Shared motion signals for human perceptual decisions and oculomotor actions

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A fundamental question in primate neurobiology is to understand to what extent motor behaviors are driven by shared neural signals that also support conscious perception or by independent subconscious neural signals dedicated to motor control. Although it has clearly been established that cortical areas involved in processing visual motion support both perception and smooth pursuit eye movements, it remains unknown whether the same or different sets of neurons within these structures perform these two functions. Examination of the trial-by-trial variation in human perceptual and pursuit responses during a simultaneous psychophysical and oculomotor task reveals that the direction signals for pursuit and perception are not only similar on average but also co-vary on a trial-by-trial basis, even when performance is at or near chance and the decisions are determined largely by neural noise. We conclude that the neural signal encoding the direction of target motion that drives steady-state pursuit and supports concurrent perceptual judgments emanates from a shared ensemble of cortical neurons.

Keywords: area MT, area MST, oculometrics, dorsal stream, extrastriate, efference copy, tracking, choice probability

Introduction

It has been proposed that there are two major visual processing pathways in the primate cortex (Ungerleider & Mishkin, 1982), a "ventral" stream subserving visual perception and a "dorsal" stream subserving visuomotor control (Goodale & Milner, 1992). However, in the case of smooth pursuit (voluntary eye movements used to track a moving object of interest), a number of behavioral studies have shown that human oculomotor performance is more closely related to the perceived motion of the target object than to the raw sensory motion of the object's retinal image (Yasui & Young, 1975; Steinbach, 1976; Wyatt & Pola, 1979; Ringach, Hawken, & Shapley, 1996; Stone, Beutter, & Lorenceau, 1996, 2000; Dobkins, Stoner, & Albright, 1998; Beutter & Stone, 1998, 2000). These studies focused on response accuracy (how well the average response matches the stimulus) and revealed a strong link between the average perceptual and pursuit responses, in some cases even when the percept was erroneous (for a review, see Krauzlis & Stone, 1999). However, these accuracy studies could not disprove the hypothesis that the response similarities were in fact produced by different sets of neurons performing similar computations in parallel. A few studies have focused on response precision (how much the responses vary for repeated presentations of the same stimulus) and found a clear relationship between the precision of perceptual and oculomotor responses (Kowler & McKee, 1987; Watamaniuk & Heinen, 1999; see however, Churchland, Gardner, Chou, Priebe, & Lisberger, 2003). However, because they measured pursuit and perception in separate blocks of trials, these precision studies could not disprove the hypothesis that separate rate-limiting noise sources for perceptual and oculomotor processing were fortuitously similar. Therefore, neither earlier accuracy nor precision studies refute the possibility of separate-but-equal cortical processing for visual motion perception and pursuit. Lastly, a number of neurophysiological studies have shown that cortical regions in the dorsal stream, specifically the middle temporal (MT) and medial superior temporal areas (MST), are involved in both visual motion perception and smooth pursuit eye movements (Newsome, Wurtz, Dürsteler, & Mikami, 1985; Dursteler & Wurtz, 1988; Newsome & Pare, 1988; Komatsu & Wurtz, 1989; Britten, Shadlen, Newsome, & Movshon, 1992; Salzman, Murasugi, Britten, & Newsome, 1992; Pasternak & Merigan, 1994; Lisberger & Movshon, 1999; Rudolph & Pasternak, 1999). Although they demonstrate that the dorsal stream supports both perception and pursuit, because these studies did not examine them at the same time, they could not rule out the possibility that similar visual motion-processing signals within MT and MST or earlier are segregated according to perceptual and motor function. For example, a cortical signal related to motion in depth appears to drive a short-latency smooth oculomotor response, independent of perception (Cumming & Parker, 1997; Masson, Busettini, & Miles, 1997).

This study sheds new light on this issue by examining the trial-by-trial covariation of perception and oculomotor

responses measured during a simultaneous direction discrimination and oculomotor tracking task. We measured both the pursued and perceived directions in response to a white spot moving over a dark background. Although two separate neural pathways theoretically could perform identical processing and thereby yield identical average performance, the observed trial-by-trial covariation reveals the presence of shared neural units that contribute both their signals and their signature noise to the final perceptual and oculomotor responses. Preliminary results were presented at the Annual Meeting of the Associate for Research in Vision and Ophthalmology (Stone & Krauzlis, 2000).

Methods

Stimuli

The stimulus was a small (0.8 deg), bright (24 cd/m^2) white spot moving at constant speed and direction over a dark (9 cd/m^2) gray background. We used a raster display with VGA resolution (60-Hz noninterlaced), which, at the viewing distance used (62 cm), had a spatial resolution of 29 pixels/deg. In selecting the directions of stimulus motion, care was taken to minimize any spatio-temporal aliasing, but more importantly, any small residual artifacts would not affect the covariation of pursuit and perceptual responses.

Each trial followed a standard step-ramp paradigm (Rashbass, 1961). First, a central fixation cross appeared. Then, a random time (1000 to 1500 ms) after the observer's gaze fell within a fixation window, the fixation cross was extinguished and the target spot appeared offset by 1.5 deg (chosen to reduce the probability of a catch-up saccade) and immediately began to move for 600 ms at 10 deg/s toward the vicinity of the center of the display along one of 9 linear trajectories within the 6° bracketing the four cardinal axes (specifically, deviated by 0°, ±1°, ±2°, ±3°, and ±6° from purely straight up, down, left, or right). In addition, for each of these 36 (= 4 x 9) directions, to minimize the usefulness of any absolute position cues, we jittered the starting point (along the axis orthogonal to the general trajectory direction) to one of three positions (0 deg and ±4 deg). We used the method of constant stimuli, and presented a sequence of 5 to 8 blocks of the 108 (= 3 x 36) randomly permuted target trajectories, during two ~45-min sessions run on different days.

Eye Movements

We measured the position of the right eye using scleral search coils embedded in silastin rings (Collewijn, van der Mark, & Jansen, 1975), yielding a measurement precision better than 0.01 deg at a sampling rate of 1 kHz.

To reduce noise and to avoid aliasing, analog eye-position signals were low-pass filtered (–3dB at 180 Hz) prior to sampling. Horizontal and vertical eye-speed traces were obtained by applying a low-pass filtered differentiator (29-point FIR filter) to the eye-position traces. Saccades were detected by applying eye velocity and acceleration thresholds (Krauzlis & Miles, 1996). Pursuit latency was determined using an objective linear regression algorithm previously described in detail (Krauzlis & Miles, 1996). Trial-by-trial inspection was used to reject those few trials (~10%) with an unstable baseline, anticipatory pursuit, a saccade just prior to the initiation of pursuit, a bad fit of the initial pursuit by the latency algorithm, or an obviously incorrectly specified latency. This process left 1,041 trials in our analyses for LS and 1,575 for RK. The Cartesian data were then converted to polar coordinates and the mean direction and speed were computed for the analysis interval, 250 to 350 ms after pursuit onset. Averaged across stimulus directions, the median pursuit latency was 183 ms for LS and 191 ms for RK. These somewhat long latencies are appropriate for stimuli with large spatial and directional uncertainty (in our case, 12 possible starting points and 36 possible directions). The median pursuit gain (ratio of pursuit speed to target speed in the analysis interval) was 92.0% for LS and 91.7% for RK.

Task

Two observers (the authors) were asked to fixate a central cross to initiate a trial. Once the target began to move, the task was to track it as well as possible. At the end of each trial, observers made a yes-no perceptual judgment. For vertical trials, they made the binary decision whether the target moved leftward or rightward of pure vertical. For horizontal trials, they made the binary decision whether the target moved upward or downward of pure horizontal. Using the same strategy as in previous similar studies (Kowler & McKee, 1987; Watamaniuk & Heinen, 1999), we ran only highly experienced observers whose motion-perception and pursuit performance was over-practiced. In this way, we could examine as close to optimal human performance as possible with trial-by-trial performance variability limited by internal neural constraints by keeping other sources of variability (e.g., learning effects, criterion drift, and finger errors) at a minimum. Furthermore, given that a large number of randomly interleaved rapid-fire trials (less than 1 s in duration) were presented during sessions lasting up to three-quarters of an hour, it is highly unlikely that any attempt to use a cognitive strategy to link the perceptual and pursuit decisions could have generated the well-behaved, high-precision data trends observed. In addition, any such strategy is inconsistent with the observed results (see "Discussion").

Psychometrics

Standard psychophysical techniques were used. For each group of trials associated with a particular cardinal direction, the percentages of rightward or downward perceptual decisions were plotted as a function of stimulus direction (with zero representing the central cardinal direction). These psychometric curves were then fit to cumulative Gaussians using Probit analysis (Finney, 1971). This yielded measures of bias and precision (the mean and SDs of the best-fitting Gaussian).

Oculometrics

To allow direct comparisons between pursuit and perception, for each trial, we converted the pursuit response into a binary decision by comparing the mean direction in the analysis interval to a threshold (Beutter & Stone, 1998). This approach is simpler and slightly different than the receiver operating characteristic (ROC) method (Green & Swets, 1966) used in other studies to examine the relationship between motion-perception and pursuit (Kowler & McKee, 1987; Watamaniuk & Heinen, 1999) or between perception and neural responses (Britten et al., 1992). However, it is specifically designed for the single-interval yes-no psychophysical paradigm used here, in which a single stimulus is compared to an internal reference. We set the pursuit decision threshold to be the median of all of the responses for a given cardinal direction (the small motor bias) minus the point-of-subjective equality of the corresponding psychometric curve (the small perceptual bias), which were both very close (within ~1°) to the cardinal directions of 0°, 90°, 180°, and 270°. The reasons for using this bias-matched threshold (as opposed to the raw cardinal directions) were (1) to remove the small biases caused by eye-tracker calibration errors and (2) to remove the effect of any tilt misalignment between the head and display. The goal was to eliminate these small artifactual differences in the average perceptual and oculomotor responses, so as to focus our analysis on the variability around the median. However, using the raw cardinal directions as the thresholds yielded the same qualitative findings. The binary pursuit decisions were then plotted as a function of stimulus direction and the resulting oculometric curves were fit to cumulative Gaussians using the same methods as for the psychometric curves.

Trial-by-Trial Covariation (%Same)

To quantify the trial-by-trial covariation of the perceptual and pursuit decisions, we computed the percentage of trials for which the two were the same, the %Same. In earlier studies of the relationship between perception and pursuit, our attempts to examine trial-by-trial covariation (Beutter & Stone, 2000) had only limited success because the measurement noise of our video-based eye-tracker dominated the observed variability of the pursuit response, thereby obscuring the underlying biological variability. Our %Same analysis is similar in intent to the sender operating characteristic (SOC) or "choice probability" analysis pioneered by others (Britten et al., 1992) to examine the trial-by-trial covariation between perceptual and neural responses, but is specifically designed for the single-interval yes-no psychophysical paradigm used here. The observed %Same can be compared to that predicted by chance (i.e., by the chance correlation of two independent binary decisions consistent with the oculometric and psychometric curves). For example, for stimulus motion along the cardinal directions, the perceptual and pursuit decisions are nearly random (~50% rightward/downward), and chance predicts that they should be the same ~50% of the time. Any covariation significantly above this therefore indicates that the two direction decisions were not performed by completely separate and independent systems. For stimulus motion in a direction not aligned with the cardinal axes, the logic is the same, except that chance covariation is higher than 50% and can be computed using the following equation:

$$\%\text{Same(chance)} = p_{\text{pursuit}}\, p_{\text{perception}} + (1 - p_{\text{pursuit}})(1 - p_{\text{perception}})$$

with $p_{\text{perception}}$, the probability of a rightward (or downward) perceptual decision and p_{pursuit}, the probability of a rightward (or downward) pursuit decision. The observed %Same was reported as significantly higher than chance by performing a one-tailed t test using the binomial distribution to compute the SE.

Noise Model

Our noise model simply postulates that the noise dominating the trial-by-trial variation in the perceptual and pursuit decisions includes three sources: σ_{v} representing the "visual" noise in the neural representation of motion direction shared by perception and pursuit, σ_{p} the "perceptual" output noise specific to the perceptual judgments, and σ_{m} the "motor" output noise specific to the pursuit response. The model predictions were made by performing 10 runs of 5,000 Monte-Carlo trials for the 9 "signal" directions (i.e., 0°, ±1°, ±2°, ±3°, and ±6°). For each trial, the perceptual and pursuit decisions were determined by adding the signal to pairs of noise samples chosen from three scaled Gaussian distributions and comparing the total to a threshold of zero. For the perceptual decisions, one sample was taken from the σ_{v} distribution and the other from the σ_{p} distribution. For the pursuit decisions, the same σ_{v} sample was combined with a sample from the σ_{m} distribution. The simulations had a single free parameter, σ_{v}, the visual-noise SD. The two other parameters σ_{p} (perceptual-noise SD) and σ_{m} (motor-noise SD) were completely constrained because the total perceptual and pursuit noise is set by the directional precision measured

from the oculometric and psychometric curves. The sum of the visual and perceptual variances must equal the psychometric variance (i.e., $\sigma_v^2 + \sigma_p^2 = \sigma^2$ of the psychometric curve), and the sum of the visual and motor variances must equal the oculometric variance (i.e., $\sigma_v^2 + \sigma_m^2 = \sigma^2$ of the oculometric curve).

Although this simple Gaussian model does a good job of simulating our results, its psychometric and oculometric predictions show small but consistent deviations from our psychometric and oculometric data, which then force it to incorrectly estimate the covariation, especially at high signal strengths. To prevent this small artifact from cascading into the %Same simulations, we used an *ad hoc* scaling factor to make small adjustments to the effective signal strength for all nine directions independently (i.e., we allowed for a small nonlinearity in

the stimulus response mapping). This allowed us to match the actual observed instance of psychometric and oculometric performance when computing the %Same predictions, as opposed to simply using the expected performance of the mean Gaussian fit. The added degrees of freedom of this "enhanced" model were used exclusively to generate perfect replicas of the averaged psychometric and oculometric curves for both observers. Any impact on the %Same simulations was completely emergent.

Results

Figure 1 shows examples of raw eye-movement responses for observer LS. Figure 1A shows two individual saccade-free trials in response to "Rightward
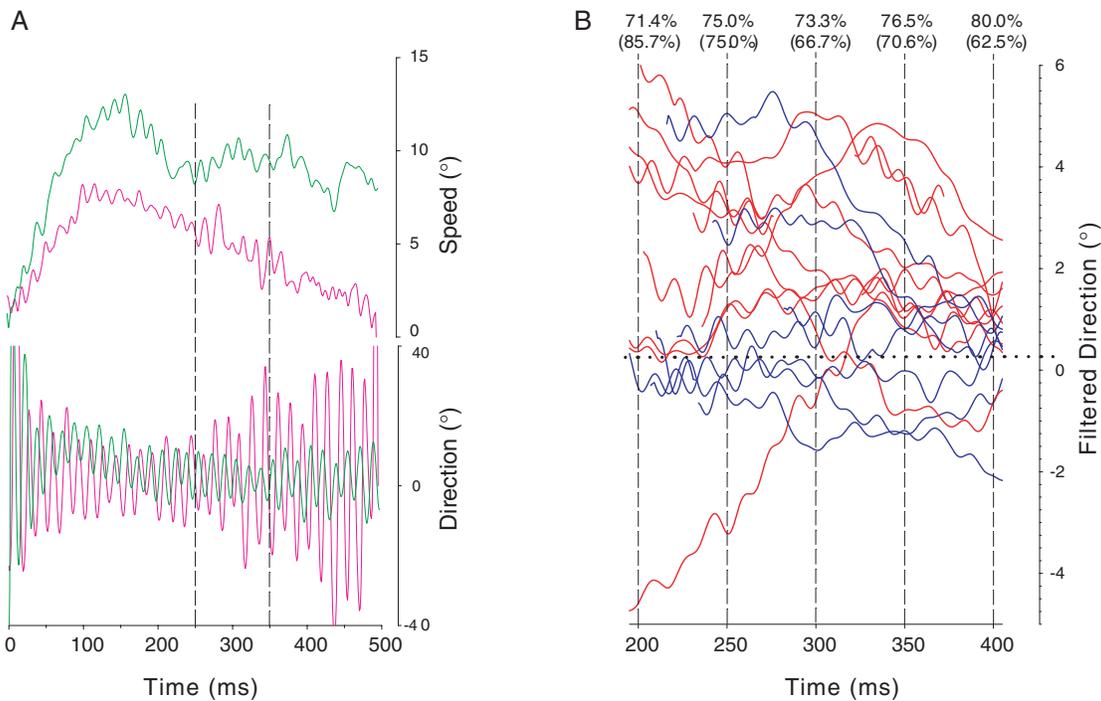

Figure 1. Converting pursuit responses into oculometric data. A. Two examples pursuit responses to rightward plus 1° upward (R+1) stimulus motion illustrate the range of response variability. The upper two traces show the eye-speed time courses, while the lower two traces show the corresponding eye-direction time courses. The apparent oscillations are simply 60-Hz noise that tends to be synchronized by our latency algorithm and amplified by the ratio taken to compute direction. To minimize this artifact, we chose a 100-ms analysis interval (indicated by the vertical dashed lines) that lies after the initial transient, but before the end-of-trial pursuit slowing (see purple eye-speed trace). B. Boxcar-filtered direction traces for all 18 R+1 trials within a single session illustrate the robustness of our analyses to changes in analysis interval. The boxcar filter converts each time-point of the raw response into the mean value over the 101-ms interval centered on that point. Thus, our analysis interval in A corresponds to the single point at t = 300 ms in B. Oculometric performance (% upward) is computed by dividing the number of traces above threshold (indicated by the horizontal dotted line) by the total number of traces. The upper row of nonparenthetic numbers above the vertical dashed lines show the measured % upward pursuit decisions for 5 different candidate analysis intervals, ranging from 150 to 250 ms after pursuit onset to 350 to 450 ms after pursuit onset. Covariation is evident by the fact that, for identical stimuli, trials associated with upward perceptual decisions (red traces) tend to be associated with upward pursuit decisions (traces above threshold). Conversely, trials associated with downward perceptual decisions (blue traces) tend to fall below threshold. The %Same is computed by dividing the sum of the number of red traces above threshold and the number of blue traces below threshold by the total number of traces. The lower row of parenthetical numbers above each vertical dashed line represent the measured %Same for the same 5 candidate analysis intervals. Gaps in the traces are due to saccades.

plus 1° Upward" (R+1) stimulus motion. They were selected to illustrate two extremes; some trials showed a very vigorous onset with significant overshoot (green traces), whereas others were more sluggish and/or decayed dramatically toward the end of the trial (purple traces). To compare directly and quantitatively the precision of the perceptual decision with that of pursuit, we combined standard psychometric techniques and an oculometric analysis (Kowler & McKee, 1987; Beutter & Stone, 1998) to generate equivalent metrics for perceptual and oculomotor performance. Thus, we compared traditional "psychometric" curves (plots of % rightward or downward binary perceptual decisions vs. the actual stimulus direction) with equivalent "oculometric" curves (plots of % rightward or downward pursuit decisions vs. the actual stimulus direction).

Psychometric decisions were recorded using a button press and oculometric decisions were determined by comparing the pursuit direction to a threshold (see "Methods"). Figure 1B shows the average pursuit direction for a series of analysis intervals centered on time points from 200 to 400 ms after the onset of pursuit. These data were obtained from all of the R+1 trials of a daily session for the same observer as in A. The non-parenthetic numbers above each vertical dashed line represent the percentage of upward pursuit decisions for the analysis interval centered on that line. To generate an oculometric curve, the process of determining the percentage of upward trials is repeated for the full range of directions bracketing each cardinal direction. Note that the percentage of upward decisions varies from 71.4% to 80.0% as the center-point varies from 200 to 400 ms after pursuit onset. All of these values are well above random guessing (50%) and are similar. The percentage of trials for which the perceptual and oculomotor decisions were the same, which we call %Same, is also not greatly affected by the choice of analysis interval. For the trials in Figure 1B, it varies from 62.5% to 85.7% (parenthetical values above the dashed lines) as the center-point varies from 200 to 400ms after pursuit onset. All of these values appear well above chance (~53% across all R+1 trials for this observer) and are roughly similar. We chose an analysis interval centered on 300 ms (bracketed by the vertical dashed lines in Figure 1A) because it largely overlaps with a region of minimal measurement noise and because it occurs after any overshoot is over but before any deceleration becomes severe. We chose an analysis interval length of 100 ms because it contains an integral number of cycles (exactly 6) of 60-Hz noise, which minimizes this artifact in the averaging process, and because it has been used successfully by others (Kowler & McKee, 1987).

Figure 2 plots the psychometric and oculometric curves for observer LS for the 4 cardinal directions. Note that the two types of curves largely superimpose. The SD of the best-fitting cumulative Gaussian provides a quantitative measure of direction uncertainty. For this observer, the direction uncertainty for perception was 1.30°, 1.29°, 1.30°, and 1.30° for up, down, left, and right, respectively, whereas that for pursuit was 1.16°, 1.53°, 1.43°, and 1.64°. On average, the uncertainty for perception was therefore 1.30°, whereas that for pursuit was 1.44°. The results for the other observer were similar; on average, the uncertainty for perception was 1.27°, whereas that for pursuit was 1.88°. The direction uncertainty for pursuit is quite similar to that for perception, albeit slightly larger. Figure 3(A, B, D, and E) plots the psychometric and oculometric data averaged across all 4 cardinal directions for both observers (circles) along with the average Gaussian fit (blue lines).
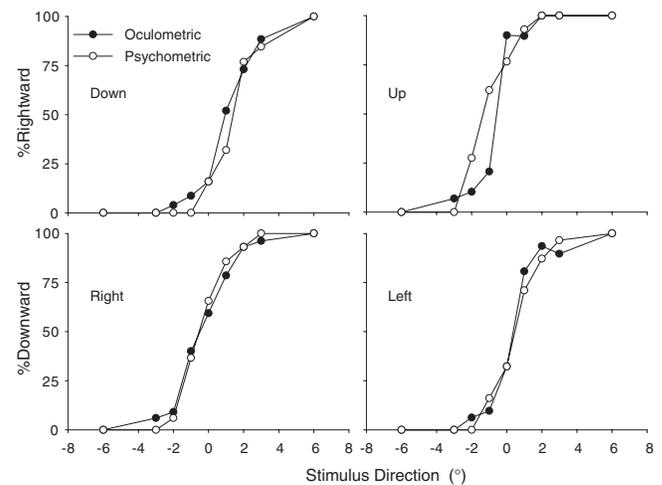

Figure 2. Psychometric and oculometric curves for observer LS for all 4 cardinal directions. Each panel plots the percentage of rightward decisions for vertical trials and of downward decisions for horizontal trials, for both the perceptual and oculomotor tasks with ~30 trials per point. The % rightward (or downward) perceptual decisions were computed directly from the observer's button-press forced choice, whereas the associated pursuit decisions were computed as illustrated in Figure 1B and described in detail in the "Methods."

Although the average precision results suggest that a similar process underlies both the perceptual and pursuit responses, they do not resolve the issue of whether or not these processes are actually performed by the same neural circuits. We therefore examined the trial-by-trial covariation between the perceptual and pursuit responses. In such an analysis, trials exactly along a cardinal direction are particularly revealing because there is no correct answer. The variability is therefore entirely dominated by the neural noise in the direction signal used to make the perceptual and oculomotor decisions. Although performance should be random (~50% rightward/downward), the %Same can vary from ~50% if the two processes are completely independent (such as two people flipping different coins) to ~100% if the two processes are completely dominated by the same noise source (such as two people responding to the same coin
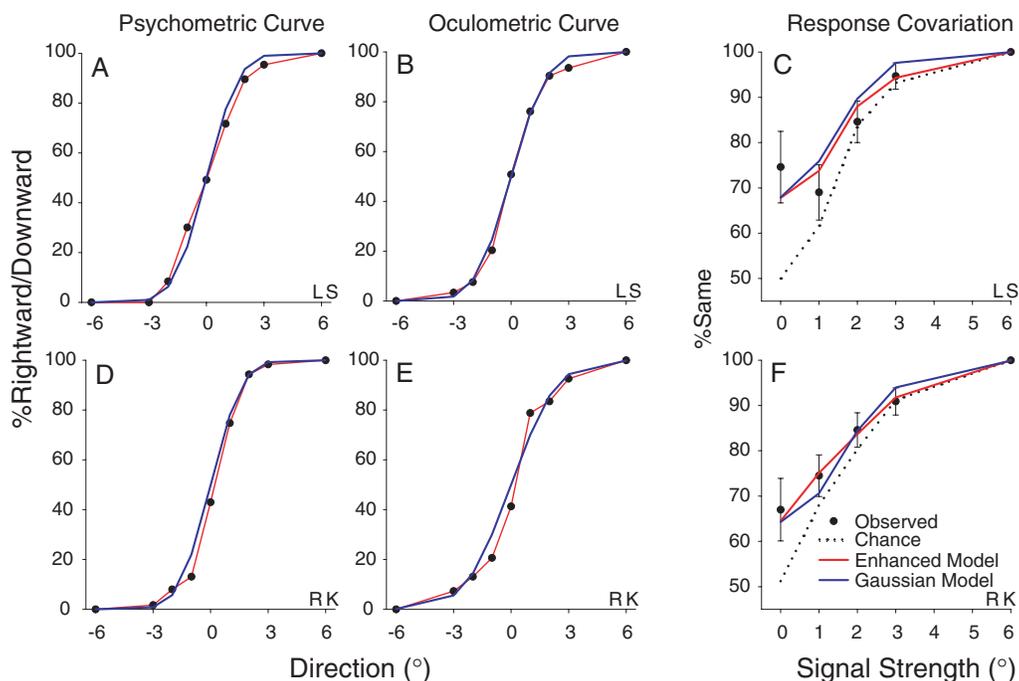
Figure 3. The relationship between perceptual and pursuit direction decisions for both observers. A and D. The psychometric data of both observers averaged over cardinal directions (black circles). The percentage of trials for which the perceptual decision was rightward or downward is plotted as a function of the direction of stimulus motion (~120 trials per point for LS; ~180 trials per point for RK). B and E. The oculometric data of both observers averaged across cardinal directions (black circles). The percentage of trials for which the pursuit decision was rightward or downward is plotted as a function of the direction of stimulus motion. C and F. The response covariation between the perceptual and pursuit decisions. The percentage of trials for which the pursuit and perceptual decisions were the same (%Same) is plotted (black circles) as a function of the absolute value of the angular deviation from the cardinal direction (signal strength), combined across cardinal directions. The error bars are the 95% confidence intervals computed from the binomial distribution. Note that the observed covariation is systematically greater than that expected by chance (dotted line), is well predicted by the Gaussian model (blue line), and is statistically indistinguishable from that predicted by the "enhanced" model (red line). See "Methods" for modeling details.

flip). For the two observers, averaged across the cardinal directions, the %Same in our analysis interval was 74.6±4.0% (SE) and 67.0±3.5% (SE), both significantly higher than that predicted by chance ($p < .001$).

The above analysis can be extended to all directions with the caveat that the number of matches occurring by chance increases with the number of overall correct decisions (e.g., if two completely separate processes make 100% correct decisions, then the decisions must be the same 100% of the time despite the fact that the processes may not be at all linked). Figures 3C and 3F plot the observed %Same (black circles) for all tested signal strengths (i.e., the angular deviation from motion purely along a cardinal direction) as well as that predicted by chance alone (dotted line). Both observers showed a consistent pattern of covariation above chance. For observer RK, this elevation was significant ($p < .05$) at signal strengths of 0°, 1°, and 2°; for observer LS, the elevation was significant at signal strengths of 0° and 1°.

This observed covariation must be due to shared noisy neural signals that cause correlated trial-by-trial variations in both perception and pursuit. To examine

this hypothesis quantitatively, we performed simulations of a simple perception and pursuit noise model (Figure 4), which assumes (1) that pursuit and perception share a neural signal that encodes the visual direction of motion and is corrupted by additive Gaussian noise (σ_v), (2) that pursuit is also influenced by additional independent Gaussian additive motor output noise (σ_m) (e.g., random fluctuations in brainstem or motoneuron signals and eye-tracker noise), and (3) that perception is also influenced by additional independent Gaussian additive perceptual output noise (σ_p) (e.g., criterion drift and finger errors). The data in Figure 3 are well explained using $\sigma_v = 1.0°$ as the single free parameter for the shared visual noise for both LS and RK, and with the two other parameters ($\sigma_p = 0.8°$ and $\sigma_m = 1.0°$ for LS; $\sigma_p = 0.8°$ and $\sigma_m = 1.6°$ for RK) fixed by the measured precision of the psychometric and oculometric data. The model simulations, represented by the blue lines in Figure 3, generate good fits to the psychometric, oculometric, and covariation data for both observers. Nevertheless, the simple model shows small but consistent deviations from the averaged psychometric and oculometric data due to the stringent constraint imposed

by the use of unbiased Gaussian response distributions. However, if the model is allowed to fit the averaged psychometric and oculometric data exactly (see "Methods"), this "enhanced" model (red lines in Figure 3) has the emergent property of fitting the %Same data even better (compare red and blue lines in Figure 3C and 3F). We emphasize that the extra degrees of freedom of the enhanced model were used exclusively to fit the psychometric and oculometric data; the covariation predictions were given no additional degrees of freedom and the only free parameter remained fixed at 1°. The simulations in Figure 3, therefore, show that the noise model in Figure 4 provides a parsimonious, quantitative explanation of the link between the perceptual and oculomotor responses in our task.
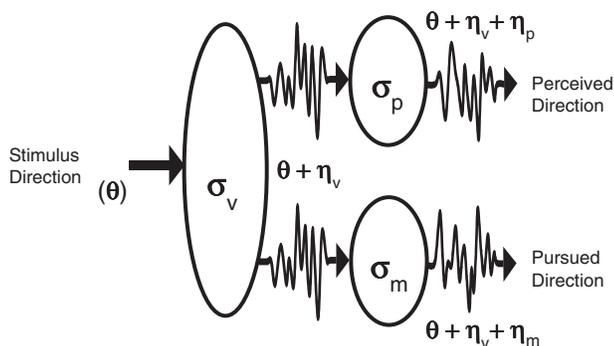

Figure 4. A schematic model of the visual direction noise dominating trial-by-trial variations in the perceptual and pursuit decisions. In response to a stimulus direction θ, the visual motion processing areas generate a noisy signal $\theta + \eta_v$ for each trial by sampling a Gaussian distribution of SD, σ_v. This signal is relayed to both perception and pursuit, each of which repeat the process by adding their own additional Gaussian noise sources (σ_p and σ_m, respectively) to yield output signals $\theta + \eta_v + \eta_p$ and $\theta + \eta_v + \eta_m$ that drive the perceptual and pursuit responses, respectively, for that trial. These two signals are each compared with a threshold to generate two binary (left/right or up/down) decisions that are partially correlated because of their shared noise η_v. The "enhanced" model allows θ in the output signals to be tweaked for each stimulus direction to fit the psychometric and oculometric curves perfectly. However, the trial-by-trial covariation above chance is still determined by η_v.

Discussion

We have found a significant correlation in the trial-by-trial variations in perceptual and pursuit responses to repeated randomly interleaved stimulus presentations. This indicates that the pursued and perceived directions are influenced by the same stochastic noise source, presumably from a shared neural mechanism encoding the direction of target motion. However, the lower than 100% correlation shows that pursuit and perception are also influenced by additional independent sources of direction noise.

Visual Motion Signals for Perception and Pursuit

Our results and conclusions are consistent with and extend previous behavioral findings that the precision of pursuit speed and perceived speed are comparable (Kowler & McKee, 1987) and that the spatial integration of direction signals for perception and pursuit are limited by similar mechanisms (Watamaniuk & Heinen, 1999). The latter study's finding that the absolute direction precision for pursuit is considerably worse than that for perception is, however, somewhat at odds with our findings. Their noisier pursuit responses may have been due to the fact that they used an extremely short analysis interval (20 ms) and that they used an eye-tracker with higher measurement noise. Alternately, the difference between our findings and theirs may simply reflect a difference between the oculomotor response to a single small spot versus that to random dots. The above issues illustrate the inherent difficulty in interpreting absolute precision; it is vulnerable to the analysis interval and the experimental conditions used (see Kowler & McKee, 1987). Indeed, even similar precision measures (our Figure 2; and Kowler & McKee, 1987) could result from the fortuitous (or judicious) choice of analysis interval or experimental conditions. The strength of the %Same analysis is that firm conclusions become independent of these factors. Although the magnitude of the covariation is somewhat sensitive to the analysis interval chosen (see, Figure 1B), and this could affect the values of any fitted model parameters, the mere existence of covariation significantly above chance for any analysis interval indicates shared neural noise. Indeed, given that the perceptual decisions were not likely based on the entire stimulus interval, it would be entirely justified to find the analysis interval that maximized the measured covariation between perception and pursuit. Because no effort was made to perform such an optimization, our reported %Same values actually represent a conservative estimate of a potentially higher actual covariation.

Our results are also consistent with and extend previous neurophysiological studies of primate extrastriate visual cortex. Previous stimulation (Komatsu & Wurtz, 1989; Salzman et al., 1992; Celebrini & Newsome, 1995), lesion (Newsome et al., 1985; Dursteler & Wurtz, 1988; Newsome & Pare, 1988; Pasternak & Merigan, 1994; Rudolph & Pasternak, 1999), and single-unit recording (Newsome, Wurtz, & Komatsu, 1988; Britten et al., 1992; Lisberger & Movshon, 1999) studies of MT and MST together indicate that these two areas play a critical role in both pursuit and motion perception. Our findings further demonstrate that the neural machinery that limits the precision of the computation of motion direction

must be shared, and therefore argue against the possibility of separate parallel pathways through these areas, one for perception and one for pursuit.

A recent study examining pursuit direction (Chuchland et al., 2003) takes an opposing view. They found little anisotropy in the directional precision of pursuit as opposed to the well-known "oblique effect" for perception (i.e., direction perception is less precise for oblique directions than for cardinal directions [Ball & Sekuler, 1987]). Churchland and colleagues conclude that the neural noise that produces the oblique effect and limits perceptual judgments of direction must occur downstream from any shared visual processing with pursuit, and that their results therefore reveal functional segregation of visual motion processing for perception and pursuit. Placed in the context of the model in Figure 4, they interpret the lack of an oblique effect for pursuit to indicate that the shared σ_v is isotropic and that the oblique effect for perception is due to an anisotropic σ_p in a cortical area "not shared with pursuit and downstream from or parallel to area MT (p. 1006)." However, the basic noise model in Figure 4 provides an alternate scenario, in which an earlier shared σ_v is responsible for the oblique effect, but an isotropic σ_m reduces (or abolishes) this effect for pursuit downstream. For our observers, both of whom showed larger σ_m than σ_p, our noise model indeed predicts smaller oblique effects for pursuit than for perception even if they are both driven by the same initial anisotropic visual motion signal.

Neural Locus of the Shared Direction Noise

Because we examined performance during steady-state pursuit, our data cannot fully resolve the extent to which

the trial-by-trial covariation we observe is due to neural signals related to retinal motion versus those related to eye movement (see Pola & Wyatt, 1989). Figure 5 elaborates on the basic noise model in Figure 4 to explore the possible cortical loci of the shared noise. More specifically, pursuit and perceptual noise could be generated within shared early visual pathways (i.e., retina through V1), in early motion processing signals in retinal coordinates (MT), or in later motion processing signals in head-centric or world-centric coordinates (MST and beyond), including any associated efference-copy (EC) signals, or could be generated at the motor and perceptual output ends.

One possibility (red neural pathway) is that the shared direction noise that limits performance is associated with early visual processing. It could result from a shared visual signal and noise (σ_r) encoded in area V1 or earlier, consistent with the later segregation of perceptual and motor pathways into the dorsal and ventral streams, as proposed by Goodale and Milner (1992). However, in primates, the receptive fields of neurons prior to primary visual cortex are not directionally selective. Even in V1, directional selectivity is relatively rare and confounded with orientation tuning. If the shared direction noise is in early visual pathways, it is more likely generated within MT (σ_d), the earliest cortical area within the dorsal stream where nearly all neurons are truly directionally tuned and a true 2D object-motion direction signal first emerges (Movshon, Adelson, Gizzi, & Newsome, 1985; Rodman & Albright, 1989). Although all of these early visual areas undoubtedly support both motion perception and pursuit (Newsome et al., 1985; Segraves et al., 1987; Newsome & Pare, 1988; Azzopardi & Cowey, 2001), this fact is not likely the cause of our observation for two reasons. First, the motion signals in V1 and MT are exclusively in retinal
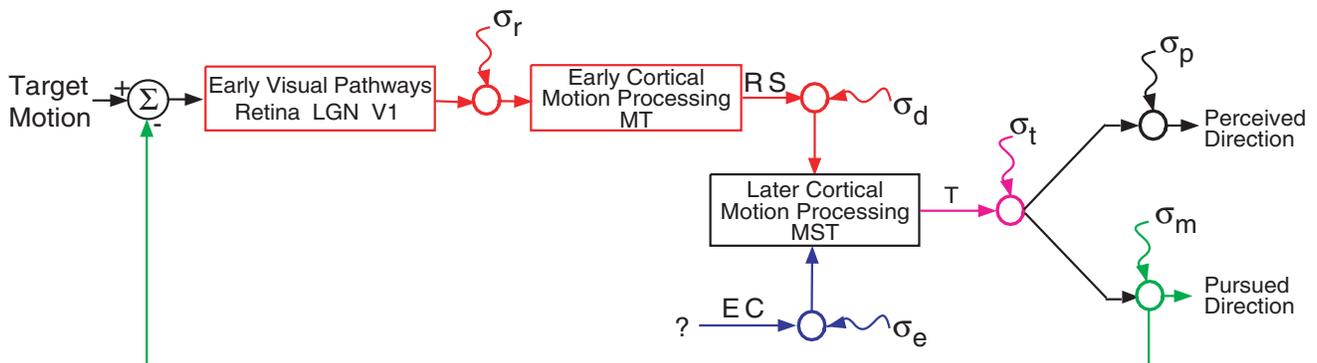

Figure 5. Visual and efference-copy (EC) contributions to perceptual and pursuit decisions. These decisions could be affected by at least six different noise sources. Early visual pathways are lumped together (red) with σ_r representing the noise contributed by all sources up to and including primary visual cortex (V1), and with σ_d representing the direction noise in the retinal slip signal (RS) contributed at the level of MT. σ_e represents the direction noise in the EC signal whose origin remains unknown (blue). σ_t represents the noise in the target direction signal (T) contributed at the level of MST or further downstream (purple). σ_p and σ_m represent the output noise of the perceptual and oculomotor systems, respectively.

coordinates. Therefore, if V1 and/or MT motion signals were limiting perceptual performance, one would generally expect a *negative* correlation between perception and pursuit because retinal direction and eye direction are physically anti-correlated (e.g., upward eye motion generates downward – or at least less upward – motion of the retinal image), yet a positive correlation was observed. Second, in our analysis interval, pursuit gain is close to one, so the residual retinal motion is quite small (~0.8 deg/s) and the output signals much reduced in both V1 and MT (Maunsell & Van Essen, 1983; Orban, Kennedy, & Bullier, 1986; Newsome et al., 1988; Logothetis, 1994). The signal driving perception and pursuit in the steady state is dominated by a signal representing ongoing eye or target velocity, which appears only later in the cortical pathway.

A second possible scenario is that an EC signal provides the shared limiting noise (blue pathway). The positive correlation between perceptual and pursuit decisions is consistent with this view. However, if σ_e dominates pursuit and perceptual direction noise during steady-state pursuit, one would expect different direction thresholds during fixation (when σ_r dominates), unless σ_r and σ_e were fortuitously the same. However, perceptual thresholds for a small spot measured during pursuit in this study (LS: 0.88° and RK: 0.97°, when converted to a semi-interquartile just noticeable difference [JND]), appear no larger than those measured under optimal conditions during fixation (e.g., ~1° at 6.66 deg/s and ~0.75° at 15 deg/s in Figure 2 of Westheimer & Wehrhahn, 1994). Indeed, a recent study that directly compares direction discrimination thresholds during fixation and pursuit found no difference between these two conditions (Krukowski, Pirog, Beutter, Brooks, & Stone, 2003). Our data are not inconsistent with a pure EC signal as the source of the shared noise, but the above facts suggest that this is unlikely.

A third possibility is that the shared target direction signal (T) is dominated by noise (σ_t) intrinsic to motion processing areas later in the dorsal pathway (purple signal). The positive correlation, together with the fact that direction discrimination thresholds appear unaffected by pursuit (see above), is consistent with the perceptual and pursuit decisions both being driven by a neural signal downstream from where retinal-motion and eye-movement information are combined to derive a signal related to target motion in the world (see Stone et al., 2000; Krukowski et al, 2003). Given the problems with the alternate scenarios described above, we propose that the shared noise, σ_v of Figure 4, is σ_t of Figure 5, the noise in a target direction signal encoded downstream from MT. Given that MST neurons have been shown to carry such combined signals and are highly active during steady-state pursuit (Newsome et al., 1988), our findings suggest that MST neurons (or neurons further downstream) are the likely source of the observed covariation, as opposed to MT neurons, which do not

carry EC signals and which respond only weakly during steady-state pursuit (Newsome et al., 1988). It should also be noted that, if the EC command is generated by local positive feedback within MST and/or surrounding cortical areas as opposed to being provided through some brainstem or cerebellar feedback loop, this scenario merges with the previous one as σ_t and σ_e become one and the same. Lastly, an apparently discrepant finding that perceptual judgments of motion direction appear more related to retinal than object motion in the world (Festinger, Sedgwick, & Holtzman, 1976) was likely due to the fact that those perceptual judgments were of a second nontarget object and not of the tracked target. This finding and those of others (Khurana & Kowler, 1987; Ferrera & Lisberger, 1997; Krauzlis, Zivotofsky, & Miles, 1999) suggest that target selection or attention may play an important role in linking motion perception and pursuit.

Closed Loop Caveats

Because of the closed-loop negative-feedback configuration of the pursuit system (i.e., eye motion alters retinal motion), it is possible that feedback of pursuit noise is driving early visual noise, which then dominates the perceptual responses (green signal). In this scenario, even if the early visual motion pathway for perception were not shared with pursuit or its intrinsic noise too small to limit either pursuit or perception, during steady-state pursuit, one might expect pursuit direction noise (σ_m + earlier sources) to add sufficient variability to the retinal motion stimulus itself to dominate any noise intrinsic to the early visual pathway. This feedback could create an external link between pursuit and perceptual decisions that might explain the observed covariation. However, there are three facts that argue against this scenario. First, if the noise in perceptual responses were dominated by noise in the retinal motion, pursuit-driven noise in the retinal stimulus would generate a *negative* correlation between perception and pursuit (see previous section), yet a positive correlation was observed. Second, this scenario predicts that psychometric thresholds would be larger or equal to oculomotor thresholds. The opposite was observed both here and by others (Watamaniuk & Heinen, 1999). Third, unless σ_p completely swamps perceptual responses (which is not consistent with the observed covariation), this scenario predicts that perceptual thresholds would be higher during pursuit than during fixation. If σ_m is large enough to drive covariation, it is large enough to add noise to direction perception during pursuit. This prediction is inconsistent with empirical observations (see previous section).

Cognitive Strategies

One might argue that a cognitive strategy in which observers based their perceptual judgments on some

sensation of their actual eye movements could trivially explain our observed covariation. However, such a strategy would require high-precision conscious access to eye-displacement information. Absolute eye-position information would not be useful given the position jitter in our stimulus, so observers would have to reliably detect eye displacements of ~0.1 deg along one axis in the presence of a simultaneous ~5-deg displacement along the orthogonal axis to account for the observed steep oculometric curves. First of all, the ability to consciously judge eye displacement with this level of precision is not plausible (Steinbach, 1987; Pola & Wyatt, 1989; Bridgeman & Stark, 1991). Secondly, even if this ability were possible, the above cognitive strategy would result in perfect correlation (%Same = 100%), unless additional noise (either by the output end or by the inconsistent application of this strategy) was added to the perceptual judgment. This additional noise could lower the covariation to the observed values, but only at the expense of increasing the uncertainty of the perceptual judgments. This would make the psychometric curves systematically flatter than the oculometric curves, yet the converse was observed. In other words, it is difficult to reconcile any strategy of monitoring the oculomotor output to perform the perceptual task simultaneously with similarly steep oculometric and psychometric curves (Figure 2) and the much less than perfect covariation (Figure 3).

Conclusions

A shared neural noise source limits the precision of perceptual judgments of motion direction and of steady-state pursuit direction. Although a few older studies suggested that pursuit might be driven by motion signals shared with perception (e.g., Yasui & Young, 1975; Steinbach, 1976; Wyatt & Pola, 1979), only more recently has there been compelling quantitative evidence to that effect (Kowler & McKee, 1987; Ringach et al., 1996; Stone et al., 1996, 2000; Beutter & Stone, 1998, 2000; Dobkins et al., 1998; Watamaniuk & Heinen, 1999), which has allowed the refutation of earlier specific claims to the contrary (Mack, Fendrich, & Pleune, 1979; Mack, Fendrich, & Wong, 1982) as well as the general claim of segregated visual streams for perception and action (Goodale & Milner, 1992). However, despite the many documented quantitative similarities between perceptual and pursuit behavior, none of these earlier behavioral findings, or even the existing physiological data (see above), is inconsistent with a separate independent set of neurons within shared motion-processing pathways limiting perceptual and pursuit performance. The trial-by-trial correlation between perception and pursuit reported here rules out this possibility. Furthermore, our data make it unlikely the observed covariation is due to shared signals at the level of MT or earlier and provide strong evidence that

perception and, at least one of its associated motor actions, share the same neural circuitry that computes target motion direction at the level of MST or further downstream. Lastly, trial-by-trial covariation analysis is a powerful tool that can be used to examine the relationship between the neural signals underlying perception and oculomotor behavior under other conditions in other tasks (e.g., visual detection and discrimination during search [Beutter, Stone, & Eckstein, 2000; Beutter, Eckstein, & Stone, 2001]).

Acknowledgments

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