Vergence Target Selection in Rhesus Monkeys: Behavior and Modeling

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Abstract

Previous studies have shown that a LATER (Linear Approach to Threshold with Ergodic Rate) race model can be used to explain saccadic target selection and latencies. The goal of the present study was to determine whether a comparable model could be applied to the underlying decision-making processes involved in target selection for transient vergence eye movements in rhesus monkeys. Luminance contrast of near and far Gabor pair stimuli were manipulated in a forced-choice paradigm to investigate their influence on vergence target selection. The distributions of responses and their latencies were evaluated by cumulative recinormal and reciprobit plots. With all targets set to 20% luminance contrast, animals showed a bias for the divergent target. Increasing luminance contrast of the near Gabor pair, while holding the far Gabor at the base contrast, resulted in increasing selection of the convergent target. This change in bias from divergent to convergent target selection correlated with decreases in convergent latency and increases in divergent latency. Monte Carlo simulations were used to estimate the internal rates of the divergent and convergent decision-making processes which, given a fixed threshold, would result in the observed distributions of vergence responses and their latencies. Statistical tests show that the LATER race model can predict observed values, and strongly suggests that competition between internal convergent and divergent target selection processes determines relative frequencies and latencies of these movements.


1. Introduction

1.1. Vergence eye movements

In animals with frontal vision, such as primates and cats, horizontal vergence eye movements are binocularly coordinated to fixate objects at different distances (Howard & Rogers, 1995). The two eyes rotate in opposite directions to align the image of the target of interest on the foveas of both retinas (see Judge, 1991, for a review). At least three stimuli can elicit horizontal vergence from a resting, tonic vergence state. These stimuli are retinal disparity (e.g. Regan, Erkelens, & Collewijn, 1986), retinal blur (e.g. Cumming & Judge, 1986), and looming cues (e.g. McLin, Schor, & Kruger, 1988). Interactions among these three stimuli are thought to drive eye movements through a vergence channel that is reciprocally cross-linked to a separate channel controlling accommodation (McLin et al., 1988; Schor, Alexander, Cormack, & Stevenson, 1992).

1.2. Trigger and fusion-lock components of disparity vergence

In humans, disparity-induced vergence eye movements appear to be composed of two visually-driven components. The first component, the transient component of vergence eye movements, is triggered even though the images in the two eyes are dissimilar and cannot be fused (Westheimer & Mitchell, 1969). The second component, which is sustained, closely maintains the vergence response within the limits of Panum’s fusional area to ensure sensory-fusion of target images on the foveas. For the sustained component to be engaged, images must be similar (Panum, 1858; Riggs & Niehl, 1960).

Functionally, the two components have been referred to as the trigger and fusion-lock components (Howard & Rogers, 1995). The function of the trigger (transient) component is to
shift vergence from one plane of depth to another, toward a particular target. At this point, the fusion-lock (sustained) component is activated. Large disparities from other depth planes are ignored; instead the target of interest is "locked on", and the sustained vergence component responds to small errors in target disparity (Schor, 1980).

1.3. Aim of study

The trigger and fusion-lock components of vergence eye movements have been studied extensively in humans, and the operating characteristics of vergence eye movements in rhesus monkey are similar to humans (Harwerth, Smith, & Siderov, 1995). However, to our knowledge, no experiments that investigate vergence target selection have been conducted in rhesus monkey. Furthermore, LATER race models, which have been used to describe saccade target selection and latencies in both human and monkey (Carpenter, 1981; Carpenter & Williams, 1995; Hanes & Schall, 1996; Hanes and Carpenter, 1999; Liston, Chukoskie, & Krauzlis, 2003), have not yet been applied to vergence target selection. Since behavioral studies can be integrated with electrophysiological techniques, characterizing these vergence responses in rhesus monkey provides the foundation for studying the underlying neural mechanisms of vergence target selection.

Previous studies in humans have shown that luminance contrast is a visual cue that strongly influences vergence target selection. Schor and colleagues used a forced-choice paradigm to investigate how luminance contrast influences the transient vergence system. They used Gabor stimuli presented with stimulus duration of 500 ms and disparities of 2.5 and 5.0 deg. Edwards, Pope, & Schor (1998) found that the transient vergence system uses a low-pass, binocular channel that selects paired stimuli with the highest combined luminance contrast. They
also found that this channel is used after a bias to dichoptic stimuli, with the same orientation and luminance polarity (Pope, Edwards, & Schor, 1999).

We used a similar experimental approach to Schor and colleagues to examine target selection by the trigger (transient) component of vergence in rhesus monkey. Our results clearly demonstrate a target selection process that can be explained by a competitive linear rise-to-threshold model. Thus, we can extend the LATER race models that have been used to describe saccadic decision making (Carpenter, 1981; Carpenter & Williams, 1995; Hanes & Schall, 1996; Hanes and Carpenter, 1999; Liston et al., 2003) to include decision making for vergence eye movements.

2. Methods

2.1. Animals

Three adult, emmotropic rhesus monkeys (*Macaca mulatta*), two male and one female, were used in this study. Facilities and care for these animals were provided by the Division of Animal Resources at the University of Alabama at Birmingham. The Division of Animal Resources is fully accredited by the American Association for Accreditation of Laboratory Animal Care, and operates in compliance with the US National Institutes of Health Public Health Service Policy on Human Care and Use of Laboratory Animals. Animal care and all experimental procedures in this study were performed in accordance with an approved Animal Welfare Assurance reviewed by the Institutional Animal Care and Use Committee.

Monkeys were placed on a water-controlled schedule, and sat in a plexiglass-restraining chair during training and recording sessions for periods of no longer than 4 to 5 hours each day. During these experimental sessions, their heads were held stationary by a head holder fastened to
a frame on the plexiglass chair. Monkeys had to sit comfortably so that they could learn the visually guided, oculomotor tasks in exchange for liquid reward.

2.2. Surgery

Sterile surgeries were performed on anesthetized monkeys to implant head-holders and scleral eye coils for measurements of eye movements. Ketamine (10 mg/kg, i.m.) was used to anesthetize animals before and after surgeries to relieve stress of transportation to and from the operating room. During surgical procedures, animals were respirated under general anesthesia (isoflurane) in an aseptic surgical suite. A veterinarian or scrub technician closely monitored vital signs. After completion of surgery, an analgesic (buprenex, 0.01 mg/kg) was administered (i.m.) as needed to minimize discomfort.

For each animal, the head-holder was implanted first. Four stainless steel plates were fastened to the skull by titanium bone screws. One end of each plate was bent up approximately 1 cm at the top center of the skull to support the placement of a lightweight, aluminum post (head post), which was cemented to the four plates by dental acrylic. The scalp was then sutured closely around the margins of the dental acrylic.

Next, so that eye position could be measured by a magnetic search coil technique (Robinson, 1963; Fuchs & Robinson, 1966), a coil of teflon-coated, stainless steel wire was inserted under the conjunctiva of one eye (Judge, Richmond, & Chu, 1980). Eye position was sampled at 1 KHz and stored on computer for later analysis. Behavioral training started with animals making simple saccades to small, cross-shaped targets on a 90° x 70° rear-projection screen. This initial training period lasted from 3 to 6 weeks. When eye-tracking ability reached a
satisfactory level of performance, a second coil was inserted under the conjunctiva of the other eye. Animals were then trained to make vergence eye movements.

2.3. Stimuli

Animals initially were trained to make vergence eye movements to light-emitting diodes (LED) placed at different viewing distances. After mastering this task, animals were required to make disjunctive saccades to either near or far targets presented by shutter stereoscope. Stimuli were generated by a Cambridge Research Systems VSG 2/4 graphics card running on a computer-based, VisionWorks™ system (Swift, Panish, Hippensteel, 1997). Presentation was on a 21” monochrome monitor (ultra-short persistence P46 phosphor) capable of producing a maximum luminance of 100 cd·m⁻². Animals viewed the stimuli presented on the monitor at a distance of 75 cm. Actual screen size on the monitor was 30x20 cm with a resolution of 736x500 pixels. Stimuli were presented dichoptically using ferro-electric, shutter glasses synchronized to the graphics card at 200 Hz (100 Hz per eye). The fast switching time (50 µs) and high extinction ratio (>1000:1) of these shutter glasses ensured minimal cross talk between the left and right eye stimuli.

The vergence demand of the stimuli was calculated in meter angles (MA). One-meter angle (MA) corresponds to the reciprocal of the target distance measured in meters and is equivalent to units of diopter. The range of vergence demand for our experiments was 1.4 to 4.1 MA to minimize interactions with the accommodative system.

Animals were initially required to track small (1.5 deg) cross-shaped targets, then Gabor stimuli. The mean luminance for each Gabor stimuli was held constant at 25 cd·m⁻², equal to the
monitor background. The standard deviation (σ) of Gabor stimuli was 0.5 degrees, and spatial frequency was 2 cycles per degree.

2.4. Forced-choice paradigm

A forced-choice paradigm was used to measure visual selectivity once animals were able to track Gabor stimuli reliably. The paradigm, shown in Fig. 1, was similar to the one used by Schor and colleagues (Edwards et al., 1998). Animals initially fixated binocularly on small crosses at a vergence angle of 5 degrees (2.7 MA). Animals were optically corrected to achieve the comparable accommodative demand of 2.7 D. The contrast polarity of crosses was randomly reversed to minimize the effects of adaptation. Fixation period varied between 1000 and 2000 ms by 100 ms increments. Then, for 500 ms, a Gabor stimulus was presented to one eye while two Gabor stimuli, corresponding to near targets at 7.5 degrees (4.1 MA) and far targets at 2.5 degrees (1.4 MA), were presented to the other eye. Equal numbers of randomly assigned trials were conducted while the left or right eye viewed the two Gabor stimuli.

Fig. 1 here

Monkeys were required to maintain eye position within a 2x2 degree window for the eye viewing the single Gabor stimulus while the other eye was required to make an eye movement to either the near or far target. In some of the recording sessions, monkeys were trained to return fixation to the crosses after Gabor presentation. Eye positions were sampled at 1 KHz and stored onto computer disk for later analysis.
2.5. Data Analysis

A computer equipped with interactive graphics was used to analyze the data off-line. Software was developed in-house to display traces showing position and velocity of all eye movements. Vergence angle was calculated by subtracting the horizontal position of the left eye from the horizontal position of the right eye. The derivative of vergence angle, vergence velocity, was used to determine direction and latency of vergence movement. After the presentation of the Gabor stimuli, a vergence velocity of 0.5 deg·s$^{-1}$ above a baseline measure was used as the criterion for the occurrence of a vergence movement. This point in time was labeled as the vergence response onset, and was used to report the latency and direction of movement (Fig. 2).

Fig. 2 here

When convergence and divergence latencies were analyzed using a normal time scale, the distributions were clearly asymmetric with a tail extending toward longer latencies. This asymmetry was measured using a formula for Skew (Press, Flannery, Teukolsky, & Vetterling, 1988).

$$\text{Skew}(x_1,...,x_N) = \frac{1}{N} \sum_{j=1}^{N} \left[ \frac{x_j - \bar{x}}{\sigma} \right]^3$$

Normal distributions that are symmetric have values of Skew that approach zero. Distributions with tails extending toward negative values have negative Skew and those with tails extending toward positive values have positive Skew. Similar asymmetries have been noted for saccadic latency measurements, and Carpenter (1981) has used a transform to minimize this
asymmetry. In this latter approach, histograms are made recinormal: frequencies of latencies are plotted on reciprocal time scale, which transform data (as rates) to Gaussian distributions. The reciprocal time scale was oriented so that zero was at axis right (infinite time), keeping with the convention, longer latencies to the right. Recinormals were then converted to cumulative histograms to better compare different distributions. Extrapolations to points at 50% cumulative probability represented medians of distributions. Cumulative histograms were plotted on a probit scale, making reciprobit plots. If distributions were normal, reciprobit plots generated straight lines, where slopes are directly related to standard deviations of the distributions. A probit scale has major ticks at each Normal Equivalent Deviation (N.E.D), plus 5. A probability of 50% corresponds to 0 standard normal deviates, or 5 probits, also the mean of the distribution. Data between probits of 4 and 6 represent ± 1 standard deviation (s.d.) or 68.2% of the distribution. Fig. 3 shows an example of a data set and analysis of its distribution.

Fig. 3 here

Computers using MatLab©, Release 13, by MathWorks performed Monte Carlo simulations to model competing internal rates of activities between divergence and convergence. A race model between divergence and convergence predicted observed latencies and the relative frequency of these responses (cf. Results).

3. Results

3.1. Vergence responses at base luminance contrast

Responses to the forced-choice paradigm were determined at a base level of 20% luminance contrast for all targets. At this base contrast, all monkeys showed a strong bias to
diverge toward the far Gabor pair. Examples of eye movements are shown in Fig. 2 for monkey 068. Fig. 2A shows a rare convergent response (latency = 148 ms) to the near Gabor stimuli with the right eye viewing the two Gabor stimuli, and Fig. 2B shows a more prevalent divergent response (latency = 111 ms), with the left eye viewing the two Gabor stimuli.

An example of distributions for divergence latencies when all three Gabor stimuli were at 20% luminance contrast is shown in Fig. 3A. The shape of the distribution is asymmetric with a tail extending toward longer latencies. The raw histogram of the latencies (Fig. 3A) had a distribution that was positively skewed (Skew = 1.15). The mean (184 ms) of the distribution was shifted away from median (168 ms). After frequencies of latencies were plotted on a reciprocal time scale, which converted latencies to rates (Fig. 3B), the histogram more closely approximated a Gaussian (Skew = 0.65). The mean of the rates (6.33 s\(^{-1}\)) closely aligned with the median (5.95 s\(^{-1}\)): expressed in units of time, mean (158 ms) and median (168 ms). The scale for rates is shown at the bottom of Fig. 3D. Zero for the rate scale is at axis right in the direction of infinite time. The pooled distribution from all latencies measured in our study (N = 5,119), convergence (N = 2,147) and divergence (N = 2,972), showed similar skewness. Distribution of latencies (Skew = 1.25) was skewed nearly two times more than associated transformed distribution of rates (Skew = 0.72).

Recinormals were converted to cumulative histograms (e.g. Fig. 3C) to examine how distributions were affected by luminance contrast of Gabor stimuli. Sigmoid functions were fit to cumulative histograms and used to extrapolate median values. The cumulative histogram in Fig. 3C is well fit (R\(^2\) = 1.00) with a median of 6.06 s\(^{-1}\), nearly matching observed median, 5.95 s\(^{-1}\). When cumulative histograms of the recinormals were plotted on a probit scale, data generated straight lines. Reciprobit plot in Fig. 3D was fit well by linear regression (R\(^2\) = 0.94),
representative of a rate distribution that is nearly normal. Extrapolated mean from the fit was 6.58 s\(^{-1}\), again nearly matching observed mean, 6.33 s\(^{-1}\).

### 3.2. Reversal of vergence responses

Increasing the luminance contrast of the near Gabor pair, while holding the far Gabor at base level, resulted in a reversal of the response bias towards convergence. In Fig. 4, we show average responses obtained from monkey 068 at luminance contrast of 20% (bottom), 60% (middle), and 100% (top). Divergence responses are plotted as a function of time in Fig. 4A; convergence responses are plotted in Fig. 4B. Traces are mean responses obtained from one recording session with dotted envelopes denoting ± 1 s.d. At 20% luminance contrast, 7% of responses were convergent (93% divergent). At 60% luminance contrast, 46% of responses were convergent (54% divergent). At 100% luminance contrast, 76% of responses were convergent (24% divergent).

The reversal of response bias, from divergence to convergence, was also strongly correlated with well-defined changes in vergence response latencies. As luminance contrast of the near pair was increased from 20% to 100%, the mean latency of divergent responses increased from 110 ms ± 24 ms (s.d.) to 199 ± 59 ms (Fig. 4A). In contrast, as luminance contrast of the near pair was increased from 20% to 100%, the latency of convergent responses decreased from 177 ± 42 ms to 118 ± 12 ms (Fig. 4B).

Fig. 4C shows recinormal distributions of latencies from four recording sessions at each level of luminance contrast. Red bars are divergence and blue bars are convergence. Since
recinormal distributions are reciprocal transformations of latencies, recinormal histograms essentially express the distributions of latencies as rates. The scale for rates is shown at the bottom of Fig. 4C, and the zero for the rate scale is at axis right in the direction of infinite time. As the near pair Gabor stimuli were increased, rates of divergent responses decreased (latencies increased) and rates of convergent responses increased (latencies decreased).

Recinormal distributions for pooled data from three monkeys (068, 89t, and r50; 11 recording sessions) showed the same reversal in frequency of movements and shifts by latencies, along with their associated rates (Fig. 5). Recinormal plots are shown for levels of luminance contrast of 20% (Fig. 5E), 40% (Fig. 5D), 60% (Fig. 5C), 80% (Fig. 5B), and 100% (Fig. 5A). Divergent mean rates decreased from 7.14 ± 0.10 s⁻¹ (median = 6.49 s⁻¹) at 20% luminance contrast (Fig. 5E) to 5.71 ± 0.17 s⁻¹ (median = 5.05 s⁻¹) at 100% luminance contrast (Fig. 5A, cf. arrow heads in Fig. 5A through 5E). Variability of means is ± standard error (s.e.). Convergent mean rates increased from 5.15 ± 0.31 s⁻¹ with median = 4.41 s⁻¹ (Fig. 5E) to 6.99 ± 0.05 s⁻¹ with median = 7.19 s⁻¹ (Fig. 5A). Rates are summarized in Table 1.

**Fig. 5 here**

**Table 1 here**

The majority of observed rates (>95%) in these distributions were less than 10 s⁻¹ (i.e. latencies > 100 ms). However, a small proportion of movements, which were faster than 10 s⁻¹ (cf. Busettoni, Miles, & Krauzlis, 1996), produced a bimodal rate distribution suggesting that these may be analogous to those “express movements” that are seen for saccadic eye movements (e.g. Carpenter & Williams, 1995). This small group of “express movements” was excluded from our subsequent modeling studies since these assumed unimodal distributions of rates.
To better compare effects of luminance contrast on distributions, recinormals were plotted as cumulative histograms (Fig. 6A and 6B) and reciprobits (Fig. 6C through 6G). As the luminance contrast of the near pair Gabor stimuli increased, divergent rates decreased (red arrow pointing right in Fig. 6B), and convergent rates increased (blue arrow pointing left in Fig. 6A). Summary of median values and $R^2$ fits of sigmoid functions are shown in Table 1. Reciprobit plots showed similar shifts by rates (Fig. 6C through 6G). Additional information was provided by linear regressions. As the luminance contrast of the near pair Gabor stimuli increased, slopes of the convergence responses (blue lines) increased along with probit-intercepts, going from 7.2 (Fig. 6G) to 9.4 (Fig. 6C). Slopes for divergence data (red lines), on the other hand, changed little but probit-intercepts clearly decreased from 8.5 (Fig. 6G) to 7.8 (Fig. 6C). Summary of mean values and $R^2$ fits of regression lines are shown in Table 1.

Fig. 6 here

3.3. Controls

Effects of luminance contrast on response bias were also determined for two animals (89t and r50) when the luminance contrast of all three Gabor stimuli was changed in unison. In this case, the response bias did not change and continued to be divergent: 11 ± 4% convergence at 20% luminance contrast, 24 ± 8% convergence at 60% luminance contrast, and 19 ± 6% convergence at 100% luminance contrast (cf. bottom of Table 1). Although the response bias direction did not change, response rates did change. As the luminance contrast of the Gabor stimuli were increased, rates increased for both divergent and convergent responses. As shown in Table 1, divergent rates increased from 6.33 ± 0.12 s$^{-1}$ (median = 5.95 s$^{-1}$) at 20% luminance contrast to 6.90 ± 0.10 s$^{-1}$ (median = 6.54 s$^{-1}$) at 100% luminance contrast. Convergent rates
increased comparably from 5.68 ± 0.57 s⁻¹ (median = 4.20 s⁻¹) to 6.90 ± 0.30 s⁻¹ (median = 5.78 s⁻¹).

Recinormals were plotted as cumulative histograms (Fig. 7A and 7B) and reciprobits (Fig. 7C through 7E). As luminance contrast of all three Gabor stimuli increased, divergent rates increased (red arrow pointing left in Fig. 7B). Convergent rates also increased (blue arrow pointing left in Fig. 7A). Summary of median values and R² fits of sigmoid functions are shown in Table 1. Reciprobit plots showed similar shifts by rates. Again, additional information was provided by linear regressions. As luminance contrast increased, probit-intercepts increased, going from 8.3 (Fig. 7E) to 9.0 (Fig. 7C) for divergence (red lines) and 6.8 (Fig. 7E) to 8.2 (Fig. 7C) for convergence (blue lines). Slopes changed little. Summary of mean values and R² fits of regression lines are shown in Table 1.

**Fig. 7 here**

The influence of luminance contrast on vergence responses to single targets, either far or near, was also examined for monkey r50. As the luminance contrast of the Gabor stimuli were increased, rates increased. Mean rates for divergence were 4.41 ± 0.11 s⁻¹ at 20% luminance contrast (N = 442), 5.99 ± 0.11 s⁻¹ at 60% luminance (N = 427), and 7.46 ± 0.11 s⁻¹ at 100% luminance contrast (N = 305). Mean rates for convergence were 4.52 ± 0.21 s⁻¹ at 20% luminance contrast (N = 63), 6.76 ± 0.14 s⁻¹ at 60% luminance (N = 487), and 8.33 ± 0.07 s⁻¹ at 100% luminance contrast (N = 475).
3.4. Statistics

Data from all three monkeys were assembled to determine statistically significant differences and relationships among means (Fig. 8). Fig. 8A shows that bias reversal from divergence to convergence was well correlated with the luminance contrast of the near Gabor pair stimuli. Luminance contrast is plotted on a log scale. At 20% luminance contrast, frequency of convergence was 11 ± 4%, divergence bias. By increasing the near pair luminance contrast, bias was shifted to convergence. Reversal occurred between 50 and 60% luminance contrast and was greatest at 100% luminance contrast, frequency of convergence was 75 ± 5% (cf. Table 1). Means were fit by linear regression ($R^2 = 0.99$) and were significantly different from one another (ANOVA, $p < 0.001$). Table 2 summarizes statistics.

**Fig. 8 here**

**Table 2 here**

Fig. 8D shows the influence of target contrast on vergence responses for each individual monkey. The response bias of monkey r50 (diamonds) switched from divergence to convergence between 20 and 30% luminance contrast ($R^2 = 0.91$, $p < 0.001$). The response bias of monkey 068 (squares) switched from divergence to convergence at approximately 50% luminance contrast ($R^2 = 0.90$, $p < 0.01$). Finally, the response bias of Monkey 89t (triangles) switched from divergence to convergence at approximately 90% luminance contrast ($R^2 = 0.97$, $p < 0.001$).

Mean rates of divergence and convergence shifted in opposite direction as a function of luminance contrast (Fig. 8B). Decrease in divergence rates (Kruskal-Wallis, $p < 0.001$) was accompanied by increase in convergence rates ($p < 0.001$). Linear regressions also fit well to
both, divergence ($R^2 = 0.95$) and convergence ($R^2 = 0.90$). Results from individual monkeys were similar (Fig. 8E and 8F). Rates for convergence increased (Fig. 8E) and rates for divergence decreased (Fig. 8F) as a function of luminance contrast. All changes in mean rates in individual monkeys were statistically significant (cf. Table 2), except for the decrease of rates for divergence movements in monkey r50 (Fig. 8F, asterisk).

Linear fits to divergent and convergent rates intercepted at 58% luminance contrast (Fig. 8B), which closely matches that at which the divergence response bias reverses to convergence (Fig. 8A). The difference of rates, divergence minus convergence, was plotted in Fig. 8C. Linear fit to difference of rates ($R^2 = 0.96$) closely matched the frequency of convergence as a function of luminance contrast. Data from individual monkeys are shown in Fig. 8G.

Frequency of convergence responses was also plotted as a function of the difference of rates (Fig. 9). Regression line (black line, $R^2 = 0.97$) fit to averaged responses showed zero difference between rates at 52% convergent response. Data from individual monkeys are also shown, fit by blue regression lines (068, squares: $R^2 = 0.95$; 89t, triangles: $R^2 = 0.98$; and r50, diamonds: $R^2 = 0.59$).

Fig. 9 here

Mean rates for convergent and divergent responses were also significantly shifted toward faster rates when luminance contrast of all three Gabor stimuli were increased in unison ($p < 0.001$). The same was true for rates measured in response to single paired targets; mean rates were increased by increasing luminance contrast ($p < 0.001$).
3.5. *LATER race model predicts distribution of rates*

We used a LATER race model (Carpenter, 1981; Carpenter & Williams, 1995; Hanes & Schall, 1996; Hanes and Carpenter, 1999; Liston et al., 2003) to describe the distributions of internal rates that would give rise to the observed distributions of external rates: the reciprocals of the observed latencies. Monte Carlo simulations were used to generate distributions of internal rates from given means and standard deviations. Internal rates were assumed to form Gaussian distributions (Fig. 10B) with a given mean ($\mu_d$ for divergence and $\mu_c$ for convergence) and standard deviation ($\sigma_d$ and $\sigma_c$). A fixed threshold was assumed. The faster of the two internal rates would exceed this threshold first and hence determined the direction and latency of the vergence response.

Values for the means of the internal rates and their standard deviations were iteratively selected until predicted external distributions closely fit the actual observed distributions. A close fit was indicated when the actual distribution of rates was not significantly different from simulated distributions (Kolmogorov-Smirnov, $p > 0.05$). Fitted values of simulated internal and external rates along with standard deviations are shown in Table 3. The model successfully accounted for the observed distributions by adjusting internal mean rates while keeping the values for the standard deviations relatively uniform. The average value for standard deviations across all conditions of luminance contrast was 2.17 s$^{-1}$; no individual selected value differed from this average by more than 15%.

Table 3 here
To demonstrate the model more clearly, simulated internal rates for convergence and divergence are shown in Fig. 11A, as the luminance contrast of the near Gabor stimuli was increased. Red (divergence) and blue (convergence) lines represent single simulations; black lines represent averages. When all three Gabor stimuli are at 20% luminance contrast, the majority of simulated rates for divergence are faster than simulated rates for convergence, and movements are biased to divergence (Fig. 11A, bottom). As the luminance contrast of the near pair increases, the internal rates for divergence decrease while rates for convergence increase. This change in internal rates is evidenced as a reversal in vergence bias occurring at 60% luminance contrast. When the near pair is presented with 100% luminance contrast, there is a clear shift to a convergent bias (Fig. 11A, top).

Simulated external rates are represented as dotted lines in Fig. 11B and 11C. Red bars in Fig. 11B are actual distributions of rates for divergence, and blue bars in Fig. 11C are actual rates for convergence. Black lines in histograms are averages of simulated distributions (N = 100) generated from 800 randomly selected internal rates, which approximated the data sample size. The simulation runs for the data when luminance contrast of all three Gabor stimuli were changed together had a tested data pool (N = 400), being based on data from two monkeys as opposed to three monkeys.

**Fig. 11 here**

Means of simulated internal rates are plotted in Fig. 12A and are well fit by regression lines. As the luminance contrast of the near pair increases, the internal rates for divergence decrease while rates for convergence increase: divergence, slope (m) = -3.7, R² = 0.96; convergence, m = 5.7, R² = 0.97. The long-dashed line in Fig. 12A is a regression line fit to the
average of combined rates, convergence plus divergence: m = 0.99, R² = 0.91. The short-dashed line is the regression line fit to the combined average rates determined by Monte Carlo simulations when luminance contrast of Gabor stimuli were changed in unison: m = 1.4, R² = 1.00. The slopes are similarly skewed positive (cf. Discussion).

Fig. 12 here

Simulated values of external mean rates, shown in Fig. 12B, closely matched actual values and are also well fit by regression lines. Rates for divergence decrease (m = −0.94, R² = 0.97), and rates for convergence increase (m = 2.7, R² = 0.98), with increasing luminance contrast of near pair stimuli. Long-dashed line is regression line fit to the averaged rates: m = 0.88, R² = 0.95. Short-dashed line is average of rates when luminance contrast of Gabor stimuli were changed in unison: m = 1.4, R² = 1.00. Again slopes for combined rates are skewed positive.

Simulated frequencies of convergent responses also closely matched observed frequencies (Fig. 12C), and regression line fits data well: R² = 0.99. All simulated external parameters shown in Fig. 12 deviated from actual observed values by less than 10%.

4. Discussion

4.1. Target selection of vergence guided by luminance contrast

The experimental design of this study required an eye movement decision in a forced-choice situation with constant and equal probability of convergent and divergent targets. Despite the equal target probability, our results show that vergence target selection has an initial bias towards divergence that can be reversed by increasing the luminance contrast of the convergent
pair. This suggests, as in humans, that vergence target selection in monkeys, although reflexive and preprogrammed in many ways (Semmlow, Hung, Horng, & Ciuffreda, 1993; Semmlow, Hung, Horng, & Ciuffreda, 1994), has an initial bias and is weighted toward binocular targets with highest luminance contrast (Edwards et al., 1998; Pope et al., 1999).

Reversal of the bias, from divergence to convergence, by increasing the luminance contrast of the near Gabor pair, is accompanied by shifts in both internal and external rates, which favor the preferred movement. Pooled data show that as divergent rates become slower and convergent rates become faster, the movement bias switches from divergence to convergence.

4.2. Luminance contrast effects

Effects of luminance contrast were examined under control conditions, when vergence target selection was non-competitive. When luminance contrast of single targets, near and far, were increased, rates increased. Likewise, when all three Gabor stimuli were increased in unison, rates increased for both divergence and convergence (cf. Table 1 and Fig. 7). The direction of the bias also did not change. Furthermore, averages of combined rates, divergent plus convergent, are also positively correlated with increases in luminance contrast for internal (Fig. 12A) and external values (Fig. 12B). Slopes of linear regression lines are similar under both competitive and non-competitive conditions, when only contrast of near Gabor pair are changed (i.e., long-dashed lines) and when contrast of all three Gabor stimuli are changed in unison (i.e., short-dashed lines). Similar effects of luminance and contrast on single targets are observed for saccades in humans (Doma & Hallett, 1988; Hanes & Carpenter, 1999). Studies in monkeys also show that latencies of saccades change with luminance of the target and after
adaptation to different background conditions (Straube, Robinson, & Fuchs, 1997; Liston et al., 2003). Our results suggest that the influence of luminance contrast on vergence is similar to that on saccades.

4.3. Divergent and convergent processes compete in a LATER race model

The race model for saccades (Carpenter, 1981; Carpenter & Williams, 1995) has been extended to account for the interaction between go and stop processes, by assuming independent processes increasing linearly toward a threshold (Hanes & Carpenter, 1999). Their results along with behavioral data from other countermanding tasks (Logan & Cowan, 1984) support the existence of such independent processes. Recent work by Liston et al. (2003) examined how saccadic target selection could be manipulated by varying the signal strength of targets against noisy backgrounds in a forced choice situation. In their study, monkeys were rewarded for making saccades to a correct choice, which was the brighter of two targets presented. Targets were presented simultaneously on opposite sides of the visual field, spatially distinct from each other. Interestingly, in this study it was found that the data were best fitted by the assumption that while the mean internal rate for correct choices increased as a function of luminance, the mean rate for incorrect choices did not change.

We have developed a race model for vergence that supports competing convergent and divergent target selection processes. Our results show mean rates of divergence that decrease and rates of convergence that increase when luminance contrast of near pair Gabor stimuli are increased (Fig. 8 and Fig. 12). The frequencies of movements correlate with the differences of the rates (Fig. 9), which in turn correlate with luminance contrast of the near Gabor pair (Fig. 8C and 8G). These data clearly indicate that the selection processes for divergent and convergent targets are competing against one another, and strongly suggest that a competitive LATER race model can adequately
describe the distributions of internal rates for convergence and divergence that underlie
distributions of external rates: the reciprocals of observed latencies.

4.4. Effects of luminance contrast on LATER race model parameters

Using probit plots, it is possible to identify how stimulating conditions are affecting race
model parameters: underlying mean rates ($\mu_d$ for divergence and $\mu_c$ for convergence), threshold
values, and variability of rates, $\sigma_d$ and $\sigma_c$ (Carpenter, 1981). If mean rates of excitation change
for convergence and divergence, y-intercepts of probit plots will be altered, but not slopes. If
threshold levels change for convergence and divergence, slopes will be altered, but not y-
intercepts. Lastly if variability changes for mean rates of convergence and divergence, both y-
intercept and slope will be altered.

Our results show y-intercepts of probits that change during bias reversal by luminance
contrast (cf. Fig. 6C through 6G). Slopes of probit plots change for convergence, but not for
divergence. Under control conditions when all three Gabor stimuli are changed, y-intercepts
change, but slopes change little (cf. Fig. 7C through 7E). This supports the idea that mean rates
of excitation for convergence and divergence are affected by luminance contrast of targets, with
less effect on the variability of the rates, and with threshold levels for convergence and
divergence that remain the same. This is in keeping with the results from an experiment
investigating saccadic target selection while recording activity from single cells in the frontal eye
fields of monkey (Hanes & Schall, 1996). Their results favored a model for decision making
using a variable rate model with constant threshold. Likewise, electrophysiological recordings
could address these issues directly by determining if neuronal activities associated with vergence
eye movements correlate with these model parameters as they are changed by stimulating conditions.

4.5. Possible neuronal mechanism

Studies of V1 neurons clearly show that as target contrast is increased, the neural response is decreased in latency and increased in magnitude (e.g. Reich, Mechler, & Victor, 2001). Assuming that neural activity in V1 is reflected in the internal rates of the target selection processes, then, in our paradigm, increasing target contrast of the near target pair would result in an increased mean internal rate for convergent target selection. However, this does not explain the observed decrease in mean internal rate for divergent target selection. This latter observation is best fit by the assumption that the target selection process is competitive. Such competing divergent and convergent target selection processes could arise from an attentional selection mechanisms such as “biased competition”, in which selection of targets is determined by competitive interactions, mutually suppressive, among extrastriate cortical neurons that represent all targets present in the visual field (see Desimone, 1998, for a review, cf. Ferrara & Lisberger, 1995). Evidence of biased competition appears in both dorsal and ventral visual streams and can include ‘bottom-up’ or ‘top-down’ feedback mechanisms. In our study, since divergence and convergence to targets are rewarded equally, it appears that a ‘bottom-up’ process based on the luminance contrast of targets is driving competitive interactions. In support of this, latency and gain changes in V4 neurons have been shown to match attentional selections that are guided by contrast (Reynolds & Desimone, 2003). In addition, one of the tenets of the biased competition model is that competitive interactions are strongest when competing stimuli are spatially close to one another (Desimone, 1998). This may explain why in our experiment we found vergence
target selection processes that were competitive, while the study by Liston et al. (2003), in which the targets were spatially segregated, reported independent saccadic target selection.

Acknowledgements

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References


Figures Legends

Fig. 1. Forced-choice paradigm. Animals initially fixated on small binocular crosses (Time 1). Then, a Gabor stimulus was presented to one eye while two Gabor stimuli, corresponding to near and far targets, were presented to the other eye (Time 2). Near pair match is encoded by blue circles; far pair match is encoded by red circles. Equal numbers of randomly assigned trials were conducted while the left or right eye viewed the two Gabor stimuli (Forced-choice to left eye or Forced-choice to right eye). The Gs represent Gabor stimuli. Diagrams are not to scale.

Fig. 2. Vergence responses from monkey 068 at luminance contrast (20%). Example of a convergent response (A) when the right eye viewed two Gabor stimuli (Forced-choice to right eye), and a divergent response (B) when the left eye viewed two Gabor stimuli (Forced-choice to left eye). Onsets of responses were calculated by comparison to a base vergence state (black bar) that preceded Gabor stimuli (white bar). Blue and red marks indicate response onsets on traces of vergence angle (VA) and vergence velocity (VV). Blue encodes onset of convergent response, latency = 148 ms; red encodes onset of divergent response, latency = 111 ms. HR-horizontal right eye position, HL-horizontal left eye position.

Fig. 3. Analysis of latency distributions. Example of data pooled from three monkeys for latencies of divergence (red bars and red circles). Distribution of latencies is plotted in a histogram binned at 10 ms (A). The distribution is positively skewed, Skew = 1.15, reflected by a shifted mean, 184 ms (large red arrow head), away from the median, 168 ms (small red
arrow head). Distribution of latencies plotted on a reciprocal time scale (i.e., recinormal distribution) transforms the plot to a distribution of rates (B). To maintain convention, longer latencies are to the right, the scale is set so that infinite time, whose reciprocal is zero, is to the right. The distribution is Gaussian and not significantly skewed, Skew = 0.65; and the mean of the rates, 6.33 s\(^{-1}\) (large red arrow head) closely aligns with the median, 5.95 s\(^{-1}\) (small red arrow head). Rates plotted as a cumulative histogram and fit with a sigmoid function, R\(^2\) = 1.00: median rate, 6.06 s\(^{-1}\) (C). When plotted on a probability scale (probit scale), a Gaussian cumulative distribution of the rates (i.e., reciprobit plot) is transformed into a straight line, R\(^2\) = 0.94: mean rate, 6.58 s\(^{-1}\) (D). N.E.D. - Normal Equivalent Deviation. Scale for rate is shown at bottom.

Fig. 4. Average divergence responses (A) and convergence responses (B) for monkey 068 during one recording session. Far Gabor was held at 20% luminance contrast while luminance contrast of the near Gabor pair were increased: 20% (bottom), 60% (middle), and 100% (top). Onsets of responses are marked red for divergence and blue for convergence. Dotted envelopes are ± standard deviations (s.d.). At 20% luminance contrast, bias is divergence. As luminance contrast of the near pair increase, frequencies of convergence responses increase. Along with the bias reversal, divergence latencies increase and convergence latencies decrease. Distributions of latencies for divergence (red bars) and convergence (blue bars) from monkey 068, four recording sessions (C). Histograms are plotted on reciprocal time scales which transforms latencies to rates (i.e., recinormal plot). Large arrow heads denote means of rates; small arrow heads, medians. Rate scale is shown at bottom.
**Fig. 5.** Pooled data from three monkeys (068, 89t, and r50) when the far Gabor was held at luminance contrast (20%) and luminance contrast of the near Gabor pair was increased. Recinormals are shown for levels of luminance contrast at 100% (A), 80% (B), 60% (C), 40% (D), and 20% (E). Large arrow heads denote means of rates; small arrow heads, medians (cf. Table 1). Rate scale is shown at bottom.

**Fig. 6.** Cumulative histograms fit with sigmoid functions for convergence (A) - blue circles and blue lines and divergence (B) - red circles, red lines. Data is derived from Fig. 5. As the luminance contrast of the near pair increases, convergence rates increase, and divergence rates decrease. Reciprobit plots fit by regression lines for levels of luminance contrast at 100% (C), 80% (D), 60% (E), 40% (F), and 20% (G). For summary of medians, means, and R² values of fits (cf. Table 1).

**Fig. 7.** Cumulative histograms fit with sigmoid functions for convergence (A) - blue circles, blue lines and divergence (B) - red circles, red lines. Distributions are from data obtained when luminance contrast of all three Gabor stimuli were changed in unison. As the luminance contrast of all three Gabor stimuli increases, convergence rates increase. Divergence rates also increase. Bias movement remains divergence (low frequency of convergence) when all three Gabors are changed in unison (cf. Table 1). Reciprobit plots fit by regression lines at 100% (C), 60% (D), and 20% (E). For summary of medians, means, and R² values of fits (cf. Table 1).

**Fig. 8.** Pooled data from monkey 068, 89t, and r50 (circles) when the far Gabor was held at threshold luminance contrast (20%), and luminance contrast of the near Gabor pair were
increased (A, B, and C). Luminance contrast is plotted on a log scale. Data is from 11 recording sessions. Black vertical bars are ± standard error (s.e.) of the Means. When all three Gabor stimuli were at 20% luminance contrast, bias movement was divergent. As luminance contrast of the near pair were increased, frequencies of convergence responses increased (A). Reversal from divergence bias to convergence bias occurred between luminance contrast of 50 and 60%. Mean rates for divergence (red circles) and convergence (blue circles) are plotted as a function of luminance contrast (B). With increasing luminance contrast of the near pair, divergence rates decrease, and convergence rates increase. Difference of rates, convergence minus divergence, is plotted as a function of luminance contrast (C). Data from individual monkeys, squares – monkey 068, diamonds – monkey r50, and triangles – monkey 89t (D, E, F, and G). Plots were fitted by linear regression. Pooled and individual relationships among means of the data showed statistically significant differences with exception of one. Mean divergence rates were not significantly different for monkey r50 (*). For summary of statistics and R² values of linear fits (cf. Table 2).

**Fig. 9.** Frequencies of convergent responses plotted as a function the difference of rates, convergence minus divergence. Data from each monkey are shown, diamonds – monkey r50, squares – monkey 068, and triangles – monkey 89t. Data are fit by regression lines (blue lines). Regression line to pooled data is also shown (black line). R² values: pooled = 0.97, monkey r50 = 0.59, monkey 068 = 0.98, and monkey 89t = 0.95.

**Fig. 10.** Race model between divergence (red) and convergence (blue) processes determines target selection (A). At the start of target presentation (Go), decision signals rise at constant rates
for divergence ($r_d$) and convergence ($r_c$) toward their thresholds (dotted line). Here starting
levels and thresholds are shown to be equal. Internal rates of activities determine which response
occurs first and subsequently the executed latency (e.g. here divergence has won). Internal rates
vary randomly from trial to trial in Gaussian fashion (B) having means ($\mu_d$ for divergence and
convergence for $\mu_c$) and associated standard deviations ($\sigma_d$ and $\sigma_c$). To preserve convention, long
latencies to the right, the rate scale is plotted with its zero at the right.

**Fig. 11.** Monte Carlo simulations reveal internal rates of activities that are shifted by the
luminance contrast of Gabor stimuli (A). When all three Gabor stimuli are at 20% luminance
contrast, bias movement is divergence (bottom plot). Simulated rates for divergence (red lines)
are faster than simulated rates for convergence (blue lines). As the luminance contrast of the
near pair is increased, internal rates shift: internal rates for divergence are slowed, rates for
convergence increase. Bias reversal occurs at 60% luminance contrast making convergence rates
faster than divergence rates. The first process to reach threshold determines movements which in
turn predicts the observed rates of activities, i.e., latencies (B and C). Simulated distributions
(black dotted lines) match observed distributions of rates for divergence (B) -red bars and
convergence (C) -blue bars. Observed distributions are not significantly different from simulated
distributions (cf. Table 3, Kolmogorov-Smirnov, $p > 0.05$). Rates are binned at 4.8 s$^{-1}$. Scale for
latencies is shown for comparison. Observed rate included for fit by Monte Carlo simulations were
those less than 10 s$^{-1}$ (cf. Results). Black lines in histograms are averages of simulated
distributions (N= 100) from 800 randomly selected values.
Fig. 12. Internal mean rates of convergence (blue +) and divergence (red x) determined by Monte Carlo simulations (A). The average standard deviation for internal rates, convergence and divergence combined, was 2.17 s\(^{-1}\); percent differences of individuals from average were less than 10% for fits to data when only luminance contrast of near Gabor stimuli were increased (cf. Fig. 11A and Table 3, top). Differences of individuals from average were less than 15% when contrast of all three Gabor stimuli were increased in unison (cf. Table 3, bottom). Regression lines (black): convergence, \(y = 5.7 \log(x) + -5.0, R^2 = 0.97\); divergence, \(y = -3.7 \log(x) + 11, R^2 = 0.96\). Long-dashed line is regression line fit to average of combined rates, convergence plus divergence: \(y = 0.99 \log(x) + 2.9, R^2 = 0.91\). Short-dashed line is regression line fit to combined average rates determined by Monte Carlo simulations when luminance contrast of Gabor stimuli were changed in unison: \(y = 1.4 \log(x) + 2.0, R^2 = 1.00\). External mean rates (B): simulated values (black + and x) and actual observed values (blue circles - convergence, red circles - divergence). Regression lines (black): convergence, \(y = 2.7 \log(x) + 1.2, R^2 = 0.98\); divergence, \(y = -0.94 \log(x) + 7.4, R^2 = 0.97\). Long-dashed line is regression line fit to the averaged rates: \(y = 0.88 \log(x) + 4.3, R^2 = 0.95\). Short-dashed line is average of rates when luminance contrast of Gabor stimuli were changed in unison: \(y = 1.4 \log(x) + 3.2, R^2 = 1.00\). Simulated frequencies of convergent responses closely match observed frequencies (C). Fit by regression line (black): \(y = 101 \log(x) – 120, R^2 = 0.99\). Simulated external parameters; mean convergent rates, mean divergent rates, and frequency of convergent responses; deviated from actual observed values by less than 10%.
Figure

Time 1

Left eye    Right eye

Time 2

Far match

G

Near match

G

Left eye    Right eye

Far match

G

Near match

G

Left eye    Right eye

or

Forced choice to left eye

Forced-choice to right eye
Figure A  Forced-choice to right eye

Figure B  Forced-choice to left eye
A
Near Pair Luminance Contrast = 100%
N=23

B
76% Convergence
N=73

C
100%
Near Pair Luminance Contrast

60%
Near Pair Luminance Contrast

20%
Near Pair Luminance Contrast

1 deg

Time (ms)

Rate (s⁻¹)

Latency (ms)

N=41

N=35

N=65

1 deg

Figure
Figure

A 100%

B 80%

C 60%

D 40%

E 20%
Figure

A

B

C

100%

80%

60%

40%

20%

Near Pair
Luminance
Contrast

40%
60%
80%
100%
Figure A

![Graph A showing Internal Mean Rate vs Luminance Contrast](image)

Figure B

![Graph B showing External Mean Rate vs Internal Mean Rate](image)

Figure C

![Graph C showing Convergent Response vs Luminance Contrast](image)
Table 1
Rates

<table>
<thead>
<tr>
<th>Luminance Contrast (%)</th>
<th>Frequency of Convergent Responses (% ± se)</th>
<th>Divergent Rates</th>
<th>Convergent Rates</th>
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<td>Mean ± se</td>
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<tr>
<td></td>
<td>(s⁻¹)</td>
<td>(s⁻¹)</td>
<td>(s⁻¹)</td>
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<tr>
<td>Far Gabor Near Gabor Pair</td>
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<tr>
<td>20 20 11 ± 4</td>
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<td>20 60 50 ± 10</td>
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<td>20 100 75 ± 5</td>
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<td>60 60 24 ± 8</td>
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Table 2  
Summary of statistics

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<th>Difference of Rates vs. Luminance Contrast</th>
<th>Convergent Response vs. Difference of Rates</th>
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Table 3
Monte Carlo simulated rates: internal and external

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