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Visual motion integration for perception and pursuit

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Abstract. To examine the relationship between visual motion processing for perception and pursuit, we measured the pursuit eye-movement and perceptual responses to the same complex-motion stimuli. We show that humans can both perceive and pursue the motion of line-figure objects, even when partial occlusion makes the resulting image motion vastly different from the underlying object motion. Our results show that both perception and pursuit can perform largely accurate motion integration, ie the selective combination of local motion signals across the visual field to derive global object motion. Furthermore, because we manipulated perceived motion while keeping image motion identical, the observed parallel changes in perception and pursuit show that the motion signals driving steady-state pursuit and perception are linked. These findings disprove current pursuit models whose control strategy is to minimize retinal image motion, and suggest a new framework for the interplay between visual cortex and cerebellum in visuomotor control.

1 Introduction

For primates in general and humans in particular, visual motion information is critical both for perception and for many motor behaviors: from walking to swinging in trees to catching a ball. Some researchers have proposed two separate visual pathways (Mack et al 1979, 1982; Goodale and Milner 1992), one controlling motor action and one determining perception. Others have emphasized the shared nature of the visual pathways for motor actions and perception (Yasui and Young 1975; Steinbach 1976; Wyatt and Pola 1979; Smeets and Brenner 1995; Beutter and Stone 1998; Dobkins et al 1998). Because of mechanical simplicity and ease of measurement, eye movements have been extensively studied as model systems of sensorimotor control. More specifically, there are two complementary types of eye movements underlying the voluntary control of gaze (Carpenter 1988): saccades, which rapidly shift gaze position from one location of interest to another; and pursuit, which generates smooth eye motion to follow a moving object. In the present study, we measured motion perception during the pursuit of specially designed, partially occluded stimuli to shed light on the relationship between the visual motion processing for perception and action.

Over the past forty years, important properties of pursuit have been elucidated by using a small moving dot as the target stimulus. Rashbass (1961) demonstrated that pursuit is largely a response to motion, so current pursuit models appropriately emphasize a motion-control loop, although position errors may also play a role (Pola and Wyatt 1980; Lisberger et al 1987; Morris and Lisberger 1987; Krauzlis et al 1997). Pursuit tends to reduce retinal slip (image motion in head-centered coordinates minus eye motion) and thus is physically constructed with negative feedback, but greater stability and accuracy would be achieved if target velocity in the world drove pursuit (Young et al 1969).

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A neural target-velocity signal, capable of sustaining steady-state pursuit despite negative feedback, could be created by the addition of eye/gaze velocity and retinal slip (Yasui and Young 1975). This view is supported by the considerable physiological and behavioral evidence for the combination of visual motion inputs and eye-velocity positive feedback in the cerebellum (Miles and Fuller 1975; Lisberger and Fuchs 1978; Kase et al 1979; Miles et al 1980; Stone and Lisberger 1989, 1990). These results led to the proposal of pursuit models (Robinson et al 1986; Krauzlis and Lisberger 1989, 1991; Ringach 1996) that incorporate both mechanical negative feedback and neural positive feedback, in an effort to minimize retinal slip.

The dot stimuli used in these previous pursuit studies are, however, somewhat trivial to process because the 'local' motion in the image and the 'global' motion of the dot-as-object are identical, unlike most natural stimuli. In the real world, moving objects have complex contours and the motion of their edges must be segregated from static or moving backgrounds, and selectively integrated to recover the motion of objects. In addition, given that objects are often partially occluded or have regions in which the edges or corners are invisible, object motion often must be reconstructed from an incomplete subset of edge motions while resolving the inherent ambiguity associated with determining which pieces to combine and which to keep separate. Visual psychologists have recognized these complexities in visual motion processing for some time (eg Adelson and Movshon 1982; Hildreth 1982; Braddick 1993), yet, by focusing on the pursuit response to a small moving dot, previous oculomotor studies have not addressed these critical issues. Furthermore, steady-state pursuit of dots is associated with negligible residual retinal motion, thereby constraining the meaningful analysis of visual motion inputs to the initial hundred or so milliseconds of the pursuit response (Lisberger and Westbrook 1985). We used partially occluded moving line-figure stimuli as a new tool for exploring the issue of motion integration for pursuit and its relationship to perception. In particular, partial occlusion causes significant and unavoidable retinal motion even during perfect steady-state pursuit, thereby allowing the meaningful examination of visual motion processing even during steady-state pursuit.

In this study, we show that the pursuit system does not merely attempt to minimize retinal motion, and is indeed capable of recovering object motion through a motion-integration process more veridical than the simple vector averaging of retinal motion. We also reveal a link between the motion integration used for perception and pursuit. These findings indicate that significant changes to current pursuit models are needed. We therefore propose a new control strategy consistent with our results, within the context of primate cortico-cerebellar pathways. Preliminary results have appeared elsewhere (Beutter and Stone 1997; Stone and Beutter 1998; Krauzlis and Stone 1999).

2 Methods

2.1 *Visual display*

The visual stimuli were displayed on a 21-inch Philips Brilliance 21A monitor running at 60 Hz noninterlaced, using an AT Vista display card hosted by a 486 PC. At the 57 cm viewing distance used, the display subtended 38 deg × 29 deg and the pixel size was 0.06 deg.

2.2 *Eye-movement recording and analysis*

Eye position was measured with an infrared video-based eye tracker (ISCAN Inc) sampling at 240 Hz with a precision of ~0.15 deg. Observers used a bite bar to minimize head movements. Calibration was performed prior to each run by having observers fixate nine known locations arranged in a 4 deg × 4 deg grid and linearly fitting the tracker data (Beutter and Stone 1998). Saccades were identified by thresholding a filtered version of the eye-position traces with a 7-point saccade template. We fit (minimum χ^2)

sinusoids to the saccade-free portions of the last full cycle of the horizontal and vertical eye-position traces (allowing the optimal offset for each intersaccadic interval). The amplitude of the best-fitting sinusoid at the stimulus temporal frequency defined the pursuit amplitude.

2.3 *Experiment 1*

Three observers (one naïve) were asked to track the center of a moving line-figure object, viewed through stationary apertures, and to respond whether the object moved leftward or rightward of straight down in a yes–no method-of-constant-stimuli paradigm. The object, a flattened diamond, moved sinusoidally (0.94 Hz) along 4.5 deg linear trajectories for 1.6 s (1.5 cycles) under two aperture conditions (figure 2, top). Its possible object-motion trajectories deviated by 0°, ±6°, or ±12° from straight down. Using basic trigonometry, it can be shown that the vector-average direction (θ_{VA}) is related to the true object-motion direction (θ) by the following equation (with α being the internal diamond angle bisected by the horizontal meridian),

$$\theta_{\mathrm{VA}} = \arctan\left(\tan^2\frac{\alpha}{2}\tan\theta\right). \tag{1}$$

Note that θ_{VA} deviates from θ when the diamond is not square (ie when $\alpha \neq 90°$). In experiment 1, $\alpha = 40°$ (figure 2, top left) so, for the range of directions examined, vector averaging predicts a nearly linear trend between the pursuit and object-motion directions with a slope of ~0.13. Because the orientations of the various component segments were fixed throughout the trial and were the same for all conditions, the different oblique object motions were therefore distinguishable only by subtle differences in the vertical 'bobbing' motion of the components. To reduce the perceptual usefulness of any cues other than object motion itself (eg the relative vertical separations of the segments or changes thereof), we added a random leftward or rightward initial object position offset (±0.7 deg) and zoom (±10% over the trial duration). The pixel luminance was 93 cd m^{-2} for the line segments. The visible apertures were dark (0.2 cd m^{-2}) and the invisible apertures were equiluminous with the background (38 cd m^{-2}).

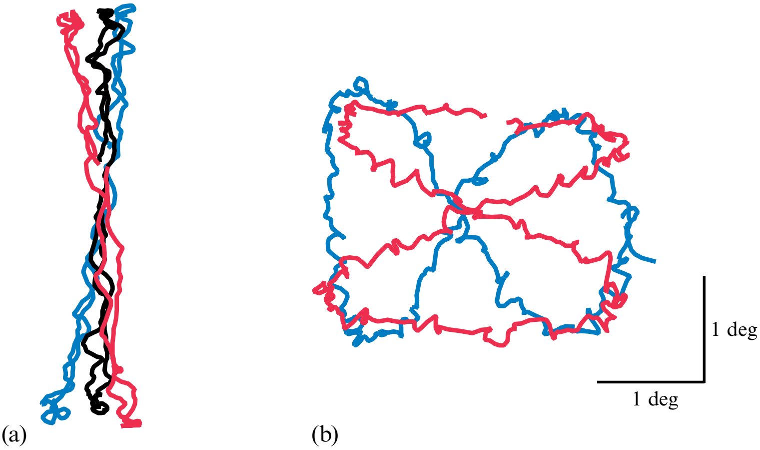

Figure 1. Raw eye-movement traces. (a) Eye-position trajectories for three visible-aperture trials in experiment 1 (blue: −12° condition; black: 0° condition; red: +12° condition). Note that, despite the fact that the segment motion in the display is always vertical, the directions of the eye-position trajectories can be oblique and appear monotonically related to object direction. (b) Eye-position trajectories for two trials reported as coherent in experiment 2 (red: 'eight' condition; blue: 'infinity' condition). Note that, despite the fact that segment motion in the display is again purely vertical, the eye-position trajectories are largely accurate representations of the 2-D object-motion trajectory.

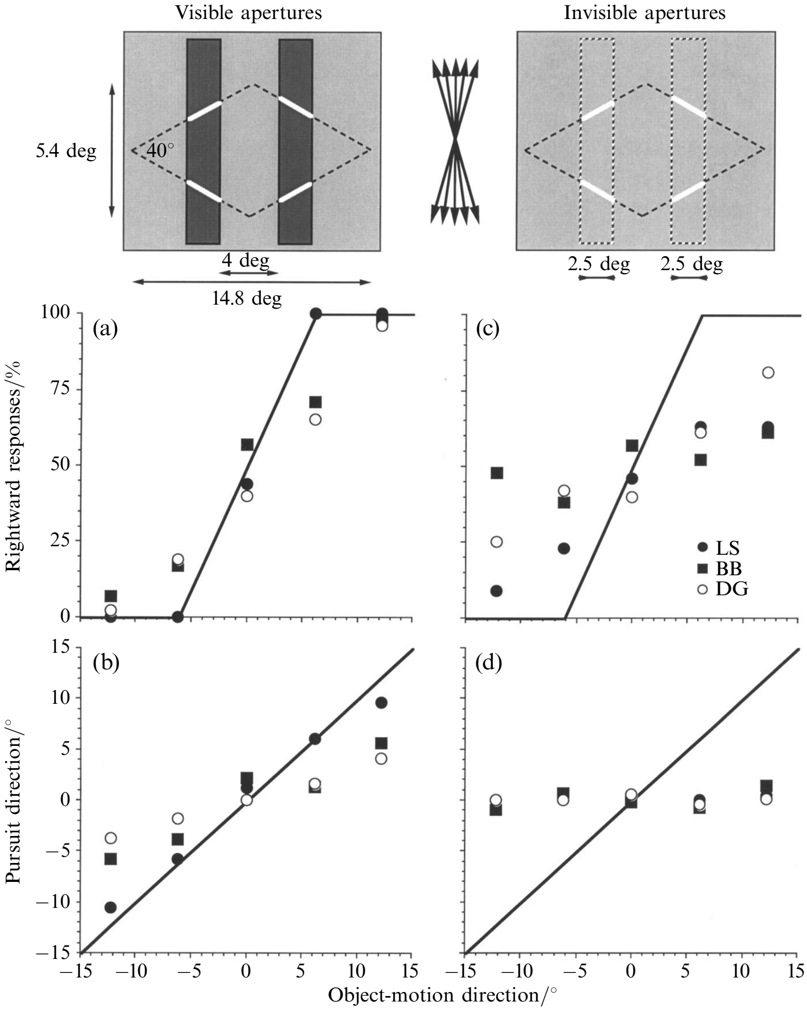

Figure 2. Experiment 1. The upper panels illustrate the physical layout of the stimulus objects (right and left) and trajectories (center). The dashed lines here and in figure 2 indicate the invisible (occluded) portions of the object and the invisible borders of apertures. (a) Psychometric functions for all three observers (symbols) and best possible perceptual performance (solid line) for the visible-aperture (high-coherence) condition. Assuming a binomial distribution, the number of trials per point (~48) yields standard errors in (a) and (c) always $< 7\%$, but generally much smaller. (b) Mean pursuit direction for all three observers (symbols) and perfect pursuit of object motion (solid line) for the visible-aperture condition. Average standard errors were 1.1°, 1.9°, and 2.2° for LS, BB, and DG, respectively. (c) Same as (a) for the invisible-aperture (low-coherence) condition. Note that the psychometric functions are flatter than in (a). (d) Same as (b) for the invisible-aperture condition. Note that the pursuit direction is always nearly vertical (0°), independent of the object-motion direction. Average standard errors were 0.6°, 1.1°, and 1.8° for LS, BB, and DG, respectively.

Observers performed two runs in each aperture condition in alternate blocks. Each block consisted of six presentations of 20 randomly interleaved stimuli (5 directions × 2 offsets × 2 zooms). Pursuit direction was computed as the mean (across trials, offsets, and zooms) of the arctangent of the ratio of the vertical to horizontal pursuit amplitudes. Figure 1a shows raw eye-position trajectories from three trials and illustrates the orderly relationship between object-motion direction and pursuit direction observed in the visible-aperture condition. Eye-position traces in the invisible-aperture condition (not shown) show a greater number of saccadic intrusions interspersed with nearly purely vertical smooth portions regardless of the object-motion direction (see figure 2 of Krauzlis and Stone 1999). Psychophysical direction-discrimination thresholds were derived by fitting the psychometric curves (percentage of rightward judgments versus object-motion direction) with cumulative Gaussians. Direction threshold was defined as half of the distance between the 25%-correct and 75%-correct points on the curve (ie 1.48 times the standard deviation of the fitted Gaussian).

2.4 *Experiment 2*

Four observers (three naïve) were asked to track the center of a line-figure object, viewed through two invisible stationary vertical apertures, and to report whether it appeared as a single object moving coherently throughout the trial in a yes–no paradigm. The object moved for 3.125 s (1.25 cycles) along Lissajous trajectories produced by sinusoidal vertical and horizontal motion at temporal frequencies of 0.4 and 0.8 Hz (or vice versa) and peak-to-peak amplitudes of 4 deg (figure 3, top). To further reduce the predictability of the stimulus, we used four possible initial directions of motion, always starting from the same central fixation point. The luminance was 44 cd m^{-2} for the visible line segments

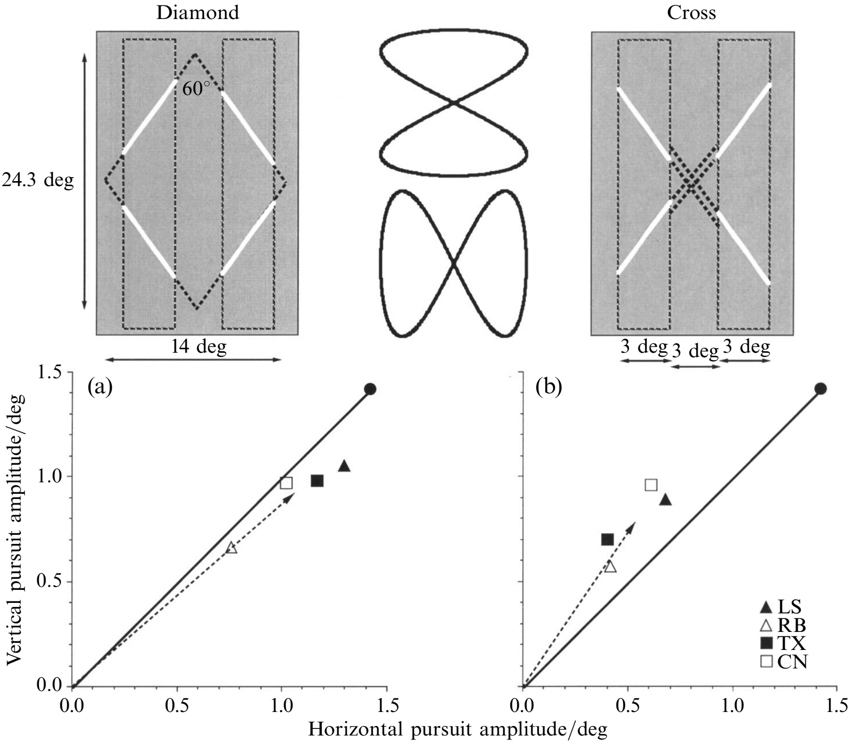

Figure 3. Experiment 2. The upper panels illustrate the physical layout of the stimulus objects (right and left) and trajectories (center). (a) Mean vertical versus horizontal pursuit amplitudes for all four observers (symbols) for the diamond stimulus. The solid line indicates pursuit trajectories with aspect ratios of 1, the solid circle perfect pursuit of object motion (gain = 1), and the dashed arrow the pursuit response averaged across observers. Note that the average response vector is shorter than perfect (gain ~ 0.7) and slightly below the solid line. This indicates a small ($\sim 15\%$) horizontal bias, consistent with the commonly reported small horizontal–vertical pursuit anisotropy. (b) Same as (a) for the cross stimulus. Note that the average response vector is much shorter (gain < 0.5) and has rotated counterclockwise relative to the diamond condition. The response shows a large ($\sim 50\%$) vertical bias, consistent with the observed perceptual bias toward the incoherent motion of the vertical segments. Within-subject *t*-tests indicate that all observers showed significant ($p < 0.001$) differences in both pursuit gain and aspect ratio for the two objects. The standard errors (averaged over horizontal and vertical) for both conditions were 0.02 deg, 0.01 deg, 0.02 deg, and 0.03 deg for observers LS, RB, TX, and CN, respectively.

and 38 cd m^{-2} for the background and apertures. The object was either a vertically elongated diamond or a cross (created by shifting the positions of the upper and lower segments of the diamond). Observers performed at least four runs, each with four repetitions of sixteen different randomly interleaved stimuli (2 objects × 2 trajectories × 4 initial motion directions). The total gain was computed as the total amplitude of eye motion [the square root of the sum of the squared mean (across trials, trajectories, and initial directions) horizontal and vertical pursuit amplitudes] divided by the total amplitude of the object motion. The mean aspect ratio was computed as the ratio of the mean vertical to horizontal pursuit amplitude. Again, with basic trigonometry, it can be shown that the aspect ratio predicted from vector averaging (R_{VA}) is related to the true stimulus aspect ratio (R) by the following equation,

$$R_{\mathrm{VA}} = R\cot^2\frac{\alpha}{2}\,. \tag{2}$$

So, as in experiment 1, the vector-average prediction deviates from veridical because the diamond is not square ($\alpha \neq 90°$). In experiment 2, $\alpha = 120°$ (figure 3, top left) so, by equation (2), vector averaging predicts a vertical-to-horizontal aspect ratio of ~ 0.33. Figure 1b shows raw eye-position trajectories for two trials of diamond motion reported as coherent and illustrates the relatively accurate tracking of the two object-motion trajectories (the 'eight' and the 'infinity'). Eye-position trajectories of cross trials (not shown) generally showed many saccadic intrusions such that the shape of any underlying smooth component of the trajectory was not readily apparent from the raw traces.

3 Results

In the two experiments presented here, we used independent approaches to manipulate the perceived motion of partially occluded line-figure objects without actually changing either the local motion of their edges or the global motion of the object. More specifically, we altered static aspects of the stimulus (aperture luminance in experiment 1 and object geometry in experiment 2) to change the perception from that of a single coherently moving object to that of multiple, incoherently moving line segments. Observers were asked to perform perceptual judgments while pursuing the moving object viewed through vertical stationary apertures, which always concealed all object vertices (ie no unambiguous feature points on the moving object). Under all conditions, only four line segments (local edges) were displayed, each oscillating up and down within the apertures (top panels of figures 2 and 3). Such stimuli are powerful probes of motion integration for pursuit and perception for three reasons.

First, both pursuit and perception are forced to perform motion integration to recover object motion, because the image motion is restricted to the ambiguous vertical motion of line segments. Second, we can determine if human pursuit is driven exclusively by the vertical image motion or if its behavior is more closely linked to perceived object motion, because the stimulus pairs in each experiment have identical segment and object motions yet are nonetheless perceived differently. Third, the fact that object geometry constrains the vector-average direction without impacting the actual object motion (Lorenceau 1998) allows us to construct specific stimulus objects that generate large differences between the predictions of motion-integration models that veridically derive object motion (eg Adelson and Movshon 1982) and those that use simple vector averaging of the local motions as a crude estimate of object motion (eg Wilson et al 1992; Lisberger and Movshon 1999).

3.1 *Experiment 1: The effect of aperture contrast on perceived and pursued direction*

In this experiment, we use the fact that the luminance of the static aperture has a powerful effect on perception (Lorenceau and Shiffrar 1992; Shiffrar and Lorenceau 1996). When the apertures are visible, dark relative to both the background and the line segments (figure 2, top left), the sense of occlusion is powerful and the stimulus is generally perceived as a coherently moving diamond. When the apertures are invisible, equiluminous with the background, and the line contrast is high (figure 2, top right), the sense of occlusion is weak and the bright line segments are generally perceived as a jumbled set of independent local vertical motions. Despite this dramatic difference in the perceived motion, the physical motion in the two aperture conditions is identical [ie the luminance Fourier spectrum (Watson and Ahumada 1983, 1985; Adelson and Bergen 1985) is identical except for the stationary term]. The line-segment motions were always consistent with them being part of a partially occluded diamond moving sinusoidally along a linear trajectory, whose axis deviated by small amounts from pure vertical (figure 2, top middle). Observers were asked to pursue the diamond and to respond whether its motion was leftward or rightward of straight down.

In the visible-aperture condition, observers were able to judge the direction of object motion rather precisely (figure 2a). The average perceptual direction threshold was 3.9° (range: 0.8° to 5.5°) with little or no systematic bias (average: 0.7°; range: 0.0° to 2.0°). Similarly, mean pursuit direction was linearly related to the object-motion direction (figure 2b). Averaged over observers, linear regression of the latter accounted for 96.3% of the variance in the mean pursuit direction (r^2 range: 90.5% to 99.4%). Although the regression slope was less than unity (average: 0.54; range: 0.31 to 0.85), it was always considerably higher than the 0.13 slope predicted by vector averaging. In the invisible-aperture condition, the same observers were much poorer at judging object-motion direction (figure 2c). The average direction threshold was five times higher than in the visible-aperture condition (average: 21.0°; range: 10.1° to 40.8°). The mean pursuit direction was not strongly related to the object-motion direction (figure 2d). On average, the latter accounted for only 24.1% of the variance in mean pursuit direction (r^2 range: 0.9% to 46.3%). The regression slope was nearly zero (average: 0.032; range: 0.003 to 0.052) indicating nearly pure vertical pursuit regardless of the object-motion direction, consistent with pursuit of the vertical motion of the individual segments.

These data show that the pursuit response to identical image motion is quite different depending on perceptual coherence. The visible-aperture (high coherence) condition is associated with both precise perceptual object-direction discrimination and pursuit in a direction closer to that of the object than to that of the segments. The invisible-aperture (low coherence) condition is associated with nearly random object-direction discrimination and nearly pure vertical pursuit (presumably of segment motion). These findings are at odds with any control strategy that uses retinal slip alone. Accurate steady-state pursuit of coherent object motion in this experiment (as illustrated in figure 1a and quantified in figure 2b) cannot be achieved by attempting to drive retinal slip to zero; perfect pursuit is actually associated with considerable uncorrectable retinal slip of the segments. However, it is possible that the observed pursuit behavior in the coherent condition could be achieved by minimizing the orthogonal component of the segment motion (while ignoring the parallel component), a strategy not inconsistent with known properties of cortical motion processing (eg consistent with minimizing the output of motion-sensitive striate cortical neurons). Furthermore, it could be argued that, by altering segment contrast, our manipulation of the static luminance of the aperture affected the low-level neural responses to local motion and thereby altered pursuit, with the observed perceptual changes merely an epiphenomenon; or that the precision of the direction judgments does not directly measure the level of perceptual coherence; or that the simplicity of the linear trajectories led to a fortuitous link between pursuit and perception. To address these concerns, we performed a second experiment in which we held segment contrast constant, object motion followed complex two-dimensional (2-D) trajectories, and coherence was measured directly.

3.2 *Experiment 2: The effect of spatial shuffling on coherence judgments and pursuit trajectories*

In the second experiment, we again used line-figure stimuli occluded by two vertical apertures. The apertures in this experiment were always invisible, but perceptual coherence was promoted by using low-contrast segments (Lorenceau and Shiffrar 1992; Shiffrar and Lorenceau 1996). The object motion was along either horizontally or vertically oriented figure-eight trajectories (figure 3, top middle). Two objects were used (figure 3, top): a diamond or a cross. The only difference between the two was that the positions of the upper and lower segments within each aperture were swapped. In particular, the segment orientations and the segment and object motions for the diamond and cross were identical. Thus, the two object conditions had identical velocity-space descriptions (Adelson and Movshon 1982), so any difference in either perception or pursuit would indicate that purely velocity-domain based models, including intersection-of-constraints (Fennema and Thompson 1979) and vector-averaging (Wilson et al 1992, Lisberger and Movshon 1999) models, are inadequate (Lorenceau and Zago 1999). Observers were asked to pursue the moving object and to indicate whether the stimulus appeared to move coherently as a single object.

In the diamond condition, observers nearly always reported that the motion was fully coherent (average across observers: 91.2% of trials reported as coherent; range: 81.5% to 99.3%) and pursuit was largely accurate (figure 3a). Averaged across observers, the total gain on trials reported as coherent was 0.71 (range: 0.51 to 0.84) and the mean aspect ratio was 0.87 (range: 0.81 to 0.96). These findings are similar to those for standard pursuit of the complex 2-D motion of small dots or unoccluded line-figure objects; at similar temporal frequencies, gain is below unity yet gaze-trajectory shape is largely accurate (Kettner et al 1996; Stone et al 1996). Vector averaging, however, predicts significantly distorted trajectories with an aspect ratio of only 0.33, and segment-terminator tracking would result in an infinite aspect ratio (pure vertical pursuit). In the cross condition, observers generally reported that the motion was not fully coherent (average: 7.4% coherent; range: 0.0% to 25%) and pursuit was less accurate than for the diamond (figure 3b). Averaged across observers, the total gain on cross trials reported as incoherent (mean: 0.48; range: 0.36 to 0.58) was significantly ($p = 0.025$, two-tailed paired t-test) reduced by 31.5% relative to the coherent diamond trials, and the mean aspect ratio was significantly ($p = 0.007$) increased to 1.50 (range: 1.30 to 1.74).

The data above demonstrate that pursuit is not merely attempting to minimize retinal slip or even the orthogonal component of slip because the identical velocity-space descriptions of the diamond and the cross stimuli would have produced identical pursuit behavior. Furthermore, they provide additional evidence for a shared motion-integration stage for perception and pursuit by showing parallel changes in both perceptual coherence and pursuit performance linked to changes in the geometry of the target object. Lastly, further evidence for a direct link between perceptual coherence and pursuit is provided by a comparison of the diamond trials judged coherent with those few trials judged incoherent. Across observers, incoherent trials show a significant ($p = 0.013$) gain reduction (mean: −13.9%; range: −6.4% to −18.1%) relative to coherent trials, for identical physical stimuli.

4 Discussion

In this study, we performed two independent experiments that demonstrate that the visual motion signal driving steady-state pursuit is not retinal slip, but rather an integrated visual motion signal more closely related to object motion. Furthermore, we have shown that the motion-integration process supporting pursuit is more accurate than mere vector averaging. Lastly, we have also found that manipulations of perceptual coherence yield parallel changes in the perceived and pursued directions, suggesting a link between motion integration for perception and pursuit.

In each experiment, a different stimulus manipulation was used to generate a perceptual change, while keeping the physical motion within the image unchanged. Thus, we cleanly disambiguated raw retinal motion from perceived object motion. For each experiment individually, it could be argued that the pursuit effects were more related to the specific static stimulus manipulation performed, rather than to the change in motion perception per se. But this logic becomes more difficult to sustain in the face of the combined results, with perceptual coherence the only manipulation common to both experiments. Our findings are neither dependent on the specific psychophysical task (in experiment 1, an objective but indirect coherence measure; and in experiment 2, a subjective but direct measure), nor on the specific object or aperture spatial configuration (figure 2 versus figure 3), nor on the specific trajectory (linear versus 2-D). Furthermore, the observed pursuit differences are not likely the primary cause of the perceptual differences, because contrast-induced differences in perceptual coherence occur even during fixation (Lorenceau and Shiffrar 1992; Lorenceau 1998). Thus, if there is a causal relationship between perception and pursuit, the perceptual coherence differences must generate the pursuit differences. Lastly, our previous finding that smooth eye movements and perception show similar systematic errors in response to manipulations of aperture shape (Beutter and Stone 1998), together with the dual perceptual and oculomotor effects of stimulation and lesions within extrastriate visual cortex (Pasternak and Merigan 1994; Celebrini and Newsome 1995; Britten and van Wezel 1998; Rudolph and Pasternak 1999), support the view that the link between perception and pursuit is direct, and not merely due to similar but distinct motion-processing mechanisms. Although previous studies have shown that smooth eye movements can be driven by a number of non-visual motion stimuli (eg Steinbach 1969; Lackner 1977; Mather and Lackner 1980) and even purely cognitive inputs (eg Barnes et al 1997), our results shed new light specifically on the nature of the visual component of the target-motion signal driving pursuit. Indeed, our findings and those of these earlier studies suggest a more expansive view of (potentially multimodal) target signals for pursuit as well as saccades, that reflect converging attentional, perceptual, and cognitive inputs (for a review of this view, see Krauzlis and Stone 1999).

4.1 *Caveats*

In the first experiment, the less-than-unity slope in the coherent condition indicates that the pursued direction was not veridical, but was biased towards vertical. This pattern of errors could be due to a number of factors: incomplete coherence, a priori expectation of largely vertical motion, or inaccurate motion integration, to name a few possibilities. More pointedly, it is distinctly possible that the perceived and pursued directions, while in some way linked, are nonetheless significantly different. Unfortunately, because we used a left/right forced-choice paradigm, we cannot know if there was also a compressive perceptual error (ie a vertical bias). Future experiments using the method of adjustment (eg Beutter et al 1996) will be needed to resolve this issue. However, in a previous study with plaid stimuli under different visual conditions, we indeed found quantitatively similar overall biases in both the perceived and pursued directions (Beutter and Stone 1998), so it is not unreasonable to suspect that the systematic pursuit inaccuracies observed in experiment 1 may be shared by perception. Also, in a control experiment with fully visible diamonds, we observed slopes very close to unity suggesting that a priori expectation is not a major contributor to the low slopes observed in experiment 1, although a differential effect of expectation for ambiguous versus unambiguous stimuli cannot be ruled out.

In the second experiment, the large difference in coherence reported subjectively for the cross and diamond conditions indicates a significant qualitative difference between the average perceptual state generated by the two stimuli, but should not be used as a quantitative measure of the absolute level of coherence. Because of criterion drift, the binary subjective judgment given by our observers is a poor metric of absolute coherence, which varies continuously from fully rigid, to nonrigid, to partially incoherent, to fully incoherent, and can also vary over time throughout a trial. In addition, we asked observers to report a trial as coherent only if the object was fully coherent, ie it appeared to move as a single object throughout the entire trial. Therefore, although the cross was rarely reported as coherent, the fact that pursuit still had a significant horizontal component suggests that the stimulus was not fully incoherent on trials reported as 'incoherent'. Indeed, the invisible-aperture high-contrast diamond stimulus of experiment 1 appeared subjectively more incoherent than the cross stimulus of experiment 2 and, for the former stimulus, we found little or no evidence for a horizontal component of pursuit. The indirect but objective measure of coherence used in experiment 1 has its problems as well. Even in the invisible-aperture condition, observers could sometimes use other cues to cognitively deduce the direction in which the diamond must have moved, even when no coherent object motion was perceived. This yielded less than random performance in the direction-discrimination task, even though the stimulus was perceived as largely, if not completely, incoherent.

In view of these caveats, the gain, aspect ratio, or some other parameter of the pursuit response may ultimately prove to be a better metric of perceptual coherence than current psychophysical measures, because they potentially can provide a continuously variable (ie non-binary) measure of performance that can be monitored over time.

4.2 *Behavioral implications*

The issue of perceptual versus retinal motion driving pursuit has been addressed previously (Yasui and Young 1975; Steinbach 1976; Wyatt and Pola 1979; Mack et al 1979, 1982; Zivotovsky et al 1995), but has remained unresolved for want of a stimulus to manipulate perception without changing the physical motion in the stimulus. An early attempt by Young and colleagues (Yasui and Young 1975) to link perception and pursuit was inconclusive because they measured changes in the vestibulo-ocular reflex that could be accounted for without invoking a role for pursuit. Steinbach (1976) also proposed a link between perception and pursuit, but there was no measurement of perceived object direction and no quantitative assessment of the extent to which either perceived or veridical object motion was pursued. Indeed, the human ability to generate horizontal pursuit in response to his wagon-wheel stimulus (a rolling wheel defined by illuminated dots along its implied circumference) could be explained by the tracking of the motion of the image centroid by a low-level, low-spatial-frequency motion detector without invoking perception or motion integration. More recently, it was shown that the vergence component of a 3-D tracking response (which may represent pursuit in depth) can track changes in perceived depth defined only by the integration of motion cues (Ringach et al 1996); however, in this study, the conjugate component (pursuit) could have been driven simply by retinal slip.

Others have disputed the view that perception drives pursuit by showing that humans appear to pursue retinal motion even in the presence of illusory (induced) motion (Mack et al 1979, 1982; Zivotovsky et al 1995). These findings are inconclusive for two reasons. First, this approach makes perceived motion different from retinal 'target' motion by adding additional 'non-target' motion to the stimulus, so the perceptual–retinal dichotomy is confounded by issues of target selection and motion–motion interactions. Second, the observed smooth eye-movement response is likely the sum of a pursuit response to perceived motion and an optokinetic response to the inducer.

Thus, these results are inadequate to support the view that steady-state pursuit can be driven by image motion, independent of perception.

Recent studies, however, suggest that the earliest component of smooth eye-movement responses may reflect different visual processing. The earliest component of the human vergence response to disparity appears independent of perceived motion in depth (Masson et al 1997). Pursuit initiation in monkeys may perform vector averaging when the monkeys are confronted with multiple dot motions (Lisberger and Ferrera 1997; Lisberger and Movshon 1999), although vector averaging is not observed under different behavioral conditions (Ferrera and Lisberger 1997). Interestingly, vector averaging has also been reported for perception of briefly presented stimuli (Wilson et al 1992). Further studies examining the perceptual and pursuit responses to the same brief stimuli are needed to see if these two apparent vector-averaging phenomena are related.

Lastly, the relationship between pursuit and speed perception has been extensively examined (eg Kowler and McKee 1987; Pola and Wyatt 1989; Brenner and van den Berg 1994; Freeman and Banks 1998; Turano 1999). These studies have established a link between pursuit and speed perception, but they have generally focused on the interaction between retinal 'sensory' signals and extra-retinal 'motor' signals. Furthermore, because they used dot targets, they did not address the issue of the relative contribution of raw retinal motion versus integrated object motion.

4.3 *Computational implications*

Our finding that humans can pursue the motion of partially occluded line-figure objects cannot be accounted for by current pursuit models (Robinson et al 1986; Krauzlis and Lisberger 1989, 1991; Ringach 1996). They also indicate that neither pursuit nor perception can be fully accounted for by any visual mechanism that merely performs velocity-space or motion-energy calculations to derive object motion (eg Adelson and Movshon 1982; Adelson and Bergen 1985; Watson and Ahumada 1985; Wilson et al 1992). In particular, our data show that a simple vector average of the local motion signals is not responsible for steady-state pursuit, and complement the recent finding that the perceived aspect ratio of 2-D trajectories also cannot be accounted for by a vector-averaging strategy (Lorenceau 1998). These results suggest that perception and pursuit share a similar motion-integration rule (ie rule by which local motions are combined to yield object velocity), extending previous findings that found correlations between the direction of smooth eye-movement responses to moving plaid patterns and perceived direction (Beutter and Stone 1998; Dobkins et al 1998).

In addition, our data provide evidence that pursuit and perception share similar segmentation rules (ie criteria used to decide whether to integrate local motions or to segregate them), extending our previous analysis of the effect of coherence on pursuit temporal phase (Stone et al 1996). However, even if pursuit and perception share a common motion-processing stage, this would not preclude the motor output pathways from possibly contributing additional processing and/or noise exclusively to the pursuit signals (Watamaniuk and Heinen 1999; Stone and Krauzlis 2000).

4.4 *Physiological implications*

Accurate estimation of object motion in the world requires both the spatiotemporal integration of multiple local motion signals and the addition of an extra-retinal signal related to eye/gaze motion. Although the integration of local motion signals likely begins in the middle temporal (MT) area (Movshon et al 1986; Rodman and Albright 1989; Stoner and Albright 1992; Dobkins et al 1998), the medial superior temporal (MST) area, with its extra-retinal pursuit signal (Newsome et al 1988), appears particularly critical in the generation of perceived object motion. Stimulation and lesions of MST affect both motion perception (Pasternak and Merigan 1994; Celebrini and Newsome 1995; Britten and van Wezel 1998; Rudolph and Pasternak 1999) and pursuit

(Dursteler and Wurtz 1988; Komatsu and Wurtz 1989), although these studies do not demonstrate that the same neurons are involved in both. Our data provide evidence that the perceptual and pursuit signals within MST are linked and may even be one and the same.

In addition, our results demonstrate that pursuit does not function by attempting to minimize retinal slip. This conclusion is consistent with the previous finding that, after MST lesions, pursuit velocity remains erroneous without correction even in the steady state (Dursteler and Wurtz 1988), a phenomenon that cannot be explained by any model dominated by negative-feedback error correction. A parsimonious explanation is that MST lesions compromise an object-motion signal leading to perceptual deficits (Pasternak and Merigan 1994; Rudolph and Pasternak 1999) as well as sustained erroneous pursuit (Dursteler and Wurtz 1988), despite the presence of large retinal-motion errors that fail to drive smooth corrective responses.

If steady-state pursuit is instead driven by an object-motion signal originating in MST, then the role of the efferent pathways through the brainstem and cerebellum must also be reassessed. It has been proposed that a positive-feedback loop through the cerebellum provides eye-velocity memory during steady-state pursuit (Miles and Fuller 1975; Lisberger and Fuchs 1978; Kase et al 1979; Miles et al 1980; Stone and Lisberger 1989, 1990). However, the sustained response of MST neurons during steady-state pursuit in the absence of retinal motion (Newsome et al 1988) demonstrates that MST is as capable of providing this signal as is the cerebellum. Indeed, the sustained response of cerebellar Purkinje cells in the floccular lobe during steady-state pursuit (Stone and Lisberger 1989, 1990) could simply reflect a descending input from extrastriate cortex.

Lastly, Ungerleider and Mishkin (1982) proposed that extrastriate visual cortical pathways could be divided into two branches: a dorsal stream, which includes MT and MST, that focuses on spatial-information processing ('where' pathway) and a ventral stream that focuses on pattern recognition ('what' pathway). Goodale and Milner (1992) extended this dichotomy by proposing that the dorsal stream controls visual processing for action, while the ventral stream supports perception. However, our findings as well as the MT and MST lesion and stimulation studies (Dursteler and Wurtz 1988; Komatsu and Wurtz 1989; Pasternak and Merigan 1994; Celebrini and Newsome 1995; Britten and van Wezel 1998; Rudolph and Pasternak 1999) are inconsistent with theories that preclude a role for the dorsal pathway in visual perception. Indeed, taken collectively, these results suggest that MT and MST are part of a neural substrate for visual motion processing shared by perception and at least those motor systems controlling eye movements. Furthermore, our finding in experiment 2 that changing the object geometry, but not its motion, affects both the perception and pursuit of its trajectory may reflect the influence of the higher-level object recognition within the ventral stream on motion processing for both perception and motor action, although lower-level spatial interactions may also be responsible (Lorenceau and Zago 1999).

4.5 *A new control strategy for pursuit*

To explain our data, current pursuit models must be updated at the very least to include a front-end motion-integration mechanism that computes object-slip (object motion—eye motion) instead of relying on raw retinal slip, its derivatives, or the vector average of these signals (Robinson et al 1986; Krauzlis and Lisberger 1989, 1991; Ringach 1996; Lisberger and Movshon 1999). An object-slip signal related to both perception and pursuit could be computed within MT (Stoner and Albright 1992; Dobkins et al 1998). Such a perceived object-slip signal, although still in retinal coordinates, could represent the beginning of a selective motion-integration process, which is then completed in MST where the signal is transformed into head-centered coordinates. Nevertheless, an object-slip signal in retinal coordinates is unlikely the dominant input directly driving steady-state pursuit, given the major projection of MT to MST (Ungerleider and Desimone 1986), the evidence for an object-motion signal in head-centered coordinates in MST (Newsome et al 1988), and the dramatic effects of MST lesions and microstimulation on pursuit (Dursteler and Wurtz 1988; Komatsu and Wurtz 1989). A parsimonious interpretation of these data is that the eye-velocity signal in MST supports a coordinate transformation from retinal to head-centered coordinates at the level of the cerebral cortex that sustains steady-state pursuit (Newsome et al 1988). If so, eye-velocity positive feedback through the cerebellum must play a different role than integrating retinal errors to sustain steady-state pursuit (for a review of this older view, see Lisberger et al 1987).

Our data together with the MST findings suggest a more fundamental change in control strategy (figure 4). We propose that object motion in head-centered or possibly world coordinates is computed in the cerebral cortex for both perception and pursuit, within a network that includes areas MT, MST, and possibly the frontal eye fields or FEF (Gottlieb et al 1994) and supplementary eye fields or SEF (Heinen and Liu 1997). The cerebellar positive-feedback loop would then compensate for the sluggish

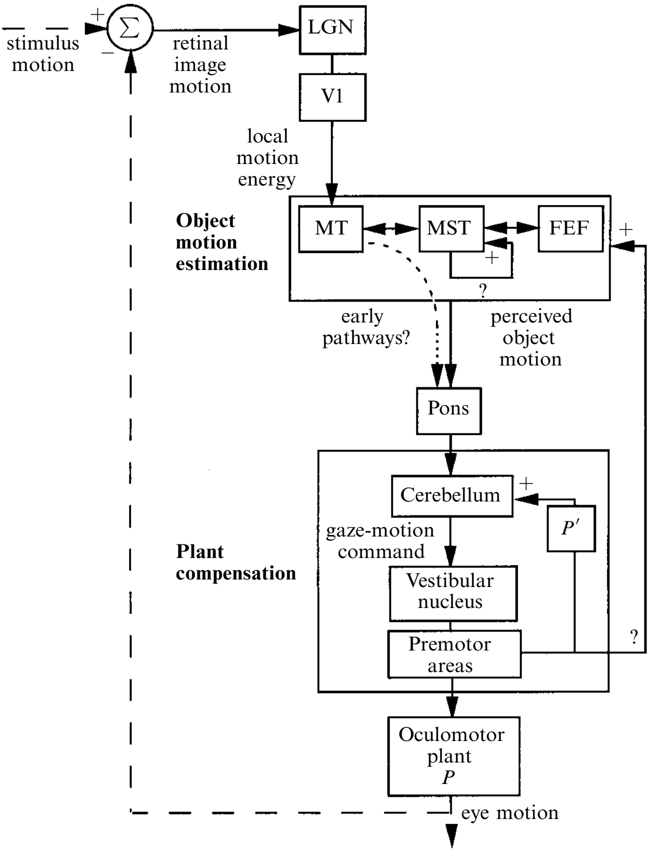

Figure 4. Proposed control strategy for pursuit. Rather than raw retinal image motion, the main driving input is perceived object motion in head-centered (or possibly world) coordinates, which is computed within a cerebral cortical network that includes the reciprocal connections between MT, MST, and the frontal eye fields (FEF). The extra-retinal pursuit signal in MST could be generated either via local positive feedback or true efference copy from the brainstem. Once object motion is computed, the remaining transformation needed to optimize performance is compensation for the dynamics of the oculomotor plant. This can be achieved by positive feedback through the cerebellum [ie by setting $P' \sim P$, to eliminate the lag associated with the transfer function P—see Stone et al (1996)].

dynamics of the oculomotor plant, caused by the viscoelastic properties of the eye muscles and orbit. Indeed, plant compensation is the only remaining control transformation necessary once object motion is derived, and others have suggested that it could be accomplished within the floccular lobe of the cerebellum (Shidara et al 1993; Krauzlis and Lisberger 1994; Krauzlis 2000). The proposed cerebral – cerebellar division of labor in figure 4 is consistent with our data and with the profound non-retinotopic directional pursuit deficits that occur after MST lesions in monkeys (Dursteler and Wurtz 1988) and occipito-parietal lesions in humans (eg Morrow and Sharpe 1993). Furthermore, this new framework is not at odds with older findings with dot stimuli, because, for dots, object and retinal motion are indistinguishable. Lastly, the skeletal framework of figure 4 clearly needs to be fleshed out to include higher-order visual and cognitive processes, such as attention, expectation, and prediction, that also play important roles in pursuit (eg Yasui and Young 1984; Khurana and Kowler 1987; Kowler 1990; Kettner et al 1996; Barnes et al 1997; Pola and Wyatt 1997).

5 Conclusions

Visually driven human steady-state smooth-pursuit eye movements are not merely a response to local image motion, but rather to a spatiotemporally integrated visual signal, related to object motion and at the very least influenced by perception. Pursuit models must be modified to include a front end that is capable of performing this motion integration and to do so more veridically than simple vector averaging. The view that the cortical input signal driving steady-state pursuit is more related to object motion than to retinal errors has important implications for the role of the cerebellum-brainstem output pathways. We therefore propose a new framework in which cortical pathways reconstruct object motion from retinal and extra-retinal signals, while cerebellum-brainstem pathways support plant compensation.

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