

Reflexive tracking eye movements and motion perception: One or two neural populations?

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Motion-sensitive neurons in the middle temporal (MT) and medial superior temporal (MST) areas perform the sensory analysis required for both motion perception and controlling smooth eye movements. The perceptual and oculomotor systems are characterized by high variability, even when responding to identical stimulus repetitions. If a single population of neurons performs the motion analysis driving perception and eye movements, errors in perception and action might show similar direction-dependent biases, or their variability might be correlated across trials. However, previous studies have produced conflicting reports of the presence of significant single-trial correlations between motion perception and the velocity of smooth pursuit, a volitional tracking eye movement. We studied ocular following, a reflexive tracking eye movement, simultaneously measuring eye movement direction and perceived direction of a moving random dot field. Oculomotor errors were largest for near-cardinal directions, providing the first evidence for cardinal repulsion in reflexive eye movements. Biases in perceptual and oculomotor errors were correlated across test directions, but not across single trials with the same direction. Based on the similar direction-dependent anisotropies in eye movements and perception, there is reason to believe that partially overlapping populations of sensory neurons underlie motion perception and oculomotor behaviors, with independent downstream sources of noise masking trial-by-trial correlations between perception and action.

Introduction

A prevailing theory of visuo-cortical organization is that separate, but interconnected pathways mediate action and perception (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). However, both smooth eye movements and visual motion perception depend

on sensory processing by neurons in a single area—the middle temporal area (MT; Born & Bradley, 2005). Thus, visual motion processing provides an attractive model for understanding and distinguishing the neuronal mechanisms that mediate action and perception. The speed and direction of eye movements (Kawano & Miles, 1986; Kowler & McKee, 1987) and perceptual judgments about the speed or direction of visual motion (De Bruyn & Orban, 1988; Loffler & Orbach, 2001; Watamaniuk & Heinen, 1999) are highly variable, even in response to repetitions of the same stimulus. Correlated variability in oculomotor and perceptual responses would provide evidence that a single population of sensory neurons is responsible for the motion analysis driving both action and perception. However, while some studies have reported significant perceptual-oculomotor correlations (Krauzlis & Adler, 2001; Stone & Krauzlis, 2003), others have not (Boström & Warzecha, 2010; Gegenfurtner, Xing, Scott, & Hawken, 2003; Tavassoli & Ringach, 2010). For reviews see Schutz, Braun, and Gegenfurtner (2011) and Spering and Montagnini (2011). These contradictory findings may be accounted for by differences in the perceptual task (e.g., judgments of direction, relative speed, or speed perturbations), and the time windows used to characterize eye movement.

Both perceptual and oculomotor variability must, at some level, depend on the well-characterized near-Poisson variability in neuronal spiking (Churchland et al., 2010; Tolhurst, Movshon, & Dean, 1983). Neural activity in MT and the downstream medial superior temporal area (MST) is critical for motion perception (Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996; Newsome, Britten, & Movshon, 1989; Rudolph & Pasternak, 1999), the generation of smooth pursuit eye movements (Groh, Born, & Newsome, 1997; Huang & Lisberger, 2009; Komatsu & Wurtz, 1989; Lisberger & Movshon, 1999; O'Driscoll et al., 2000) and ocular

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following eye movements (Buttner, Ono, Glasauer, Mustari, & Nuding, 2008; Ibbotson, Price, Crowder, Ono, & Mustari, 2007; Kawano, Shidara, Watanabe, & Yamane, 1994). Thus, although neuronal variability within MT and MST is likely to account for some of the variability in oculomotor behavior and perceptual judgments (Huang & Lisberger, 2009; Osborne, Lisberger, & Bialek, 2005), it is unclear if a single population of sensory neurons in MT/MST is responsible for driving both perception and action.

Comparing oculomotor and perceptual responses evoked by the same stimuli may give insights into the level of neural processing shared between these two systems. Broadly speaking, this has been achieved using three methods: comparison of speed or direction discrimination thresholds; comparison of direction-dependent biases such as the oblique effect and cardinal repulsion; and single-trial correlations between eye movements and perception. Behavioral studies comparing psychophysical and oculomotor discrimination of speed and direction have found similar *thresholds* for smooth pursuit and perception (Beutter & Stone, 1998; Kowler & McKee, 1987; Watamaniuk & Heinen, 1999). However, in these studies, ocular and psychophysical data was not recorded from the same trials, and other studies have failed to report similarities in perceptual and oculomotor thresholds (Churchland, Gardner, Chou, Priebe, & Lisberger, 2003).

The presence of systematic *biases* common to perception and oculomotor behavior is also controversial. For example, human observers are more accurate at discriminating orientations and motion directions around cardinal (horizontal and vertical) axes compared to oblique directions, a phenomenon known as the oblique effect. While this finding is robust for perception (Ball & Sekuler, 1980; Gros, Blake, & Hiris, 1998; Heeley & Buchanan-Smith, 1992), there is disagreement as to whether it is evident in pursuit eye movements (Churchland et al., 2003; Ke, Lam, Pai, & Spring, 2013; Krukowski & Stone, 2005; Rottach et al., 1996). Although many such studies are based on a limited number of observers, a recent study of 20 untrained observers found no systematic differences between smooth pursuit in cardinal and oblique directions (Ke et al., 2013). Moreover, to our knowledge, the presence of the oblique effect has not been investigated with respect to reflexive eye movements. Another directional bias in perception is reference repulsion, the observation that observers overestimate the angle between cardinal axes and a test direction (Grunewald, 2004; Rauber & Treue, 1998, 1999; Szpiro-Grinberg, Spring, & Carrasco, 2011). Ocular cardinal repulsion from the horizontal axis has been reported for smooth pursuit eye movements, described as an overestimation of eye movement direction relative to the perceived horizontal (Szpiro, Spring, &

Carrasco, 2012). However, the presence of anisotropies in oculomotor behavior has not been explored across a wide range of directions nor with the ocular following response. Asymmetries have been reported in smooth pursuit, with precision and gain favored in horizontal over vertical, and downward over upward eye movements (Baloh, Yee, Honrubia, & Jacobson, 1988; Collewijn & Tamminga, 1984; Ke et al., 2013; Rottach et al., 1996).

If oculomotor and perceptual systems rely on the same population of sensory neurons, then their precision could be limited by the same sources of noise, leading to the hypothesis that errors in oculomotor behavior and perception should correlate on a trial-by-trial basis. Some studies have reported significant correlations between the trial-by-trial variability of pursuit eye movements and perceived direction (Krauzlis & Adler, 2001; Stone & Krauzlis, 2003). However, no significant correlations have been reported between smooth pursuit eye movements and perceptual judgments of brief perturbations in stimulus speed (Gegenfurtner et al., 2003; Tavassoli & Ringach, 2010). Interestingly, while smooth pursuit is a volitional eye movement, in studies using unexpected perturbations, the changes that occur in eye speed are effectively involuntary. Irrespective of the discrepancies regarding the presence of trial-by-trial correlations, it is commonly agreed that there is an initial shared source of motion processing after which independent noise sources affect the perceptual and motor systems separately (Gegenfurtner et al., 2003; Stone & Krauzlis, 2003). However, because of these uncertainties, it remains in question whether the precision and accuracy of perceptual and oculomotor responses errors are limited by common or independent sources of noise (Tavassoli & Ringach, 2010).

Prior research comparing oculomotor performance and perception has been largely concerned with smooth pursuit eye movements, which require tracking a moving target and have typical latencies of 100–140 ms depending on target speed (Ilg, 1997; Robinson, 1965; Tychsen & Lisberger, 1986). In contrast, the ocular following response, a reflexive eye movement with latencies of 70–100 ms that is driven by similar sensory systems to those that drive smooth pursuit, is less well studied (Gellman, Carl, & Miles, 1990; Miles, Kawano, & Optican, 1986). Ocular following has the major advantage of being reflexive, and therefore involves little, if any, cognitive processing. Furthermore, the open-loop phase of ocular following is a short, early phase in the response where eye movements are based only on external visual information in an observer's surrounds. That is, eye movements do not affect the speed and direction of retinal image motion. To our knowledge, only one study has used ocular following to explore the relationship between eye movements and

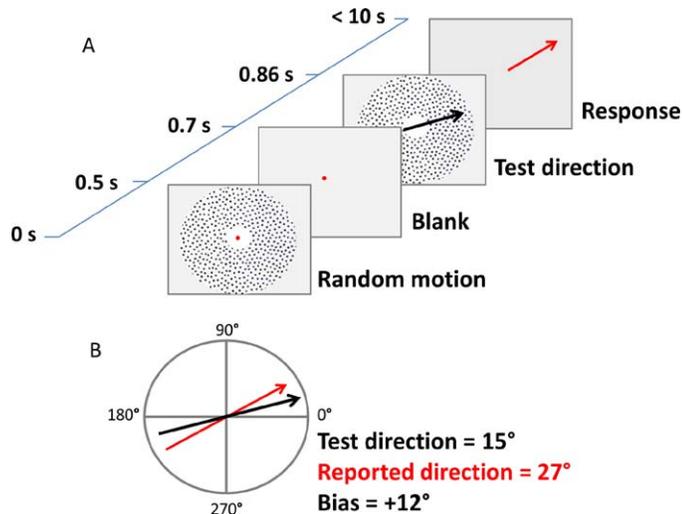


Figure 1. Stimulus and task. (A) Each trial had four periods. Initially, dots moved randomly for 500 ms with 0% motion coherence; then, following a 200-ms blank period, test motion was presented for 160 ms. All dots moved at 16 deg/s with 90% coherence in one of 24 probe directions. Finally the participants were given a 10-s window in which they used a computer mouse to drag an arrow to indicate their perceived direction of motion. (B) Calculation of perceptual error on a single trial. For this trial, the true direction is 15° with a reported direction of 27°, resulting in a bias of 12°. This illustrates reference repulsion away from the horizontal axis.

perception. In their study, Boström and Warzecha (2010) found no trial-by-trial correlation between the speed of eye movements and perceptual judgments of stimulus speed.

A common link between studies that fail to find a correlation between perception and action in the context of visual motion is that they focus on judgments of speed and depend on neuronal motion analysis in very short time periods such as detecting or discriminating motion onset or brief perturbations (Schutz et al., 2011; Spering & Montagnini, 2011). We explored whether errors in the direction of reflexive, ocular following eye movements would covary with perceptual errors, both at the level of systematic biases, such as the oblique effect and cardinal repulsion, and on a trial-by-trial basis. We compared observers' perceptual judgments of a wide-field motion stimulus with the direction of reflexive eye movements in different time periods relative to motion onset. We found evidence for cardinal repulsion and the oblique effect in the perception of 160-ms motion periods, but only cardinal repulsion was present in simultaneously recorded oculomotor responses. Further, while there was a correlation between *mean* perceptual and oculomotor errors across a range of test directions and this correlation grew over time, there was no systematic correlation between *trial-by-trial* errors. Our results are

consistent with two distinct populations of motion-sensitive neurons performing the sensory analysis required to drive smooth eye movements and direction perception. However, based on the similar direction-dependent anisotropies in eye movements and perception, there is reason to believe that a single, or two partially overlapping, neural populations are involved in the sensory motion analysis, with independent downstream sources of noise that mask trial-by-trial correlations between perception and action.

Methods

Participants

Seven observers (four male, three female; ages 18–65), including one of the authors (JB) participated in the experiment. All had normal or corrected to normal vision. Volunteers gave informed consent, had no prior psychophysical experience, and were reimbursed for their time. Before data collection commenced all observers completed 10–20 trials to familiarize themselves with the stimulus and task. Data from one participant was excluded as their pattern of responses indicated that they did not understand the task.

Stimulus and procedure

Participants were comfortably seated facing a 34.8 × 30 cm CRT monitor (IBM 6558 P202; 100 Hz refresh rate; 1,280 × 1,024 pixels). Stimuli were generated using MATLAB (MathWorks, Natick, MA) and the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997). A chin and forehead rest was used to maintain a viewing distance of 74 cm and stabilize the head.

The stimulus was a random dot pattern comprising black dots (1.2 cd/m²) on a grey background (15 cd/m²). Dots were limited to an aperture of 22.9 deg with a dot density of 3 dots/deg². Note that we use “deg” to indicate spatial angles (e.g., stimulus size) and “°” to indicate rotational angles (e.g., motion directions). To minimize eye movements during the initial phase of the stimulus, participants were required to maintain eye position within 1.2 deg of a central red fixation spot (radius 0.2 deg) surrounded by a grey annulus (1 deg) in which there were no dots. This helped eliminate intentional and accidental tracking of individual dots.

An individual trial consisted of four stages (Figure 1): an initial 500 ms “random motion” period, in which every dot was randomly replotted within the stimulus aperture on every frame; a 200-ms “blank” period consisting of a grey screen in which only the fixation

spot was visible; a 160-ms “test motion” period, in which limited lifetime dots moved in one of 24 test directions; and a response period limited to 10 s. During the test period, 10% of dots were randomly selected on each frame and replotted at a random position within the stimulus aperture. The remaining 90% of dots were displaced by 0.16 deg in the test direction, giving a test speed of 16 deg/s. If a participant failed to respond within 10 seconds of the end of a trial, the next trial started automatically. The random motion cued the test period and ensured that participants were fixating accurately, thus reducing the likelihood of postsaccadic enhancement due to eye movements prior to the motion period (Kawano & Miles, 1986). The motion direction during the test period was chosen randomly on each trial from 24 uniformly distributed directions (i.e., 15° resolution). Critically, no fixation point was visible in the test period. During the response period, the random dot pattern disappeared and the fixation point reappeared. Participants reported their perceived direction of motion by using a computer mouse to click and drag an arrow emanating from the fixation point until it aligned with the perceived direction of the motion. Observers were urged to report perceived direction as precisely as possible and were informed that response time was not being measured.

Each participant completed 9–27 blocks of 80 trials, yielding 540–1,620 trials. A five-point calibration procedure for the eye tracker was repeated every 20 trials. To minimize eye tracker signal loss, participants were encouraged to blink between, rather than during, trials. In all trials viewing was binocular and no feedback was given as to the accuracy of the perceptual responses.

Analysis

Individual trials were manually inspected to reject those that contained a saccade or signal loss (e.g., due to a blink) in the interval from 200 ms before to 300 ms after the start of the test period. In addition, any trial in which eye position deviated by more than 1.5 deg from the mean eye trajectory for each test direction was rejected. We further rejected three trials from one participant that had perceptual errors $>90^\circ$, under the assumption that they were guesses. After manual inspection, each participant had 371–1,370 usable trials (mean 847), representing 71%–92% (mean 81%) of the total trials that they completed. For each trial we determined perceptual and oculomotor errors as the difference between the perceived or eye movement direction and the actual test direction (Figure 1B). To determine eye movement directions, the unfiltered eye position data from the eye tracker was filtered with a

fifth-order Savitzky-Golay filter with a frame size of 35 ms and a 3 dB cutoff of 97 Hz. Savitzky-Golay filters perform least-squares fitting of a polynomial of the specified order at each time point, permitting noise reduction while retaining local peaks and troughs in the data. Thus, they are ideal for retaining the high frequency components associated with the onset of an eye movement; they typically have very flat pass-band, at the expense of a noisy stop-band. After filtering, we calculated the average eye movement direction between the eye positions at the start and end of time windows defined relative to eye movement onset. To determine eye movement latencies we fit a piecewise continuous linear function of the form:

$$e(t) = \bar{e} \quad \text{for } -150 \leq t \leq t_{Late} \quad (1)$$

$$e(t) = at + b \quad \text{for } t_{Late} \leq t \leq t_{Late} + 60 \quad (2)$$

where $e(t)$ is the eye speed at time t relative to stimulus motion onset, \bar{e} is the average eye speed from 150 ms before motion onset until t_{Late} ms after motion onset, and $\bar{e} = at_{Late} + b$. The raw horizontal and vertical eye speeds were obtained from the corresponding eye position traces using a central difference algorithm with time-step of 15 ms. For the cardinal probe directions, we averaged the component of eye velocity in the same direction as the target direction across all trials, yielding a single mean-speed trace. The value t_{Late} was varied between 40 and 120 and the onset of ocular following was defined as the value of t_{Late} that maximized the goodness of fit (r^2) of the equation above to the mean-speed trace for each participant. Latencies varied from 79–92 ms across participants.

Our initial analysis focuses on three metrics applied to both the perceptual and oculomotor data: (a) bias, quantified as the sign and magnitude of the mean error across trials; (b) accuracy, quantified as the mean absolute error across trials; and (c) precision, quantified as the standard deviation of errors, across trials. For the oculomotor metrics, we focused on the initial, open-loop phase of the ocular following response, from 20–80 ms after eye movement onset. Earlier time windows (e.g., 0–60 ms after tracking onset) produced qualitatively similar, but weaker results, because eye speed is lower, leading to higher variability in the calculated direction.

Eyetracker precision

Eye movements were recorded using a noninvasive infrared eye-tracker with a sampling resolution of 1000 Hz (EyeLink 1000, SR Research, Mississauga, ON, Canada). A detailed analysis of the precision of this eyetracker using an artificial eye suggests that measurement noise associated with both static and moving eye positions are negligible (Boström & Warzecha, 2010). To

supplement this, we performed two separate analyses of precision during fixation and slow eye movements.

First, we quantified the precision of fixation for the two authors. Each observer fixated a stationary spot for 2–3 minutes. This fixation period was divided into 0.5 second “trials,” and for each trial, we calculated the standard deviation (SD) of the raw, unfiltered horizontal and vertical eye position across time. Trials containing blinks or saccades greater than 1 deg in amplitude were removed, leaving 252 (NP) or 339 trials (JB), each containing 500 eye position samples. Smaller saccades were retained in the data set, but note that this can only impair our estimate of eye position precision. The 25th, 50th, and 75th percentiles of the distributions of SD in eye position were 0.068, 0.078, and 0.095 deg (NP) and 0.068, 0.076, and 0.088 deg (JB). Thus, eye position precision across 0.5-s periods was almost always better than 0.1 deg. For both observers, 95% of trials had a *range* of eye movement positions less than 0.4°, matching the diameter of the fixation spot.

Second, for all test participants, we quantified the precision of eye movement direction during ocular following *across time*. Note that this is a measure of within-trials precision (standard deviation across time), whereas the remainder of the paper describes between-trials precision (standard deviation across trials). We focused on the period 20–80 ms after tracking starts, even though ocular speed and gain in this period are low. For each trial, we determined the directional error at each time point, relative to the mean eye movement direction across the 60 ms time window. As high frequency changes in eye position are not relevant, direction errors were resampled at 100 Hz, using the MATLAB (MathWorks) *decimate* command, which applies an eighth-order Chebyshev low-pass filter with cutoff frequency 40 Hz before resampling. Finally, we determined the standard deviation of the directional errors for each participant, collapsing data across all stimulus directions, trials and time points. For the six participants, these standard deviations were 29.8°, 33.4°, 37.9°, 27.4°, 38.3°, and 34.8°. Collectively, the precision of eye position and eye movement direction across time suggests that despite the low gain and speed of eye movements evoked during ocular following, we are able to obtain reliable estimates of eye movement direction in short time windows.

Results

Anisotropies in ocular and perceptual responses

The distribution of perceptual and oculomotor errors varied with test direction. These direction anisotropies are shown in Figure 2 as violin plots for

naïve participant 1 and author JB (participant 6). Notably, the range of perceptual errors is consistently smaller for cardinal (0°, 90°, 180°, 270°) than oblique directions (45°, 135°, 225°, 315°), which is characteristic of the well-known “oblique effect” (Ball & Sekuler, 1980; Gros et al., 1998; Heeley & Buchanan-Smith, 1992). Both perceptual and ocular responses also show systematic biases, such that mean errors are typically positive for test directions in quadrants 1 and 3 ($Q_{1,3}$: 15°–75° and 195°–255°; red symbols), and negative for test directions in quadrants 2 and 4 ($Q_{2,4}$: 105°–165° and 285°–345°; blue symbols). Positive errors indicate reported directions that were anticlockwise from the true direction. These systematic biases, in which directions are reported as further from the horizontal meridian than is veridical, are consistent with the phenomenon of “cardinal repulsion” (Grunewald, 2004; Rauber & Treue, 1998, 1999).

Directional asymmetries

To quantify the direction dependent effects of cardinal repulsion and the oblique effect observed within the perceptual and ocular following data, we compared the size and distribution of errors for the cardinal and oblique directions. We grouped trials with cardinal and oblique test directions, and calculated the accuracy for each participant as the mean absolute error across trials, and precision as the circular standard deviation of the error.

A significant oblique effect was present in the perceptual reports of all six participants, evident as higher accuracy (mean absolute error) and precision (standard deviation of errors) for cardinal directions than obliques. The mean absolute error was significantly higher for oblique than cardinal directions, $t(5) = 4.19$, $p = 0.0086$ (Figure 3A). In addition, $p < 0.01$ for all participants: $t_{P1}(442) = -2.41$; $t_{P2}(119) = -6.06$; $t_{P3}(294) = -9.12$; $t_{P4}(139) = -8.43$; $t_{P5}(479) = -13.5$; $t_{P6}(343) = -14.8$. Similarly, standard deviations were significantly higher for oblique than cardinal directions, $t(5) = 3.55$, $p = 0.016$ (Figure 3C). In addition, these differences were individually significant for five of six participants: $F_{P1}(205, 237) = 0.83$, $p = 0.09$; $F_{P2}(56, 63) = 0.13$, $p < 0.001$; $F_{P3}(145, 149) = 0.09$, $p < 0.001$; $F_{P4}(62, 77) = 0.11$, $p < 0.001$; $F_{P5}(244, 235) = 0.15$, $p < 0.001$; and $F_{P6}(174, 169) = 0.03$, $p < 0.001$.

The oblique effect was not observed in the ocular following data, $t_{accuracy}(5) = -0.45$, $p = 0.67$; $t_{precision}(5) = -1.28$, $p = 0.26$, with only participant 1 showing individually significantly higher accuracy, $t_{P1}(442) = -4.00$, $p < 0.001$, and precision, $F_{P1}(205, 237) = 0.63$, $p < 0.001$, of eye movements, and all other participants showing no significant difference between accuracy and

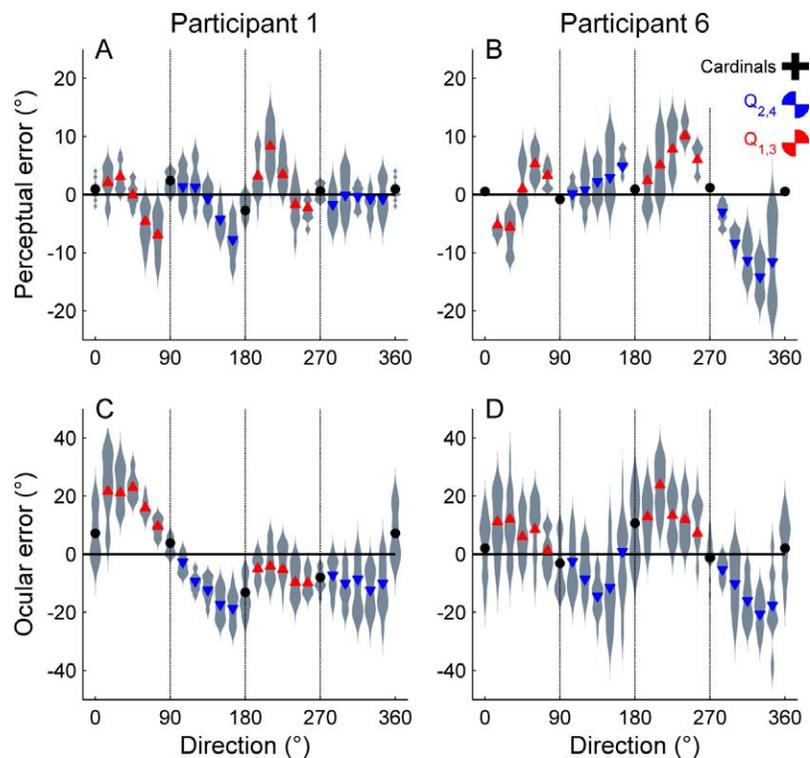


Figure 2. Perceptual (A, B) and oculomotor (C, D) errors associated with each stimulus direction are shown for naïve participant 1 and author JB (participant 6). A minimum of 56 trials (mean = 75) were completed for each of the 24 test directions. Perceptual and oculomotor responses were recorded from the same trials. Filled symbols show the mean error across trials. Violin plots show the distribution of the interquartile errors for each test direction. In the perceptual data, error distributions are highly compressed around 0° error for cardinal test directions (black data points in A, B).

precision for oblique and cardinal test directions (Figure 3B, 3D).

Figure 2 highlights that both perceptual and ocular following errors are commonly repelled from cardinal axes, and in particular the horizontal meridian. To quantify this horizontal cardinal repulsion for individual observers, we combined responses from noncardinal test directions in quadrants 1 and 3 together ($Q_{1,3}$), and compared them with the distribution of responses combined from noncardinal test directions in quadrants 2 and 4 ($Q_{2,4}$). If horizontal repulsion is present, we should expect errors in $Q_{1,3}$ to be positive and errors in $Q_{2,4}$ to be negative. Mean errors within the two direction-groupings are shown for the perceptual (Figure 3E) and ocular following (Figure 3F) data. At the population level, mean perceptual errors were significantly different from zero for $Q_{1,3}$ [$t(5) = 2.78$, $p = 0.039$], but not $Q_{2,4}$ [$t(5) = -1.25$, $p = 0.27$], and mean ocular errors were significantly different from zero for $Q_{2,4}$ [$t(5) = -4.53$, $p = 0.0062$] but not $Q_{1,3}$ [$t(5) = 2.12$, $p = 0.088$]. For 5/6 participants, the mean perceptual errors for $Q_{1,3}$ were significantly greater than zero; similarly, for 5/6 participants, the mean perceptual errors for $Q_{2,4}$ were significantly less than zero: $Q_{1,3}$ [$t_{P1}(568) = 0.28$, $p = 0.39$; $t_{P2}(160) = 1.72$, $p = 0.04$; $t_{P3}(332) = 6.09$, $p < 0.001$; $t_{P4}(183) = 7.31$, $p < 0.001$;

$t_{P5}(620) = 1.82$, $p = 0.03$; $t_{P6}(425) = 6.52$, $p < 0.001$]; and $Q_{2,4}$ [$t_{P1}(594) = -4.02$, $p < 0.001$; $t_{P2}(152) = -2.20$, $p = 0.015$; $t_{P3}(371) = -6.56$, $p < 0.001$; $t_{P4}(195) = -4.22$, $p < 0.001$; $t_{P5}(573) = 22.0$, $p = 1$; $t_{P6}(429) = -7.12$, $p < 0.001$]. In 4/6 participants, the mean ocular errors for $Q_{1,3}$ and $Q_{2,4}$ were significantly greater, and less than zero, respectively: $Q_{1,3}$ [$t_{P1}(568) = 6.99$, $p < 0.001$; $t_{P2}(160) = 0.45$, $p = 0.33$; $t_{P3}(332) = 5.20$, $p < 0.001$; $t_{P4}(183) = -3.39$, $p = 0.99$; $t_{P5}(620) = 5.12$, $p < 0.001$; $t_{P6}(425) = 9.33$, $p < 0.001$]; and $Q_{2,4}$ [$t_{P1}(594) = -14.2$, $p < 0.001$; $t_{P2}(152) = -4.02$, $p < 0.001$; $t_{P3}(371) = -7.58$, $p < 0.001$; $t_{P4}(195) = -0.30$, $p = 0.38$; $t_{P5}(573) = -8.444$, $p < 0.001$; $t_{P6}(429) = -7.87$, $p < 0.001$]. Thus, in the majority of participants, we observe the oblique effect in only the perceptual reports, but observe cardinal repulsion in both perceptual and oculomotor reports.

While directional asymmetries have previously been reported for smooth pursuit, we observed no significant differences in eye movement precision between horizontal and vertical ocular following across participants, $t(5) = -0.30$, $p = 0.78$, and although two of six participants individually showed a significant asymmetry between upward versus downward motion directions, one participant favored upward tracking and the other downward.

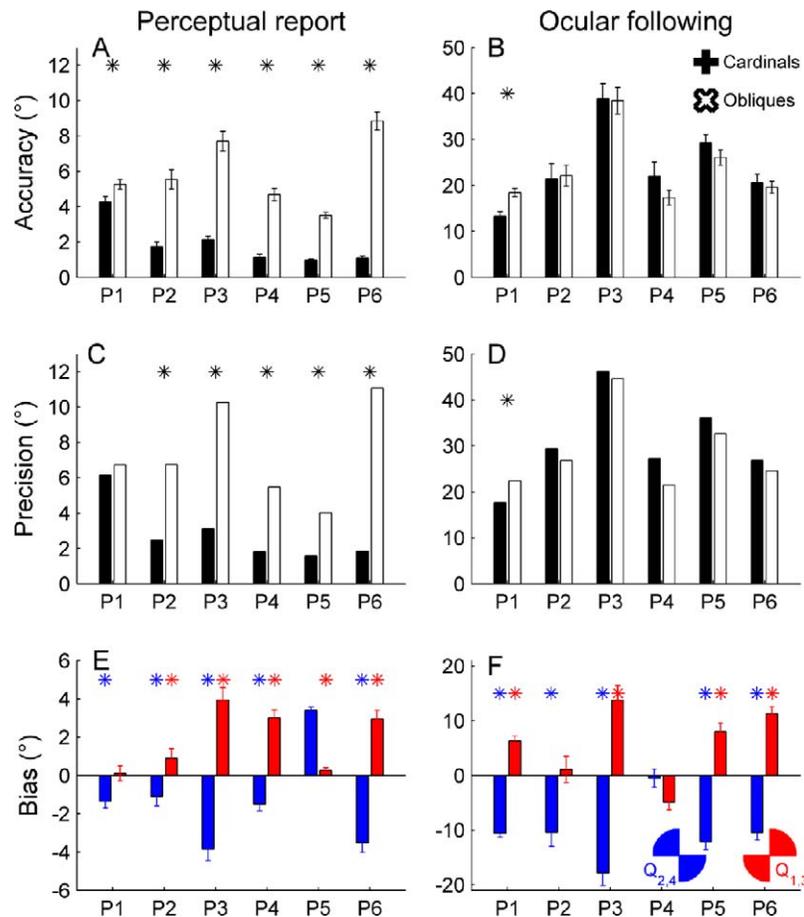


Figure 3. Accuracy (A, B), precision (C, D), and bias (E, F) of perceptual reports and eye movement directions during ocular following. Labels on the x-axis are participant IDs, and are used throughout subsequent Figures. Note the difference in scale between the left and right columns. In A–D, trials were grouped into cardinal and oblique directions. Perceptual accuracy (A) and precision (C) metrics were significantly higher (i.e., larger errors) for oblique than cardinal directions, consistent with the oblique effect. The oblique effect was not observed in the accuracy (B) or precision (D) of eye movements. Participants with significant differences in accuracy, two-sample t -test, $p < 0.01$, and precision, two-sample F -test, $p < 0.01$, are marked *. In E–F, the bias, quantified as the mean error, was calculated separately for trials with test directions in quadrants 1 and 3 (red) and quadrants 2 and 4 (blue). Data for each quadrant that is significantly different from zero are marked * (t -test, $p < 0.05$).

Correlations between perceptual and oculomotor responses

Previous studies have observed correlations between the perceived directions of motion and eye movement direction during smooth pursuit tasks (Krauzlis & Adler, 2001; Stone & Krauzlis, 2003). We explored the correlation between perceived direction and the ocular following response in two ways; first, we examined the correlation between the mean perceptual and oculomotor biases across test directions. Second, we examined the correlation between perceptual and oculomotor biases on a single trial basis. In the latter case, errors were z -scored within each test direction before collapsing across directions.

Positive correlations were observed between mean perceptual and oculomotor biases in five of six

participants, and these correlations were significant for two participants (Figure 4A, P3 & P6). We combined the z -scored mean errors for each participant (Figure 4B) and this population data showed a significant positive correlation between the mean perceptual and oculomotor responses, $r(142) = 0.23$, $p = 0.006$.

To examine trial-by-trial covariation between perceptual and oculomotor errors on single trials, we z -scored the data separately for each test direction and then combined all of the data for each participant. Given the correlations evident in mean error (Figure 4), z -scoring the single-trial data for each test direction is necessary to remove a potentially spurious correlation when the errors are collapsed across test directions. We observed no significant trial-by-trial correlation between perceptual reports of direction and oculomotor biases for any of the six participants (Figure 5). Similarly, no significant correlation was observed when

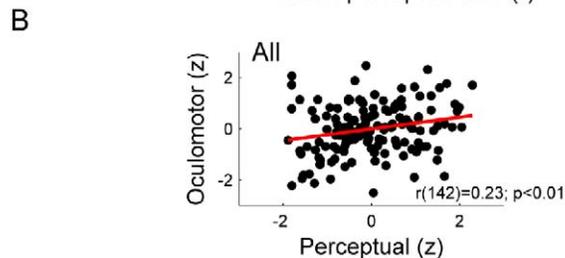
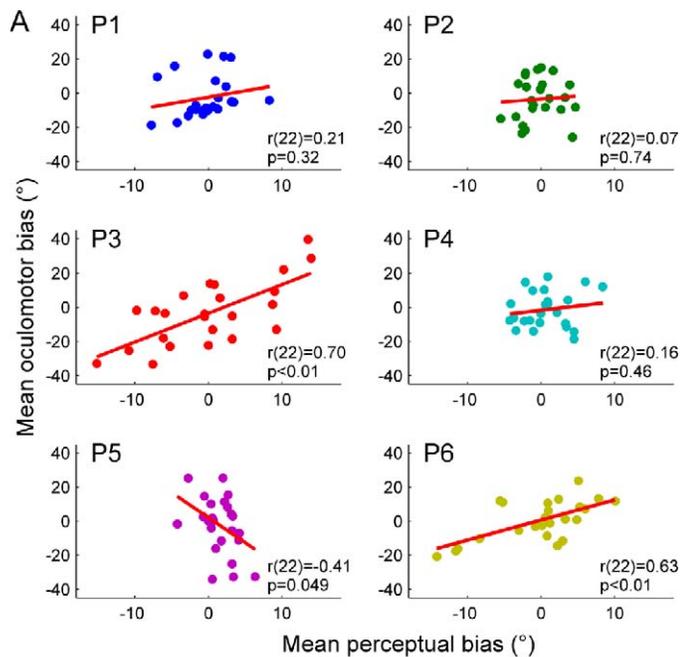


Figure 4. Correlations between perceptual and ocular following biases. Each data point represents the mean perceptual and oculomotor error for a single test direction. Data is shown separately for each participant (A) and combined across participants after z-scoring (B).

the data from all six participants were combined. In calculating these correlations, we excluded data points greater than three standard deviations from the mean (i.e., $|z| > 3$) to avoid outliers.

More cells in V1 and MT preferentially respond to cardinal than oblique directions (Li, Peterson, & Freeman, 2003; Xu, Collins, Khaytin, Kaas, & Casagrande, 2006), thus we explored whether significant trial-by-trial correlations were present if we only considered cardinal or oblique directions. No systematic correlations between perceptual and oculomotor biases were seen for either cardinal or oblique directions, at the level of individual participants or the population.

Temporal changes in ocular following precision and accuracy

Thus far, we have examined eye movements in a fixed time window from 20–80 ms after the onset of

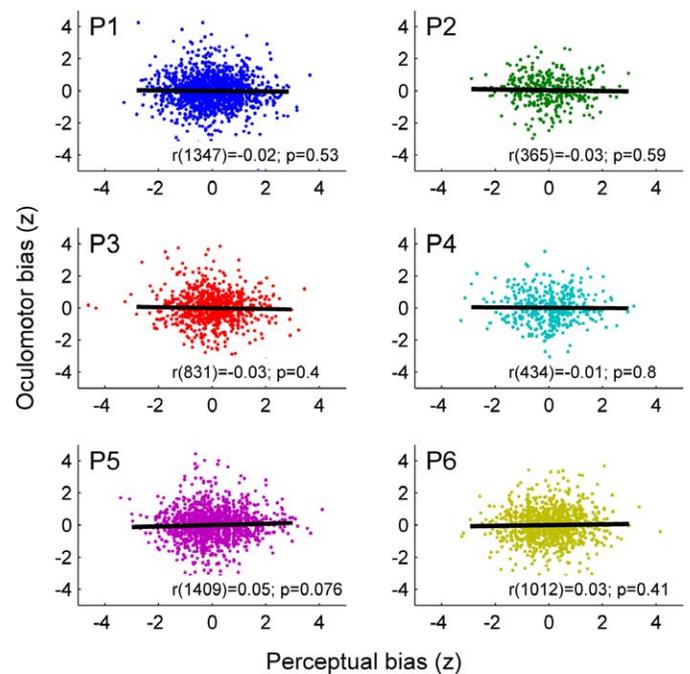


Figure 5. Single-trial covariation between perceptual and oculomotor biases. Ocular and perceptual data were z-scored and then collapsed across directions for each participant. No participant showed a significant correlation between errors in perception and the ocular following response.

tracking. We now quantify how the accuracy, precision and bias of ocular following changes over time, and how this affects the strength of the correlation between perceived and ocular direction. We perform identical analysis to that shown in Figure 3, but with two types of temporal analysis: (a) “sliding” 20-ms windows, with end times ranging from 50 ms before until 160 ms after tracking begins; and (b) “growing” windows, with a fixed start time matched to the onset of each observer’s tracking eye movements.

Using a sliding 20-ms window, accuracy and precision improved over time (Figure 6A, 6B). This improvement is most dramatic around 20 ms after the onset of tracking, as eye speed increases. Accuracy and precision increased monotonically with increasing duration of the analysis time window. We did not examine time windows ending later than 160 ms after eye movement onset, as the stimulus motion lasted only 160 ms and saccades frequently interrupted the smooth tracking later in each trial. Note that a uniform random distribution of directions, as expected early within each trial, has a mean absolute error (accuracy) of 90° and circular standard deviation (precision) of 79.8° . Under noiseless conditions we would expect accuracy and precision to be 0° . The observed values reflect a combination of noise in the eyetracking measurements and the commonly reported intertrial variability in

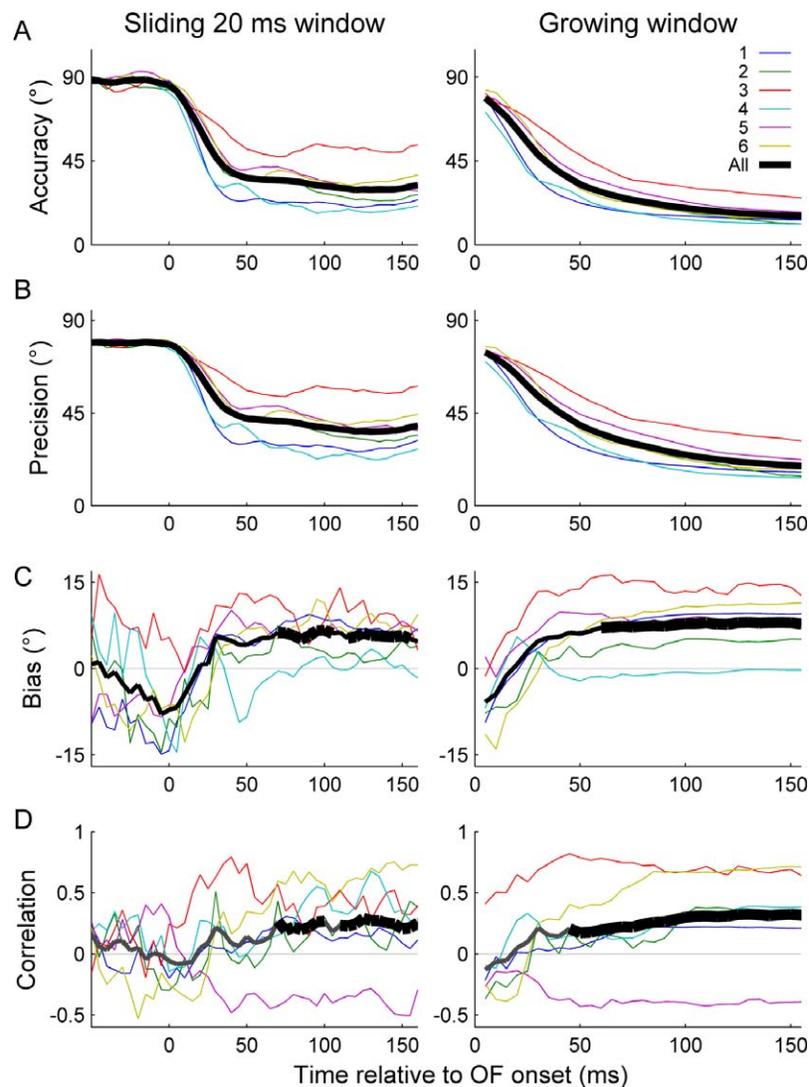


Figure 6. Temporal changes in accuracy, precision, bias, and perceptual–ocular correlations. Two types of time window were used: a sliding 20-ms time window (left column) and a window that grew in duration from the start of each observer’s ocular following (right column). Accuracy (A) and precision (B) are smallest in the latest and longest time windows. Bias (C) saturates soon after the onset of tracking eye movements. Thick black lines in C indicate periods in which the mean bias was significantly greater than zero ($\alpha = 0.05$, corrected for FDR). The correlation (D) between mean eye movement direction and perceived direction was strongest late in the trial. An average correlation was determined by combining the z-scored data for each participant (thin black line) and was significant only late in a trial, or for time windows at least 45 ms in length ($\alpha = 0.05$, corrected for FDR; thick black line).

ocular following eye movements (Boström & Warzecha, 2010).

In Figure 3F, we compared the mean bias in eye movement direction for quadrants 1 and 3 with the bias for quadrants 2 and 4. Here, we create a single metric of bias to quantify the average effect of cardinal repulsion in each time window: $\text{Bias} = (\text{Bias}_{Q1,3} - \text{Bias}_{Q2,4}) / 2$. Positive bias indicates cardinal repulsion; negative values indicate cardinal attraction. Averaged across observers, bias was significantly greater than zero for sliding 20 ms time windows ending from 70–155 ms after tracking onset, and growing time windows 60 ms or longer (thick line in Figure 6C shows points that are

significantly different from zero after correction for multiple comparisons using the Benjamini-Hochberg procedure to control the false discovery rate, $\alpha = 0.05$, $p_{\text{critical},20\text{ms}} = 0.016$ and $p_{\text{critical},\text{growing}} = 0.032$). In the growing time windows, bias plateaued for time windows longer than ~ 50 ms, suggesting that the effects of cardinal repulsion do not increase in strength over time, and follow a different time course to the change in accuracy and precision.

Correlations between perceived direction and eye movement direction measured in 20-ms windows were positive for 5/6 participants from 70 ms after tracking onset (Figure 6D). We determined a population-level

correlation by collapsing across participants after z -scoring each participant's data (as in Figure 4B). This population-level correlation was significantly greater than zero only late in the trial, for all time windows ending 70–160 ms after tracking onset except the window ending at 105 ms (thick black line in Figure 6D shows correlations that are significant after correction for multiple comparisons using the Benjamini-Hochberg procedure to control the false discovery rate, $\alpha = 0.05$, $p_{\text{critical},20\text{ms}} = 0.021$). In the growing time window, the population-level correlation was significantly greater than zero for almost all time windows longer than 45 ms and the strength of the correlation did not change with increasing window duration, $\alpha = 0.05$, corrected for FDR, $p_{\text{critical},\text{growing}} = 0.039$.

We performed a similar analysis of the single-trial correlations (e.g., Figure 5), but observed no significant correlation between perceived direction and eye movement direction, even when collapsed across subjects and with the longest analysis time windows.

Discussion

In the current study, we observed the commonly reported anisotropies of perception, the oblique effect and cardinal repulsion (Ball & Sekuler, 1980; Gros et al., 1998; Heeley & Buchanan-Smith, 1992). For the first time, we also report cardinal repulsion in reflexive ocular following eye movements. Averaged across all participants, we found a significant correlation between the mean perceptual and oculomotor biases across a range of test directions, but no correlation between these errors on a single-trial basis. We argue that the sensory motion analysis required for generating ocular following and motion perception may be performed by a single population of neurons with an anisotropic distribution of preferred directions. Independent sources of noise downstream from the sensory neurons may account for the lack of a single-trial correlation between perceptual and motor errors in the short time windows that we were able to analyze.

Correlations in the mean bias of eye movements and motion perception indicate similar neural anisotropies

The presence of both cardinal repulsion, and correlated biases across test directions in ocular following and motion perception, suggests that a single population of sensory neurons underlies motion perception and action. This neural population is likely to have an anisotropic, direction-dependent distribution of preferred directions, bandwidths or connectiv-

ity. While we have provided the first report of cardinal repulsion in ocular following, we found no evidence for the oblique effect. This matches previous studies that reported no direction-dependence in the precision of smooth pursuit eye movements (Churchland et al., 2003). Our oculomotor thresholds were significantly larger than the perceptual thresholds, attributable to the short time windows used for analyzing eye movement direction. As characterizing the oblique effect depends on comparing response precision, the large variability in our oculomotor, compared to our perceptual, responses could account for why we observed no oculomotor oblique effect.

Numerous studies have linked both direction perception and the initiation of smooth eye movements to motion analysis performed by neurons in cortical areas MT and MST (Born & Bradley, 2005; Newsome & Pare, 1988). Neurons in these areas are likely to have an anisotropic distribution of direction tuning. Although an electrophysiological study of macaque MT reported isotropic distributions of preferred direction, tuning bandwidth and peak response, this may have been due to the relatively small sample size of 220 neurons (Churchland et al., 2003). Optical imaging in owl monkey MT has reported an overrepresentation of cortical territory representing cardinal versus oblique orientations (Xu et al., 2006). Similarly, V1, which provides the dominant input to MT, has widely reported orientation-tuning anisotropies, based on a range of methods including electrophysiology in cats and monkeys (De Valois, Yund, & Hepler, 1982; Li et al., 2003), optical imaging in ferrets (Chapman & Bonhoeffer, 1998; Coppola, White, Fitzpatrick, & Purves, 1998) and human fMRI (Furmanski & Engel, 2000; Mannion, McDonald, & Clifford, 2010).

Under what condition are eye movements and motion perception correlated across trials?

The presence of significant trial-by-trial correlations has been the hallmark evidence for previous studies arguing that a single population of sensory neurons underlies the generation of smooth eye movements and motion perception. However, relatively few studies have found such correlations. To our knowledge, only one other study has compared errors in the ocular following response and perception. Although they focused on speed, rather than direction, no significant correlation was reported (Boström & Warzecha, 2010). Significant trial-by-trial correlations have been reported for the perceived direction and reflexive tracking of bistable stimuli such as plaids (Beutter, Mulligan, Stone, & Null, 1995; Beutter, Stone, & Null, 1996). In contrast, using a binocularly rivalrous stimulus, in which orthogonal gratings are presented separately to

each eye, perception and reflexive eye movements are dissociated: perception follows the component motion of one of the gratings, while eye movements follow the pattern motion associated with the plaid produced by combining the two gratings (Spering, Pomplun, & Carrasco, 2011). A major difference between our study and those using bistable and rivalrous stimuli is that we examined “fine” correlation between errors around a single possible target direction. In contrast, studies using bistable stimuli examine “coarse” perceptual-motor correlations as the possible choices are separated by 90°. The presence of a correlation therefore depends on the perceptual and oculomotor systems weighting or decoding the sensory activity in the same way.

Prior research comparing errors in oculomotor performance and perception has largely been concerned with smooth pursuit eye movements, which require volitional tracking of a small moving target (Robinson, 1965). Significant correlations have been reported between the direction of smooth pursuit eye movements and perceived direction (Krauzlis & Adler, 2001; Stone & Krauzlis, 2003). However, when observers discriminate increases from decreases in speed, no correlation has been reported between eye movement speed and perception (Gegenfurtner et al., 2003; Tavassoli & Ringach, 2010). The brevity of the stimulus perturbation in the latter studies means that eye speed changes subconsciously and involuntarily in an attempt to match the target velocity (Buttner et al., 2008). Thus, it appears that the variability in eye movements and perception is not shared when the eye movements are reflexive in nature, or when eye movements depend on motion analysis in short time windows, as is the case for ocular following and speed perturbations in smooth pursuit. The fact that action–perception correlations are only observed by some experimenters suggests that if a single population of sensory neurons introduces significant error covariation between action and perception, the detectability of this correlation at the behavioral level is limited by downstream noise injected in independent, downstream perceptual or oculomotor-related areas (Boström & Warzecha, 2010; Gegenfurtner et al., 2003).

Timescales of ocular following and smooth pursuit

We observed improved accuracy, decreased variability, and enhanced correlations between mean biases in eye movement direction and perceived direction in both *later* and *longer* time windows. Similar preliminary evidence was reported by Kumbhani, Spering, and Movshon (2011) whereby the ocular following response and perceptual judgments of direction to single component gratings were less correlated on a single trial basis in the early phases of ocular following (<100

ms after tracking begins) compared to the closed loop tracking period (100–300 ms after tracking begins).

That performance improves with increasing *length* of the analysis window may trivially reflect that measurement variability decreases with longer observation windows. Previous studies of pursuit have shown that perceptual and oculomotor speed thresholds are higher in short time windows (120 ms) than long time windows (200 and 500 ms) (Gegenfurtner et al., 2003), and became more similar with increasing in stimulus duration (Krauzlis & Adler, 2001). However, in response to stimuli with ambiguous motion information such as plaids and diamonds (i.e., distinct component and pattern directions), early phase ocular following and smooth pursuit eye movements initially follow local features of a stimulus (Barthelemy, Fleuriet, & Masson, 2010; Masson & Castet, 2002; Masson & Stone, 2002). Later phases of either ocular following or smooth pursuit, however, follow the veridical direction of stimulus motion, showing that some motion integration process must take place later in the stimulus presentation. As our dot stimulus contains no strong orientation components, similar refinement of sensory motion processing that lead to tracking of pattern or object motion could account for the improvements in precision and accuracy that we see over time.

Furthermore, the biases in perception and eye movements reported by Krauzlis and Adler (2001) converged with increasing stimulus duration. The longest saccade-free time window that we analyzed was 160 ms, which may explain the lack of single-trial correlation in both this study and other studies using ocular following or stimulus perturbations, as these explicitly require short analysis time windows (Boström & Warzecha, 2010; Gegenfurtner et al., 2003; Tavassoli & Ringach, 2010).

Improvements in accuracy and precision in *later* analysis windows require a different explanation. The late improvements may reflect the timescales over which different types of motion analysis are performed. Eye movements may be biased to short-latency, low-accuracy responses in order to stabilize the retinal image as quickly as possible. In contrast, motion perception may be biased to longer-latency, higher-accuracy responses, meaning that oculomotor–perceptual correlations cannot emerge until late after motion onset. Alternatively, it is possible that sensory information begins to influence oculomotor processing, or vice versa, after some delay. An efferent copy of oculomotor commands is likely to reach sensory motion processing areas (Ibbotson et al., 2007; Wurtz, Joiner, & Berman, 2011); thus, the late emergence of significant perceptual–oculomotor correlations may be due to the time taken to integrate an efferent motor signal into sensory processing.

Conclusion

This is the first study to report cardinal repulsion in reflexive tracking eye movements and similar directional biases in ocular following and perceived direction. Similar to previous studies, we failed to observe single trial correlations between oculomotor and perceptual errors, likely due to independent downstream noise in the perceptual and motor systems swamping common variability introduced in sensory processing. Our results are consistent with partially overlapping populations of neurons performing the sensory motion analysis required to drive smooth eye movements and direction perception, accounting for the common anisotropies in mean biases of perception and ocular following.

Keywords: ocular following response, trial-by-trial correlation, direction perception, sensory noise, oculomotor system

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