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The Role of Attention in Binocular Rivalry as Revealed through Optokinetic Nystagmus

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Abstract

When stimuli presented to the two eyes differ considerably, stable binocular fusion fails, and the subjective percept alternates between the two monocular images, a phenomenon known as binocular rivalry. The influence of attention over this perceptual switching has long been studied, and although there is evidence that attention can affect the alternation rate, its role in the overall dynamics of the rivalry process remains unclear. The present study investigated the relationship between the attention paid to the rivalry stimulus, and the dynamics of the perceptual alternations. Specifically, the temporal course of binocular rivalry was studied as the subjects performed difficult nonvisual and visual concurrent tasks, directing their attention away from the rivalry stimulus. Periods of complete perceptual dominance were compared for the attended condition, where the subjects reported perceptual changes, and the unattended condition, where one of the simultaneous tasks was performed. During both the attended and unattended conditions, phases of rivalry dominance were obtained by analyzing the subject's optokinetic nystagmus recorded by an electrooculogram, where the polarity of the nystagmus served as an objective indicator of the perceived direction of motion. In all cases, the presence of a difficult concurrent task had little or no effect on the statistics of the alternations, as judged by two classic tests of rivalry, although the overall alternation rate showed a small but significant increase with the concurrent task. It is concluded that the statistical patterns of rivalry alternations are not governed by attentional shifts or decision-making on the part of the subject.

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1 Introduction

When the two retinal images are largely different, normal binocular fusion becomes impossible, and the visual system lapses into an unstable state. When one artificially creates such situation, by placing completely non-matching stimuli in the two eyes, the brain's tendency is to choose rather than compromise. This "choice" manifests itself in complete perceptual suppression of one of the competing stimuli while the other remains entirely visible, a phenomenon known as *binocular rivalry*. The dominance of the visible stimulus is only temporary, however, and after a few seconds the suppressed stimulus rises to the conscious level, as the previously dominant stimulus fades away. The resulting alternations in the identity of the perceived stimulus characterize binocular rivalry, and have been studied extensively. Each individual phase of complete perceptual dominance, where one of the rival stimuli is unitarily visible, lasts between several hundred milliseconds and many seconds, and the alternation process is stochastic, with successive dominance phases durations being independent (Fox and Herrmann, 1967; Blake et al., 1971).

The rivalry phase times (durations of complete perceptual dominance) form a characteristic distribution. Specifically, if each of the phase times is expressed as a fraction of the mean phase time, the resulting frequency histogram that resembles a normal distribution skewed towards longer times. This distribution has often been modeled with a gamma function whose r and λ parameters fall within a relatively narrow range (Levelt, 1965; Walker, 1975; Fox & Herrmann, 1967; Blake et al., 1971). Although it is not understood why such a distribution emerges, it is a consistent characterization of rivalry alternation in both humans and monkeys (Leopold and Logothetis, 1995; Myerson et al., 1981).

Rivalry can be initiated by stimuli that conflict across nearly any stimulus dimension. Rivaling stimuli can consist of colored patches (Breese, 1899), simple contours (Walker, 1975), textures (Julesz and Miller, 1975), conflicting directions of motion (Fox et al., 1975), or higher order stimuli such as faces (Yu and Blake, 1992; Sheinberg et al., 1995b). The rate of perceptual switching, besides exhibiting large intersubject variability, is dependent upon the type rivaling stimuli and the "strength" (i.e. contrast, speed, spatial frequency content, etc.) of each stimulus. However, the *distribution* of phase times, when normalized to the mean phase, remains largely invariant to all of these factors, and even substantially different alternation rates yield distributions that are virtually indistinguishable.

When the monocular stimuli presented during rivalry differ in strength, the mean dominance times for the two eyes changes in a predictable manner. Levelt (1965) summarized these effects with four propositions, rephrased here:

1. The fractional dominance of a stimulus increases with its strength.
2. The mean dominance time of a stimulus does not increase with its strength.
3. The overall alternation rate increases with an increase in the strength of one of the stimuli.
4. The overall alternation rate increases with an increase in the strength of both of the stimuli.

The first and second of these propositions, when considered together, predict that a decrease in the strength of Stimulus A (in one eye) will significantly increase the mean dominance time of Stimulus B (in the other eye), while leaving the mean time of Stimulus A unchanged. An alternate perspective reveals that increasing the strength of Stimulus A decreases its mean duration of perceptual suppression. This pattern can be seen for both threshold level (Blake, 1977) and suprathreshold stimuli of all types (Fox and Rasche, 1969; Leopold & Logothetis, 1995) (also, Sheinberg personal communication) in both humans and monkeys (Leopold & Logothetis, 1995).

1.1 Attention and Binocular Rivalry

One of the first explanations of the rivalry phenomenon, put forth by Helmholtz, was based on attention (Helmholtz, 1866). Helmholtz felt that during binocular rivalry, only one stimulus is perceived at any one time because attention strives to produce singleness of vision based on normal visual experience, and that switches in perceptual dominance are caused by attentional shifts. He also claimed that there was significant attentional control over binocular rivalry, and that the 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). Attention can only be used to affect the timecourse of the alternation process, primarily by increasing or decreasing the rate of alternation, yet the limits of this conscious control remain unclear (Meredith and Meredith, 1962; Lack, 1969, 1970).

To study the effects of attention on binocular rivalry, 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 oppositely moving rivalrous stimuli alternate in their visibility, the OKN changes according to the *perceived* direction of motion (Enoksson, 1963, 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 can influence the rate of the perceptual alternations experienced during binocular rivalry, does it also affect the stochastic nature of rivalry and the relation of mean suppression of the eye to the stimulus strength? In other words, do relative dominance phases show their usual gamma-like distribution if neither of the rivaling stimuli is attended by the subject? And, does the stimulus strength of the unattended rivaling stimuli still have the same impact on the inhibitory,

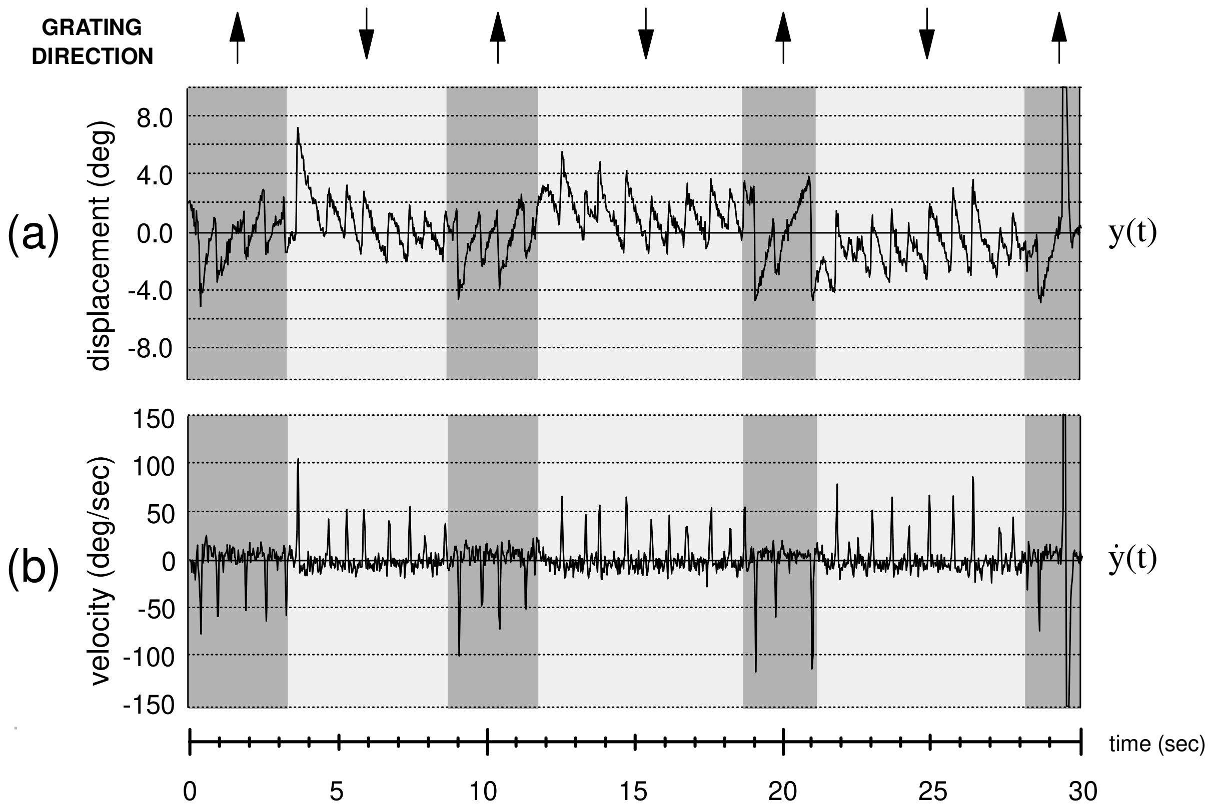

Figure 1: Optokinetic nystagmus (OKN) of a subject during nonrivalry, as measured by and electrooculogram. Throughout the observation period, the grating stimulus is always congruent. The direction of motion changed at random intervals between 1 and 8 seconds. The light gray regions correspond to periods 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 saccade back to the original position (*fast phase of OKN*). The direction of the slow phase indicates the direction of the drifting grating. The large, upward deflection at the end of the observation period is the result of a blink from the subject. During full analysis of the eog trace, blinks were automatically spliced out of the eye movement traces by the 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 downwards saccades, identifying regions of upward grating drift, and vice versa.

competitive interactions occurring during binocular rivalry?

Our interest in these questions is threefold. First, we want to know whether the study of the mechanism underpinning perceptual bistability requires the conscious participation of the subject. The rationale of this inquiry is that we are primarily interested in the neurophysiological investigation of binocular rivalry in the nonhuman primate. It is therefore of great importance to know whether the activity of single neurons in the visual system can be studied during continuous observation of rivalrous stimuli in a fixation task, or whether the participation of the animal is required – and thus excessive training of the animal is necessary – for the interpretation of possible response modulation. Second, we seek to determine the expected alternation rate in different tasks. The latter is of importance in rivalry is otherwise unaffected by the attentional state of the subject, since it could hint at the expected mean time for the neuron's response modulations. Finally, the study of the reaction times for the OKN and manual transitions, together with the possibility of a consistent lag between the two, can also provide significant information as to the time windows within which cell activity may best be studied in electrophysiology experiments.

In these experiments, the alternation process is examined using OKN as the subject performs simultaneous tasks requiring concentration, essentially removing his attention from the rivalry stimulus. First, the reliability of the phase extraction process is assessed by comparing individual extracted phases with matching phases reported by the subject in the attended condition. Next, the phase statistics for this condition are compared with those derived while the subjects were concentrating their attention on a difficult concurrent task.

2 Methods

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

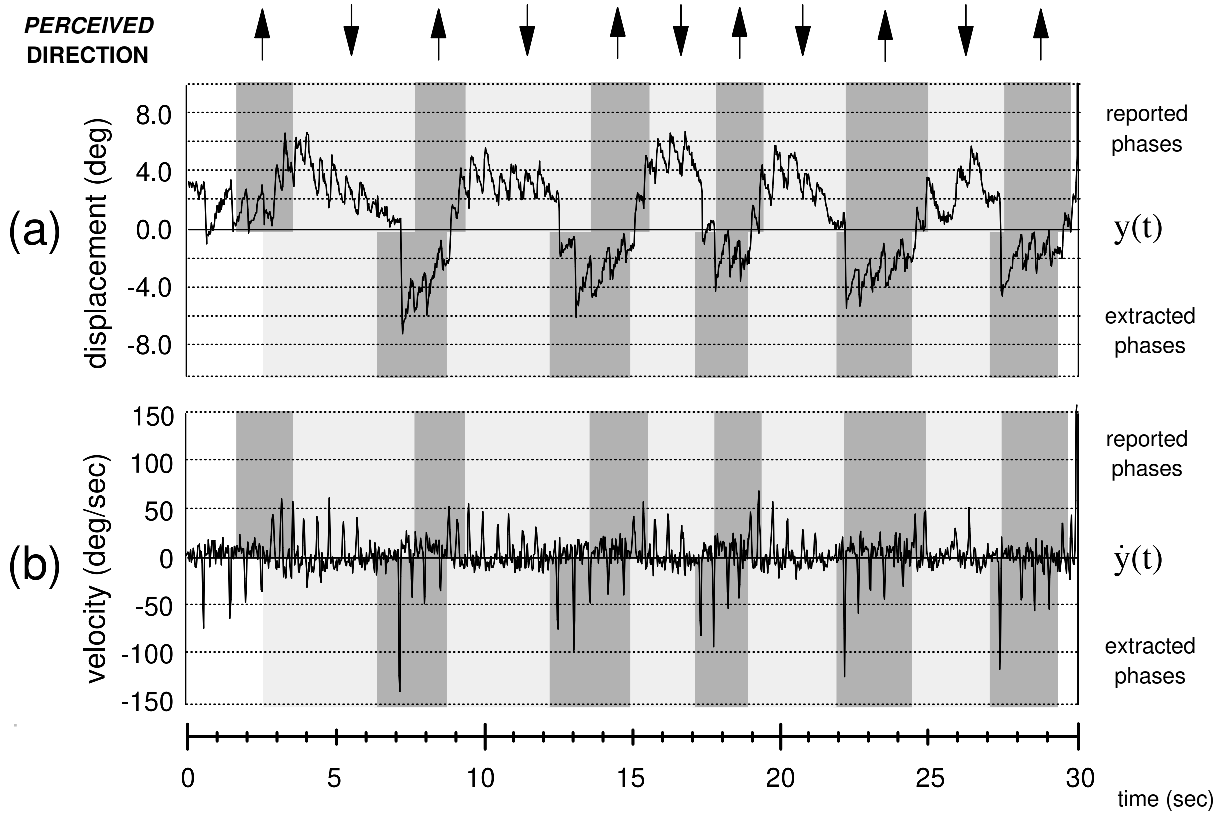

Figure 2: Optokinetic nystagmus (OKN) of a subject during binocular motion rivalry. The subject viewed stereoscopically presented dichoptic gratings, moving upward in one eye and downward in the other. The polarity of the OKN reflected the subject's *perceived* direction of motion. The shading in the 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 downwards OKN 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.

could pass a basic stereo vision test. One of the subjects was one of the investigators, and the other was a paid medical student. The use of all subjects was approved by the Baylor Affiliates Review Board for Human Subject Research.

2.1 Visual Stimuli

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 deg x 10.5 deg,) drifting gratings, bordered by a white frame, 0.26 deg 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 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.

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. In these trials, the physical stimulus never changed.

In experiments conducted for generating the frequency distributions, the contrast of the gratings in the two eyes was fixed at 33%. During the variable contrast

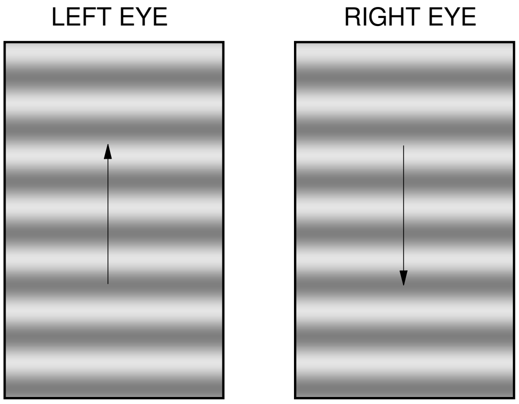

Figure 3: Rivalry stimulus. The stimulus consisted of sinusoidal, low contrast, low spatial frequency gratings drifting upward in the left eye and downward in the right. The gratings were sinusoidally modulated with a spatial frequency of 0.5 cycles/deg, a contrast of 33%, and a speed of 8 deg/sec.

experiments the contrast of one of the gratings was always 33%, while the contrast of the other grating varied between 23% and 33%. On half the trials the variable grating was the in the right eye and on the other half it was in the left.

2.2 Electrooculogram

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.

2.3 Testing Procedure

During the first few 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 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 each of the experiments, the gratings were rivalrous, moving upward in the left eye and downward in the right eye. 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.

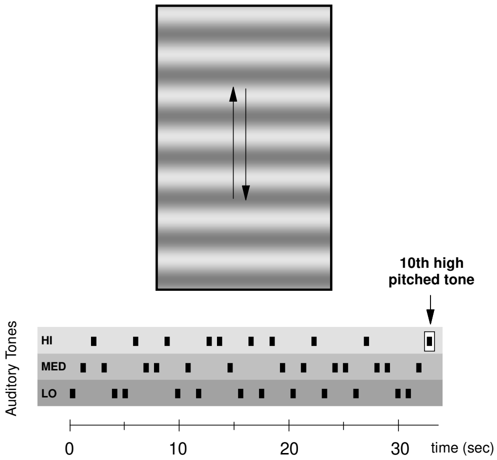

Figure 4: Counting Task. Subjects were required to concentrate on a sequence of auditory tones played by the computer while gazing at the central rivalry stimulus, which was identical to that in Experiment 1. Low, medium, and high pitched tones lasting 150 msec were played at intervals randomized between 300 and 900 msec. The subject was instructed to press a button after the tenth tone of a specified pitch. As the subjects performed the psychophysical task, their OKN was continually recorded.

2.3.1 Experiment 1: Rivalry Report

In the first experiment, the subject attended to the direction of motion of the stimulus, and indicated the perceived direction of motion at each point in time by pressing one of two buttons on a button box. Subjects were instructed to concentrate on the visible direction of the rivalry stimulus. When an upward direction was perceived, the subject depressed the top button, and when a downward direction was perceived the subject depressed the bottom button. During ambiguous phases, the subject was instructed not to press either button.

2.3.2 Experiment 2: Counting Task

In the counting experiments, subjects continued to gaze toward the central region of the rivalrous moving gratings. However, in this case, the subject was required to complete a difficult auditory counting task. During each observation period, a series of low, medium, and high pitched tones were played (see Figure 4). Each tone was 150 msec in duration, and the interval between tones was 600 msec $\pm 50\%$. Subjects listened carefully to the auditory stimulus, counting the tones of a specified pitch, while gazing blankly at the rivalry pattern. The subject was required to press a button after the tenth tone of a specified pitch. Pressing the button before the tenth tone, or failure to press the button in time was counted as an incorrect response. This task demanded considerable attention, and each subject required approximately 30 minutes of practice in order to perform the task with greater than 90% accuracy.

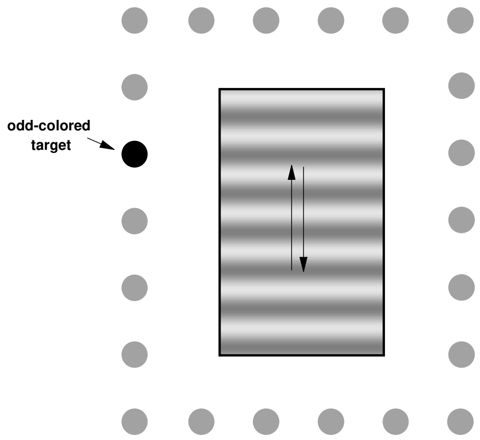

Figure 5: Multiple popout task. Peripheral "popout" stimuli consisted of brief presentations of small red or yellow filled circles surrounding the central rivalrous gratings. After each presentation, subjects were required to report whether all stimuli flashed in the periphery were of the same color, or if one was colored differently from the rest. Again, the OKN of the subjects was recorded during all observation periods.

2.3.3 Experiment 3: Multiple Popout Task

In the final experiment, a concurrent visual task was performed as the subject gazed at the moving rivalry stimulus. The subject was required to attend 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 5). 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 the rest by pressing one of two buttons. The position of the odd stimulus was randomized with each presentation. This "multiple popout" task required constant visual attention from the subject, who again required several practice observation periods to reach 90% reliability.

2.4 Analysis of EOG signal

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 1 illustrates the eye movements during a typical observation period of nonrivalrous, dioptic stimulation. Figure 1a is the filtered EOG signal. In addition to the 40Hz cut-off 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 $y(t)$ (Figure 1a), the slow and fast phases of OKN are easy to distinguish, as are changes in the polarity of the signal. Nonetheless, to facilitate the identification of distinct phases of upward and downward OKN, the time derivative $\dot{y}(t)$ was taken of the filtered signal to yield a continuous representation of the eye's vertical velocity. Peaks in this trace represent saccades, whereby upward peaks are are upward saccades, and downward peaks are downward saccades. Phases containing upward saccades represent phases of perceived downward motion, during which the slow phase of $y(t)$ moves downwards. Likewise, regions of downward velocity peaks represent periods of upward perceived motion.

In order to extract phases from the OKN signal, two of the 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 $\dot{y}(t)$ (see Figure 1a), 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

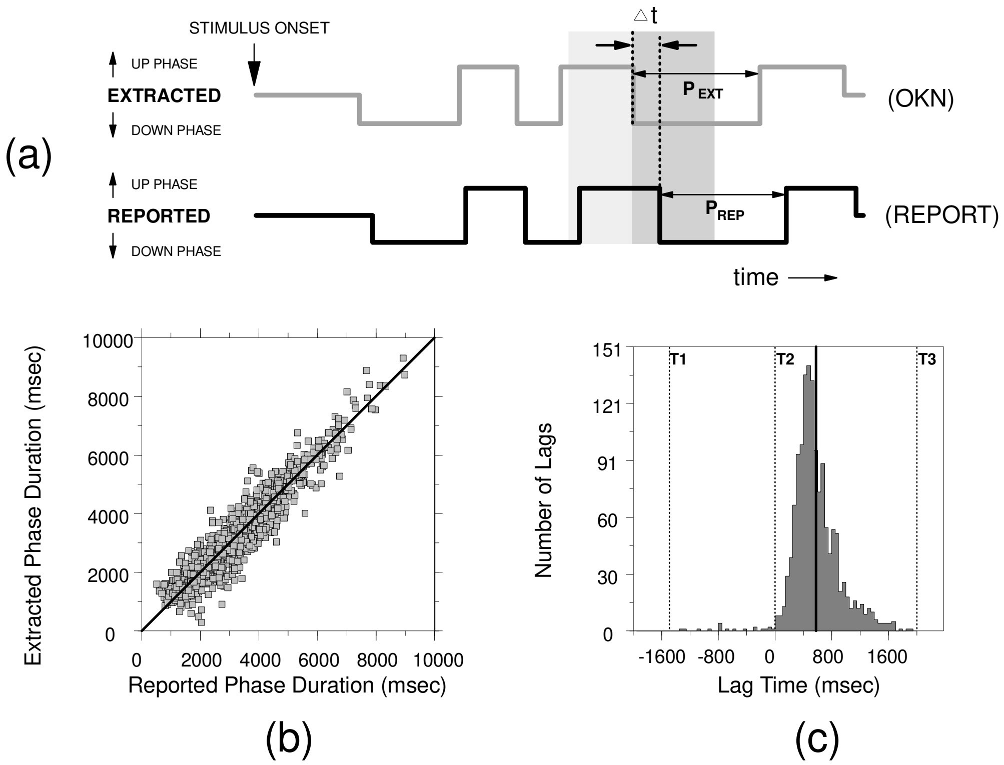

Figure 6: Comparison of reported and extracted dominance phase data. (a) For the observation periods during which the subjects reported their perceived direction of motion, there were two means of evaluating dominance phases. The gray lines represent phases of upward and downward perceptual dominance determined from the OKN (e.g. P_{EXT}). The black lines correspond to the subjective report of upward and downward motion derived from the subject's button press (e.g. 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 transition, and positive values that the extracted transition occurred first. Lines 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.

for this, stimuli that remained dominant for longer than 10 seconds before the end of the observation period are included in the analysis.

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

Table 1: Comparison between extracted and reported transitions: number of phases (N), correlation coefficient (R), mean lag ($\bar{L}$), and percentage of matched phases (%) for each of the two analysts.

The OKN and rivalry report data from Experiment 1 were used to evaluate the reliability of OKN as an objective rivalry indicator. It should be noted that in all cases, the extracted phase information was based entirely on the shape of the eye movement trace. At no time did the analysts consult the button responses of the subject to aid in determining phase transitions.

3 Results

3.1 OKN as an Objective Indicator of Binocular Rivalry

In order to utilize OKN as a measure of the subject's perceived direction of motion, it was necessary 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 percieved direction of motion has previously been established in both humans (Fox et al., 1975) and monkeys (Logothetis and Schall, 1989). A similar approach to the former study was used in the analysis of Experiment 1, 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. Specifically, each extracted phase was compared to the subject's reported direction of motion at that time. Figure 6a 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 in figure 6a. Hence, even the longest reaction times would not be eliminated during the analysis. Finally, a reported transition was not permitted to occur more than 1500 msec *before* a matching extracted transition (the lightly shaded region in Figure 6a). It was necessary to allow the button report to occur before the extracted transition because, occasionally, infrequent saccades resulted in the first post-transitional saccade occurring after the subject's report of that transition. Using these criteria, it was possible to clearly match $> 90\%$ of all extracted phases with corresponding reported phases (see Table 1).

Figure 6b shows the correlation between all matched extracted and reported phase durations for one subject (N = 1558). The correlation between phase times demonstrates a high degree of reliability in the method, with a correlation coefficient of 0.95 for each analyst. Note that the timing constraints applied in the matching process were relatively weak, and are not responsible for the high correlation of the two phase times. Figure 6c further illustrates the reliability of the extracted phases by plotting the lags between the extracted OKN transitions and the reported phase changes. In this figure, negative values indicate that the reported transition occurred before the extracted transition, and positive values that the extracted transition occurred first. Note that the distribution is composed nearly entirely of positive lags, where the button was pressed after the change in OKN, with a mean of 550-575 msec. This suggests that the initiation of the OKN transition roughly reflects the time of the perceptual transition, and that the distribution of lags corresponds to a standard reaction time distribution, where the stimulus onset is the perceptual transition. Table 1 summarizes the reliability of the extraction process during rivalry for two independent analysts.

When phases of upward and downward OKN were extracted in a similar manner for the nonrivalry (dioptic) trials, and correlated with the physical change in the direction of the grating, the mean lag between the stimulus change and the first sign in the OKN signal was 120 msec. This reflects the latency of the OKN's response to changes in the physical stimulus.

3.2 Experiment 1: Rivalry Report

The first experiment required the subject to actively attend to the visible direction of motion during rivalry, and to report the direction of the dominant stimulus by pressing one of two buttons. This was the control condition, and was expected to yield normal rivalry statistics.

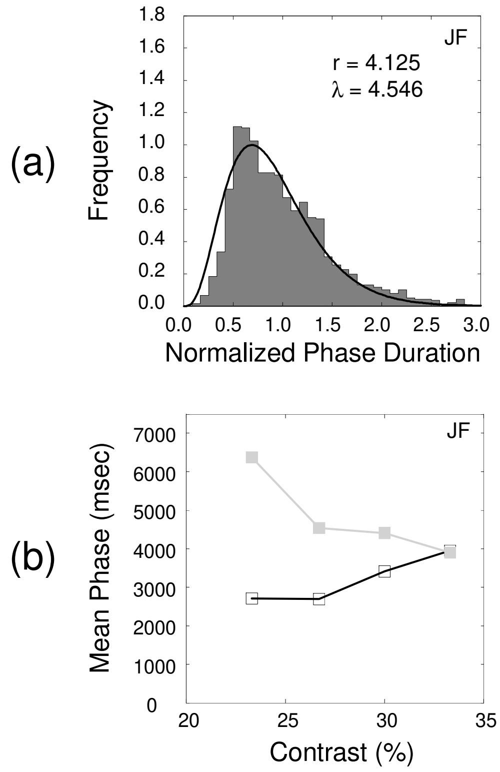

Figure 7: Rivalry phase statistics during Experiment 1, the attended condition. Table 2 lists distribution parameters for two independent analysts.(a) Distribution of phase times. Each phase time is expressed as a fraction of the mean for the distribution. A gamma function is fit to the bin values of the frequency histogram, and the values of the parameters, r and λ, closely resemble values previously reported in the literature for rivalry induced by 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 of the other eye's grating was varied. Lowering the contrast of one of the gratings 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).

The results are shown in Figure 7.

In the first part of Experiment 1, phase times were collected during fixed contrast stimulation, and their distribution was compared with the standard rivalry phase time distribution. In generating this distribution, each phase time is expressed as a fraction of the mean. The results are shown in Figure 7a. As in many previous studies (Levelt, 1965; Fox & Herrmann, 1967; Walker, 1975) a gamma function was fit to the bin values of the frequency histogram, and the optimal parameter values were evaluated. The values are listed for each of the analysts in Table 2. Note that the parameters of the theoretical distributions were estimated by nonlinearly approximating the frequency histogram data, and not computed from the mean and standard deviation of the distribution. The parameters of the gamma distribution are in agreement with values reported in previous stud-

analyst	$\bar{t}$	$\%t$	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 2: Attended condition. Mean dominance time ($\bar{t}$), 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.

ies of binocular rivalry (Levelt, 1965; Fox & Herrmann, 1967).

The second part of Experiment 1 examined the effects of changing the interocular contrast on the mean dominance time for the stimuli in each eye (Figure 7b). In each observation period, the contrast of one of the rivaling gratings was fixed at 33%, while the contrast of the second grating was varied between 23% and 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 result, as expected, are also consistent previously reported findings, where changes in the strength of one of a pair of rivalry stimuli primarily affect the mean duration of the unchanged stimulus (Blake, 1977; Fox & Rasche, 1969; Bossink et al., 1993).

analyst	$\bar{t}$	$\%t$	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 3: Counting task. Mean dominance time ($\bar{t}$), 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.

3.3 Experiment 2: Counting Task

The concurrent counting task had little or no effect on the binocular rivalry alternation. Optokinetic nystagmus continued to occur with alternations, even though the subject was engrossed in a task which required considerable attention. The quality of the OKN signal was slightly less in this condition than the attended trials, however, the net result was simply an increase in the percentage of ambiguous periods. Also, the overall alternation rate was slightly higher during this task. However, the statistics of the phases derived from the OKN signal very closely matched the results of Experiment 1. Figure 8a shows the distribution derived from the equal contrast

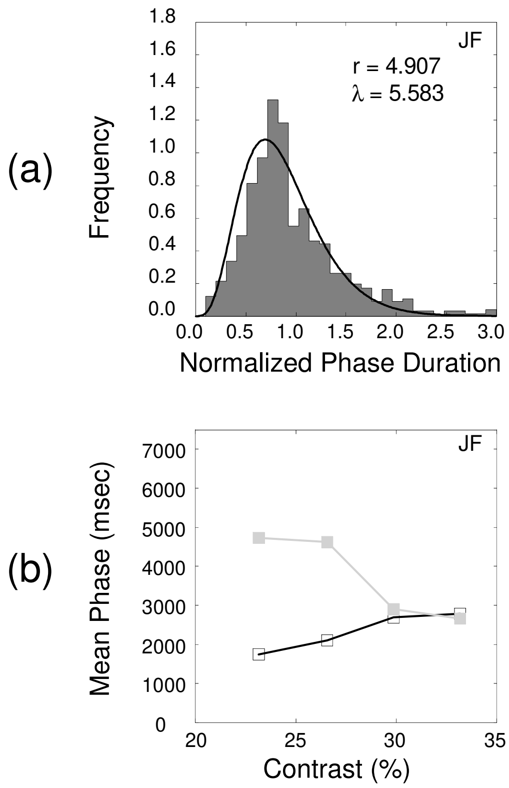

Figure 8: Rivalry phase statistics during Experiment 2, counting task. Table 3 lists distribution parameters for two independent analysts.(a) Distribution of phase times. The distribution of phase times generated during the counting task is remarkably similar to that generated when the subject was actively reporting her perceived direction of motion. (b) Changes in the contrast of one of the gratings affected the mean dominance times in the same fashion as when the subject was actively reporting the rivalry changes.

condition in Experiment 2. As in the first experiment, the distribution of fixed contrast dominance phases was modeled well with a gamma function, with parameters that were again in the expected range for normal rivalry (Table 3). The second part of Experiment 2 examined the effect of the counting task on changes in interocular stimulus strength. As the contrast of one of the pair of rivalry stimuli was systematically decreased, the effect on the mean dominance time of each stimulus was nearly identical to the attended condition (Figure 8b).

3.4 Experiment 3: Popout Task

The final task, requiring the subject to attend multiple short stimulus presentations in the periphery, also had little or no effect on the dynamics of the binocular rivalry alternation, again with the exception of a slight rate increase. The gamma function approximating the distribution in this experiment (Figure 9a) had slightly higher parameters than in the other two experiments (Table 4), 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.

analyst	$\bar{t}$	$\%t$	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 4: Popout task. Mean dominance time ($\bar{t}$), 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.

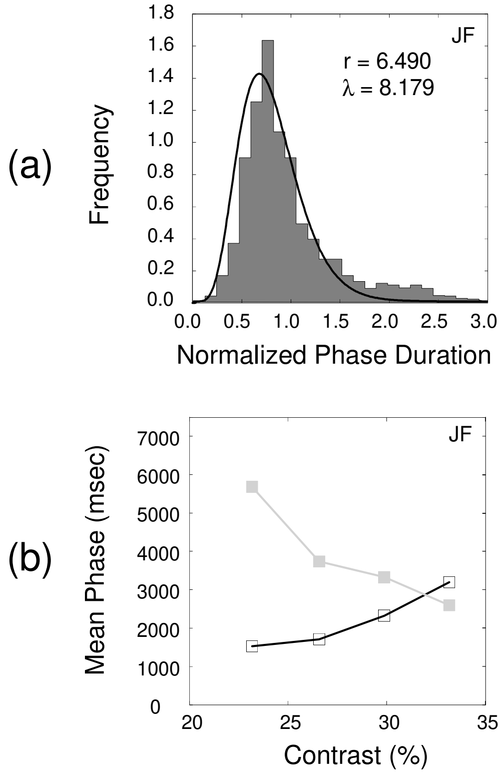

Figure 9: Rivalry phase statistics during the concurrent popout task. (a) Distribution of phase times for constant contrast stimuli in Experiment 3. The normalized distribution was again fit with a gamma function, whose parameters are listed in Table 4. The concurrent visual task has little effect on the overall shape of the distribution of phase times. The values for r and λ are slightly higher than in the attended rivalry condition, however they are still within the range of parameters observed in studies of binocular rivalry. (b) Results of Experiment 3b. Changing the contrast of one of the gratings during the popout task yielded results nearly identical to the condition where the subject actively attended to the direction of motion.

The effect of changes in interocular contrast (Figure 9b) was again extremely close to 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.

4 Discussion

The relationship between binocular rivalry alternation and conscious attention is poorly understood, despite over a century of inquiry (Helmholtz, 1866). On the one hand, it has been clear since the first studies of rivalry that perceptual changes can be controlled to some degree by the subject (Helmholtz, 1925; Breese, 1899). On the other hand, 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 (George, 1936; Washburn and Gillette, 1933). One consistently observed effect of attention on binocular rivalry is ability to control the rate of alternation (Meredith & Meredith, 1962; Lack, 1969, 1970, 1973). 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 the statistical profile of the dominance times that characterizes its dynamics. 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 the rivalrous stimuli yielded a small (21%) decrease of alternation rate. It should be noted that in these experiments the subjects were not instructed to either slow down or increase the alternation rate of rivalry, but rather to report rivalry, attending the rivaling stimuli, or perform an entirely different task. Thus the change in alternation rate reported here is not directly comparable to that reported in previous experiments.

4.1 Gamma Distribution

As shown above, the distribution formed by the normalized dominance intervals during rivalry can be modeled well with a gamma function whose parameters fall within a relatively narrow range. Gamma distributions have been commonly interpreted as representing the waiting time for the rth event when a single event is a Poisson process of waiting time λ. Levelt (Levelt, 1965) hypothesized that the fourth order gamma distribution (where $r = 4$) formed by the rivalry phase times is likely to be the consequence of a mechanism that requires the summation of four independent events to occur before a perceptual transition. Levelt speculated that these events could be "excitation spikes", caused by small eye movement shifts over a contour (Levelt, 1965). However, the eye movement hypothesis was weakened when it was subsequently shown that the distribution of phases during binocular rivalry remains unchanged even when the rivaling images are retinally stabilized (Blake et al., 1971).

Why then are the rivalry phase times distributed in this way? Although Levelt's "excitation spikes" are not likely to be the underlying events in a Poisson process, it is possible that the distribution does reflect the summation of r independent events in a more central process (Blake et al., 1971). For example, independent events could take the form of high order correlations of adapting and regenerating cells in the cortex. If perceptual transitions are the result of one neuronal network becoming dominant over another in a region of cortex, the independent random events in question could be the activation (or fatigue) of a number of smaller cell assemblies, each acting as its own functional unit. As individual units are activated, a summative process could, after a threshold is reached, boost the entire network into dominance. Conversely, as individual units are fatigued, the dominant network could be weakened enough to be overcome by the other, previously quiescent, one.

Alternatively, the gamma-like distribution observed during rivalry could have nothing to do with a Poisson process, and could arise either because of dynamics imposed by attention shifts, or even by the decision making process itself. Because every rivalry experiment known to the investigators has involved the subject attending to the rivalry and making judgements as to the dominant stimulus, it is possible that the statistics of the timing intervals reflect the dynamics of the highest level.

The data presented here eliminate the possibility that the attention or decision-making process of the subject is responsible for the shape of the gamma distribution. When the subject is forced to perform a difficult concurrent task, directing his attention away from the rivalry stimulus, the dynamics of the process seem largely unaffected. The distribution of phase times extracted from the OKN during the concurrent tasks is not significantly different from the distribution obtained during the attended rivalry condition.

4.2 Physiological Implications

Levelt's propositions predict that the mean dominance time of the variable contrast stimulus should remain unchanged while the mean time of the fixed contrast stimulus should be significantly affected. Later experiments showed that although the mean dominance time of the variable stimulus may change slightly with increasing contrast (Bossink et al., 1993), the major influence in mean dominance phase occurs in the eye opposite the stimulus being varied (Levelt, 1965; Fox & Rasche, 1969; Blake, 1977; Leopold & Logothetis, 1995).

This dependence of dominance of one eye on the stimulus strength of the other was found entirely unaffected by whether or not the subjects of this study attended the rivaling stimulus. Under all three attention conditions, a monocular decrease in contrast increased the mean dominance time of the stimulus in the other eye, while affecting that for the changed stimulus very little. A possible implication of this finding is, that if binocular rivalry reflects the workings of fundamental mechanism underlying perceptual organization, then this mechanism operates on the image data at a preattentive state, perhaps in the early extrastriate areas of the visual cortex.

Psychophysical, clincial, and theoretical work suggests that the processes underlying segmentation may occur early in the visual system, and that such processes are likely to reflect the functional architecture and connectivity of the striate and peristriate areas (Ullman and Shashua, 1988; Ullman, 1990; Field et al., 1993; Nakayama et al., 1989; Shimojo et al., 1989; Grüsser and Landis, 1991). For example, clinical literature shows that the processes of grouping of local elements in a visual scene into larger-scale contours, regions, or surfaces can break down selectively when parts of the striate and prestriate cortex is damaged. Specifically, a group of patients suffering from *Apperceptive Agnosia* exhibit dramatic deficits in simple object discriminations, when the only difference between objects is the shape (see Humphreys and Riddoch, 1987a, 1987b; Damasio et al., 1990; Farah, 1990; Grüsser & Landis, 1991, for a thorough review). Such patients have adequate elementary visual functions, such as acuity, luminance, chrominance, motion thresholds, and stereoscopic vision (Goldstein and Gelb, 1918; Landis et al., 1982). They have no cognitive deficits, and they can identify objects utilizing color and size cues, or other senses, such as tactile information. However, they show severe "shape-blindness", and often a dependence on local continuity.

Similarly, the capability of such patients to separate figure from ground breaks down when the figure is intercepted by other lines. The patients are capable of recognizing and reading letters or words when presented alone, fail to do so when the words are "scratched" with a line having the same color as the words (Goldstein & Gelb, 1918; Landis et al., 1982). Lines differing in color from the test-words do not affect perception, suggesting a dissociation between segmentation based on color and that based on orientation (Landis et al., 1982). All these patients suffer from diffuse brain lesions – typically caused by intoxication, such as carbon monoxide and mercury poisoning – primarily damaging the interlaminar connections (Benson and Greenberg, 1969), and axons (Landis et al., 1982) of the lateral aspects of the occipital lobe, affecting the perifoveal striate and most of the prestriate areas (Abadi et al., 1981; Campion and Latto, 1985). These visual areas probably correspond to the areas V1, V2, V3, V4, and other analogous areas in the dorsal stream of the monkey (Sereno et al., 1995), which are also known to play an important role in pattern recognition (Logothetis and Sheinberg, 1996).

Is there evidence, however, that binocular rivalry may indeed be the manifestation of a break down of normal processes of grouping and segmentation? Theories of binocular rivalry have often proposed bottom-up models, where perceptual suppression results from the inhibition of populations of early monocular neurons (Lehky, 1988; Mueller, 1990; Blake, 1989) to models, where perceptual changes are directly guided by attention (Helmholtz, 1866; Ooi and He, 1995). Alternatively, however, rivaling percepts may reflect a competition between mutually exclusive pattern representations, and therefore may reveal some fundamental mechanisms that underlie our perceptual organization.

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). Further, 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). Similarly, 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). Finally, the fact that the temporal dynamics of binocular rivalry are greatly 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.

In support to this notion is recent physiological evidence in the behaving monkey showing that cell activity modulations during rivalry are by no means limited to or even most predominant in striate cortex. Neural interactions subserving the singleness of vision – 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. Yet, the majority of neurons that showed pronounced modulations during rivalry were found in areas MT, V4, and IT (Leopold & Logothetis, 1995; Logothetis & Schall, 1989; Sheinberg et al., 1995a); areas known to be involved in image segmentation (Logothetis, 1994; Stoner and Albright, 1994; Bradley et al., 1995; Kobatake and Tanaka, 1994; Schiller, 1995). If this hypothesis proves to be true, then our current results provide further evidence of segmentation occuring early in the visual system, before the object selection processes that may operate in close relation to the attentional state of the subject.

Finally, a result obtained in these experiments may aid the analysis of data in physiological experiments on binocular rivalry in monkeys. This is refers to the finding that the time lags between different report types vary only to a limited extent, with a mean delay between the transition derived from the EOG trace, and that reported by the subject of 550-575 msec. This, together with the distribution of eye movement reaction times (mean latency $\approx$ 120 msec), suggest a mean manual reaction time to perceptual changes may be at the order of 675-700 msec.

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