of a stimulus, but does not provide an explicit perceptual representation. As emphasized in the opening chapter, this dissociation is often difficult to explore, but there is now mounting evidence in support of this hypothesis from psychophysical data (He, Smallman et al. 1995; Kolb and Braun 1995; He, Cavanagh et al. 1996), electrophysiology in primates (Gur and Snodderly 1997), and human lesion studies (Humphrey, Gooddale et al. 1995) (for a recent review, see Koch and Braun (1996)).

The present formulation of rivalry, as an apperceptive agnosia resulting from a conflict in the first binocular cortical stages, supports the notion that striate cortex is more closely allied to sensation than to perception. Contour conflicts are continuously present, and thus the activity of these cells remains relatively constant. But we don't *perceive* this constant conflict in V1, just as the apperceptive agnosics don't perceive their scotomata. Perception is instead dictated by the activity of neurons receiving direct and indirect input from these neurons, representing the perceptual apparatus in a continual struggle to lock onto a unique and stable solution. Consider the dynamic mosaic in piecemeal rivalry. Often zones of unitary perception appear to sweep across the stimulus, recruiting neighboring zones to join in to create a more parsimonious representation. However, the high density of conflicting monocular contours disrupts this struggle for parsimony, and the neighboring zones are continually shuffled and regrouped into an infinite number of unstable perceptual solutions. Compare this activity with the dynamic perception of Figure 71 (Marr 1982), where ambiguous grouping of neighboring elements similarly results in a continually changing, piecemeal pattern. According to the model presented here, these changes would not be reflected in the activity of neurons in V1, but would certainly be seen in V4, perhaps involving the same cells that were the strongest modulators during binocular rivalry. In short, we *see* the output of the perceptual apparatus, not the input, and striate cortex represents the input.

Final Comments

I began the first chapter by considering the first instance that a human being reflected upon his or her own perception, and made the point that it may well have been in response to a visual illusion or bistable scene. Or perhaps it was in the recollection of a dreamed episode or the experience of a hallucination. In any of these cases it was the isolation of perception from sensation that brought forth the realization that we do not live directly in the world, but in our private cognitive (re)construction of the world. Studying mechanisms that our brains, through hundreds of millions of years of evolution, have developed to subjectively represent our environment in a meaningful way is arguably one of the most fascinating human endeavors, whether approached from a biological, psychological, or even philosophical angle. Binocular rivalry is only a small, insignificant phenomenon that more than likely represents a “side-effect” of evolution, but in studying its mechanisms, and further specifying how patterns of brain activity specifically reflect perceptual events, it may be possible to uncover general principles underlying the neural mechanisms of perceptual organization.

APPENDIX

EXTRACTION OF EYE MOVEMENT DATA

The measurement of eye position is extremely important in the present physiological experiments for a number of reasons elaborated in the physiology chapter. Aside from the behavioral control it affords the experimenter over when the animal is performing its task correctly, an accurate and precise knowledge of the direction of gaze is invaluable for understanding the factors that make cells in the cortex fire in the awake animal.

In the present experiments, we have measured the position of the eye using the *scleral search coil technique* (Robinson 1963). Although a complete description is out of the scope of the present discussion, I will briefly describe the basic principles. First, a small ring of wire, about 1.0-1.5 cm in diameter is implanted in one eye of a monkey during sterile surgical procedure. The ring consists of 2-3 loops laid over each other, and wrapped a final time, with the ends of the wire coming together to form a lead. The ring is permanently fastened to the sclera with sutures and/or medical adhesive, and positioned evenly around the limbo-scleral margin with the lead exiting the orbital cavity laterally and running subcutaneously to a connector in the monkey's head post. During experimental sessions the monkey sits in a magnetic fields consisting of both horizontal and vertical components on the frontal plane. Faraday's law

$$e \propto -N\frac{df}{dt}$$

governs the voltage generated in the loop as the monkey moves his eyes, where e is the measured voltage signal, N is the number of turns of the coil on the eyeball, and $\frac{df}{dt}$ is the change in magnetic flux through the coil through time. When the monkey looks straight ahead, and the loop is perfectly on the frontal plane, there is no flux through the coil, and hence no measurable voltage. When, however, he deviates his eye slightly in any direction,

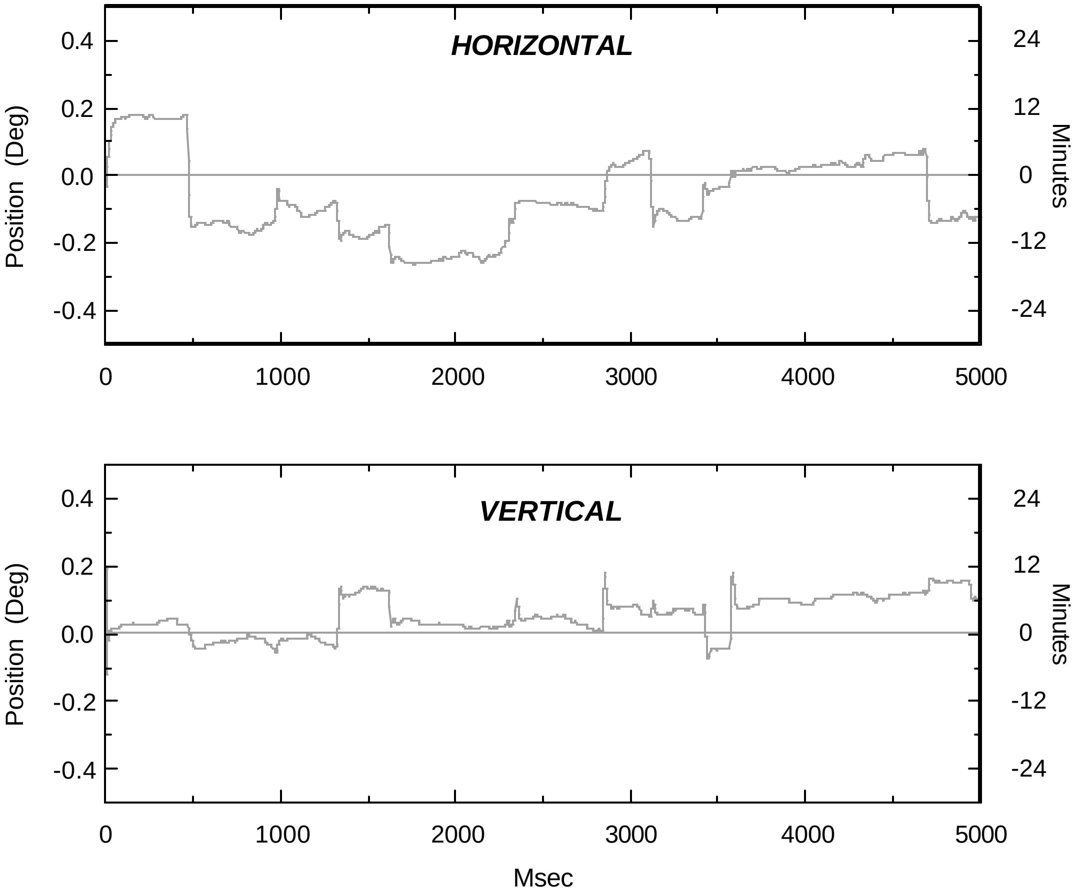


Figure 72 Raw eye movement signal collected during binocular rivalry task.. A 0.15 degree fixation square was present in the center of the image, and the monkey was not allowed to deviate more than 0.4 degrees in any direction from this point..

the flux, and therefore the measured voltage signal, will change. Horizontal and vertical components of the eye position signal can then be deconvolved because their respective magnetic driving fields differ with respect to phase or frequency. In the present we use the CNC Engineering Inc. eye monitoring system, and obtain an precision of better than 1 minute of arc. An example of a typical eye movement trace is shown in Figure 72.

Saccade Identification

One can see that the signal in consists of periods of relative stability occurring between quick jumps in eye position, corresponding to fixation epochs and saccades, respectively. In the present study we were interested to accurately extract all the possible information about saccades and fixation periods in order to determine the relationship of eye movements to perception, as well as to physiological responses of individual neurons.

During data collection the eye movement signal is continuously sampled at 200 Hz for the horizontal and vertical components independently. In this section I describe the initial saccade identification applied to each of the traces individually. First, the 5 msec intervals in the traces were interpolated using a cubic spline algorithm and expressed again at 1 msec intervals. This method was chose because it was data-driven, it preserved the positions at each of the original data points, and it eliminated high velocity artifacts arising from the 5 msec sampling. The general strategy in detecting saccades entails finding peaks in eye velocity. In this first pass, the velocity was calculated by differentiating the position signal, peaks greater than 3.0 deg/sec were considered to be candidates for saccades. This value was arrived at empirically, and was selected so that even small saccades could be detected as long a they met with the other criteria listed below.

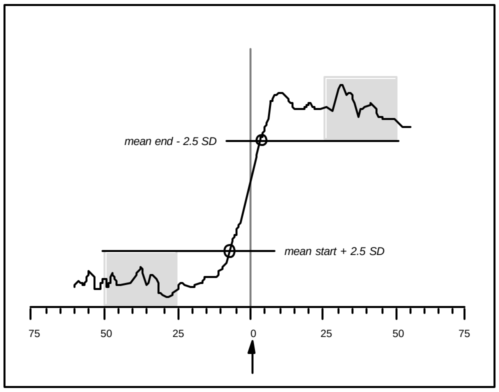


Figure 73 Identification of saccades in the individual traces. Deviation was measured in the stable fixation periods before and after the saccade itself (gray area). This was used to determine accurately the beginning and end of saccades, based upon monotonic increases outside of the normal fixational noise. Open circles represent the start and stop times for a single trace. These were later refined when information from the horizontal and vertical traces was combined.

Next we evaluated each of the prospective saccades to make certain it resembled a saccade in aspects other than just its peak velocity. This entailed, for one, verifying that any saccades consisted of fast, monotonic changes in position. In order to do this, we needed a measure of the normal deviation (noise) in eye position during a stable fixation period. Based on the initial first pass detection described, candidate stable periods were identified between the saccades. The mean and standard deviation of the position signal was calculated for each trace for the intervals from -49 msec before to -25 msec before the saccade time (velocity peak) and +25 msec after to +49 msec after the saccade time (shown in grey in Figure 73). These periods were chosen because they did not include the saccade itself, but would give a good measure of the noise in the stable periods.

The mean standard deviation found for both horizontal and vertical eye traces was 0.003 degrees (about 11 seconds of arc), which is in agreement with previous measurements of positional deviation in fixation due exclusively to drift and tremor (Barlow 1952; Carpenter 1988). Saccades were only accepted if they departed from the normal variability found in fixation periods noise (>2.5 times the measured s.d.) and followed a monotonic positional

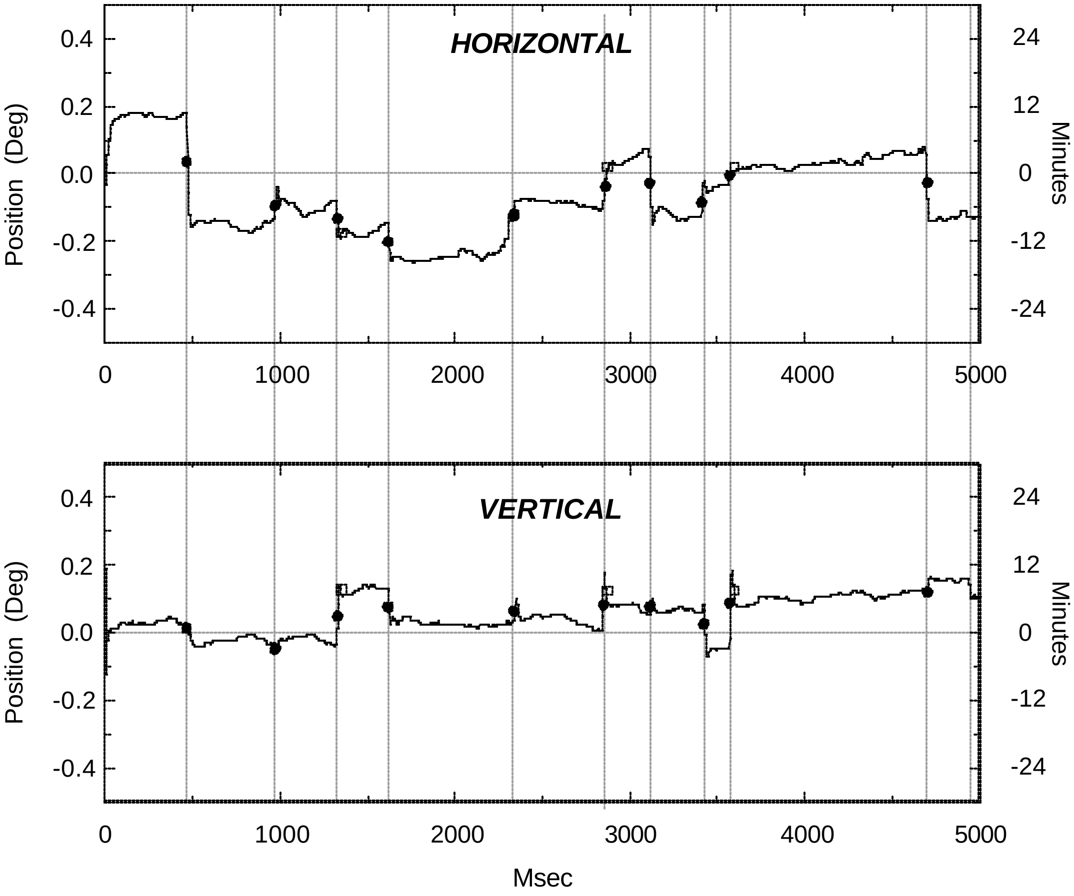


Figure 74 Detected saccades on the trace from Figure 72. The filled circles correspond to real saccades, while the open squares represent corrective saccades.

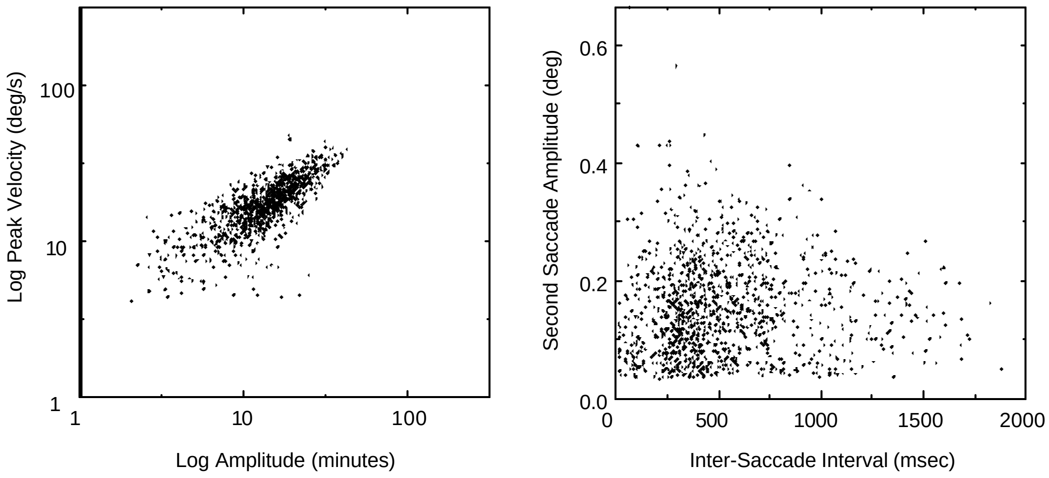


Figure 75 Statistics of microsaccades during nonrivalrous fixation trials. In the left panel is plotted the saccades peak velocity vs. amplitude, and on the right is shown the saccade amplitude against the waiting time since the last saccade.

change in the same direction as the velocity peak for at least 10 msec. Using this method, the beginning and end of the saccades were identified (open circles in Figure 73).

The saccades extracted from the velocity peaks were classified based on their passing the tests described above, and those that did were classified as *real*. If a potential saccade failed to either have a well-defined monotonic region, or was not preceded or followed by a stable period, it was not analyzed further as a saccade, nor was it incorporated into the stable fixation periods described below. The exceptions to this rule were saccades which occurred within 40 msec after a real saccade, which were categorized as *corrective* and were not immediately preceded by a stable period.

Detecting saccades in two dimensions relied largely on first calculating the one-dimensional solutions and then comparing them. Peak in the velocity trace occurring within 15 msec of each other were considered horizontal/vertical matches. Since roughly horizontal and roughly vertical saccades are represented by a deviation in only one of the two traces, we did not reject unmatched saccades, but kept them and labeled them as such. Two dimensional saccade positions (initial and final), amplitudes, directions, and classification types were registered. Figure 74 shows the saccades detected in the eye traces in Figure 72 using this technique. The black circles corresponds to the real saccade times, and the open squares to the corrective saccades. . Real saccades were assessed for their similarity to those described for humans in the literature. The relationship between their individual amplitudes and peak velocities, as well as their amplitudes and intersaccadic intervals are shown in Figure 75, and these patterns match very closely those observed previously (Carpenter 1988).

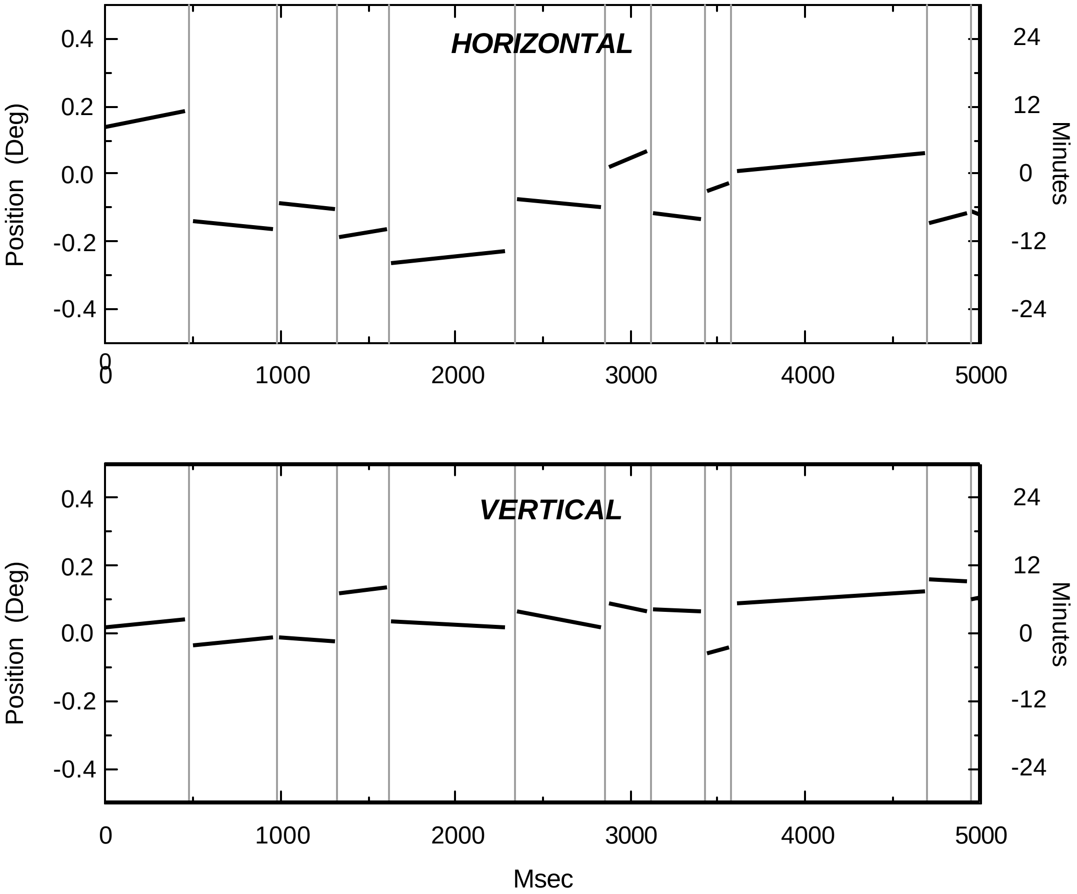


Figure 76 Extracted fixation periods from the raw trace shown in Figure 72.

Stable Fixation Periods

Stable fixation periods were considered to be those regions between the identified saccades. These periods typically were characterized by low amplitude noise superimposed on a slow, constant drift (between 3-6 minutes of arc per second). For each of these periods, the beginning and end times were registered, as well as the mean position, the drift velocity, and the standard deviation of the noise (above and beyond the drift itself). The extracted fixation periods were subsequently used in the analysis to get the best possible estimate of eye position and refixation effects.

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Thus science marches on blindly, without regard to the welfare of the human race or to any other standard, obedient only to the psychological needs of the scientist…

<u>The Unabomber Manifesto</u>

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