BINOCULAR MOTION RIVALRY IN MACAQUE MONKEYS: EYE DOMINANCE AND TRACKING EYE MOVEMENTS

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Abstract—When the two eyes are exposed to markedly different patterns, perception becomes unstable, falling into oscillations, so that the image of one eye is seen first and then that from the other. With large stimuli the alternation is piecemeal, whilst when small stimuli are used the whole pattern alternates in unison. The purpose of this study was to determine whether a reliable, objective indicator of the perceptual state during binocular rivalry could be developed in the nonhuman primate. Monkeys (*Macaca mulatta*) were trained to discriminate direction of motion when presented with vertically drifting gratings moving in opposite directions in the two eyes. A high correlation was found between the direction of the slow phase of the optokinetic nystagmus (OKN) elicited by the drifting gratings during rivalry and the direction of motion reported by the monkey even though the gain of the OKN was reduced during rivalry, and the latency was longer. Behavioral eye dominance during rivalry varied significantly over time, between individuals and as a function of interocular contrast differences. Since the direction of tracking eye movements can be used to reliably monitor perceptual state during binocular motion rivalry, the opportunity exists in nonhuman primates to study the neurophysiological mechanisms underlying motion perception during the perceptually ambiguous condition of binocular rivalry.

Binocular rivalry   Eye dominance   Optokinetic nystagmus   OKN   Motion perception
Macaque monkey (*Macacca mulatta*)   Visual perception

INTRODUCTION

Sensation and perception are commonly thought to be distinct. If by sensation we mean that which is given by the retinal stimulus configuration and by perception we mean that which is derived from the stimulus, then most often there is a one-to-one correspondence between perception and sensation. This correlation makes an experimental investigation of perceptual processes independent of sensing processes difficult. However, there are stimulus configurations which allow more than one percept. The Necker cube is a common example. To the extent that the line drawing of the Necker cube projected on to the retina does not change (ignoring eye movements), we can say that the sensation does not change. However, the perception of depth in this ambiguous stimulus alternates. Thus, perception can be dissociated from sensation using ambiguous stimuli.

When identical images are presented to corresponding regions of the two retinae, the binocular visual system derives a single image through a process known as binocular fusion. However,

when the two eyes are presented with different visual stimuli, for instance horizontal stripes in the right eye and vertical stripes in the left eye, then binocular fusion does not derive a composite image such as a plaid or a checker-board. Instead, if the stimuli are large, the perceptual state decomposes into horizontal and vertical patches; whereas, if the stimuli are smaller, the perceptual state alternates between the image in the right eye and the image in the left eye. The phenomenon is well known as binocular rivalry (reviewed recently by Walker, 1978; Sloane, 1985; Wolfe, 1986; Blake, 1989). Binocular rivalry occurs between stimuli of sufficiently different orientation, spacial frequency or color. Similarly, an alternation in the perception of the direction of motion is observed when gratings moving in different directions are presented to each eye (Enoksson, 1961, 1963, 1968; Fox, Todd & Bettinger, 1975; Wade, De Weert & Swanston, 1984; see also De Weert & Wade, 1984).

It seems that the cyclopean visual system cannot cope with this highly conflicting situation and instead one eye's view is suppressed

from phenomenal awareness for a period. The alternating periods of dominance and suppression of one of the views are the most salient attributes of the process of binocular rivalry and are considered the characteristic dependent variables of this phenomenon. The mechanism of binocular rivalry as well as the locus of phenomenal suppression have been of interest for many years, and a number of neuronal models have been proposed (Sperling, 1970; Abadi, 1976; Sugie, 1982; Cogan, 1987; Lehkey, 1988; Blake, 1989), but a paucity of neurophysiological data has made it impossible to realistically evaluate these models. The purpose of this study was to investigate the extent to which the visuomotor behavior of macaque monkeys experiencing unitary binocular motion rivalry can be used as a reliable indicator of the monkey's perceptual state with reference to motion direction. If such an objective indicator of the subjective state can be developed, then it provides a means by which to study the neurophysiological mechanisms underlying the phenomenal alternation during binocular rivalry.

A moving visual field such as a random dot pattern or a luminance grating induces a series of conjugate tracking eye movements known as optokinetic nystagmus (OKN). As long as the pattern is not moving too fast, the subject's eyes tend to track the pattern as it moves. When the gaze is carried too far from the primary position a compensatory saccadic eye movement returns the eye to the primary position. The first type of eye motion is known as the slow phase and the second type, as the quick phase of the OKN.

OKN has been used in the past as an objective indicator of defective color perception (Pitt, 1944; Moreland Kogan & Smith, 1975). Recently OKN elicited by the minimum motion stimulus (Anstis & Cavanagh, 1983) has been recorded in normal and color-defective adults (Cavanagh, Anstis & Mather, 1984) as well as in infants (Anstis, Cavanagh, Maurer & Lewis, 1987). In all of these experiments a drifting color grating, could be seen moving in either of two opposite directions. Under these conditions, the direction of the slow phase of the nystagmus was correlated with the direction of motion perceived by the subject. Logothetis and Charles (1990), also using the minimum motion method, extended these observations to nonhuman primates, providing a simple and accurate measure of isoluminance points that can be used in physiological experiments.

Similarly, previous studies in humans have demonstrated that the direction of nystagmic eye movements during binocular motion rivalry corresponds to the perceived direction of motion (Enoksson, 1961, 1963, 1968; Fox et al., 1975). We were, therefore, specifically interested in whether the direction of the slow phase of the optokinetic eye movements is correlated with the direction of motion a monkey responds that it sees during binocular rivalry.

Part of this work has been presented in preliminary form (Logothetis & Schall, 1988).

METHODS

Subjects

Three male, juvenile rhesus monkeys (*Macaca mulatta*) provided the data for this study. The animals were cared for in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and the guidelines of the Massachusetts Institute of Technology Committee on Animal Care.

Surgery

All surgical procedures were accomplished under barbiturate anesthesia using sterile technique. Each animal underwent an eye coil and head-post implantation procedure as follows: antibiotics (tribrissen 0.11 ml/kg s.c., p.o.) were administered one day before the operation. The animal was restrained with ketamine (10 mg/kg i.m.) preceded by atropine (0.10 mg/kg i.m.). Following catheterization, surgical anasthesia was induced with pentobarbital (15 mg/kg i.v.), and the monkey was intubated. The surgical sites were scrubbed with betadine, nolvasan and ethanol. An additional dose of antibiotic and an initial dose of analgesic (butorphenol 0.05 to 0.1 mg/kg, i.m.) were given and the animal was placed on the surgical table and rescrubbed. Somatic responses were tested, particularly during surgical manipulations and before making incisions or placing the animal in the stereotaxic head holder. The incisions and pressure points were infiltrated with local anesthetic (2% lidocaine). Throughout the surgical procedure the animal was given 5% dextrose in lactated Ringer's solution at a rate of 15 ml/kg/hr i.v. Heart rate, pulse and respiration rate were monitored constantly. Body temperature was kept at 37°C using a heating pad. Maintenance of anesthesia was accomplished with pentobarbital (5 mg/kg as needed). A scleral search coil was implanted subconjunctivally in one eye

(Judge, Richmond & Chu, 1980), and a stainless steel post to restrain the head was attached to the skull using stainless steel screws embedded in acrylic cement. At the end of the surgical procedure the animal was allowed to recover and extubated; when the monkey could sit unassisted and moved spontaneously it was returned to its cage. Antibiotics were administered for 3 days after the operation.

Task

The monkeys were trained to perform a direction of motion discrimination task. Two drifting horizontal gratings (square or sinusoidal) were generated by an Adage 3000 raster display system and presented on a Hitachi monitor at a viewing distance of 57 cm. The monitor was calibrated, the luminous output was linearized and the spatial inhomogeneity of the monitor was corrected with software to provide a uniform luminance distribution depending only on the input values of the lookup table. The gratings were presented independently to the two eyes through a prismatic stereoscopic viewer (Fig. 1A). The gratings were drifted in either the same or in opposite directions. Only vertically drifting gratings were used to prevent any vergence movements that may have resulted from gratings drifting horizontally in opposite directions.

Figure 1B illustrates the course of a single trial. Each trial began with the appearance of a central fixation spot. After the monkey fixated it for a specified period (300–500 msec), the drifting gratings were presented. After a specific presentation period (500–1500 msec), the gratings were replaced by two spots on either side. If the monkey perceived upward motion, then he was rewarded for making a rightward saccade; a leftward saccade was required following downward movement. When the gratings appeared in half of the trials, the fixation spot was removed to permit tracking eye movements. In the other half the fixation spot remained visible to suppress nystagmic responses.

In trials in which nonrivalrous gratings were presented, the monkeys were rewarded for responding correctly to the explicit direction of motion. However, in trials in which ambiguous, rivalrous motion was presented, it was necessary to reward the monkeys for either response since there was no externally defined correct response. This raises the obvious question about whether the monkeys respond appropriately in the rivalrous trials since direct access to the monkeys' perception is impossible. In an effort to insure insofar as possible that the monkeys' response in rivalrous trials accurately reflected their perceptual state, their training proceeded as follows: each monkey was trained using only nonrivalrous motion until their performance exceeded 95% correct. Rivalrous trials were introduced gradually. Moreover, in these training sessions all trials began with a period of rivalrous stimulation lasting from 200 to 500 msec. In trials that were to be nonrivalrous the gratings switched to drifting in the same direction. This was intended to have the effect of teaching the monkeys that a period of ambiguity would be followed by resolution such that
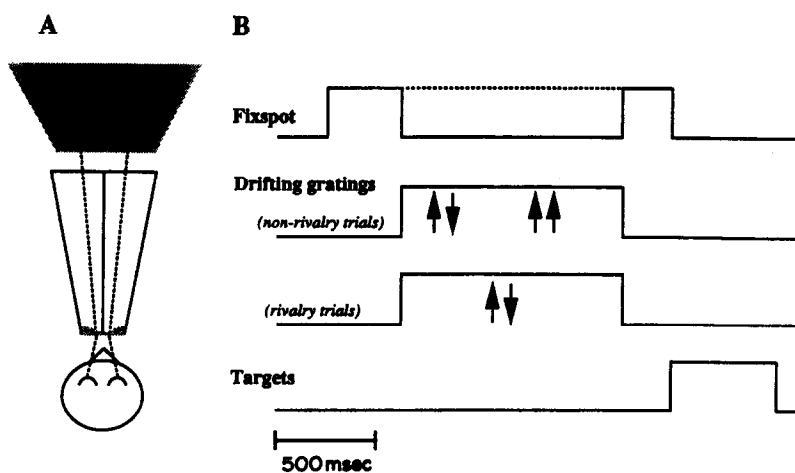

Fig. 1. (A) Diagram of stimulus presentation through a prismatic dichoptic viewer. The dichoptic viewer was a trapezoidal black box with a dark dividing septum open on the end facing the video monitor. Prisms were mounted in the viewing end to provide fusion under normal vergence. (B) Binocular rivalry motion discrimination task described in text.

in rivalry trials the monkeys would provide the resolution. In addition, during training the contrast of the gratings presented to each eye was manipulated to bias which stimulus would be dominant and thus provide an explicit reward contingency. As the monkeys gained experience with the rivalrous stimulus configuration, the proportion of rivalrous trials increased and the interocular contrast differences decreased. A monkey was considered sufficiently trained on the rivalrous stimuli when it responded with equal probability to gratings of either direction in either eye.

The gratings subtended not more than 4 deg and drifted 4–12 deg/sec. The typical stimulus subtended 3 deg, with a spatial frequency of 0.5 c/deg and drifted at 6 deg/sec. A drifting grating of this size was large enough to elicit consistent optokinetic responses (see Koerner & Schiller, 1972) but was small enough to produce unitary perceptual alternations as experienced by several human observers.

Technical controls

A disparity calibration was performed with each monkey to accurately position the gratings so that they overlapped. A spot, which the monkey fixated, was presented to each eye sequentially. The spot alternation rate never exceeded 4 Hz to prevent eliciting vergence (Owens, Wolfe & Bower, 1981). The separation of the spot location was adjusted so that the monkey made no saccade to refixate the spot; at this point we considered the fixspot to be fused within the limits of resolution of our system (0.4 deg). The gratings were centered on this fused point.

Contrast sensitivity was determined using a four alternative forced choice method with constant stimuli. Each trial began with the appearance of a fixation spot. After fixation, four circular patches were presented at eccentricities ranging from 2 to 6 deg. One of the patches was a stationary sinusoidal grating pattern that could vary in spatial frequency (0.5, 1.0, 2.0, 4.0 and 8.0 c/deg) and luminance contrast (9 steps separated by 0.05 log units). The other three patches were uniform fields of the mean luminance of the grating. The monkey's task was to discriminate the grating by making a saccade to it. The luminance contrast at which the monkeys performance dropped below 62.5% correct (half-way between chance and 100%) was taken as the contrast threshold, and the inverse of this value defined the contrast sensitivity for a par-

ticular spatial frequency. The monkeys were tested monocularly in two ways—either by placing a patch over one eye or by presenting the stimuli to one of the two eyes through the stereoscopic viewer.

Data collection and analysis

The presentation of the visual stimuli, collection of the eye movements and delivery of the juice reward were controlled by a PDP 11/73 computer. Eye movements were monitored with a scleral search coil (Robinson, 1963) and sampled at 200 Hz.

The onset and gain of the nystagmic eye movements were determined by computer algorithms. The onset of the slow phase of the nystagmus was computed by detecting a monotonic change in the eye position signal of the appropriate speed (20–130% of the grating speed) and direction that moved the angle of gaze at least 3 standard deviations from the initial fixation position. To compute the eye velocity the eye position signal was differentiated and filtered (cutoff 50 Hz, −3 dB). Saccades were detected according to velocity criteria and were excised by replacing their velocity values with the average velocity between successive saccades in a trial. The eye velocity was then obtained by computing the slope of the regression between the onset of the tracking eye movements and the end of grating presentation. Gain was given by the ratio of eye velocity to target velocity. Since the aim of this analysis was to compare the gain of the slow phase of the tracking eye movements during the rivalrous and nonrivalrous stimulus presentation, all of the gain values were normalized to the average value obtained from the responses to the nonrivalrous upward motion which always elicited the highest gain eye movements. t-Tests were used to ascertain the significance of any differences in the data.

RESULTS

Eye dominance during rivalry

Since stimuli were being presented to the two eyes independently, it was important to determine that the quality of vision in the two eyes was comparable. This was accomplished by determining the contrast sensitivity of the two eyes. The results for two monkeys are presented in Fig. 2. In interpreting the absolute sensitivities represented by these data, it is important to note that the stimuli were presented 3 deg from

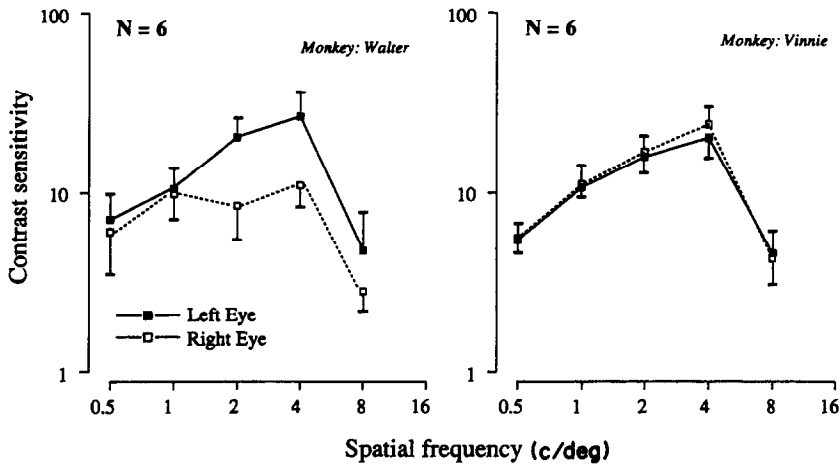## CONTRAST SENSITIVITY FUNCTION FOR SINEWAVE GRATINGS

Fig. 2. Contrast sensitivity measured in both eyes of two monkeys. Contrast sensitivity (1/threshold) for sinewave gratings is plotted as a function of spatial frequency. Error bars represent the standard error of the mean ($\pm$ SEM). Walter had a higher sensitivity in the left eye for two of the spatial frequencies tested. The contrast sensitivity in the two eyes was identical for Vinnie.

the fovea. For Walter the right eye was less sensitive ($P < 0.01$) for the spatial frequencies of 2 and 4 c/deg. For Vinnie as well as for Lily (data not shown), the contrast sensitivity of the two eyes was found to be almost identical. For the rest of spatial frequencies tested no significant difference in contrast threshold was found. In additional psychophysical experiments using random dot stereograms (Julesz, 1971) these monkeys exhibited normal stereoscopic fusion.

During binocular rivalry in humans an eye dominance has been observed; that is, in any individual the perceived stimulus during rivalry tends to be that presented to one eye more often than that to the other (Washburn, Faison & Scott, 1934; Enoksson, 1961; Coren & Kaplan, 1973). Figure 3 shows the eye dominance observed in one monkey. Eye dominance was defined as the percent of trials in which a monkey's perceptual response corresponded to the stimulus that was presented to the right eye.
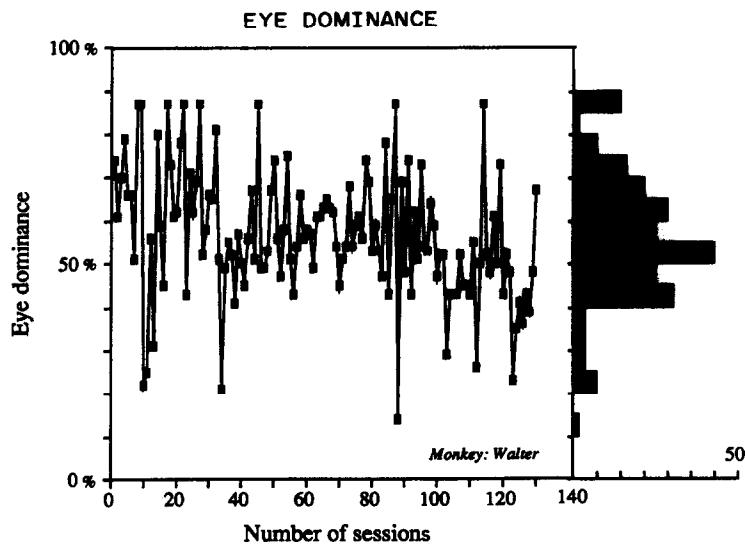
EYE DOMINANCE

Fig. 3. Eye dominance during binocular motion rivalry. The percent of trials in which one monkey's perceptual response corresponded to the stimulus that was presented to the right eye is plotted as a function of the experimental session. Stimulus contrast was equivalent for both eyes. While there was variation over the recording sessions, as shown in the histogram, the overall eye dominance is balanced.
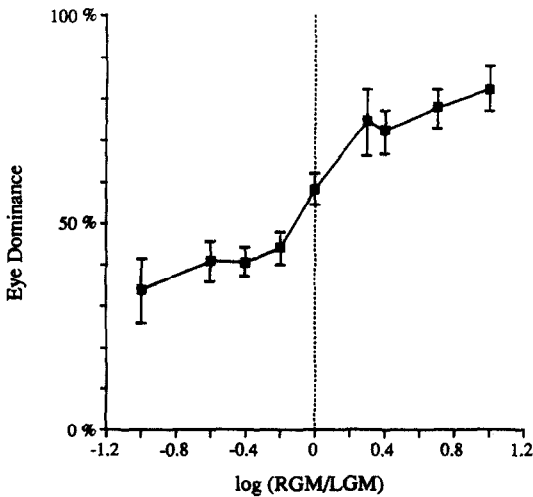
EYE DOMINANCE AS A FUNCTION OF CONTRAST

Fig. 4. Effects of interocular contrast difference on behavioral eye dominance. The percent of trials in which the monkey's behavioral response corresponded to the direction of motion presented to the right eye is plotted as a function of the log of the ratio of the right grating luminance modulation (RGM) to the left grating luminance modulation (LGM). The perceptual choice reflects the eye with the higher contrast.

There was considerable variation in eye dominance over the testing sessions; however, as shown in the histogram, over the course of the testing the eye dominance was on average balanced for this monkey. The mean right eye percentage for monkey Walter was 56% which was significantly different from an expected value of 50% (d.f. = 129, SE = 1.3%, $P < 0.001$).

Table 1. Correlation of pursuit direction and behavioral response. The percent of trials of the type indicated by the response direction and OKN direction is given for each monkey. This analysis only represent rivalry trials in which the fixation spot was absent, allowing pursuit

Response	Pursuit	Walter	Vinnie	Lily
up	up	97%	95%	90%
	down	3%	5%	10%
	none	10%	5%	9%
down	up	12%	8%	6%
	down	88%	92%	94%
	none	18%	11%	8%

The average right eye percentage for monkey Vinnie was 71% which was also significantly different from 50% (d.f. = 15, SE = 4.0%, $P < 0.001$). The mean right eye percentage for monkey Lily was 47% which was not significantly different from 50% (d.f. = 15, SE = 2.4%).

Behavioral eye dominance varied with interocular contrast differences (Fig. 4). When the luminance modulation of the gratings in one eye was reduced relative to that in the opposite eye, then the behavioral response favored the eye exposed to the higher contrast. In fact, in sessions with balanced contrast in which a monkey favored one eye, reducing the contrast in the favored eye balanced the behavioral responses.

Eye movements during binocular motion rivalry

In most trials the behavioral response corresponded to the direction of the slow phase of the tracking nystagmus (Fig. 5). Table 1 presents the correspondence between direction of the
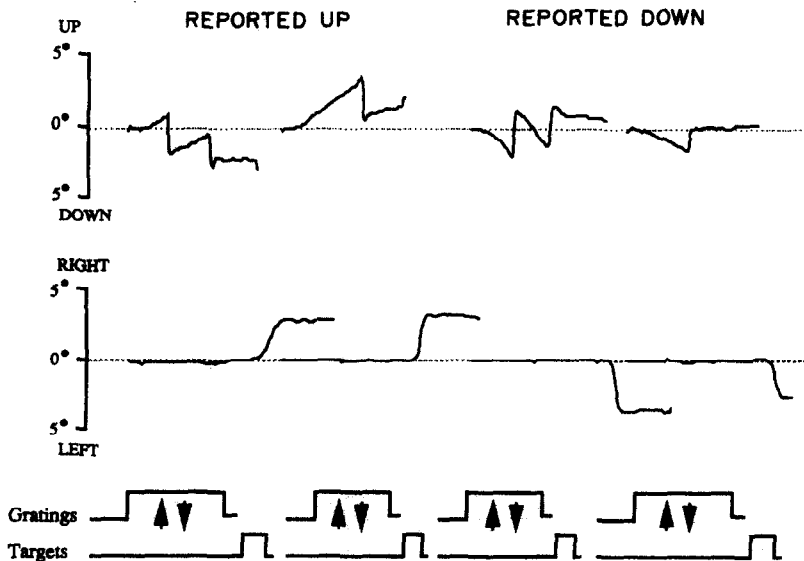

Fig. 5. Correlation of perceptual response and direction of the slow phase of OKN. Vertical (top) and horizontal (bottom) eye movement traces are shown for rivalry trials in which monkeys reported upward (left) and downward (right) motion. The monkey pursued up on the trials in which his behavioral response, indicated by the rightward saccade, was up. The converse was observed for trials in which the monkey perceived downward motion.

slow phase of the OKN and reported direction of motion for the three monkeys. Overall, in 93% of the rivalry trials the direction of the tracking eye movements was the same as the direction indicated by the perceptual choice. In the remaining rivalry trials in which OKN could be measured, the behavioral response was opposite the direction of the OKN slow phase. Finally, in 10% of the rivalry trials no OKN responses could be measured even though the monkey made a perceptual decision. An absence of measurable OKN was more common when the monkeys reported downward motion (12% for down vs 8% for up), but this may be a consequence of the additional observation that the gain of the downward OKN was less than that for the upward OKN. An OKN response could be measured in every nonrivalrous trial, and in 95% of the nonrivalrous trials the direction of the slow phase corresponded to the correct direction of motion.

The slow phase of the OKN evoked by the rivalrous and nonrivalrous grating motion was analyzed in more detail. The distributions of OKN gains for each monkey is illustrated in Fig. 6. The average relative gain for all monkeys during nonrivalrous grating presentation was 0.80 (1.00 for up, 0.61 for down). The average gain of pursuit during rivalry was 0.49 (0.49 for up, 0.49 for down). A statistical analysis of these data reveal two general trends. First, the gain of OKN during rivalrous stimulus presentation was less than that during nonrivalrous trials. In particular, the gain of upward OKN in non-rivalrous trials was significantly greater than the gain of upward OKN in rivalry trials in all three monkeys (worst case d.f. = 63, $t = 5.18$, $P < 0.001$), and the gain on downward OKN in nonrivalrous trials was significantly greater than that in rivalry trials for Walter and Lily (worst case d.f. = 63, $t = 3.34$, $P < 0.01$) but not in Vinnie. Second, the gain of downward OKN is less than that for upward OKN. Specifically, in nonrivalrous trials the OKN gain for upward motion was significantly greater than for downward for all three monkeys (worst case d.f. = 62, $t = 2.1$, $P < 0.05$). In rivalry trials the gain of upward OKN was significantly greater than that for downward OKN only in Walter (d.f. = 122, $t = 2.49$, $P < 0.02$).

The latency of the slow phase of the OKN for each monkey is shown in Fig. 7. The average OKN latency for all monkeys during non-rivalrous trials was 189 msec (170 msec for up, 199 msec for down). The average latency during
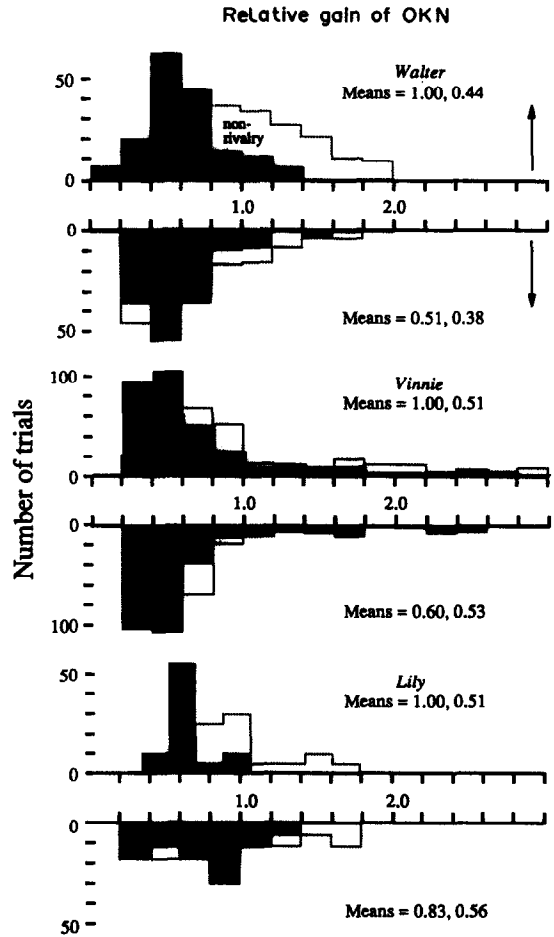

Relative gain of OKN

Fig. 6. Distribution of relative OKN gains for the three monkeys. The open histogram represents data collected during nonrivalrous trials, and the closed histogram represents data collected during rivalry trials. The top histogram in each pair represents trials in which the monkeys reported upward motion, and the bottom histogram represents trials in which the monkeys reported downward motion. The gain values were all normalized to the average value for non-rivalrous up for each monkey. The mean gain for non-rivalrous and rivalry trials are displated above each histogram. The gain of the slow phase of the OKN response during rivalry was significantly less than normal.

rivalry was 296 msec (275 msec for up, 314 msec for down). In nonrivalrous trials the slow phase latency for up was significantly shorter than that for down for all three monkeys (worst case d.f. = 198, $t = 3.4$, $P < 0.001$). Also, in rivalry trials the latency of upward tracking was significantly shorter than that for downward tracking (worst case d.f. = 223, $t = 2.38$, $P < 0.02$). The latency of upward OKN in nonrivalrous trials was significantly shorter than the latency of upward OKN in rivalry trials in all three monkeys (worst case d.f. = 199, $t = 10.00$, $P < 0.001$). Also, the latency of downward OKN in nonrivalrous trials was significantly

Latency of OKN slow phase

Walter
Means = 164, 294

Non-Rivalry

40 –

0

0   100   200   300   400   500   msec

0

Means = 211, 307

40 –

40 –

Vinnie
Means = 149, 258

0

0   100   200   300   400   500

0

Means = 174, 321

40 –

40 –

Lily
Means = 205, 288

0

0   100   200   300   400   500

0

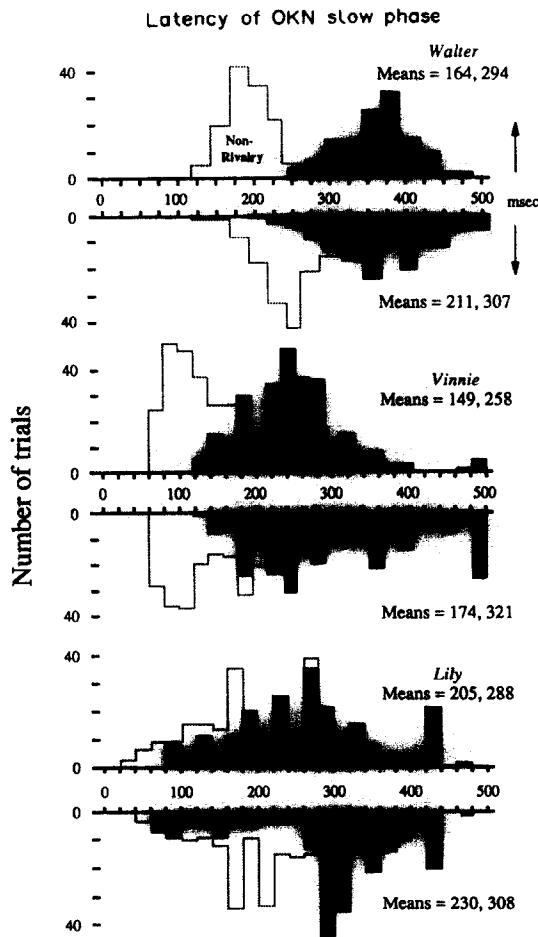Means = 230, 308

40 –

Number of trials

Fig. 7. Distribution of pursuit latency for the three monkeys. Conventions are as in Fig. 6. The latency of pursuit during rivalry was significantly longer than normal.

shorter than that in rivalry trials (worst case d.f. = 223, $t = 9.0$, $P < 0.001$). These results indicate that the latency of the eye movements elicited by rivalrous drifting gratings was longer than normal. In addition, the latency of downward tracking eye movements was consistenly longer than that for upward, although the lower gain of the downward optokinetic response may confound the measurement of the latency.

DISCUSSION

This investigation has demonstrated the following: (1) rhesus monkeys appear to experience binocular motion rivalry in a fashion similar to humans; (2) both nonrivalrous and rivalrous drifting gratings elicit good optokinetic responses, the direction of which corresponds to the direction of motion the monkey reports seeing; (3) an up/down asymmetry in OKN gain and latency was observed in response to both the nonrivalrous and the rivalrous gratings;

(4) the ambiguity of the binocular motion rivalry stimulus is expressed in the oculomotor system as evidenced by increasing latency; and (5) despite the phenomenal dominance of one eye during rivalry, the motion signal processed through the suppressed eye influences the oculomotor system as revealed by the reduced gain of the slow phase of the optokinetic nystagmus.

Relation to previous work

Rivalry in monkeys. Myerson, Miezin and Allman (1981) have previously investigated binocular rivalry in nonhuman primates; there are some notable differences between their report and the present study. First, these investigators allowed monkeys time to report several alternations during a longer rivalrous stimulus presentation. Using this paradigm, they were able to show that the frequency of alternation for monkey and human are identical and that the mean rate of alternation increases with stimulus velocity. In the present study the monkeys were allowed a single judgment about the perceived direction of motion of the rivalrous stimuli. This paradigm did not allow us to study perceptual alternation; however, preliminary psychophysical experiments with human subjects in this single judgment paradigm indicated a close correspondence between the monkey and human performance as indicated by the degree of eye dominance, the response latencies and the optokinetic eye movements.

Earlier work on rivalry in humans has shown that stimulus factors such as intensity, contrast or size can influence the prevalence of one eye over the other (Breese, 1899; Fry, 1936; Enoksson, 1963; Whittle, 1965). In this experiment we investigated the effects of varying stimulus contrast in one eye on the frequency of the reports corresponding to that stimulus. In agreement with the earlier work we found that the monkey's perceptual choice tended to correspond to the higher contrast stimulus. However, as has been shown by other investigators (Blake, 1977), even a 10-fold higher contrast of the stimulus presented to one of the eyes cannot cause perpetual suppression of the other.

Eye dominance. During rivalry in humans it has been observed that even with equal contrast stimuli, the perceptual alternation tends to favor the stimulus presented to one eye over the other (Washburn et al., 1934; Coren & Kaplan, 1973). This eye dominance has also been observed in the optokinetic response during rivalry (Enoksson, 1961, 1963). These studies have

shown that the dominant eye during binocular rivalry cannot be predicted by other measures of eye dominance such as acuity, preferred eye for sighting, or handedness.

The present results reveal a similar eye dominance in monkeys. Such an eye dominance may be an artifact of impaired vision in one of the eyes. To rule out this possibility, we determined the contrast sensitivity functions in both eyes of each monkey through the stereoviewer. The curves we obtained agree with previously published data (DeValois, Morgan & Snodderly, 1974) although since we presented the gratings perifoveally, the absolute sensitivity is lower than that observed with foveal gratings. In two monkeys, the contrast sensitivity functions were not distinguishable between the two eyes; whereas in the third animal the left eye was more sensitive at intermediate spatial frequencies. The monkey with the more sensitive left eye, however, had a right eye dominance. Furthermore, the degree of eye dominance varied considerably over time. These results support further the idea that eye dominance during binocular rivalry does not depend on any time-invariant optical or visuomotor biases and so may reflect the vicissitudes of perceptual processing.

Eye movements and rivalry suppression

The analysis of the tracking eye movements revealed an asymmetry such that gains for upward OKN were greater than those for downward. This asymmetry has been observed previously in cat, monkey and human (Pasik, Pasik, Valciukas & Bender, 1971; Matsuo, Cohen, Theodore, de Jong & Henn, 1979; Matsuo & Cohen, 1984; Grasse & Cynader, 1988; Murasugi & Howard, 1989). The OKN asymmetry in primates is in congruence with the physiological properties of the cells of the lateral terminal nucleus of the accessory optic system, a structure crucial for the generation of the vertical OKN (Mustari, Fuchs, Langer, Kaneko & Wallman, 1988).

The reduced pursuit gain during rivalry indicates that a motion signal is derived from the suppressed eye despite the phenomenal dominance of the other eye. The fact that the up-down asymmetry is preserved suggests that this motion signal is processed in the same way that it is during natural, nonrivalrous stimulation. These findings provide further evidence that suppression during rivalry is not an actual blindness of the suppressed eye; instead, it

appears to be an active inhibitory process at a relatively advanced stage of the visual system that prevents the suppressed stimulus from reaching conscious awareness.

Eye movements and rivalry dominance

An important issue in this study is whether at a given moment one can be confident that the monkey is in a particular perceptual state corresponding to one that human subjects experience. It seems acceptable to assert that monkeys experience subjective perceptions (see Nagel, 1974). However, how reliable is the monkey's report in assessing the perceptual discriminations done in this experiment? And, is the monkey doing a perceptual discrimination at all?

During the unitary rivalry that occurs with small stimuli, only two, mutually exclusive states are experienced by human observers (ignoring the transient if not instantaneous transitions from one eye to the other). The structural and functional similarities between the visual systems of man and monkey make it unjustified to posit that the monkey cyclopean visual system does not respond to rivalrous stimuli in the same alternating fashion. In fact, the remarkable similarity in the alternation frequency of dominance and suppression, and the very similar way this alternation depends on the velocity of the stimulus in both humans and monkeys (Myerson et al., 1981), suggest a common mechanism in the two species. Thus, given that monkeys can be ascribed perceptual states and that unitary alternation under rivalry occurs, we are left with the empirical matter of determining an observable behavioral correlate for each of the two subjective perceptual states. All animals used in this study performed at a level higher than 95% in the nonrivalrous motion discrimination task. They did so whether the fixation spot remained visible during presentation or not. The dissociation of the sensory from the perceptual processing that occurs during motion rivalry requires an additional behavioral indicator, since no reward contingency is possible in the rivalrous trials. The results of this study demonstrates that tracking eye movements serve this end during motion rivalry.

The credibility of this measure is attested to by the fact that during binocular motion rivalry in humans the direction of the slow phase of the optokinetic eye movements is correlated with the reported perceived direction of motion (Enoksson, 1961, 1963, 1968; Fox et al., 1975).

In fact, the degree of correlation between the direction of nystagmus and reported motion direction observed by Fox et al. in human observers (greater than 90%) coincided quantitatively with that determined in the present study of monkeys (93%). Furthermore, the incidence of anti-correlation in rivalry trials was no higher than the error rate observed with non-rivalrous motion. In addition, two other observations are consistent with the interpretation that the tracking eye movements reveal the perceptual state. First, the systematic dependence of eye dominance on interocular contrast differences provides additional evidence that the monkeys' performance in the rivalrous trials is based on an internal representation of motion direction. Second, the unusually long latency of the OKN under rivalrous conditions appears to reflect the intrinsic ambiguity of the stimulus.

In conclusion, the results of this study demonstrate that binocular motion rivalry can be used in nonhuman primates to study the perception of motion direction. This opens the avenue for neurophysiological studies of rivalry in general and motion perception in particular. In fact, we have begun recording single units in the superior temporal sulcus of monkeys experiencing binocular motion rivalry and find an intriguing variety of neuronal modulation, some of which appears to be correlated with the monkeys' perceptual state (Logothetis & Schall, 1989a,b).

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