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On the Physiology of Bistable Percepts

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Abstract

Binocular rivalry refers to the alternating perceptions experienced when two dissimilar patterns are stereoscopically viewed. To study the neural mechanism that underlies such competitive interactions, single cells were recorded in the visual areas V1, V2, and V4, while monkeys reported the perceived orientation of rivaling sinusoidal grating patterns. A number of neurons in all areas showed alternating periods of excitation and inhibition that correlated with the perceptual dominance and suppression of the cell's preferred orientation. The remaining population of cells were not influenced by whether or not the optimal stimulus orientation was perceptually suppressed. Response modulation during rivalry was not correlated with cell attributes such as monocularity, binocularity, or disparity tuning. These results suggest that the awareness of a visual pattern during binocular rivalry arises through interactions between neurons at different levels of visual pathways, and that the site of suppression is unlikely to correspond to a particular visual area, as often hypothesized on the basis of psychophysical observations. The cell-types of modulating neurons and their overwhelming preponderance in higher rather than in early visual areas also suggests – together with earlier psychophysical evidence – the possibility of a common mechanism underlying rivalry as well as other bistable percepts, such as those experienced with ambiguous figures.

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1 Introduction

1.1 Multistable Percepts

Pictures and geometric figures (Figure 1) that spontaneously change in appearance, such as depth or figure-ground reversals, have always been thought of as powerful probes for understaning the nature of the perceptual system. When we look steadily at the picture of a real object the information received by the retina remains largely constant, and so does the perception of the object, presumably because of the richness of information derived by integrating a large number of visual cues. For example, under natural conditions the perceptual representation of an object's contour, commonly considered as a primary factor for determining the figure-ground relationship, does not solely rely on the detection of spatially abrupt luminance changes, but also on a variety of other changes that usually occur close to an object's boundaries. Changes in luminance, for instance, most often occur concurrently with variations in stereoscopic depth, or alterations in color and texture. Integration of such, often redundant, cues very rarely permits alternative interpretations of a complex scene.

When the visual cues provided, however, do not suffice for one single interpretation, then rival possibilities can be entertained and perception becomes ambiguous, swiftly switching between two or more alternatives without concomitant change in the message received from the eye. Classical examples of figures eliciting different perceptions are the figure-ground and depth reversals. For instance, figure-ground reversals, *e.g.* the Goblet and Faces figure (Figure 1a), often occur when a boundary contour that results from the apposition of two adjacent surfaces can be assigned to either one surface. In general, boundary contours are due to occlusion of a surface by another surface, and are determined by the intrinsic shape of one of the surfaces, and not the other. Assignment of the boundary contour to a surface, in turn, determines one possible foreground-background configuration. Pomerantz and Kubovy (1986) give a good description of the factors that promote an image-part to appear as figure.

Depth reversals, on the other hand, are most likely due to the fact that vision begins with a projection of a three-dimensional space to a two-dimensional surface like the retina. Thus, although a straight line in the world will necessarily cast a straight line on the retina, a straight retinal line may be the projection of any one of an infinite number of lines or even curves viewed by an accidental vantage point. For example, when looking at the line-drawing of a cube (Figure 1b), the perspective of the object changes abruptly in a manner that the "front side" of the cube can suddenly be perceived as the cube's "back side", and vice versa. Perceptual depth reversals can occur even with real $3D$, transparent or wire-frame objects if disparity cues are eliminated by inspecting the objects monocularly.

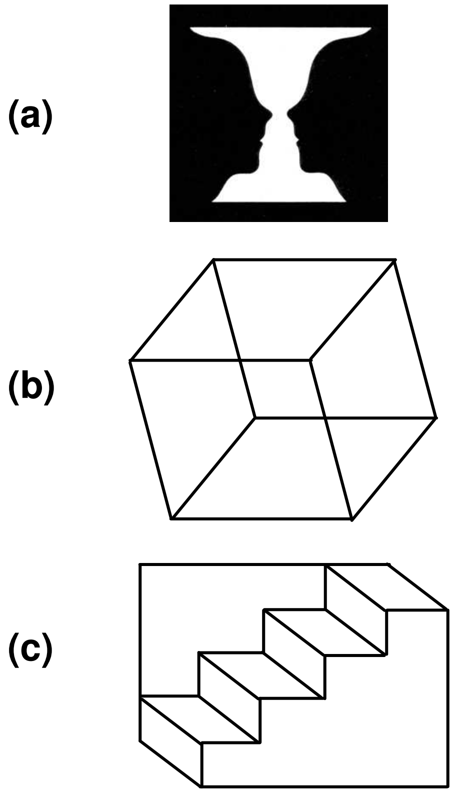


Figure 1: Examples of bistable stimuli. (a) Rubin's reversible figure-ground pattern. Either a vase or a pair of faces in profile is seen. (b) Necker cube, named for the Swiss naturalist Louis Necker. It can seen to oscillate between two alternative perspectives. (c) Schroeder staircase. Another depth reversal example with two alternative perspectives.

Understanding the neural processes underlying such perceptual alternations is a formidable task, but at the same time one of obvious importance, since the reason for the multistability probably lies in the brain's physical organization, which imposes several constraints on the processing of visual information. Why is it that our visual system fails to lock onto one aspect of an ambiguous figure? What accounts for the spontaneous changes of interpretation? If apperception corresponds to a given state of a neural network, and the perceptual alternations reflect state-changes caused by fatigue or adaptation of the network's elements, what is it that adapts, given that – at least in the case of reversible figures – most if not all of the individual units of the network may remain active when viewing either configuration?

The experiments described in this paper were motivated by these questions. To study the neural processes underlying the perceptual multistabilty experienced while viewing ambiguous figures, we set out to examine electrophysiologically the behavior of single neurons during the phenomenal alternations between two or more distinct percepts that follow when different stimuli are simultaneously presented to the two eyes – a phenomenon known as *binocular rivalry*. The rationale for the choice is simply the fact that reporting binocular rivalry can be in principle an orientation discrimination task that could be systematically taught to nonhuman primates.

1.2 Binocular Rivalry

1.2.1 Psychophysical Studies

Binocular rivalry ensues dichoptic stimulation with any dissimilar stimuli, such as patterns with very large positional disparities, images of different objects, or simple gratings that differ in orientation, spatial frequency, velocity or wavelength. The perceptual alternations characterizing binocular rivalry can also be experienced between afterimages (Breese, 1899) and optically stabilized images (for example Ditchburn and Pritchard, 1960); a fact that eliminates at once peripheral variables such as eye movements, local adaptation, and shifts in accommodation as causitive factors in the production of the alternations. Moreover, stochastic analysis of rivalry alternations produced by retinally stabilized images (using the method of enduring afterimages) revealed the same parameters as measured under normal dichoptic conditions (Blake et al., 1971). Such evidence strongly suggests that binocular rivalry is instigated by a central mechanism, and that the perceptual disappearance of the stimulus is due to a disruption of normal flow of information in later processing stages of the visual pathways.

The mechanism responsible for the neural suppression, which in turn leads to the perceptual disappearance of a suprathreshold stimulus, is triggered as long as one of the competing stimuli exceeds normal threshold visibility (Blake, 1977). Hence, contrast sensitivity for a stimulus in one of the eyes is not significantly influenced by a rivalrous contralateral stimulus, regardless of its contrast level. Once binocular rivalry is induced with suprathreshold stimuli, however, the suppressed eye suffers a general reduction in sensitivity, *i.e.* , when test-probe stimuli are presented to the eye during the suppression phase, thresholds are found substantially elevated for a variety of stimulus attributes. Increases are reported in detection thresholds (Wales and Fox, 1970; Makous and Sanders, 1978; Blake and Camisa, 1978), incremental detection thresholds (Wales & Fox, 1970), reaction times in a motion detection task (Fox and Check, 1968), letter recognition thresholds (Fox and Check, 1966), and latencies in detection of sudden spatial frequency and orientation changes (Blake and Fox, 1974b).

Based on these and other studies it has been suggested that suppression affects the whole "monocular" processing (Blake et al., 1980); that is, suppression is not selective for the rivalry-inducing stimulus, but it rather blocks the entire processing of the information coming through the suppressed eye (but see also Discussion). Exceptions are the processing of color information and of patterns with largely different spatial frequency spectra. Suppression appears to affect differentially the color-opponent and the achromatic mechanisms (Smith et al., 1982), and signals from the short wavelength-sensitive cones do not contribute appreciably to binocular rivalry (Rogers and Hollins, 1982; Stalmeier and De Weert, 1988). Simultaneous rivalry and fusion is possible, on the other hand, with images having spatial frequency spectra that are separate by at least two octaves (Julesz and Miller, 1975). Taken together, all these psychophysical investigations show that during the suppression phases of rivalry a complex, high-contrast, continuously presented visual pattern presented to one eye is rendered entirely invisible for several seconds at a time. Where in the visual system does such suppression occur?

The question has been addressed repeatedly in psychophysical experiments by exploiting two facts: (1) the magnitude of most aftereffects increases (up to a limit) with exposure duration, and (2) during rivalry the duration of physical stimulation is different from the duration of phenomenal viewing. Thus by examining the magnitude of an aftereffect during rivalry, one can infer whether or not various attributes of a stimulus are processed even while perceputally suppressed.

Results from these studies showed that binocular rivalry exerts no influence on the growth of contrast-threshold elevation and spatial frequency shift aftereffects (Blake and Fox, 1974a), of the linear motion aftereffect (Lehmkuhle and Fox, 1975), and the tilt aftereffect (Wade and Wenderoth, 1978), as the recovery time from all these aftereffects appears to be proportional to the physical and not the perceived stimulus presentation. The orientation or direction specificity of these aftereffects has been thought to indicate that the processing of information about the adapting stimulus is uninterrupted during suppression at least up to the level of striate cortex, where such stimulus-specificity is first encountered. Also unaltered by suppression is the interocular transfer of adaptation aftereffects (Wade & Wenderoth, 1978; Blake and Overton, 1979; O'Shea and Crassini, 1981), suggesting, once again, that suppression occurs in or beyond the striate cortex, the site of convergence of the monocular inputs in the primate. Interocular transfer is indeed severely reduced in humans who lack stereopsis (Movshon et al., 1972).

In contrast, the aftereffects produced by nonlinear, spiral motion (Wiesenfelder and Blake, 1990) or by subjective contours (Van der Zwan and Wenderoth, 1994) are reduced when adaptation occurs under rivalry conditions, suggesting that the disruption of perceptual processes may occur as early as in area V2 or in the visual areas of the superior temporal sulcus, known to be involved in the processing of subjective contours (von der Heydt and Peterhans, 1989; Merigan et al., 1993), and complex stimulus motions (Movshon et al., 1984; Tanaka and Saito, 1989; Graziano et al., 1994) respectively.

1.2.2 Electrophysiological Studies

Curiously electrophysiology had little to contribute in the discussion on the site of suppression. Whereas a great deal of electrophysiological research has been conducted on the neural mechanisms of stereoscopic vision (for references see Poggio, 1995), until recently no physiological research was conducted specifically pertaining to the competitive interactions that underlie binocular rivalry. Interocular interactions have been demonstrated at the level of dorsal lateral geniculate nucleus (dLGN) of the cat (Sanderson et al., 1969; Singer, 1970; Rodieck and Dreher, 1979; Pape and Eysel, 1986) and the monkey (Rodieck & Dreher, 1979; Schroeder et al., 1989), however, almost all of them were stimulus-nonspecific.

An exception was the experiment of Varela and Singer (Varela and Singer, 1987), who recorded from the dLGN of anesthetized cats and found that the cell response to a drifting grating presented to the dominant eye (the driving eye) was inhibited by stimulation with an orthogonal grating through the nondominant eye. Ablation of the visual cortex, however, abolished these feature-dependent inhibitory interactions.

Conclusive evidence of absence of any inhibition at a subcortical level in the geniculostriate system came recently from the electrophysiological finding that neurons in the lateral geniculate nucleus (LGN) of the alert monkey do not exhibit any temporal modulation of their activity when an animal is presented with moving rivalrous gratings during a fixation task (Lehky and Maunsell, 1993). Recordings from the visual cortex of cats and monkeys, however, have been somewhat inconclusive. About half of the cells in the primary visual cortex of cats showed a significant depression of their response to their preferred stimulus when a rivalling stimulus was placed in the other eye (Sengpiel et al., 1994). This orientation suppression was, however, contingent upon the neuron having been previously adapted to its preferred orientation. Simultaneous rivalrous presentation after several seconds of a blank screen did not result in suppression of the response. In another study, recordings from extrastriate cortex of monkeys experiencing binocular motion rivalry revealed a surprising diversity of neuronal responses, with 40% of the neurons showing a positive or negative correlation with the monkey's perceived motion direction. Of the remaining 60% about one half were inhibited during the entire presentation of rivalrous stimuli, while the rest were unaffected, discharging equally strongly during the dominance and the suppression phase of rivalry (Logothetis and Schall, 1989).

In an attempt to address the question of the locus of rivalry suppression and the type of neurons that may underlie the perception of the stimulus during the dominance phases of rivalry, we trained two rhesus monkeys (*Macaca mulatta*) to report their alternating perceptions during continued observation of rivalrous stimuli, and concurrently examined the activity of neurons in the striate and extrastriate cortex. In the current paper we discuss the findings from the recordings in areas V1, V2, and V4.

2 Methods

Five human subjects (DM, JP, RH, DE, FW, ages between 22 and 37 yr) participated in the psychophysical, and 2 monkeys in the combined psychophysical-electrophysiological experiments of this study. All human subjects had normal or corrected-to-normal vision and could pass a basic stereo vision test. The use of all subjects was approved by the Baylor Affiliates Review Board for Human Subject Research. The monkeys (*Macaca mulatta*, weighing 7-10 kg) were 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.

2.1 Surgical Procedures

After preliminary training, the animals underwent an aseptic surgery for the placement of the head restraint post and the scleral search eye-coil. 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 hrs before the surgery. Fifteen minutes before the preanesthetic, the monkey was injected with atropine (0.05 mg/kg IM) to avoid congestion during surgery. The animal 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 surgical sites were scrubbed with Betadine and Nolvasan. An additional dose of antibiotic (Tribrissen 0.11 ml/kg) and a initial dose of analgesic (Buprenorphine 0.01 to 0.03 mg/kg, IM) were given and the animal was placed on the surgical table and rescrubbed.

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 (2% 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 pressures and respirations were monitored constantly and recorded every 15 minutes. Body temperature was kept at 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 O_2).

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.

2.2 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 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, $R_{xy} = 0.609, 0.347,$

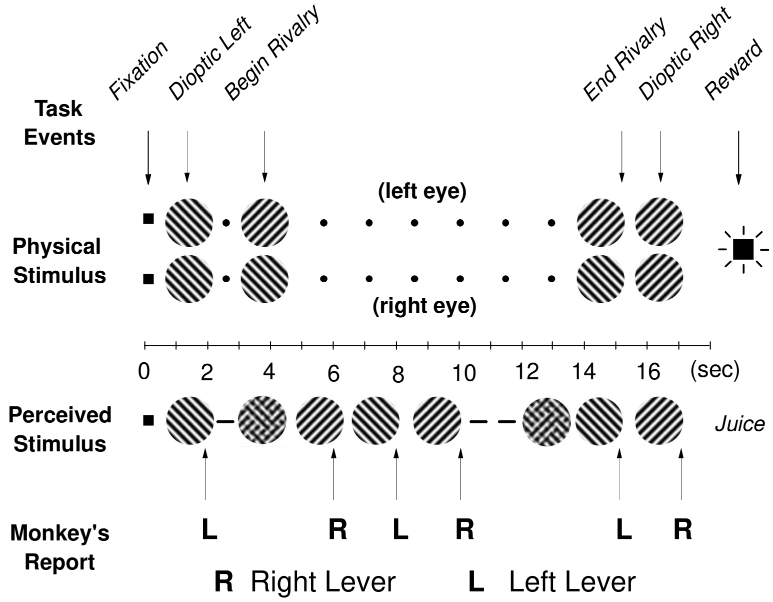


Figure 2: Single observation period during binocular rivalry task. Fixation of a small spot was followed by periods of both nonrivalrous and rivalrous stimulation. Incorrect responses to nonrivalry stimuli resulted in abort of the observation period. In all cases, juice was administered only after an entire successful observation period.

$G_{xy} = 0.286, 0.587$, $B_{xy} = 0.148, 0.076$) 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.

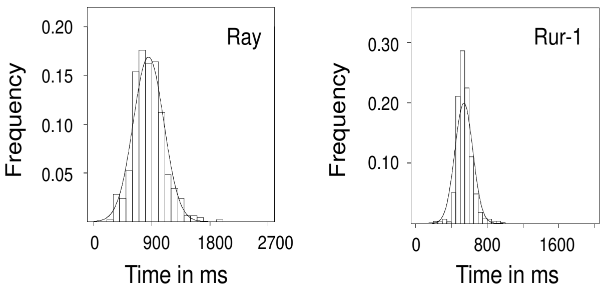
2.3 Training and Behavioral Paradigm

The monkeys were trained to perform a fixation and an orientation discrimination task. Both tasks required continuous fixation of a small central spot within a 0.8×0.8 degrees window. Eye movements were measured with the scleral search coil technique (Robinson, 1963).

In the first task, the animal fixated a yellow spot for periods of 10 to 30 seconds and responded differentially to color changes by pressing one of two levers attached to the front of a primate restraint-chair; right for yellow-to-red and left for yellow-to-green changes. During these fixation periods the neurons' specificity to different stimulus attributes was studied using computer generated bars and gratings.

In the second task, following the fixation of a blue spot, a sinusoidal grating was presented, and the orientation of which was initially alternated between ± 45 degrees up to 10 times in a period of 15 to 25 seconds. The monkeys maintained fixation and reported the stimulus orientation by pressing the right lever for a rightward and the left for a leftward tilted grating within 600–900 ms after any orientation change. The monkeys were initially rewarded for each correct response; incorrect responses or breaking fixation were punished by aborting the entire observation period. When the monkeys consistently attained better than 95% accuracy, the gratings were presented at any right/left orientation (barring orientations within $\pm 5^o$ of vertical and horizontal), and the training continued by reinforcing them after a specified average number of correct responses. Finally, the monkeys were only rewarded at the end of the entire observation period. Yet, feedback as to the correctness of the response was always given by aborting the observation period each time the monkey responded incorrectly. In the training period binocular rivalry was often "mimicked" with congruent stimuli, by smoothly fading one orientation into the other, and permitting the monkey to respond only at the end of the gradual transition. This effectively taught the monkeys that short periods of ambiguity would be followed by resolution, and eliminated quick random responses to the mixed patterns typically observed during the onset of binocular rivalry.

After the animals learned to respond rapidly and accurately to sequences of arbitrary orientation changes, progressively longer periods (from 4 to 12 seconds) of rivalry-inducing stimulation were randomly intermixed with periods of congruent stimulation in observation periods lasting up to 25 seconds. In the rivalrous periods the monkey's exactness in reporting spontaneous changes of perceived orientation was probed by introducing *catch* trials, in which the orientation of one grating was smoothly replaced after a lever-response to yield a coherent binocular stimulus of the orientation indicated by the monkey's last report, and to which the animal was



Statistics for Monkey Ray	
N OF CASES	499
MEAN	**849.148**
VARIANCE	55676.633
STANDARD DEV	235.959
STD. ERROR	10.563
SKEWNESS(G1)	0.509
KURTOSIS(G2)	1.055
SUM	423725.000
C.V.	0.278
MEDIAN	**835.000**

Statistics for Monkey Rur-1	
N OF CASES	2024
MEAN	**554.056**
VARIANCE	9446.069
STANDARD DEV	97.191
STD. ERROR	2.160
SKEWNESS(G1)	3.332
KURTOSIS(G2)	24.572
SUM	121410.000
C.V.	0.175
MEDIAN	**540.000**

Figure 3: Distribution of reaction times for two monkeys during the nonrivalry trials. The median of the reaction times of the monkeys to was 540ms and 835ms respectively.

expected not to respond. A stimulus of orthogonal orientation to that indicated by the monkey's latest report was presented at the end of an observation period. A correct response to this last stimulus was followed by an apple juice reward. The performance of the animals in both the nonrivalrous periods and in the *catch* trials was consistently above 95%. Figure 3 shows the distribution of the reaction times for the two monkeys during the orientation discrimination task with nonrivalrous stimuli.

2.4 Data Collection and Analysis

The three 18mm recording chambers were centered at (9.7P, 8.2D), (10.9P, 10.5D), and (5P, 7D), whereby the foveal representation of areas V1, V2 and V4 could be accessed in the lower half of the chamber (Figure 4). Recording of single unit activity was done using Platinum-Iridium electrodes of 2-3 Megohms impedance. Action potentials were amplified (Bak Electronics, Model 1A-B), filtered, and routed to an audiomonitor (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.

Cells were recorded from the foveal representation of the areas V1 and V2, at the V1/V2 border that represents the vertical meridian of the visual field. Based on ocular dominance preferences in a single penetration, it was often possible to separate striate from V2 neurons. However, since no histology is yet available, the cells in the two early areas will be referred to as V1/V2 neurons. On the basis of stereotaxic coordinates, preliminary mapping of receptive field size and position, and of the receptive field properties, most neurons on the prelunate gyrus or the anterior bank of the lunate were in V4.

The receptive field of each isolated neuron was first plotted with a computer controlled bar stimulus. The width and height of the optimally oriented bar were used to determine the orientation, spatial frequency and size of a test-grating. All parameters were further optimized by listening to the cell's responses while presenting the grating in the center of the receptive field. Quantitative tests of each neuron's specificity for orientation, disparity, and ocular dominance were then conducted while the monkey performed the fixation task. Each test consisted of 5 to 10 presentations in which one stimulus dimension varied at a time, holding all other properties constant at the optimal value for the cell. Subsequently each neuron was tested during the orientation discrimination task with congruent and rivalrous stimuli. The relationship between eye and preferred orientation was pseudorandomized across rivalrous observation periods, so that in each session an equal number of preferred and non-preferred orientations were presented to each eye. Experimental sessions were approximately 4 to 5 hours in duration.

The data were saved in binary files for subsequent analysis. In analyzing the data great care was taken to eliminate the confounding effects of the animal's eye movements. Foveal receptive fields are as small as 0.1 to 0.2 degrees in V1/V2, and are about 1 degree in V3/V4 (Hubel and Wiesel, 1977; Felleman and Van Essen, 1987; Desimone and Schein, 1987). For most neurons (particularly for complex cells) eye movements could in principle be ignored if the stimulus size was much greater than the receptive field of the cell. However, the size of the stimuli, which were centered in the receptive field, had to be kept as small as possible (usually about 0.7 to 1.2 degrees) to promote unitary rivalry. Thus the neuron's activity could occasionally change as a result of small eye movements moving the cell's receptive field beyond the extent of the stimulus pattern. Systematic eye movements can in such a case generate extraneous cell activity modulations, while random eye movements will dilute response modulations due to perceptual changes.

This problem can only be partially solved by reducing the monkey's fixation window, since very small windows typically result in an excessive number of aborted trials, frustrating the animals. Nonetheless, collection of a large number of trials permitted an "off-line" selection of only those trials, in which the monkey maintained accurate fixation. To select such trials, the optimal eye position, *i.e.* the position for which the neuron gave maximum responses, was calculated for each trial as follows.

Mean eye position (X, Y) and spike rate R were first calculated over 35 small time-windows (a 250 ms window that was shifted by 50 msec, beginning 1000 msec before and ending 750 msec after each lever press) during nonrivalrous periods in which the neuron was stimulated with its preferred orientation. The average $(\bar{X}, \bar{Y})$ of the X, Y values for which $R > (\bar{R} + \sigma_R)$, was taken as the center of the ellipse that represents the eye position that "centers" the stimulus within the receptive field. The slope and length of the axes of the confidence ellipses correspond to the eigenvectors and eigenvalues of the distribution of the selected eye positions. Only rivalrous trials during which the eye position remained within the

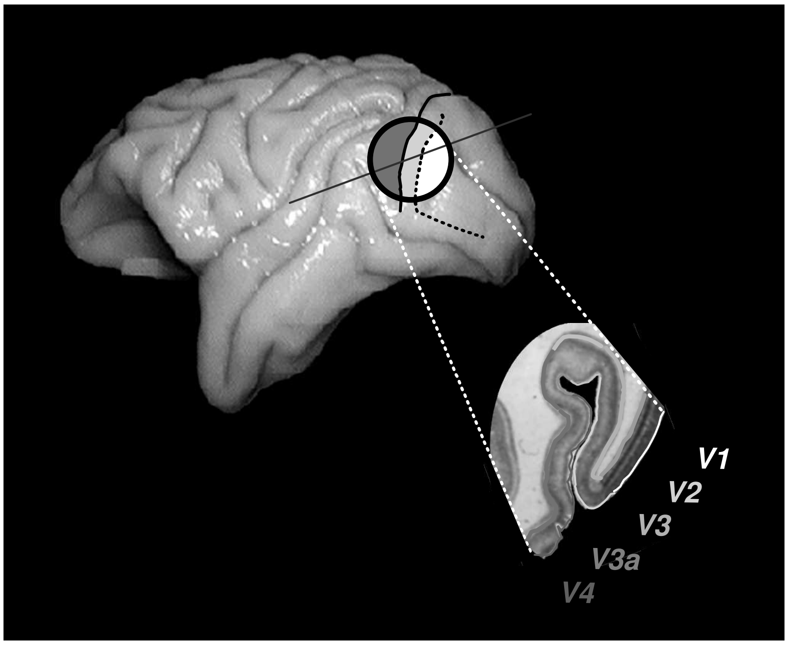


Figure 4: Lateral view of the macaque brain and placement of the recording chamber for the V1/V2 and V4 recordings. The small section on the bottom right shows approximately the location of different visual areas.

confidence ellipse were used to build the peristimulus histograms (or the spike density functions) shown in the next figures.

Figure 5 illustrates the process of selecting an "off-line" receptive field. The upper scatter plot in Figure 5 shows the monkey's horizontal and vertical eye positions during the dichoptic presentations, together with the confidence ellipse and the activity of the neuron for each position. The dark gray square bounded by the black line shows the typical 0.8 degree fixation window used during data collection. The white vertical spikes show the activity of the neuron for a given position in spikes per second. The lower plot shows only those mean eye positions (average of 50 eye position samples in a 250ms window), for which the neuron's response exceeded criterion.

To assess the distribution of different types of cells, *e.g.* neurons that were not affected by the perceptual alternations, neurons that were modulating their responses during rivalry, etc., a modulation index was computed as follows.

First, the position and width of a time-window around the monkey's report-time was determined, within which the neuron's response to the perceived right and left tilted grating showed the greatest difference in terms of mean spikes per second. Specifically, the "optimal window" was computed by determining the difference in the mean spike rate between the right and left report for different combinations of the window's position and width (within some limits; minimum window = 100 ms shift within $\pm$500 ms), by subsequently surface-interpolating these difference values, and finally computing the maximum height of the surface (Figure 6). A modulation index was defined as the square root of the Mahalanobis D^2 distance (Mahalanobis, 1936) between the responses of the neuron to the perceived right and left gratings within this optimal window.

The Mahalanobis D^2 distance (Mahalanobis, 1936) was applied here for univariate statistics, that is it was simply the difference between the mean response of a neuron to right and left perceived orientations in a block of trials, weighted by the standard deviations of the two response distributions (analogous to d' of signal detection, but for the case of unequal variances (Morrison, 1990)). Thus the modulation index in our analysis depends on the mean rate difference, as well as on the variance and number of trials.

3 Results

3.1 Temporal Dynamics of Rivalry

An analysis of the psychophysical performance of the subjects was performed to (a) obtain information regarding the mean dominance and suppression phase of the animals, and (b) to examine the ability of the animals to report reliably their alternating percepts. To this end, the two dependent characteristic parameters of rivalry – the distribution of dominance-phase durations and the effects of interocular contrast differences on the mean phase duration – were calculated and compared with those of the human subjects.

Prior analysis has shown that even though the durations of successive phases are sequentially independent random variables, and although their means vary both

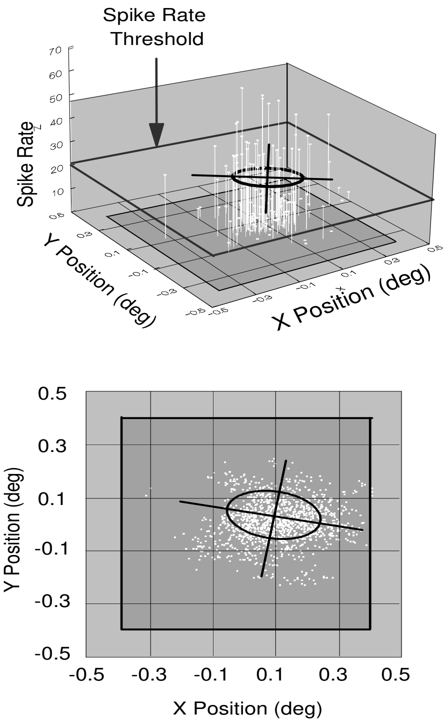


Figure 5: Off-line selection of valid eye position. **(a)** Three dimensional plot cell responses for the preferred stimulus at different eye positions. The ellipse shows the region that was assumed to be the "off-line" receptive field of the neuron, and within which presentation of the preferred stimulus always elicited a brisk response. **(b)** Computation of the confidence ellipse the horizontal and vertical eye movements (see text). The black square shows the typical eye movement window used during the data collection (0.8×0.8 degrees). The white dots show the eye positions for which the response of the neuron to the preferred stimulus exceeded criterion (see text). Only trials in which the eye position was within this ellipse are considered valid and analyzed during the binocular rivalry trials.

with subject and with stimulus type, when durations are expressed as fractions of the mean, their distribution can be reasonably well approximated by a gamma function, the parameters of which show considerable intersubject similarity for both humans and monkeys (Levelt, 1965; Fox and Herrmann, 1967; Blake et al., 1971; Walker, 1975; Myerson et al., 1981; Leopold and Logothetis, 1995).

Figure 7 shows the distribution of dominance phases for 4 human subjects. The smooth lines illustrate a nonlinear approximation of the data with a gamma function

$$f(x) = \lambda^r / \Gamma(r) \; x^{r-1} exp(-\lambda x) \tag{1}$$

where

$$\Gamma(r) = (r-1)! \tag{2}$$

The approximation was accomplished using the Levenberg-Marquardt minimization method (Marquardt, 1963).
The gamma distribution has been commonly interpreted as representing the waiting time for the rth event when

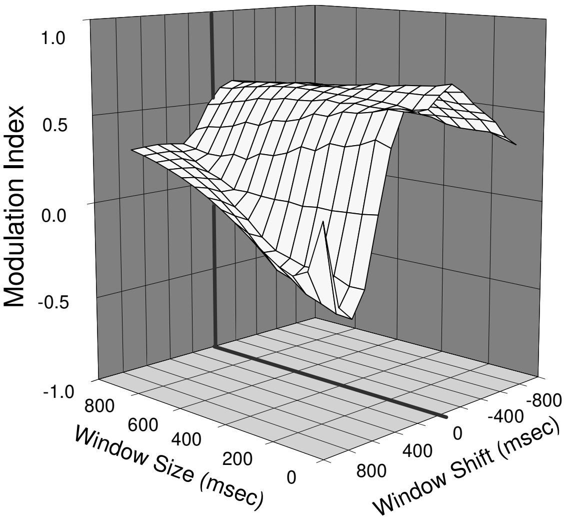


Figure 6: Determination of optimal analysis window. Both the window size and its position were varied to obtain different mean spike rates that were interpolated with the surface shown in the plot. The "highest" point of the surface was used for computing the Mahalanobis distance that in turn determined the modulation index of each cell.

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 at of a number of independent excitations the decision region. 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 not peripheral (Blake 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.

For the purposes of this study it is of secondary importance whether or not this distribution provides information about the neural events instigating binocular rivalry. Of interest here is rather the fact that the parameters of the theoretical distribution for the monkey data do not deviate significantly from those obtained for humans in this and other studies ($\bar{r} = 5.57, \sigma_r = 3.83, t_r = 0.41$, and $\bar{\lambda} = 6.02, \sigma_\lambda = 4.55, t_\lambda = 0.48$; two-tailed t-test) (Levelt, 1965; Fox & Herrmann, 1967; Walker, 1975).

In analyzing the monkey data each phase duration was normalized to the mean duration for a given recording session, to compensate for the changes in alternation rate produced by the adjustment of the stimulus parameters in order to optimize the stimulation of the neurons.

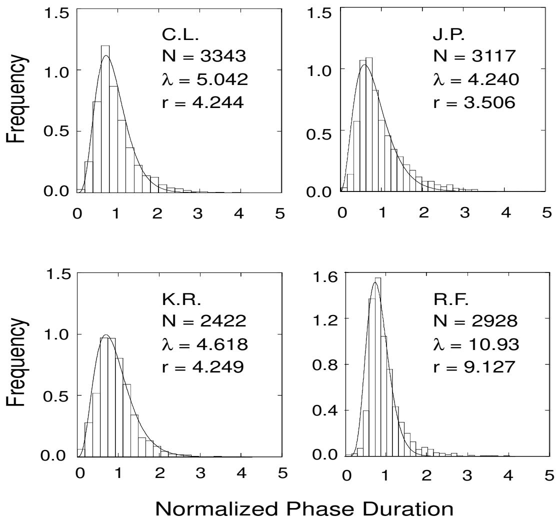


Figure 7: Distribution of dominance phase durations for 4 human subjects.

Figure 8 shows the frequency histograms of relative dominance durations obtained from one of the monkeys next to the data obtained from one of the subjects. 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 (raw $r^2 = 0.927$, corrected $r^2 = 0.878$).

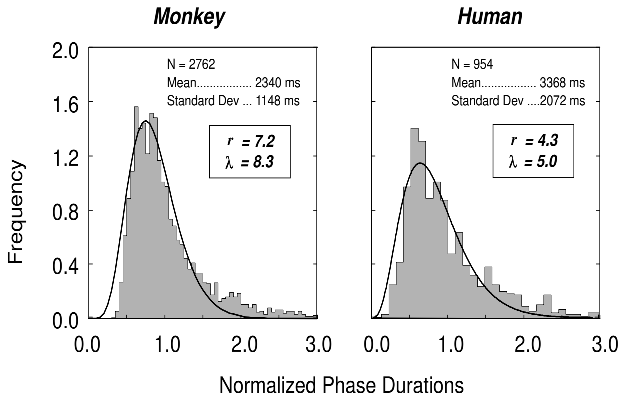


Figure 8: Distribution of dominance phase durations for monkey (left) and human (right). Phase times are normalized to the mean phase time, and each distribution is approximated with a gamma distribution.

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 (Figure 9) also deviates significantly from a gamma distribution (Kolmogorov-Smirnov one sample test) at the $p < 0.005$ level.

The similarity in the parameters of the theoretical distribution describing the monkey and human 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 perceiving binocular rivalry.

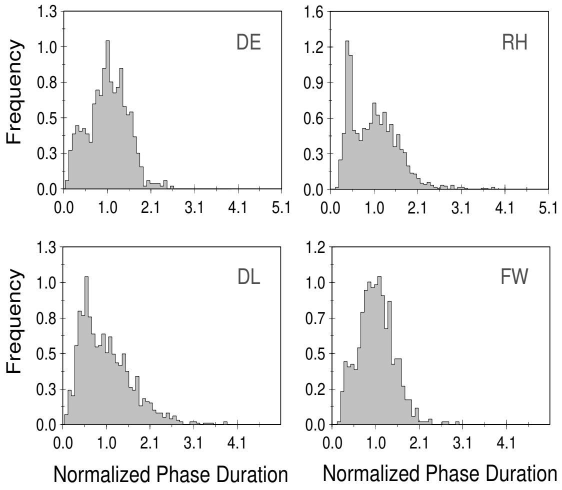


Figure 9: Distributions of "phase times" when subjects were instructed to randomly press the levers, ignoring the stimulus entirely.

However, even stronger evidence as to the reliability of the monkeys' reports comes from the study of the effects of interocular contrast differences on the mean phase-duration (Figure 10). During rivalrous stimulation, increasing the stimulus strength in one eye increases the visibility of that stimulus, not by increasing its mean dominance phase, but by decreasing the mean period for which this stimulus remains suppressed (Levelt, 1965; Blake, 1977; Fox and Rasche, 1969; Fahle, 1982). A consequence of this characteristic is also an increase in alternation rate when the strength of one eye's stimulus is increased. 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.

The difference in mean dominance duration between the two eyes for equal contrasts is most likely due to the subjects' 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 et al., 1934; Enoksson, 1961; Coren and Kaplan, 1973). 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 even the human subject) systematically adjusts its behavior for different interocular contrasts.

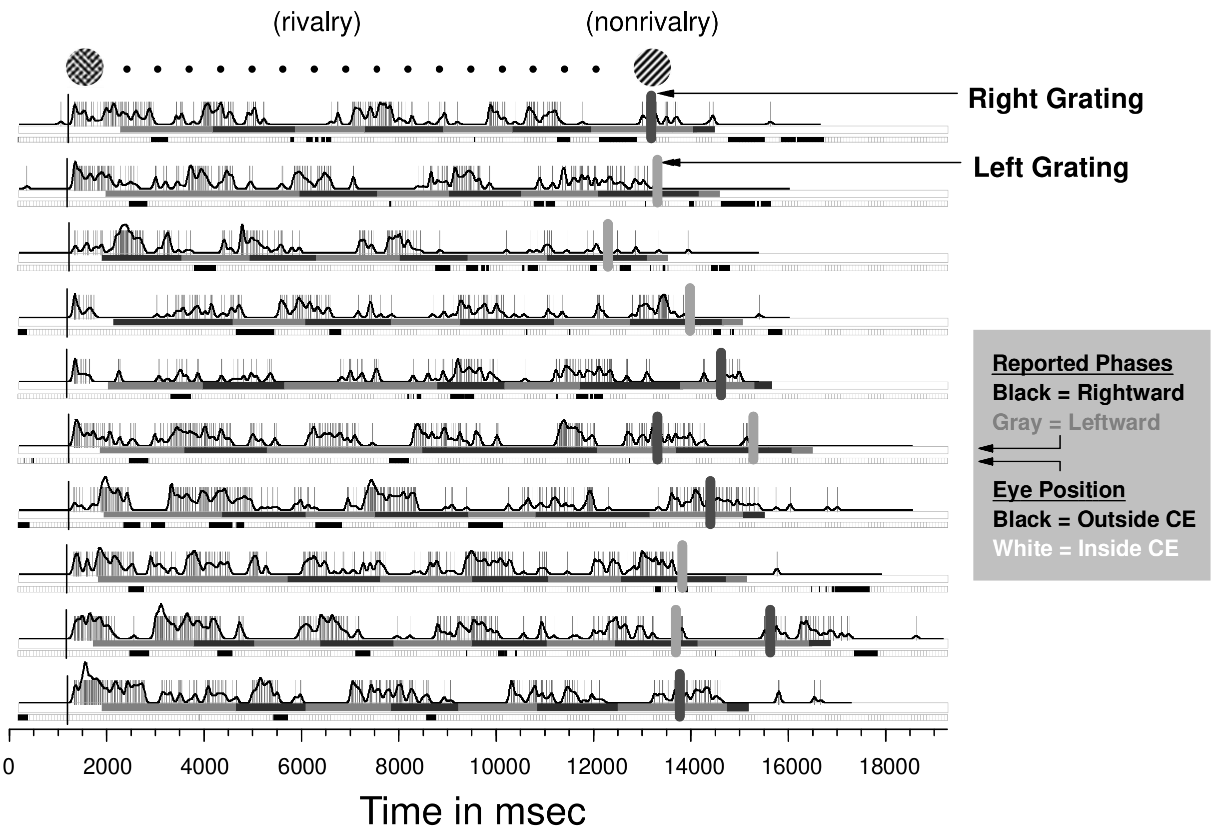


Figure 11: Examples of observation periods of cell activity during rivalry and nonrivalry stimulation. Each of the periods depicted here begins with dichoptic presentation of the two rivalrous gratings. Vertical lines represent cell action potentials. The curved black line represents the spike density function, an estimation of the probability of spike generation at each point in time. The two lower horizontal bars represent the monkey's report and eye position, respectively. In the upper one, gray and black bars represent phases during which the monkey indicates perceiving a leftward and rightward oriented grating, respectively. In the lower bar, white areas represent areas where the monkey's eyes were inside the confidence ellipse (CE) for which the preferred stimulus maximally excites the cell.

3.2 Single Unit Responses During Rivalry

Of the 156 isolated neurons, only the units (N = 101) that were tested completely in all the tasks described in the Methods section are reported here. Based on the initial plotting procedure, the average receptive field size of the V1/V2 and the V4 neurons was found to be 0.520 ± 0.157 and 0.664 ± 0.142 degrees respectively. The average position, in terms of azimuth and elevation, of the receptive field's center was (-0.008, 0.089) degrees for V1/V2, and (0.021, -0.018) degrees for V4. As tested during the fixation task 74.2% of these cells were binocular, 15.8% were monocular and 9.9% were tuned to crossed or uncrossed disparities. Seventy-three of the 101 units (72.3%) were considered orientation tuned, based on the their distributions of mean firing rates for preferred and nonpreferred stimulation. Significance was computed at the $\alpha = 0.05$ level with paired, two-tailed, approximated t-tests for samples expected to have unequal variances.

Figure 11 shows examples of single observation periods. Note the response modulations in the firing rate of the cell as the monkey reports perceptual changes during continued viewing of the same stimulus. To better illustrate the response changes occuring around the time at which the monkey reported a perceptual change, peristimulus time histograms (PSTHs) were constructed from all neural responses for the two trial types. A "trial" here indicates the time window around the animal's response to either a physical change of the stimulus, or to a perceived change during the rivalrous periods. Figure 14a shows an example of such a PSTH for the same neuron shown in Figure 11.

The response of a neuron at the V1/V2 border is illustrated in Figure 12 during both the fixation and the discrimination task. The PSTHs in Figure 12a show the cell's activity during binocular and monocular stimulation with the optimal and null (orthogonal to optimal) orientations, while the orientation tuning of the neuron is illustrated in the upper right polar-plot.

The neuron had a foveal receptive field, it was sharply

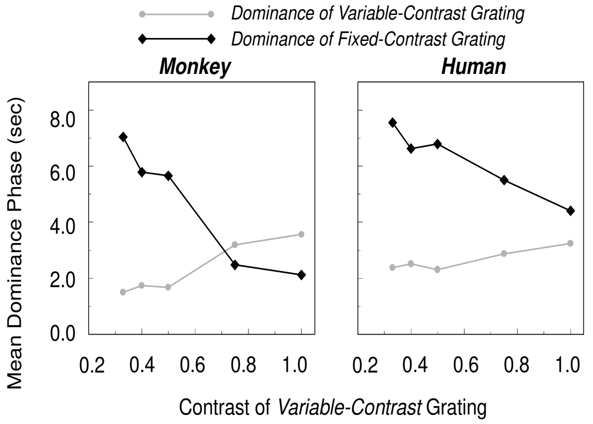


Figure 10: Effects of variation of interocular contrast on the mean dominance phase. Fixed contrast was set to 1.0. On the abscissa is plotted the varied contrast of the stimulus in one eye, and on the ordinate the mean dominance duration of the contralateral (black lines and symbols) and the ipsilateral (gray lines and symbols) eye.

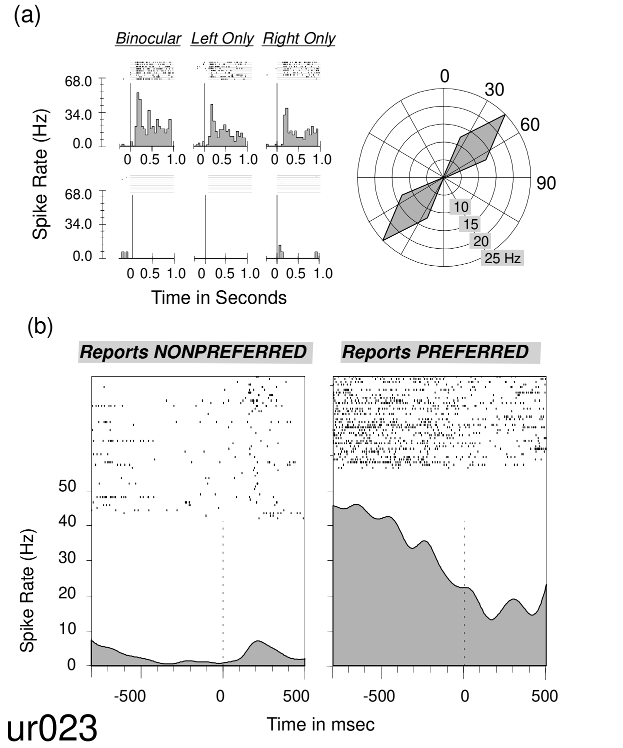


Figure 12: Complete testing of cell from the V1/V2 border during binocular rivalry. **(a)** Testing of binocularity for preferred and null directions (left). Polar plot of orientation tuning obtained during passive fixation (right). **(b)** Cell activity synchronized to the monkey's report during binocular rivalry.

orientation-tuned, and responded equally well to stimulation through either eye. During rivalrous stimulation, however, the neuron's response depended on the perceived orientation. The right plot in Figure 12b shows the spike rate of the cell averaged across all trials in which the monkey reported perceiving the preferred, and the left plot the null orientation of the neuron. The mean response was obtained after aligning the spike trains to the monkey's report. On average, this neuron's activity was suppressed for a time period of approximately 1500 ms, and it remained high for an approximately equal time period.

Figure 12 shows only those trials in which the eye position remained within the excitatory region of the receptive field. The absence of significant effects of eye position changes on the neural responses within this region of the receptive field can be seen in the Figure 13, which shows the cell activity as a function of the monkey's horizontal and vertical eye positions during the dichoptic presentations. The gray square bounded by the white line shows the typical 0.8 degrees fixation window used during data collection. Each small square depicts the spike rate for a given horizontal and vertical eye position, averaged over a 250 msec time-window; white squares show trials in which the monkey reported seeing the preferred and black the null orientation of the grating pattern. Note the different levels of activity for entirely overlapping stimulations. The dark-gray ellipse with the black perimeter shows the confidence region around the mean eye position for which the neuron was optimally stimulated.

Figure 14 shows the activity pattern of two V4 neurons. Both cells had foveal receptive fields, were orientation tuned and binocular. Note the crescendo of the first neuron's activity before the monkey reports seeing the cell's optimal orientation in Figure 14. In contrast, the neuron's activity is increasingly inhibited before the report of the orthogonal orientation. Not all modulating neurons increased or decreased activity before the animal's report. Some neurons changed activity levels clearly after the monkey's response. Moreover, some neurons discharged during the suppression of the grating in the preferred orientation as shown in Figure 14b.

Finally, some V4 neurons (N=5) were strikingly more "oriented" when the animals had to discriminate orientations (whether rivalrous or nonrivalrous stimulation), than during the fixation task, probably reflecting the different attentional requirements of the two tasks (Figure 15).

A quantitative analysis of the cell responses revealed different cell types with respect to their response to congruent and rivalrous stimuli during the discrimination task (Figure 16). About one third (31.7%) of the neurons were found to significantly (α = 0.05 paired, two-tailed, approximated t-tests for samples with unequal variances) modulate their activity during rivalry, while the rest were either inhibited during the entire presentation of the rivalling patterns, or they remained unaffected, discharging with the same rate under monocular, binocular, or rivalrous conditions. Six of the response-modulating neurons were in V1/V2 (18.2% of the total V1/V2 neurons), and 26 were in V4 (38.2% of the total V4 neurons). Interestingly, not all of these neurons were significantly tuned to a particular orientation dur-

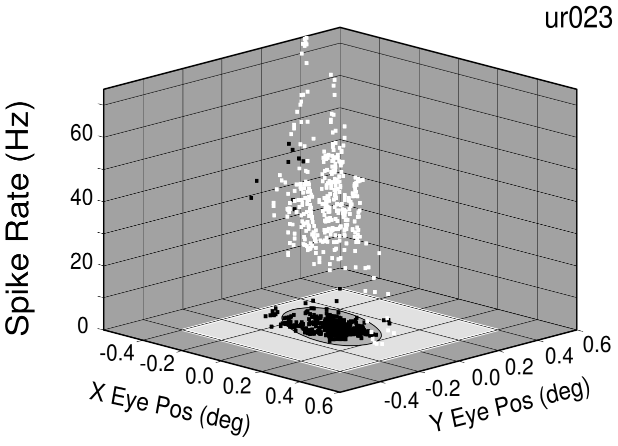


Figure 13: Three dimensional representation of cell activity vs. eye position during binocular rivalry. The white dots represent periods the monkey reported perceiving the cell's preferred orientation, and the black dots represent times the monkey reported the null orientation.

ing the discrimination task with nonrivalrous stimuli. In specific, in areas V1/V2 only half of the cells that modulated their response during binocular rivalry were orientation selective during congruent stimulation. The rest – while responding slightly better to one, rather than to the other orientation – showed no statistically significant preference for either pattern (T-test, $\alpha = 0.05$). Similar results were obtained in V4, where only 16 (61.5%) of the cells that showed activity changes during rivalry were orientation tuned when stimulated with nonrivalrous stimuli.

The orientation selective V1/V2 neurons that also exhibited response-modulations during rivalry were active exclusively when the monkey reported perceiving the neuron's preferred orientation. In contrast, of the 16 orientation selective and response-modulating V4, only 10 (62.5%) units fired best when their preferred orientation was perceived; another 6 (37.5%) cells discharged instead when their preferred orientation was perceptually suppressed. Interestingly, typical cell properties like ocular dominance, disparity tuning, end-stopping, or simple/complex type receptive field organization did not relate in any systematic manner to the neuron's behavior during rivalrous stimulation.

4 Discussion

4.1 On the Site of Phenomenal Suppression

We have reported here the different types of response modulation that cells in striate and extrastriate cortex exhibit during binocular rivalry. The response types observed in area V4 are similar to those described for the middle temporal area (MT) of monkeys experiencing binocular motion rivalry (Logothetis & Schall, 1989). In both areas some cells respond only when the stimulus pattern is perceived and some others when it is phenomenally suppressed. The latter units may be providing the inhibition underlying the truly remarkable disappearance of an otherwise clearly visible stimulus. The

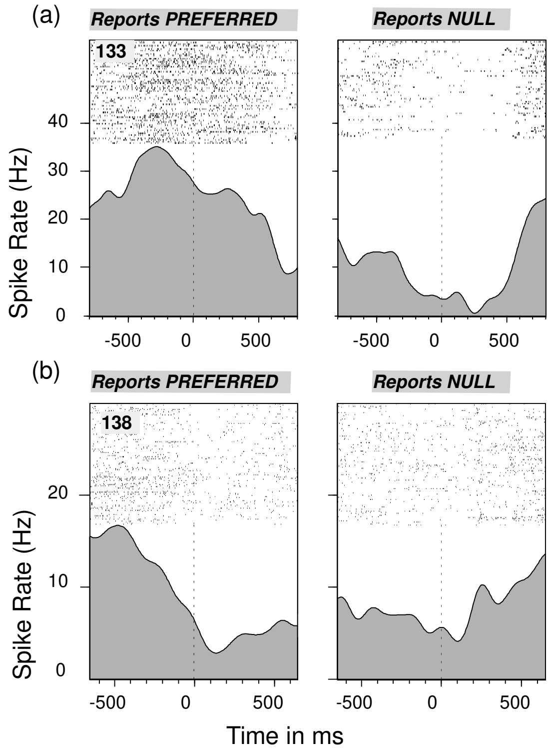


Figure 14: Two cells that modulate significantly according to the monkey's report during binocular rivalry. **(a)** This V4 cell shows maximal activity on average 300-400 msec prior to the monkey reporting the preferred orientation. When the monkey reports the null orientation, the cell's activity drops nearly to zero. **(b)** In this example, again in V4, The cell activtity gradually diminishes starting 500 msec before the monkey reports perceiving the cell's preferred stimulus.

notable fact that increasing the stimulus-strength does not affect the dominance of a rivalry-stimulus, but only its ability to overcome the inhibition exerted by the other eye or stimulus (Levelt, 1965), suggests indeed the possibility of more than one group of neurons being involved in binocular rivalry: one that underlies the perception of the stimulus, and another that may be involved in reciprocal inhibition.

Interestingly, in all studied areas a large number of neurons remained active whether the stimulus was perceived or it was phenomenally suppressed. Why is the firing of this latter group of neurons not enough to support the visibility of a stimulus? What is so special about the neurons the excitation and inhibition of which coincides with the awareness and perceptual disappearance of a pattern? Of great interest would be the cortical or subcortical connectivity and the laminar distribution of such cells (for discussion see Crick and Koch, 1995), but neither issue can be addressed here, since no histology is yet available.

A puzzling finding in these as well as in the motion rivalry experiments (Logothetis & Schall, 1989) was the differential enhancement of the responses of some

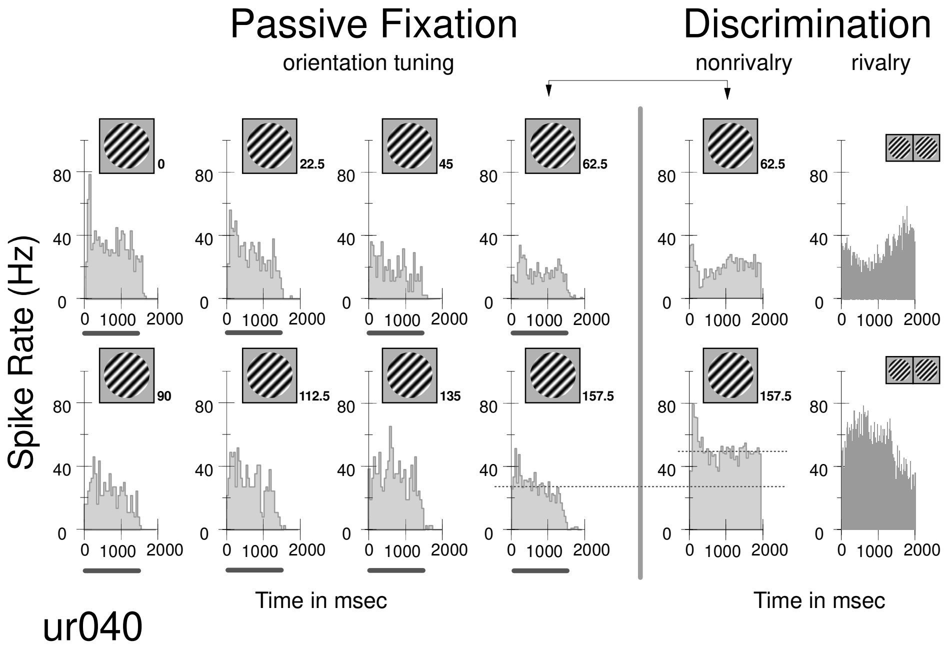


Figure 15: Example of a V4 cell showing increased differential activity during discrimination task. Note that for this cell the preferred orientation during passive fixation was vertical; however, during the rivalry task the target was chosen to be -22.5 degrees, left of vertical. During both rivalrous and nonrivalrous trials, the difference in activity between the preferred and nonpreferred reports were significantly larger than during passive fixation.

cells during only the rivalry periods of the discrimination task. Some of these neurons responded equally well to any of the presented orientations during dioptic presentations, but responded selectively to one of the two orientations used in the rivalry task. A small number of cells were significantly selective to either the vertical or horizontal orientation, neither of which could be used because the monkey discriminated between left and right orientations. Instead the next "best" orientation was paired with its orthogonal orientation, *e.g.* (22.5^o / 112.5^o) instead of (0^o / 90^o). The responses to such alternative orientations, although occasionally not selective during dioptic viewing, were signficantly different during binocular rivalry. Thus at least for some neurons the selectivity observed exclusively during rivalry may be a sensitivity "shift", reflecting some kind of disinhibition occuring during dichoptic stimulation.

The results presented in this paper are difficult to reconcile with the notion of binocular suppression occuring at a specific early cortical stage in the visual hierarchy as has been often suggested on the basis of psychophysical observations. Only a fraction of the cells in any of the tested areas appeared to modulate their response during rivalry, while many other neurons responded well during either the dominance or the suppression phase of their preferred orientation. The latter group of neurons in any of the tested visual areas could mediate all the adaptation aftereffects described above. Yet, it is not clear what the role of these units may be under normal viewing conditions, and why their activity is not sufficient for rendering the stimulus visible during rivalry. With respect to clarity and contrast, a stimulus dominating perception during binocular rivalry is indistinguishable from the same stimulus viewed dioptically. Are the response-modulating neurons during rivalry those underlying pattern perception in normal vision? If so, why does the duration of the adaptation aftereffects reflect the physical stimulus presentation and not the sum of epochs, in which these units are active? Further experimentation may provide some answers to these questions.

4.2 Multistable Percepts

The striking perceptual alternations during binocular rivalry have been attributed by some investigators to fluctuations in attention (Helmholtz, 1962; Walker, 1978) and by others to the structural organization of the visual system. Although it does not deny modulatory effects of attention on the rivalry alternations (Lack, 1978), the latter group of researchers posits that binocular rivalry reflects strong competitive interactions at the level of the visual system where the inputs from the two eyes are combined to establish single vision (Blake, 1989). Among the various models, reciprocal inhibition is the one that received a great deal of support, since it is physiologically the most plausible, and it accounts satisfactorily for the temporal characteristics of binocular rivalry. According to this model, the inputs from each eye compete at the level of convergence in such a way that whenever the strength of one input exceeds that of its

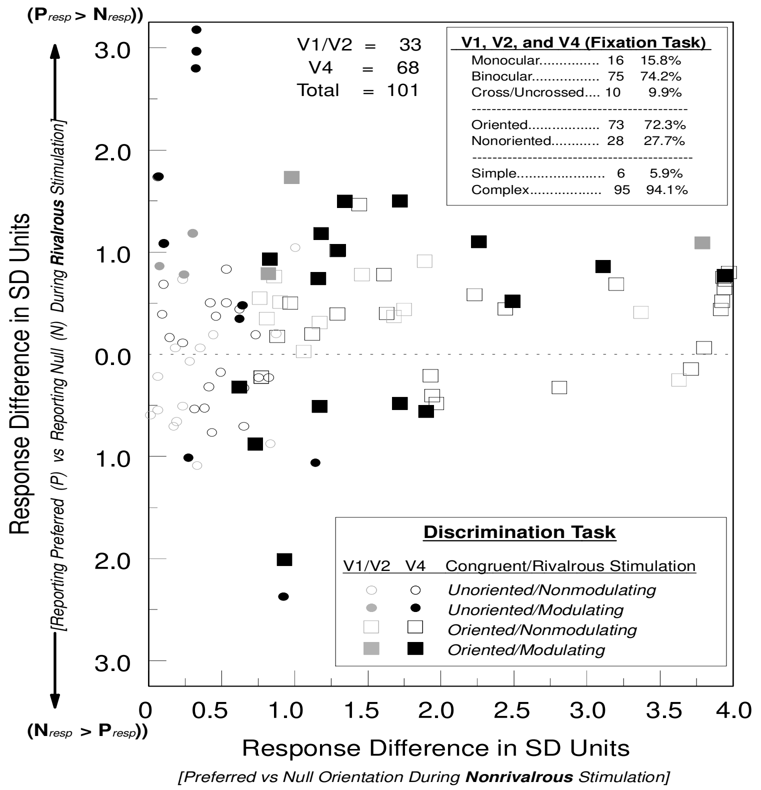


Figure 16: Scatter plot of 101 cells from the V1/V2 border and V4. Gray symbols represent V1/V2 cells and black symbols represent V4 cells. Circles represent cells that did not show significant differences for the two orthogonal orientations for congruent stimuli presented during the discrimination task, squares represent cells that did. Cells whose activity depended significantly on the monkey's reported perceived orientation during binocular rivalry have closed symbols, and those whose activity was not significantly influenced by the monkey's report have open symbols. The abcissa on the plot corresponds to the Mahalanobis distance between cell activity for the preferred stimulus and cell activity for the nonpreferred stimulus. The ordinate represents the Mahalanobis distance between the cell activity when the monkey indicates the preferred stimulus vs. the nonpreferred stimulus during binocular rivalry. For cells positioned above the dashed horizontal line, the cell fired more strongly when the monkey reported perceiving the preferred stimulus. For points below the line, the cell fired more when the preferred stimulus was in the suppressed eye.

competitor, the stronger input inhibits the weaker and temporarily dominates. It then adapts gradually, until at some point it succumbs to the competitor, and the next cycle starts, this time with the other eye dominating perception.

The notion that the perceptual alternations during rivalry are the result of reciprocal inhibition between monocular neurons (Blake, 1989), finds no support in the data presented here. Monocular neurons, many of which receive an inhibitory input from the contralateral eye (Sillito et al., 1980; Poggio and Fisher, 1977), would be expected to dominate the group of response-modulating neurons during dichoptic stimulation, were binocular rivalry exclusively associated with interocular competition; for inhibitory neural mechanisms in early visual cortex are thought to be involved in stereopsis (Poggio & Fisher, 1977), and could be critically involved in the instigation of binocular rivalry. Yet, in our recordings most monocular neurons remained entirely unaffected by the rivalry suppression. Furthermore, binocular interactions – whether among monocular or binocular neurons – would be most likely to occur between the borders of ocular dominance columns at the levels where the initial processing of the merging monocular visual inputs is carried out. However, the proportion of response-modulating cells was considerably higher in areas V4 and MT, than in areas V1/V2.

Interestingly, both areas MT (Logothetis & Schall, 1989) and V4 have cells responding to complex patterns (Movshon et al., 1985; Gallant et al., 1993; Kobatake and Tanaka, 1994), and are thought to be involved in figure/ground segregation (Logothetis, 1994; Stoner and Albright, 1994; Bradley et al., 1995). Moreover, a number of studies indicate that area V4 may be involved in the processing of shape (Kobatake & Tanaka, 1994; Schiller, 1995), and that its activity is modulated by the amount of attention that the animal is required to pay to the presented stimulus (Desimone and Duncan, 1995). Attentional effects were evident also in the data presented here, since some neurons responded significantly more vigorously to their preferred orientation during the discrimination task, than during the passive fixation task. Thus, it seems that changes in the response of neurons during binocular rivalry occur mostly in those visual areas that might be involved in grouping and segmentation, and in which neurons show sensitivity not only to complex patterns but also to the attentive state of the animal.

Evidence that rivalry may reflect more than binocular interactions can can also be found in prior psychophysical work from different laboratories. For one, the perceptual oscillations experienced during rivalry can indeed occur without simultaneous presentation of the incompatible stimuli, often surviving a dark interval of more than 100 msec (O'Shea and Crassini, 1984). They can also occur when both patterns are presented to one eye (Crovitz and Lockhead, 1967; Crassini and Broers, 1982; Wade, 1976). Monocular rivalry, as the latter phenomenon is termed, occurs in the absence of any eye movements, even with afterimages, generated by a brief intense stimulus presentation. A grid, for example, flashed to one eye perceptually breaks down into its individual grating components that compete for visibility in a manner similar to dichoptic stimuli during binocular rivalry (Sindermann and Lueddeke, 1972). The fragmentation of complex patterns while viewing stabilized images is such that, the dominance of a pattern varies according to the contingency of the parts, with perceptual entities such as simple geometrical shapes remaining in view much longer than disjoined line or curve segments (Pritchard et al., 1960). Moreover, during dichoptic stimulation, the rivaling of the neighboring stimuli is more likely to occur in synchrony when they form certain types of figures, even when they are seen by different eyes, than if the nearby stimuli are seen by the same eye but they are not part of the same figure (Whittle et al., 1968). A dissociation of the neural processes of rivalry from those related to binocular vision is also suggested by the differences in visual sensitivity during rivalry and strabismic suppression. For example, individuals with strabismus of early onset, who commonly exhibit suppression for reducing or eliminating diplopia, do not manifest any spectral sensitivity losses during suppression, as do normal observers during rivalry suppression (Smith et al., 1985).

Finally, the fact that the temporal dynamics of binocular rivalry, *e.g.* the stochastic nature of perceptual alternations, the statistical properties of distributions of dominance periods, etc., are noticeably similar to those of ambiguous figures, such as the Necker cube, the Schroeder staircase, or the honeycomb (Borselino et al., 1972), also suggests a general, common principle in the neural interactions underlying perceptual multistability, whether such multistability is generated by dichoptic stimulation or by the inability of the visual system to segment figures from the ground when the visual cues available do not suffice for a unique, stable interpretation.

The possibility thus exists, that alternating percepts during rivalry reflect a competition between mutually exclusive pattern representations, just as it occurs with ambiguous figures. Depending on the properties of the rivaling stimuli, such competition can be local, greatly involving interactions of neurons in early visual areas, or can be dominated by reciprocal inhibition of neurons or neural assemblies representing visual objects. If the latter hypothesis proves to be true, research on the neural mechanisms of binocular rivalry may reveal some fundamental mechanisms that underlie our perceptual organization.

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