



Direction and extent of perceived motion smear during pursuit eye movement

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Abstract

Smooth pursuit eye movements superimpose additional motion on the retinal image of untracked visual targets, potentially leading to the perception of motion smear and a distortion of the perceived direction of motion. Previously, we demonstrated an attenuation of perceived motion smear when the untracked target moves in the opposite direction of an ongoing pursuit eye movement. In this study, the *extent* of perceived motion smear and the *direction* of perceived smear were compared for a single bright dot that moved in a wide range of directions with respect to horizontal pursuit at 8 deg/s. Comparable data were obtained during fixation as a control. The results indicate that a significant attenuation of perceived motion smear occurs when the dot's motion includes a horizontal component in the opposite direction of eye movement. In contrast, the direction of perceived smear approximates the trajectory of the retinal image motion, during both fixation and pursuit. These results suggest a selective application of extra-retinal signals to compensate specific aspects of visual perception that results from the retinal image motion during smooth pursuit eye movements.

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1. Introduction

Pursuit eye movements keep the image of a tracked object approximately stable on the fovea. However, these eye movements produce an additional component of retinal image motion for untracked objects in the visual field, compared with when the eyes are stationary. This motion of the retinal image that occurs for untracked objects during pursuit would be expected to result in the perception of motion smear, because of the substantial temporal persistence in the visual system (Bidwell, 1899; McDougall, 1904; Burr, 1980; Coltheart, 1980; Chen, Bedell, & Ögmen, 1995). However, previous experiments found a significant reduction in the extent of perceived motion smear when

the eyes are moving, compared to when the eyes remain stationary (Bedell & Lott, 1996; Bedell & Yang, 2001; Bedell, Chung, & Patel, 2004; Bedell & Patel, 2005). Because the motion of the retinal image was comparable during eye movements and fixation, these investigations supply evidence that extra-retinal signals (ERSs), for example, efferent copy signals associated with pursuit, play a role in attenuating the extent of perceived motion smear.

In a recent study, Tong, Patel, and Bedell (2005) reported that an attenuation of perceived motion smear occurs during smooth pursuit if the target moves in the opposite direction, but not in the same direction, as the ongoing eye movement. Because the target and the eyes moved collinearly in this study, an unanswered question is to what extent perceived smear is attenuated if the retinal image motion of the untracked target contains a component that is not opposite to the direction of the on-going eye movements.

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When the target and the eyes move non-collinearly, the direction of target motion on the retina is different from its physical trajectory. This discrepancy raises the additional question of whether the *direction* of perceived smear is compensated by ERSs during eye movements. The direction of perceived smear for a moving target should be identical to the target's physical direction of motion if complete compensation for the observer's eye movement occurs. If the compensation for pursuit is incomplete, then the direction of perceived smear should be closer to the retinal motion trajectory. In the present experiments, observers reported the direction as well as the extent of perceived smear. These data allow us to compare the attenuation of perceived motion smear with the compensation for the direction of perceived smear, for untracked targets that move non-collinearly with respect to the pursuit eye movement.

2. Methods

2.1. Apparatus and stimuli

Visual stimuli were generated by a PC-controlled 12-bit Arbitrary Wave Form Generator and were presented on an X-Y monitor (HP 1311B) at a 500-Hz refresh rate. The stimuli were small spots with a nominal size of 0.4 arc min and a luminance of 2 log units ($\approx 14 \text{ cd/m}^2$) above the detection threshold in an otherwise dark environment. The stimuli were viewed monocularly through a mirror system from a distance of 4 m (Fig. 1). A spot at the center of the screen served as the fixation target during each trial of the fixation condition. After a 150–250 ms delay from the beginning of each trial, a second moving test spot was presented at a speed of 4 deg/s or 8 deg/s for a duration of 200 ms. The trajectory of test-spot motion was symmetrical with respect to the center of the screen. The

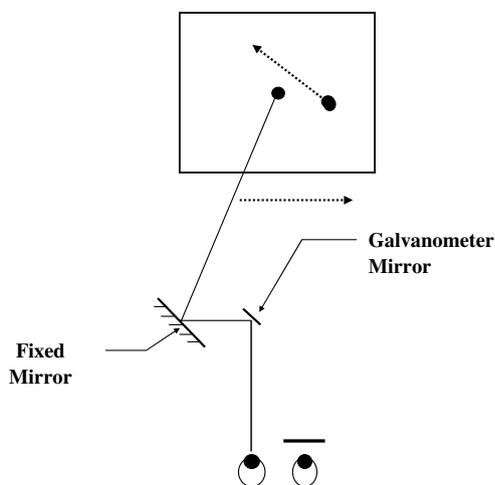


Fig. 1. Schematic diagram of the experimental set up. The stimuli on the screen were reflected to the left eye of the subject using an optical system. A patch covered the subject's right eye. The spot at the center of the screen served as the stationary fixation target in the fixation condition and the tracking target in the pursuit condition. Horizontal movement of the tracking target (as well as the test spot) was achieved by rotating a galvanometer-mounted mirror. The test spot was presented for 200 ms and moved in one of 16 different directions on the screen.

distance between the moving test spot and the fixation target reached a minimum value of 0.5° when the test spot reached the center of its trajectory.

The experimental set up in the pursuit condition was similar to that in fixation condition, except that rotation of a galvanometer-mounted mirror moved the image of the entire screen from left to right on each trial. At the beginning of each pursuit trial, the image of the screen was displaced leftward by 4° and was stable for 1 s. A smooth rotation of the mirror then caused the spot at the center of the screen, which served as the pursuit target, to move the right at a speed of 8 deg/s for 1 s. After a 400–450 ms delay after motion onset, the second moving test spot was presented for 200 ms with the same screen trajectory as in the fixation condition. Because both the pursuit target and the test spot were reflected from the moving mirror, the physical motion of the test spot on the screen produced identical retinal image motion as during the fixation condition when the pursuit gain was equal to one. Horizontal eye position was measured by IR limbal tracking and stored to a PC computer at 1 kHz. The stored eye-movement records were used to calculate the direction and speed of the retinal image motion on each pursuit-condition trial.

2.2. Procedure

In each block of 64 trials, the test spot moved across the screen at 4 or 8 deg/s in one of 16 directions between 0° and 337.5° . The specific combination of speed and direction of test-spot motion varied randomly from trial to trial. Trials in the fixation and pursuit conditions were run in separate blocks. After each presentation of the test spot, the observer used a joystick to successively adjust (1) the direction and (2) then the length of a stationary bright line to match the direction and extent of perceived motion smear. This procedure generated one estimate of the direction and length of perceived smear for each acceptable trial (see below).

2.3. Subjects and data analysis

Seven observers with normal or corrected-to-normal vision participated. Head position was maintained using a chin rest. The experimental protocol was reviewed by the University of Houston Committee for the Protection of Human Subjects and written informed consent was obtained from each subject before he or she participated. Five to twelve blocks of trials were completed for each subject to collect enough data for each combination of test-spot speed and direction of motion in the fixation and pursuit conditions.

The eye velocity on each pursuit trial was determined from the slope of the best fitting straight line during the 200-ms presentation of the test target. The pursuit gain was calculated as the ratio of the eye velocity to the velocity of the pursuit target. To ensure that comparable motion of the retinal image occurred in the pursuit and fixation conditions, individual pursuit trials were rejected if either of the following occurred: (1) pursuit gain was lower than 0.8 or higher than 1.2, or (2) a saccade or blink occurred during the presentation of the test spot or within 50 ms of its onset or offset. Averaged across observers, $\approx 30\%$ of the trials in the pursuit condition were rejected on the basis of each of these criteria (total rejected pursuit trials = 62%).

To evaluate the stability of fixation, horizontal eye position was recorded also for each observer on a sample of the trials in the fixation condition. For three observers, fixation was consistently stable (velocity $< 1 \text{ deg/s}$) and eye movement recording was discontinued for the rest of the fixation condition. For the other four observers, the eye velocity sometimes exceeded 1 deg/s. The eye movements of these observers were recorded throughout the fixation condition and a trial was rejected if the speed of eye movement was greater than 1 deg/s (less than 20% of trials). On all accepted fixation trials, the direction and speed of the retinal image motion were assumed to reflect only the direction and speed of the target motion.

The matched extent of perceived motion smear on each trial was converted from units of visual angle to units of time (Hogben & Di Lollo, 1985; Tong et al., 2005):

$$\text{Duration of perceived motion smear (s)} = \frac{\text{extent of matched smear (}^\circ\text{)}}{\text{retinal image speed (deg/s)}}$$

The extent and the direction of the perceived motion smear on each trial were placed into one of 16 bins (direction range = 22.5°), based on the calculated direction of motion with respect to the retina. The average extent and direction of perceived smear were determined for each bin and observer by vector summation. The averages for each bin did not differ substantially from the median values. Statistical analyses were performed using a repeated-measures analysis of variance (ANOVA) and piecewise local regression.

3. Results

3.1. Pursuit gain is not affected by the motion of the test target

The average pursuit gains were determined for the 16 directions of retinal image motion and both stimulus speeds for the seven observers. As seen in Fig. 2, the average pursuit gain is approximately constant and close to 1 for all stimulus directions and for both speeds. This analysis indicates that smooth pursuit was essentially unaffected by the motion of the untracked target in the present study.

3.2. Attenuation of extent of perceived motion smear during pursuit

Fig. 3 shows the averaged extent of perceived motion smear during fixation and rightward smooth pursuit, for

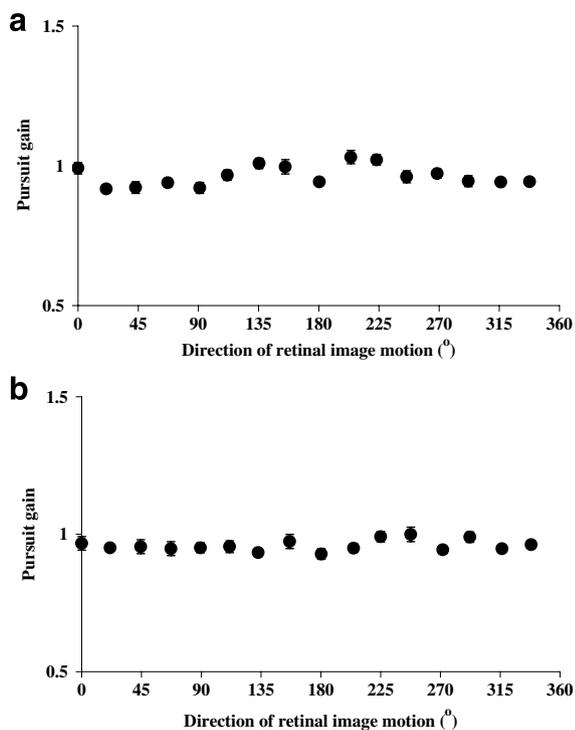


Fig. 2. Smooth pursuit gain as a function of the direction of motion of the test spot's image on the retina, for test-spot speeds of 4 deg/s (a) and 8 deg/s (b). The results are averaged across all seven observers. Error bars represent ±1 SEM.

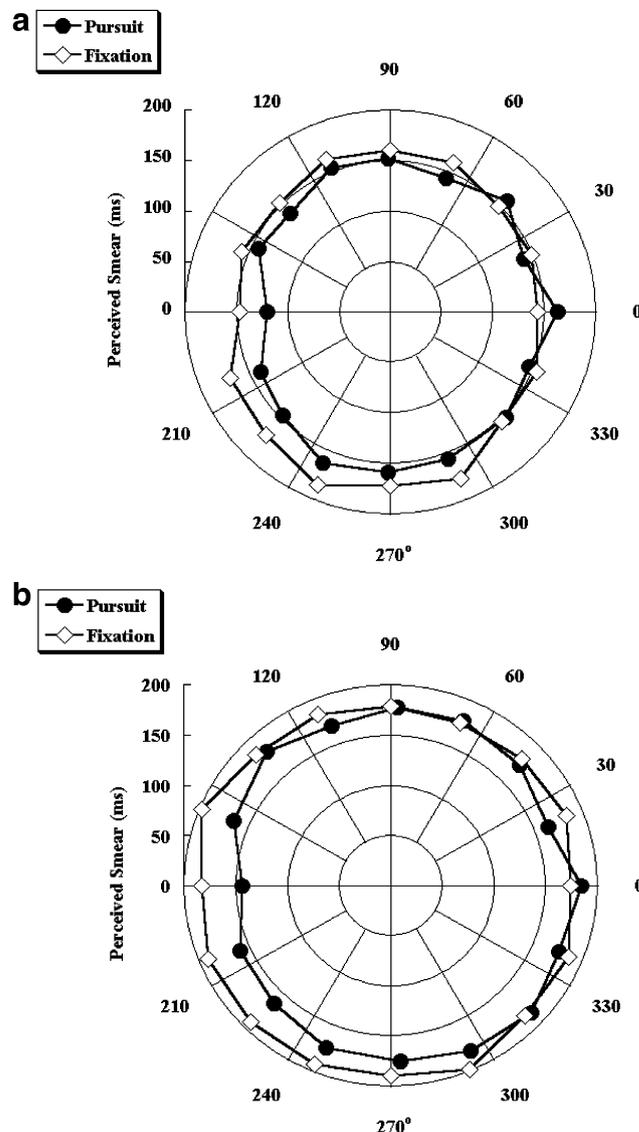


Fig. 3. Comparison of the extent of perceived motion smear as a function of the direction of retinal image motion during fixation (unfilled diamonds) and rightward smooth pursuit (filled circles). The average results of seven observers are shown for retinal image speeds of 4 deg/s (a) and 8 deg/s (b). In (a), the median SEMs across observers are 12 ms during fixation and 15 ms during pursuit. The comparable SEMs for the data plotted in (b) are 10 ms during fixation and 11 ms during pursuit.

motion of the retinal image in different directions. The results are shown separately for target speeds of 4 (Fig. 3b) and 8 deg/s (Fig. 3b). Although the observers' average matches shown in Fig. 3a are generally smaller than in Fig. 3b, an ANOVA revealed no significant effect of the target speed on the extent of perceived motion smear ($F_{[1,6]} = 1.956, P = 0.2115$). Examination of the interaction between eye-movement condition and direction of motion revealed that during fixation, the extent of perceived smear was approximately the same for all directions of test-spot motion ($F_{[df=15,90]} = 1.923, P = 0.07$), and that the extent of perceived smear during pursuit was reduced significantly for some directions of test-spot motion ($F_{[df=15,90]} = 2.53,$

$P = 0.006$). Piecewise local regression was used to fit the differences between the extent of perceived smear in the fixation and pursuit conditions, as a function of the direction of test-spot motion. To assess how perceived motion smear differed in the fixation and the pursuit conditions, a bootstrapping procedure was used to compare the area under the fitted regression function to zero. The results of this analysis confirmed that the reduction of perceived motion smear during pursuit was significant for both test-spot speeds, when the motion of the test spot included a horizontal component in the opposite direction of the pursuit eye movement (for retinal image motion at 4 deg/s, $r_{\text{regression}} = 0.24$, $p = 0.0099$; for retinal image motion at 8 deg/s, $r_{\text{regression}} = 0.30$, $p = 0.0015$).

The difference in the extent of perceived smear during pursuit and fixation is plotted as a function of the direction of test-spot motion in Fig. 4a and b. These plots illustrate that the attenuation of perceived motion smear is tuned for test-spot motion in the opposite direction of the pursuit eye movement. The maximum reduction of perceived smear corresponds to a duration of ≈ 30 ms when the retinal image motion of the test spot was 4 deg/s and to ≈ 40 ms when the retinal image motion of the test spot was 8 deg/s. To quantify the reduction of perceived motion smear in different directions, the averaged tuning results were fitted by Gaussian functions. As shown by the arrows in Fig. 4a and b, this analysis indicates that the maximum attenuation of perceived motion smear during pursuit occurs in the 207° meridian (95% confidence interval: 175° – 239°) for retinal image motion at 4 deg/s, and in the 196° meridian (95% confidence interval: 174° – 218°) for retinal image motion at 8 deg/s. The attenuation of perceived smear has a directional bandwidth of $\sim 157^\circ$ (full width at half height, denoted by dashed lines in Fig. 4) for retinal image motion at 4 deg/s and $\sim 137^\circ$ for retinal image motion at 8 deg/s.

3.3. Comparison of direction of perceived motion smear during fixation and pursuit

The results reported above indicate that a significant attenuation of perceived motion smear occurs when the motion of the test spot contains a component opposite to the direction of eye movement. However, as shown in Fig. 5, the direction of perceived smear in the pursuit condition is similar to that in fixation condition ($F_{[df=1,18]} = 0.693$, $P = 0.33$). Therefore, the direction of perceived smear during pursuit is approximately consistent with the trajectory of the retinal image motion and far from that expected on the basis of complete compensation. Indeed, the maximal compensation in the direction of perceived smear that is shown by the data in Fig. 5 is only 8%. Contrary to previous findings for the direction of perceived motion (Souman, Hooge, & Wertheim, 2005a, 2005b, 2006a, 2006b), a slight compensation in the direction of perceived motion smear only occurs when the test spot moves close to the opposite

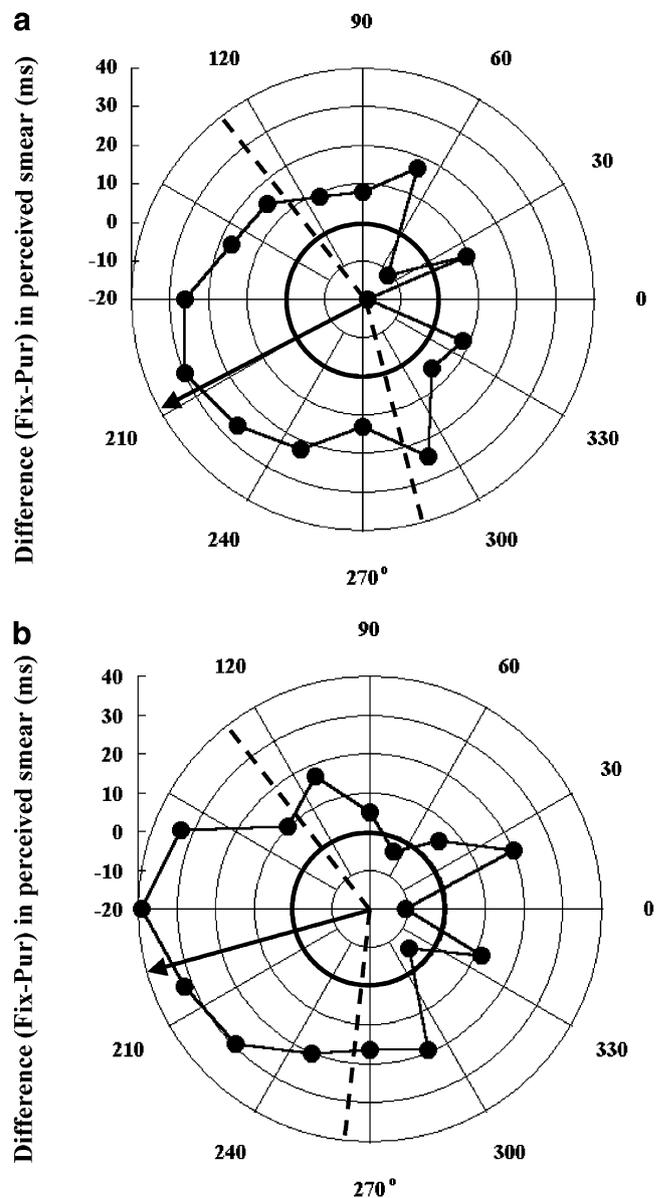


Fig. 4. Direction-tuning functions for the attenuation of perceived motion smear for speeds of the test stimulus of 4 deg/s (a) and 8 deg/s (b). Average data are plotted for seven observers. In each panel, the bold circle indicates no attenuation of perceived smear during pursuit. The results were fitted with Gaussian functions to determine the peak (arrows) and the bandwidth (full width at half height, indicated by the range between the dashed lines) of each tuning function.

direction of the pursuit eye movement (i.e., directions of motion between $\approx 135^\circ$ and 225°).

4. Discussion

4.1. Anisotropies of perceived smear and target speed during pursuit

Previous studies indicated that the extent of perceived motion smear is reduced asymmetrically when a target moves in the opposite direction of ongoing eye and/or head

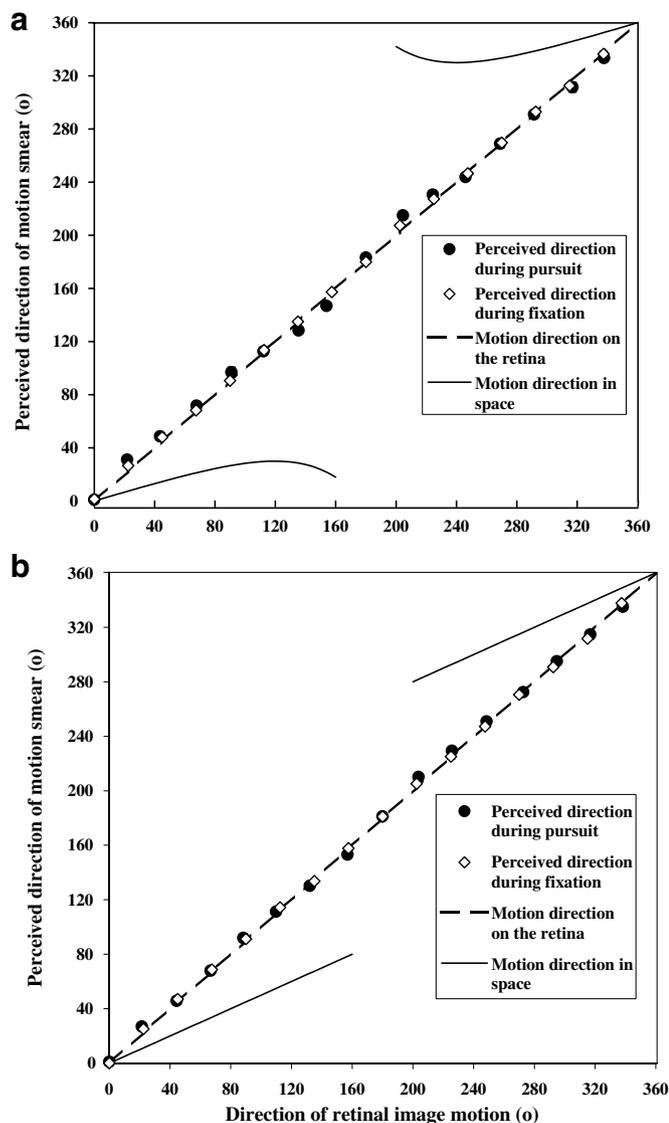


Fig. 5. The direction of perceived motion smear as a function of the calculated direction of retinal image motion, for target speeds of 4 deg/s (a) and 8 deg/s (b). Average data for the fixation and pursuit conditions are shown as open diamonds and filled circles, respectively. The dashed line in each panel represents the calculated direction of image motion on the retina, whereas the solid line represents the direction of target motion in space. Error bars (± 1 SEM) are smaller than the plotted symbols.

movements, suggesting a selective influence of ERSs on perceived smear for targets that move in this direction (Tong et al., 2005, Tong, Patel, & Bedell, 2006). Other studies revealed a comparable asymmetric influence of pursuit eye movements on the *perceived speed* of an untracked target (Wertheim & van Gelder, 1990; Turano & Heidenreich, 1999; Freeman, 2001; Turano & Masoff, 2001). Speed perception is approximately veridical for a target that moves physically in the opposite direction of pursuit, indicating that ERSs are combined with retinal information about motion to generate the perception of speed. In contrast, the perceived speed of a target that moves in the same direction as pursuit approximates the velocity of the tar-

get's retinal image motion, indicating *no* extraretinal compensation for the pursuit eye movement (Freeman, 2001; Turano & Masoff, 2001; Wertheim & van Gelder, 1990). A transition between extraretinal compensation and no compensation for pursuit occurs when the retinal image motion of the untracked target is relatively slow (Turano & Heidenreich, 1999; Freeman, 2001; Turano & Masoff, 2001).

Brenner and van den Berg (1994) reported an asymmetrical influence of an untracked moving background on the perceived speed of a pursued target. Whereas the perceived speed of the pursuit target approximates its physical speed when the background moves in the same direction as pursuit, the perceived speed reflects the difference in velocity between the tracked and untracked targets when the background moves in the opposite direction from pursuit. These findings imply that the ERS for pursuit affects perceived speed only when an untracked target moves in the *same* direction as pursuit, which appears to contradict the results summarized in the paragraph above.

A possible reconciliation of these apparently contradictory results is as follows. Previously, we suggest that the visual system rapidly categorizes an untracked stimulus as potentially stationary or moving, depending upon whether its motion is in the opposite or the same direction as an ongoing eye and/or head movement (Tong et al., 2005, 2006). Initial rapid categorization of the untracked stimulus as potentially stationary triggers the application of ERSs to reduce perceived motion smear, whereas categorization of the stimulus as moving does not. In the study by Brenner and van den Berg (1994), a rapid categorization of a background stimulus that moves in the opposite direction from pursuit as “stationary” would allow the visual system to use this background as a reference, and determine the perceived speed of the pursuit target based on its relative motion with respect to this background. On the other hand, a background that moves in the same direction as pursuit should be categorized as “moving”. Because a moving stimulus provides no direct reference, the visual system relies on ERSs instead of the relative image motion to determine the perceived speed of the pursuit target.

We suggest that a second, slower stage of analysis may be engaged when observers are required to judge the perceived speed of an *untracked* stimulus. If an untracked stimulus moves in the opposite direction from pursuit, the visual system makes an initial qualitative determination that the stimulus could potentially be stationary. Now, the visual system may compare the velocity of the stimulus' retinal image motion to the ERS for pursuit. If the speed of retinal image motion is clearly faster than the ERS for pursuit, then perceived stimulus speed is determined from a combination of these signals (Wertheim & van Gelder, 1990; Freeman, 2001; Turano & Masoff, 2001; Souman, Hooge, & Wertheim, 2006b). On the other hand, if the retinal motion signal and the ERS for pursuit are close to equal and opposite, then the stimulus is perceived to be stationary. The perceptual decision as to whether the back-

ground stimulus is stationary depends on the speed of pursuit (Wertheim, 1981; Wertheim & van Gelder, 1990) and, to some extent, on the stimulus size (Turano & Heidenreich, 1999). Finally, if the untracked stimulus moves in the same direction as pursuit, the visual system categorizes it as moving. Once this categorization is made, the visual system appears to determine the perceived speed of the untracked stimulus from its retinal image velocity alone, rather than from a combination of the retinal motion signal and ERS.

The principal new finding of the present study is that attenuation of perceived motion smear occurs not only when the target and the eyes move collinearly, but also when they move in non-collinear directions if the resulting retinal image motion includes a *component* in the same direction as a target that the visual system would categorize as stationary. The maximal attenuation of perceived smear that we found is ≈ 40 ms, which is consistent with our previous result that the extent of perceived smear for a 200-ms target is reduced by 50 ms during pursuit compared to fixation (Tong et al., 2005). The reduction of perceived motion smear during smooth eye movements becomes larger as the target duration becomes longer (Bedell & Lott, 1996; Bedell et al., 2004). This outcome is reasonable if the principal goal of reducing perceived smear is to preserve the perception of clarity in untracked background stimuli during sustained eye and head movements. Although not tested in our study, we presume that the attenuation of perceived motion smear would increase comparably with duration for *all* targets with a component of motion in the opposite direction from pursuit.

4.2. Possible sites for the reduction of perceived motion smear

Because the directions and speeds of the retinal image motion presented to our observers were close to identical in the fixation and pursuit conditions, the asymmetrical attenuation of perceived motion smear is attributed to an asymmetrical influence of the ERSs that accompany smooth pursuit eye movements. Based on the current knowledge of the visual system, at least two possible neural sites could account for the present results. One possible site is the medial superior temporal (MST) cortex, which is specialized for visual motion processing. Evidence from a number of investigations indicates that pursuit-related ERSs interact with retinal signals for motion in MST (Thier & Erickson, 1992; Yamada, Suzuki, & Yee, 1996; Ilg, 2003; Churchland & Lisberger, 2005). The directional bandwidth that we estimated for the attenuation of perceived smear (Fig. 4) is similar to that reported for individual motion-sensitive neurons in MST (Squatrito & Maioli, 1997), which suggests that MST could be the neural site for the attenuation of perceived motion smear.

On the other hand, Geisler and colleagues (Geisler, 1999; Geisler, Albrecht, Crane, & Stern, 2001) presented psychophysical and neurophysiological evidence to support

the hypothesis that motion smear is detected by orientation-sensitive neurons at an early stage of cortical processing, i.e., area V1. Several experiments indicate that the ERSs associated with *rapid* eye movements can modulate the neural activity in V1 and V2, even when eye movements are made in complete darkness (Duffy & Burchfiel, 1975; Vanni-Mercier & Magnin, 1982; Toyama, Komatsu, & Shibuki, 1984; Sylvester & Rees, 2006). In some neurons, the reported modulation is contingent on the direction of the animal's eye movement. Therefore, a second possibility is that ERSs reduce the extent of perceived motion smear at an early level of visual processing, such as area V1. However, the responses of V1 neurons to visual orientation and direction-of-motion are reported to have a bandwidth of $\approx 80^\circ$ (Albright, 1984; Gur, Kagan, & Snodderly, 2005), which is much narrower than the tuning function that we found for the reduction of perceived motion smear. Nevertheless, the effective bandwidth would be wider if ERSs were to influence a *range* of narrowly tuned neurons, each of which has a direction of maximal sensitivity that overlaps the opposite direction of eye movement.

4.3. Extra-retinal compensation for the direction of perceived motion smear

Contrary to the reduction in the extent of perceived motion smear, our data indicate little or no compensation for the direction of perceived motion smear. The direction of perceived motion smear that was reported by our observers approximates the trajectory of the image motion on the retina, rather than the direction of motion in space. Recently, Krukowski, Pirog, Beutter, Brooks, and Stone (2003) assessed observers' ability to discriminate the direction of target motion during pursuit tracking, and found that thresholds are indistinguishable from the results during fixation. These discrimination results suggest that the visual system has access to and can use precise extra-retinal information for pursuit eye movements. Why does the visual system ignore these signals of eye movement in determining the direction of perceived motion smear in the present experiment?

Li, Brenner, Cornelissen, and Kim (2002) conducted experiments to test whether 2-dimensional shape perception is distorted during pursuit eye movements, using eye and stimulus velocities that were similar to ours. During horizontal pursuit at 6 deg/s, a horizontal line moved downward at a speed between 6 deg/s and 8.5 deg/s. A horizontal gap appeared in the moving line for 180 ms to trace a rhombus on the retina. Because of ongoing horizontal pursuit, the shape drawn on the retina differed from the shape that the moving gap traced on the screen. The observers' judgments of perceived shape closely matched the shape traced on the retina, showing little or no compensation for their eye movements. Despite marked distortions in the perceived locations of visual targets, the perceived shape of a continuous figure that is flashed near the time of a saccade similarly depends on the shape of the retinal

image (Hendry, 1975; Matsumiya & Uchikawa, 2001). Related studies indicate that the perceived relative position of two targets flashed in quick succession is determined by their relative locations on the retina, both during smooth pursuit (Brenner & Cornelissen, 2000) and around the time of saccades (Sogo & Osaka, 2002; Brenner, Meijer, & Cornelissen, 2005). Similarly, the perception of stroboscopic motion during pursuit depends on the successive stimulation of two separate retinal loci, rather than two separate locations in space (Stoper, 1973). These studies suggest that ERSs are incapable of compensating perceptually for eye-movement induced distortions of the retinal image, at least for stimuli that are presented close together in time. When the spatial and temporal intervals between a series of sequentially presented dots are small enough to generate a continuous line, it is reasonable to deduce that the direction of perceived smear should be determined also by the retinal orientation of the resulting streak.

4.4. Compensation for the direction of perceived motion

A long debate exists about the extent to which the direction of retinal image motion during smooth eye movements is compensated perceptually (Dodge, 1904; Festinger & Canon, 1965; Mack, 1986; Freeman, Banks, & Crowell, 2000; van Beers, Wolpert, & Haggard, 2001). Swanston and Wade (1988) and recent reports by Souman et al. (2005a, 2005b, 2006a, 2006b) argued for an incomplete compensation of perceived motion during pursuit eye movements. On the contrary, Festinger, Sedgwick, and Holtzman (1976) investigated the perceived direction of motion of an untracked target during harmonic smooth pursuit, and found little compensation for the eye movements. Mateeff (1980) asked observers track a target that moved horizontally at 6.5 deg/s and also found that the perceived direction of an untracked target was consistent with its trajectory on the retina. Other studies suggest an orientation-specific compensation for the retinal image motion that occurs during pursuit. For example, Wallach and colleagues (Becklen, Wallach, & Nitzberg, 1984; Wallach, Becklen, & Nitzberg, 1985) reported less compensation in the direction of perceived motion for a target that moved physically perpendicular compared to collinear with respect to the direction of pursuit.

Recent evidence indicates that the discrimination of motion direction depends not only on the motion signals from the target, but also on the orientation information that results from motion smear (Geisler, 1999; Geisler et al., 2001; Burr & Ross, 2002; Edwards & Crane, 2006). Our data indicate that direction-of-motion discrimination is facilitated by perceived motion smear when the eyes are still, consistent with a weighted integration of motion and orientation signals according to the relative precision of each source of information (Tong, Aydin, Bedell, & Psychophysics, in press). During pursuit eye movements, we suggest that the direction of perceived motion also

would be biased by information about the *retinal* image orientation that is provided by perceived motion smear.

This suggestion may help to reconcile the inconsistencies about the existence of extra-retinal compensation for target motion during pursuit that were summarized above. Souman et al. (2005a, 2005b, 2006a, 2006b) set the luminance of their stimulus to 0.04 cd/m², which is probably too low to produce a substantial extent of perceived motion smear. Further, they reported more compensation for untracked stimuli that moved at a slower speed, which also would produce a smaller angular extent of perceived motion smear. With little or no perceived motion smear to generate a bias toward the retinal direction of motion, ERSs would be able to effect a greater compensation for the perceived direction of motion of an untracked visual target. In the experiments that found little or no compensation during pursuit (Festinger et al., 1976; Mateeff, 1980), the untracked stimuli were bright targets presented on a dark background, which should have generated substantial extents of perceived motion smear.

5. Conclusions

Our results indicate that the visual system uses ERSs to reduce the *extent* of perceived motion smear for targets that move in a wide range of directions with respect to the direction of a smooth-pursuit eye movement. On the other hand, the visual system overlooks these ERSs and determines the *direction* of perceived smear based essentially on the retinal trajectory alone. Evaluation of published data suggests that the visual system may use a combination of extra-retinal and retinal information to determine the direction of perceived motion for an untracked target during pursuit eye movements. Whether attenuation of the extent of perceived motion smear and compensation for the direction of perceived motion occur in the same or different neural sites needs to be investigated further.

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References

- Albright, T. D. (1984). Direction and orientation selectivity of neurons in visual area MT of the macaque. *Journal of Neurophysiology*, *52*, 1106–1130.
- Becklen, R., Wallach, H., & Nitzberg, D. (1984). A limitation of position constancy. *Journal of Experimental Psychology: Human Perception and Performance*, *10*, 713–723.
- Bedell, H. E., & Lott, L. A. (1996). Suppression of motion-produced smear during smooth pursuit eye movements. *Current Biology*, *6*, 1032–1034.

- Bedell, H. E., & Yang, J. (2001). Attenuation of perceived image smear during saccades. *Vision Research*, 41, 521–528.
- Bedell, H. E., Chung, S. T. L., & Patel, S. S. (2004). Attenuation of perceived motion smear during vergence and pursuit tracking. *Vision Research*, 44, 895–902.
- Bedell, H. E., & Patel, S. S. (2005). Attenuation of perceived motion smear during the vestibulo-ocular reflex. *Vision Research*, 45, 2191–2200.
- Bidwell, S. (1899). *Curiosities of light and sight*. London: Swan Sonnenschein.
- Brenner, E., & van den Berg, A. V. (1994). Judging object velocity during smooth pursuit eye movements. *Experimental Brain Research*, 99, 316–324.
- Brenner, E., & Cornelissen, F. W. (2000). Separate simultaneous processing of egocentric and relative position. *Vision Research*, 40, 2557–2563.
- Brenner, E., Meijer, W. J., & Cornelissen, F. W. (2005). Judging relative positions across saccades. *Vision Research*, 45, 1587–1602.
- Burr, D. C. (1980). Motion smear. *Nature*, 284, 164–165.
- Burr, D. C., & Ross, J. (2002). Direct evidence that “speedlines” influence motion mechanisms. *Journal of Neuroscience*, 22, 8661–8664.
- Chen, S., Bedell, H. E., & Ögmen, H. (1995). A target in real motion appears blurred in the absence of other proximal moving targets. *Vision Research*, 35, 2315–2328.
- Churchland, A. K., & Lisberger, S. G. (2005). Relationship between extraretinal component of firing rate and eye speed in area MST of macaque monkeys. *Journal of Neurophysiology*, 94, 2416–2426.
- Coltheart, M. (1980). Iconic memory and visible persistence. *Perception & Psychophysics*, 27, 183–228.
- Dodge, R. (1904). The participation of the eye movements in the visual perception of motion. *Psychological Review*, 11, 1–14.
- Duffy, F. H., & Burchfiel, J. L. (1975). Eye movement-related inhibition of primary visual neurons. *Brain Research*, 89, 121–132.
- Edwards, M., & Crane, M. (2006). Motion streaks lower global-motion thresholds. *Vision Sciences Society Meeting Abstracts*, 145.
- Festinger, L., & Canon, L. K. (1965). Information about spatial location based on knowledge about efference. *Psychological Review*, 72, 373–384.
- Festinger, L., Sedgwick, H. A., & Holtzman, J. D. (1976). Visual perception during smooth pursuit eye movement. *Vision Research*, 16, 1377–1386.
- Freeman, T. C. A. (2001). Transducer models of head-centered motion perception. *Vision Research*, 41, 2741–2755.
- Freeman, T. C. A., Banks, M. S., & Crowell, J. A. (2000). Extraretinal and retinal amplitude and phase errors during Fiehn illusion and path perception. *Perception & Psychophysics*, 62, 900–909.
- Geisler, W. S. (1999). Motion streaks provide a spatial code for motion direction. *Nature*, 400, 65–69.
- Geisler, W. S., Albrecht, D. G., Crane, A. M., & Stern, L. (2001). Motion direction signals in the primary visual cortex of cat and monkey. *Visual Neuroscience*, 18, 501–516.
- Gur, M., Kagan, I., & Snodderly, D. M. (2005). Orientation and direction selectivity of neurons in V1 of alert monkeys: functional relationships and laminar distributions. *Cerebral Cortex*, 15, 1207–1221.
- Hendry, D. P. (1975). Saccadic velocities determined by a new perceptual method. *Vision Research*, 15, 149–151.
- Hogben, J. H., & Di Lollo, V. (1985). Suppression of visible persistence in apparent motion. *Perception & Psychophysics*, 38, 450–460.
- Ilg, U. (2003). Visual-tracking neurons in area MST are activated during anticipatory pursuit eye movements. *NeuroReport*, 14, 2219–2223.
- Krukowski, A. E., Pirog, K. A., Beutter, B. R., Brooks, K. R., & Stone, L. S. (2003). Human discrimination of visual direction of motion with and without smooth pursuit eye movements. *Journal of Vision*, 3, 831–840.
- Li, H. O., Brenner, E., Cornelissen, F. W., & Kim, E. (2002). Systematic distortion of perceived 2D shapes during smooth pursuit eye movements. *Vision Research*, 42, 2569–2575.
- Mack, A. (1986). Perceptual aspects of motion in the frontal plane. In K. R. Boff, L. Kaufman, & J. P. Thomas (Eds.), *Handbook of perception and human performance* (pp. 16.1–16.27). New York: John Wiley.
- Matsumiya, K., & Uchikawa, K. (2001). Apparent size of an object remains uncompressed during presaccadic compression of visual space. *Vision Research*, 41, 3039–3050.
- Mateeff, S. (1980). Visual perception of movement patterns during smooth eye tracking. *Acta Physiologica et Pharmacologica Bulgarica*, 6, 82–89.
- McDougall, W. (1904). The sensations excited by a single momentary stimulation of the eye. *British Journal of Psychology*, 1, 78–113.
- Sogo, H., & Osaka, N. (2002). Effects of inter-stimulus interval on perceived locations of successively flashed perisaccadic stimuli. *Vision Research*, 42, 899–908.
- Souman, J. L., Hooge, I. T. C., & Wertheim, A. H. (2005a). Vertical object motion during horizontal ocular pursuit: compensation for eye movements increases with presentation duration. *Vision Research*, 45, 845–853.
- Souman, J. L., Hooge, I. T. C., & Wertheim, A. H. (2005b). Perceived motion direction during smooth pursuit eye movements. *Experimental Brain Research*, 164, 376–386.
- Souman, J. L., Hooge, L. T. C., & Wertheim, A. H. (2006a). Localization and motion perception during smooth pursuit eye movement. *Experimental Brain Research*, 171, 448–458.
- Souman, J. L., Hooge, L. T. C., & Wertheim, A. H. (2006b). Frame of reference transformations in motion perception during smooth pursuit eye movements. *Journal of Computational Neuroscience*, 20, 61–76.
- Squatrito, S., & Maioli, M. G. (1997). Encoding of smooth pursuit direction and eye position by neurons of area MSTd of macaque monkey. *Journal of Neuroscience*, 17, 3847–3860.
- Stoper, A. E. (1973). Apparent motion of stimuli presented stroboscopically during pursuit movement of the eye. *Perception & Psychophysics*, 13, 201–211.
- Swanston, M. T., & Wade, N. J. (1988). The perception of visual motion during movements of the eyes and of the head. *Perception & Psychophysics*, 43, 559–566.
- Sylvester, R., & Rees, G. (2006). Extraretinal saccadic signals in human LGN and early retinotopic cortex. *NeuroImage*, 30, 214–219.
- Thier, P., & Erickson, R. G. (1992). Responses of visual-tracking neurons from cortical area MST-I to visual, eye and head motion. *European Journal of Neuroscience*, 4, 539–553.
- Tong, J. L., Patel, S., & Bedell, H. E. (2005). Asymmetry of perceived motion smear during head and eye movements: evidence for a dichotomous neural categorization of retinal image motion. *Vision Research*, 45, 1519–1524.
- Tong, J. L., Patel, S., & Bedell, H. E. (2006). The attenuation of perceived motion smear during combined eye and head movements. *Vision Research*, 46, 4387–4397.
- Tong, J. L., Aydin, M., Bedell, H. E. Direction-of-motion discrimination is facilitated by visible motion smear. *Perception & Psychophysics*, in press.
- Toyama, K., Komatsu, Y., & Shibuki, K. (1984). Integration of retinal and motor signals of eye movements in striate cortex cells of the alert cat. *Journal of Neurophysiology*, 51, 649–665.
- Turano, K. A., & Heidenreich, S. M. (1999). Eye movements affect the perceived speed of visual motion. *Vision Research*, 39, 1177–1187.
- Turano, K. A., & Masoff, R. W. (2001). Nonlinear contribution of eye velocity to motion perception. *Vision Research*, 41, 385–395.
- van Beers, R. J., Wolpert, D. M., & Haggard, P. (2001). Sensorimotor integration compensates for visual localization errors during smooth pursuit eye movements. *Journal of Neurophysiology*, 85, 1914–1922.
- Vanni-Mercier, G., & Magnin, M. (1982). Retinotopic organization of extra-retinal saccade-related input to the visual cortex in the cat. *Experimental Brain Research*, 46, 368–376.
- Wallach, H., Becklen, R., & Nitzberg, D. (1985). The perception of motion during collinear eye movements. *Perception & Psychophysics*, 38, 18–22.
- Wertheim, A. H. (1981). On the relativity of perceived motion. *Acta Psychologica*, 48, 97–110.
- Wertheim, A. H., & van Gelder, P. (1990). An acceleration illusion caused by underestimation of stimulus velocity during pursuit eye movements: Aubert-Fleischl revisited. *Perception*, 19, 471–482.
- Yamada, T., Suzuki, D. A., & Yee, R. D. (1996). Smooth pursuitlike eye movements evoked by microstimulation in macaque nucleus reticularis tegmenti pontis. *Journal of Neurophysiology*, 76, 3313–3324.

