



Nonlinear contribution of eye velocity to motion perception

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Abstract

The aim of this study was to test the hypothesis that an extra-retinal signal combines with retinal velocity in a linear manner as described by existing models to determine perceived velocity. To do so, we utilized a method that allowed the determination of the relative contributions of the retinal-velocity and the extra-retinal signals for the perception of stimulus velocity. We determined the velocity (speed and direction) of a stimulus viewed with stationary eyes that was perceptually the same as the velocity of the stimulus viewed with moving eyes. Eye movements were governed by the tracking (or pursuit) of a separate pursuit target. The velocity-matching data were unable to be fit with a model that linearly combined a retinal-velocity signal and an extra-retinal signal. A model that was successful in explaining the data was one that takes the difference between two simple saturating non-linear functions, g and f , each symmetric about the origin, but one having an interaction term. That is, the function g has two arguments: retinal velocity, \dot{R} , and eye velocity, \dot{E} . The only argument to f is retinal velocity, \dot{R} . Each argument has a scaling parameter. A comparison of the goodness of fits between models demonstrated that the success of the model is the interaction term, i.e. the modification of the compensating eye velocity signal by the retinal velocity prior to combination. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

If a person moves his or her eyes to track a moving object in the scene, the retinal image is changed. The smooth pursuit eye movements add a velocity field to the visual scene, changing the speed and/or direction of the motion in the retinal image. Despite retinal image motion from eye movements, we rarely misinterpret the motion to mean there is a moving visual scene.

As early as the nineteenth century, it was hypothesized that retinal image motion from eye movements is discounted by an extra-retinal motion signal, i.e. a neural signal that carries information about the eye movement (von Helmholtz, 1962). The perception of motion was thought to be the difference between a signal reflecting retinal-image motion and the extra-retinal motion signal (von Holst, 1954; von Helmholtz, 1962). The existence of an extra-retinal motion signal

has been implicated by observations such as the movement of an afterimage or a stabilized image when it is viewed while moving one's eyes (von Helmholtz, 1962; Mack & Bachant, 1969) and more recently by a case report (Haarmeier, Thier, Repnow, & Petersen, 1997) of a patient with a cortical lesion. The patient presumably lacked the extra-retinal signal linked to eye movements and as a consequence perceived motion of the stationary background during eye movements. There is also neurophysiological evidence for the existence of an extra-retinal signal related to eye movements from single-unit recordings in the medial superior temporal (MST) area of awake monkeys (Newsome, Wurtz, & Komatsu, 1988).

While it is commonly assumed that an extra-retinal signal exists, observations suggest that the extra-retinal signal does not fully discount (or compensate for) the changes in the retinal image due to eye movements. For example, stationary backgrounds appear to move in the opposite direction of an eye movement — the Filehne illusion (Filehne, 1922), and objects appear to move slower when they are pursued than when they are viewed with stationary eyes — the Aubert–Fleischl

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phenomenon (Fleischl, 1882). Furthermore experimental studies have demonstrated perceptual errors in the speed and direction of moving objects when subjects move their eyes (Wertheim & Van Gelder, 1990; Brenner & van den Berg, 1994; Freeman & Banks, 1998; Turano & Heidenreich, 1999). This lack of compensation has been regarded as representing a less-than-unity gain for the extra-retinal signal. According to a modification of the traditional theory,

$$\dot{R} - \varepsilon\dot{E} = \dot{\psi}, \quad (1)$$

where $\dot{\psi}$ is perceived velocity, \dot{R} is retinal velocity, and $\varepsilon\dot{E}$ is estimated eye velocity. The parameter, ε , is the gain of the extra-retinal signal that relates the actual eye velocity, \dot{E} , to the estimated eye velocity.¹

Although this model can account for some findings, more recent studies (Wertheim & Van Gelder, 1990; Haarmeier & Thier, 1996; Freeman & Banks, 1998; Turano & Heidenreich, 1999) challenge this simple modification of the traditional model. For example, the compensation of eye movements for motion perception has been shown to be influenced by the relative direction of the eye movement and stimulus motion (Wertheim & Van Gelder, 1990; Brenner & van den Berg, 1994; Turano & Heidenreich, 1999), preceding stimuli (Haarmeier & Thier, 1996), and stimulus characteristics. Some of the stimulus characteristics that have been shown to affect the eye-movement compensation are size (Wertheim & Van Gelder, 1990; Turano & Heidenreich, 1999), retinal eccentricity, (Turano & Heidenreich, 1998) duration (Ehrenstein, Mateeff, & Hohsbein, 1987), and spatial frequency (Freeman & Banks, 1998). These studies indicate that the process by which the visual system compensates for changes in the retinal-image motion caused by smooth pursuit eye movements is not as simple as had been previously thought.

Freeman and Banks (1998) recently proposed a parameterized model of perceived velocity that consists of an extra-retinal signal that inaccurately estimates eye velocity and a retinal-velocity signal that inaccurately estimates the retinal velocity. The inaccuracies can be viewed as gains of the signals. In the Freeman and Banks study, the stimulus spatial frequency was shown to modify the perceived speed of the stimulus during eye movements. Their model (Eq. (2)), with a retinal-velocity signal gain that varied with stimulus spatial frequency and an extra-retinal signal gain that remained constant, could explain the data. According to Freeman and Banks (1998),

$$\rho(\Omega)\dot{R} - \varepsilon\dot{E} = \dot{\psi}, \quad (2)$$

where $\rho(\Omega)\dot{R}$ is the estimated retinal image velocity. The parameter, ρ , is the retinal velocity gain that relates the actual retinal image velocity to the estimated retinal image velocity and is affected by the stimulus's characteristics, Ω .

The aim of this study was to test the hypothesis that an extra-retinal signal is combined with a retinal-velocity signal in a linear manner as described by existing models to determine perceived velocity. To do so, we needed to determine the relative contributions of the retinal-velocity signal and the extra-retinal signal for the perception of stimulus velocity. Under normal viewing situations, movements of the eye cause the image to move on the retina. Consequently the perceived motion could be the result of the retinal image motion, the extra-retinal signal, or both. To study the relative contributions of the two signals, we employed an image stabilization method. This method allowed us to control retinal image motion independent of eye movements. Specifically, the image of the stimulus display was slaved to the subject's eye movements. The image of the display screen moved in synchrony with the eye movement so that its image remained stable on the retina, irrespective of eye velocity. With this technique, we could control the retinal velocity by manipulating the movement of the stimulus on the display.

2. Methods

2.1. Subjects

Three observers (including the first author) with normal or corrected-to-normal acuities, well trained in the fixate-pursue procedure, served as subjects.

2.2. Stimulus-generation and display apparatuses

The stimuli were generated by a Silicon Graphics OCTANE workstation and displayed on a high-resolution CRT monochrome monitor (IKEGAMI 19 in. diagonal, spatial resolution 1280 H \times 1024 V pixels, P104 phosphor). The IKEGAMI CRT display is refreshed at a rate of 60 Hz without interlace. Viewing distance was 0.57 m. The stimulus was an array of randomly positioned dots (density of 1 dot deg²) that moved horizontally within a stationary 24° \times 24° window. Each dot was composed of a 3 \times 3 pixel array (5.4' \times 5.4') and had a luminance of 28.5 cd/m². The resulting stimulus velocity for 1 pixel displacement per frame was 1.8°/s. (Desired velocities were obtained by calculating pixel positions in real numbers and then rounding to the nearest integer prior to displaying on each frame.) A single square (5 \times 5 pixel array-9' \times 9',

¹ In order to keep the sign convention simple, we specify velocities in the world coordinates. For example, a positive retinal velocity corresponds to the retinal velocity that results from viewing, with stationary eyes, a stimulus that moves to the right. A positive eye velocity corresponds to an eye movement to the right.

28.5 cd/m²), positioned within a horizontal gap (2.5°) that divided the window, served as both the stationary fixation point (in the fixate phase) and the pursuit target (in the pursue phase). Subjects viewed the display in a dark room with the light from the display as the only important source of illumination. The edges of the CRT frame were not visible due to the aperture of the eyetracker.

2.3. Eye movement recording and analysis

Eye velocity was measured using a Generation-V dual Purkinje-image eyetracker (Crane & Steele, 1985). This model has a reported noise level of 20 s of arc rms, a frequency response of ~500 Hz for eye movements up to several degrees, and a tracking range of 20° (Crane & Steele, 1985). The subject viewed the display with his or her right eye and wore an opaque patch

over the left eye. The subject's head was steadied with a bite bar and headrest. Eye velocity was determined from the voltage analogs of horizontal eye position. The voltages were fed into an analog-to-digital converter every 10 ms and stored on a computer for off-line analysis. (As pointed out by an anonymous reviewer, a sampling rate of 100 Hz is inadequate to precisely detect saccades. However, the 100 Hz sampling rate was sufficient for our purposes: to identify saccadic eye movements for the purpose of elimination and to determine average pursuit velocity.) Voltage was converted to degrees of visual angle, on the basis of each subject's calibration results. For each trial, the slopes of the eye positions over time (i.e. average eye velocities) were computed separately for the fixation interval during stimulus presentation (0.5 s) and the pursuit interval during stimulus presentation (0.5 s). Analyses were performed on the average eye velocities determined in the pursuit interval only during stimulus presentation. Eye movements were calibrated prior to data collection and voltage converted to degrees of visual angle in the manner that we have in past studies (Turano & Heidenreich, 1996, 1999). Prior to calculating smooth pursuit eye velocity, saccadic eye movements were identified and eliminated also in the manner that we have in past studies (Turano & Heidenreich, 1996, 1999).

The retinal velocity of the stimulus was controlled by the stabilization of the stimulus display with a visual stimulus deflector on the dual Purkinje image eye tracker. With this method, the eye movements were monitored by the eyetracker and the signals were sent to the servo-controlled mirrors (designated in Fig. 1 as horizontal and vertical deflection mirrors) that rotated in response to the signals to compensate for the subject's eye movements. Two General Scanning CCX-101 amplifiers drove the G300PD Optical Scanners (Crane & Clark, 1978). The scanners were set up with a 40–60 Hz square wave and adjusted so that the rise time was equal to or less than 1 ms from when the square wave was low to when the square wave was high. The maximum excursion angle of the scanners was 20° peak to peak with a linearity of 0.1% of the excursion. The pursuit (fixation) target was presented on a separate monitor from the one that displayed the stimulus, and the images on the two monitors were superimposed optically. The image on the stimulus display passed through the optically stabilized path with the result that the retinal velocity of the moving stimulus was unaffected by eye movements. For example, a stimulus moving at 2°/s had a retinal speed of 2°/s, regardless of the eye velocity. A half-silvered mirror positioned at location A produced another optical path in which stimuli presented on a separate display monitor could pass through, bypassing the optical path used for stabilization. Not drawn to scale.

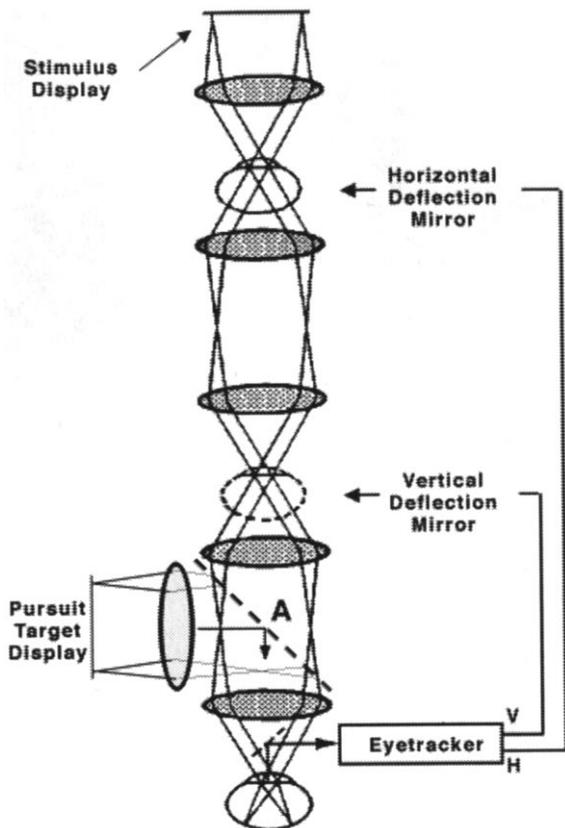


Fig. 1. An illustration (adapted from Crane and Steele, 1985) to show the critical components of the modified image-stabilizing system of the Generation V dual Purkinje image eye tracker. Eye movements are monitored by the eyetracker and the signals are sent to the servo-controlled mirrors (designated in the figure as horizontal and vertical deflection mirrors) that rotate in response to the signals to compensate for the subject's eye movements. A half-silvered mirror is positioned at location A in order to produce another optical path in which stimuli presented on a separate display monitor could pass through, bypassing the optical path used for stabilization. Not drawn to scale.

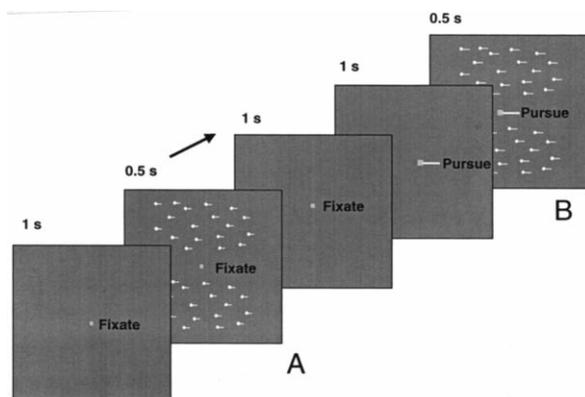


Fig. 2. Schematic of procedure. Subjects matched the velocities of two sets of dots (labeled as A and B in figure) randomly positioned within a stationary window. While viewing the first set of dots the subject kept his or her eyes fixed on a small centrally located stationary square. While viewing the second set of dots, the subject pursued the square as it translated across the screen. After the presentation of the two sets of dots, the subject indicated whether the dots in A moved faster or slower than the dots in B. Depending on the subject's response, on the next trial the speed of the dots in A was decreased or increased. This process continued until the subject reported that the two velocities were equal. Time course for each trial is shown at the top.

on this second display with the result that its retinal image undergoes changes consistent with a person's eye movements. The images (stimulus and pursuit/fixation target) on the two monitors were superimposed optically.

We used the after-image technique described by Kelly (1979) to achieve optimal stabilization. An initial gain setting of the eyetracker signal was established by having the subject alternately fixate between two unstabilized marks as he or she adjusted the potentiometer to make a stabilized dot move from one unstabilized mark to the other. After the initial gain setting was made, a finer gain setting was achieved by having the subject view a stabilized bright line as the subject moved his or her eyes back and forth. The gain of the eyetracker signal was adjusted so that the dark afterimage was positioned behind the bright line and hence could not be seen. Using these methods, the average error in repeating the optimal gain setting was 0.6%.

2.4. Procedure

On each trial, a stationary fixation point appeared in the center of the display. After 1 s, an array of dots appeared and moved at the 'test velocity' for 0.5 s. The array disappeared and the fixation point continued to be displayed for another second (for a total duration of 2.5 s for the stationary fixation point). After that, the fixation point began to move at the pursuit target velocity. After 1 s, a second array of dots appeared and moved at the 'base velocity' for 0.5 s. A depiction of the

time course is shown in Fig. 2. (Eye velocity was unaffected by the introduction of the arrays. The introduction of the array coincided with a saccade in less than 5% of the trials. In those cases, the change in eye velocity was less than 3%.)

Subjects were instructed to match the velocities of the dots (i.e. the head-centric velocities) in the two successively presented arrays. Velocity matches were made in a two-step process. The first step consisted of establishing a direction match, and the second step consisted of obtaining velocity matches to the stimuli whose directions were perceptually matched. For both direction matching and velocity matching, on each trial a moving stimulus was presented twice in succession. In the first interval, the stimulus moved at a test velocity. During this interval, the subject fixated a stationary spot. In the second interval, the stimulus moved at a base velocity, and the subject tracked the pursuit target (a spot translating across the screen). To establish direction matches, after each trial, the subject adjusted the direction of the stimulus (left or right) in the first interval to match the direction of the stimulus in the second interval. (No more than three trials were ever needed to perceptually match the directions.) Upon completion of the direction-matching step, speed matches were made using the direction-matched stimuli. To obtain speed matches, for each trial, the subject indicated whether the test speed, a pre-determined base speed \pm a delta speed, was faster or slower than the base speed in the second interval. On the next trial, the test speed was decreased or increased depending on the subject's response on the previous trial. This process continued until the subject reported that the two speeds were equal. At the point of perceptual equivalence, the test speed defined the speed match threshold. No feedback was given. (For the conditions that we tested, approximately 25 trials were required to achieve a speed match. On all trials, at the point that the speeds were perceptually matched, the subjects reported that the directions were also matched.)

In order to manipulate eye velocity in the experiment, a small square was optically superimposed on the stimulus. Subjects were instructed to keep their eyes fixed on the square that either remained stationary in the center of the display or moved across the screen. The image of the square passed through a separate optical path from the stimulus display, and it was not yoked to the subject's eye movements.

With this procedure, we are able to determine the relative contributions of the retinal-velocity signal and the extra-retinal signal for the perception of motion. In the first interval, the subject viewed the stimulus with stationary eyes so that the eye velocity was approximately 0. Perceived velocity of the stimulus in this interval had to be derived solely from the retinal velocity. In the second interval, perceived velocity of the

reference stimulus was derived from the extra-retinal signal generated from the pursuit eye movement and a constant retinal velocity from the reference stimulus. (Because the retinal velocity of the stimulus was unchanged by the pursuit eye movements with this method, we were able to hold the retinal velocity constant.) At perceptual equivalence the retinal-velocity signal from the test stimulus produced the same velocity perception as the combined extra-retinal signal and the retinal-velocity signal. By systematically varying eye velocity across a range of base velocities, we were able to map out the contributions of the two velocity signals for compensation. In the special case where the base velocity was $0^\circ/\text{s}$, the velocity of the test stimulus at perceptual equivalence revealed the retinal velocity that is perceived to be equivalent to the extra-retinal signal.

3. Experiment 1: velocity matches for a stimulus velocity of $0^\circ/\text{s}$

To obtain direct evidence of the existence of an extra-retinal visual motion signal and to determine how the illusory motion that it generates relates to eye velocity, we measured velocity match thresholds for a base velocity of $0^\circ/\text{s}$ for a range of eye velocities. The pursuit target velocities tested were ± 0.95 , ± 1.9 , ± 2.85 , ± 3.8 , and $\pm 4.75^\circ/\text{s}$. Since the eyes were stationary during the first interval, no extra-retinal signal was generated and therefore the perception of motion had to be due to the retinal image motion. In the second interval, there was no retinal-image motion. Therefore any perception of motion during the second presentation had to arise from the extra-retinal signal. At

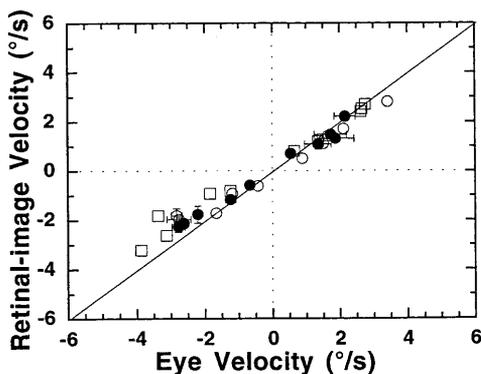


Fig. 3. Velocity match thresholds for a stationary ($0^\circ/\text{s}$) base velocity. The retinal image velocity that perceptually matches the stationary dots viewed during smooth pursuit eye movements. Each data point is the mean of three determinations. Error bars represent ± 1 SD. Negative and positive eye velocities indicate leftward and rightward eye movements, respectively. Solid line represents a perfect match between retinal image velocity and eye velocity. Data are for subjects smh (filled circles), kat (squares), and fjt (open circles). Dotted lines represent the $0^\circ/\text{s}$ eye and retinal-image velocities.

perceptual equivalence, the retinal image velocity that produced the same motion percept as the extra-retinal signal was determined.

4. Results: experiment 1

Subjects observed that when the stationary stimulus was viewed with stationary eyes the stimulus appeared stationary. However, when the stationary stimulus was viewed while the eyes were moving, the stationary stimulus appeared to move with the eyes. All subjects reported that the perceived motion of the stationary stimulus viewed while the eyes were moving was indistinguishable from a motion percept generated from a moving stimulus. Because the image of the stimulus display was slaved to the subject's eye movements and the stimulus was stationary on the display, there was no retinal image motion. The perceived illusory motion of the stimulus must be due to an extra-retinal signal that is associated with the movement of the eyes.

Subjects made perceptual matches across a range of eye velocities. Fig. 3 is a graph of the retinal velocity of a test stimulus perceived to be equal to a stationary reference stimulus viewed with moving eyes. As shown, the stationary stimulus was perceived to be moving in the same direction as the smooth pursuit eye movement, corroborating the subjective impressions. This illusory motion is the consequence of the compensation process. Because the retinal velocity of the stationary stimulus was $0^\circ/\text{s}$, the speed match threshold reflected the retinal velocity equivalence of the extra-retinal signal.

The data show that the magnitude of the speed match threshold increased with increasing eye velocity for both leftward (shown as negative eye velocity) and rightward (positive eye velocity) eye movements. The data would fall on the identity line in Fig. 3 if perceived velocity of motion appeared matched when retinal image velocity equaled eye velocity. The matches deviate from the line (with slopes of 0.84, 0.82, and 0.77 and correlation coefficients of 0.99, 0.99, 0.98 for subjects smh, kat, and fjt, respectively). These results indicate that the gain of the extra-retinal signal is less than the gain of the retinal velocity signal—corroborating earlier impressions (Fleischl, 1882; Brown, 1931; Mack & Herman, 1972; Wertheim, 1987; de Graaf & Wertheim, 1988; Freeman & Banks, 1998). This conclusion implies that the perceived illusory motion of the stationary world during a smooth pursuit eye movement would be equivalent to that produced by an 80% reduction in actual retinal image motion (if the signals add). A comparison of the motion percepts generated from eye movements and from retinal image motion indicates that the eye has to move at a speed approximately 1.25 times that of the retinal image motion to produce equivalent motion percepts.

Table 1

Average pursuit gains, i.e. eye velocity/target velocity, and standard deviations (SD) of each subject and base-velocity condition

	smh	kat	fjt
<i>Base velocity</i>			
0°/s	0.63 (0.11)	0.87 (0.23)	0.66 (0.13)
2°/s	0.79 (0.28)	0.87 (0.17)	0.66 (0.13)
4°/s	0.58 (0.24)	0.89 (0.19)	0.72 (0.36)

5. Experiment 2: velocity matches for stimulus velocities of 2°/s and 4°/s

The results of experiment 1 demonstrated that smooth pursuit eye movements generate an internal motion signal, i.e. an extra-retinal signal, that is in the same direction as the eye movement and can perceptually match the motion generated from retinal image motion. In this experiment we examined how the extra-retinal and retinal velocity signals combine. Velocity match thresholds were determined for base speeds of 2°/s and 4°/s. In these conditions the perception of motion of the dots in the second interval is the result of the combination of the base velocity (2°/s or 4°/s) and an extra-retinal signal.

6. Results: experiment 2

The average pursuit gains (i.e. eye velocity/pursuit target velocity) for the 2°/s, and 4°/s base-velocity conditions (as well as for the 0°/s base-velocity data from Exp. 1) for the three subjects are listed in Table 1. As shown, the pursuit gains remained relatively constant across conditions within a given subject, with the exception of the 2°/s condition for subject smh.

The center and bottom rows of Fig. 4 show the graphs of the velocity match thresholds for base velocities of 2° and 4°/s, respectively. The three subject's data are shown in separate columns. The retinal velocities of a test stimulus perceived to be equal to the reference stimulus viewed with moving eyes are plotted against eye velocity. Negative and positive values of eye velocity indicate eye movements in the opposite and same direction to the stimulus. As shown, the data appear to flatten out for eye movements in the same direction as the stimulus (positive values of eye velocity).

7. Fit of linear models

To determine how well the modified traditional model, $\dot{R} - \varepsilon\dot{E} = \dot{\psi}$, fit the data we performed a least squares fit. Using the statistical software program, JMP (SAS Institute, Cary, NC), we estimated the best value

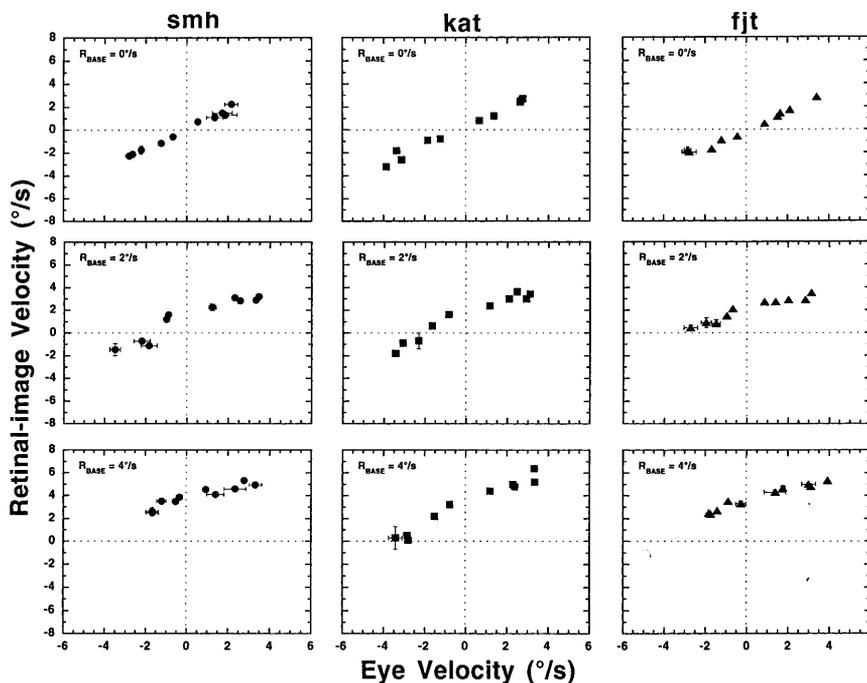


Fig. 4. Velocity-match thresholds for base velocities of 0°/s (top), 2°/s (center), and 4°/s (bottom). The retinal image velocity that perceptually matches the base velocity viewed during smooth pursuit eye movements. Negative and positive eye velocities indicate eye movements in the opposite and same direction as the stimulus, respectively. Data for subject smh, kat, and fjt are in the left, center, and right columns, respectively. Dotted lines represent the 0°/s eye and retinal-image velocities.

Table 2
Parameter values and goodness-of-fit estimates for the linear and nonlinear models

Parameters	Linear model	Ad hoc parameterized linear model			Saturating nonlinear model	Present model
		$0^\circ (\text{s}^{-1})$	$2^\circ (\text{s}^{-1})$	$4^\circ (\text{s}^{-1})$		
ρ	–	–1.248	–1.564	–1.673	0.404	0.247
ε	–0.677	1	1	1	0.377	0.785
h	–	–	–	–	0.674	1.584
α	–	–	–	–	–	0.769
RMSE	0.71	0.65			0.93	0.46

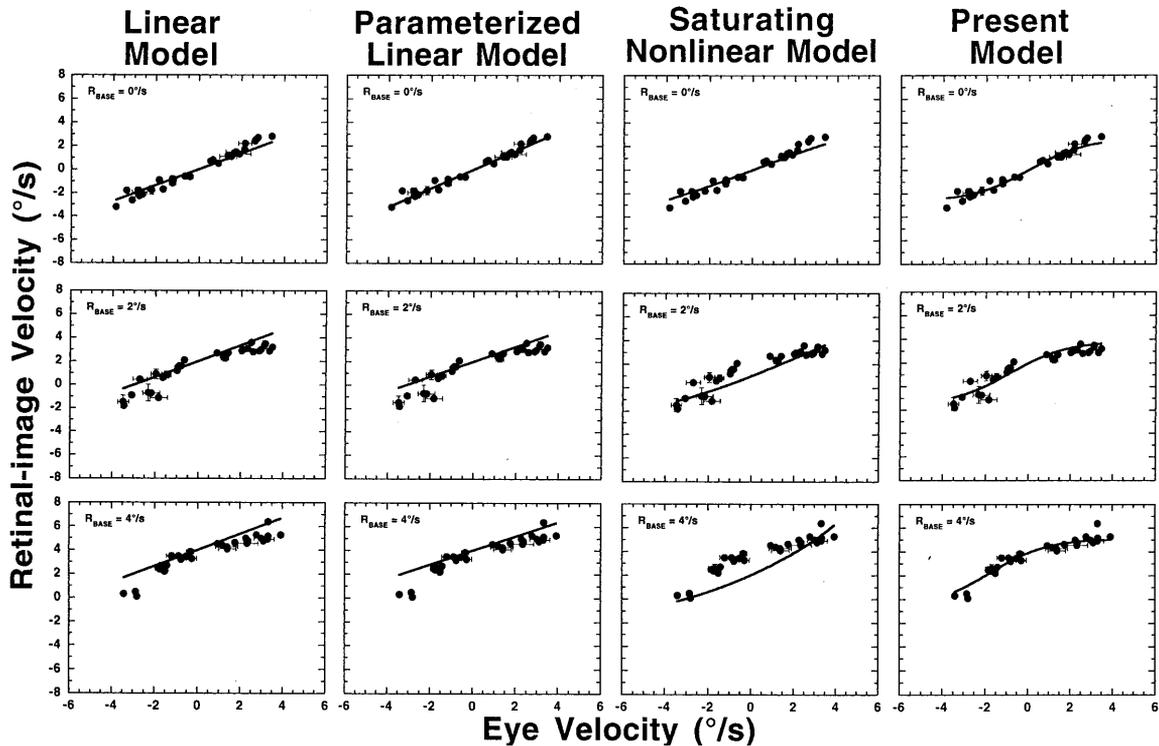


Fig. 5. Velocity-match thresholds for base velocities of $0^\circ/\text{s}$ (top), $2^\circ/\text{s}$ (center), and $4^\circ/\text{s}$ (bottom). The retinal image velocity that perceptually matches the base velocity viewed during smooth pursuit eye movements. Negative and positive eye velocities indicate eye movements in the opposite and same direction as the stimulus, respectively. Lines represent model fits to the data. Column headings indicate the respective models. Data are from three subjects.

for ε , the gain factor of the extra-retinal signal. The model was fit to the combined dataset of the three subjects and three R_{BASE} velocities (0° , 2° , and $4^\circ/\text{s}$). The best fitting value for ε was -0.677 (see Table 2). The leftmost graphs in Fig. 5 show the three subject's data with the linear model fits. The top, center, and bottom rows show the data for base velocities of 0° , 2° , and $4^\circ/\text{s}$, respectively. As shown, the model fails to account for the data of the fast eye movements.

We then determined whether or not a parameterized linear model could account for the data. The parameterized linear model, $(\rho)\dot{R} - \varepsilon\dot{E} = \dot{\psi}$, states that perceived velocity is the difference between the estimated retinal velocity signal and the estimated eye velocity

signal. The parameter, ρ , is a gain factor that relates the estimated retinal velocity to the actual retinal velocity, and ε is a gain factor that relates the estimated eye velocity to the actual eye velocity. If in the Freeman and Banks model the extra-retinal gain is fixed and the retinal gain does not vary as a function of retinal speed then the model is essentially the same as the modified traditional model and the ratio ε/ρ is -1.477 with an RMSE of 0.71. Giving the model a liberal interpretation, we applied the model separately to each of the R_{BASE} velocity datasets (0° , 2° , and $4^\circ/\text{s}$). We used JMP to perform a least squares fit to estimate the ratio ε/ρ . The best fitting ratios are shown in Table 2. These ad hoc model fits are shown as solid lines in the center left

graphs of Fig. 5 (under ‘Parameterized Linear Model’). The ad hoc parameterized linear model provides a good fit to the 0°/s base velocity data (top graph). However the model does less well in fitting the 2°/s (middle graph) and the 4°/s base velocity data (bottom graph), particularly for fast eye movements in the opposite direction.

8. Fit of nonlinear models

The observation that the linear models failed to fit the data at the fast eye speeds led us to look at simple

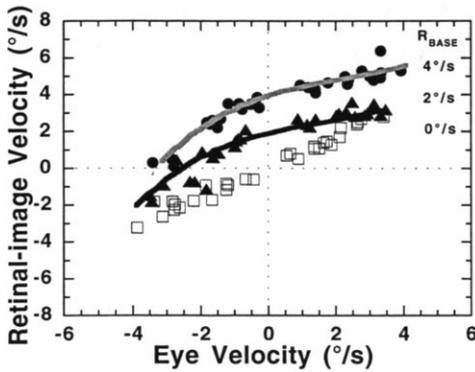


Fig. 6. Velocity-match thresholds for base velocities of 0°/s (open squares), 2°/s (solid triangles), and 4°/s (solid circles). The retinal image velocity that perceptually matches the base velocity viewed during smooth pursuit eye movements. Negative and positive eye velocities indicate eye movements in the opposite and same direction as the stimulus, respectively. Dotted lines represent the 0°/s eye and retinal-image velocities. The solid gray line represents a curve fit to the 4°/s data using the locally weighted Least Squared error method. The curve was then shifted horizontally by $-0.75^\circ/\text{s}$ and vertically by $-2.4^\circ/\text{s}$ (shown as a solid black line) to reveal a horizontal and vertical shift of the 2°/s data. Data are from three subjects.

nonlinear models for eye-movement compensation that incorporate saturating functions. We defined a nonlinear form of the traditional model as

$$f(\dot{R}) - g(\dot{E}) = \dot{\psi}, \tag{3}$$

where perceived velocity was the difference between a nonlinear function, g , that related estimated eye velocity to actual eye velocity and a non-linear function, f , that related estimated retinal velocity to actual retinal velocity. Assuming that $f(\cdot)$ and $g(\cdot)$ are approximately linear over some range, but are limited to asymptotic values at extreme velocities, we first evaluated the functions

$$f[\dot{R}] = R_{\max} \left(\frac{1}{1 + e^{-\rho \dot{R}}} - 0.5 \right) \tag{4}$$

and

$$g[\dot{E}] = R'_{\max} \left(\frac{1}{1 + e^{-\varepsilon \dot{E}}} - 0.5 \right) \tag{5}$$

which are linear near zero velocity, and asymptote at $R_{\max}/2$ or $R'_{\max}/2$ at extreme positive or negative velocities. The gain factors, ρ and ε , control the slopes of the linear portions of the functions. We determined the values for the three free parameters (ε , ρ , and R_{\max}/R'_{\max}) using a least squares fit to the combined dataset. The best fitting parameter values are listed in Table 2, and the model fits are shown as solid lines in the center right graphs of Fig. 5. As shown, this simple nonlinear model provides a poor fit to the data.

If we superimpose the velocity matches for the three base velocities (0°, 2°, and 4°/s) on a single graph (Fig. 6), we can observe both a vertical shift in the data and a horizontal shift that is dependent on \dot{R}_{BASE} . Motivated by the apparent horizontal shift in the data, we modified the simple nonlinear model to incorporate an interaction term into the compensating signal (Fig. 7). Function g , representing the compensating signal, was modified to receive two inputs: retinal velocity, \dot{R} , and eye velocity, \dot{E} . The modified function, $g[\dot{E}, \dot{R}]$, is specified as

$$g[\dot{E}, \dot{R}] = R'_{\max} \left(\frac{1}{1 + e^{-\varepsilon \dot{E} - \alpha \dot{R}}} - 0.5 \right). \tag{6}$$

We determined the values for the four free parameters (ε , ρ , R_{\max}/R'_{\max} , and α) using a least squares fit to the combined dataset. The parameter values are listed in Table 2, and the model fits are shown as solid lines in the rightmost graphs of Fig. 5. As shown in the graphs, the model provides a good fit to the data of all three base velocities, despite the fact that the model was applied to the combined dataset.

One estimate of a model’s goodness of fit is the root mean square error (RMSE) of a model’s prediction of the data. The RMSEs for the linear and nonlinear models are shown in Table 2. The ad hoc parameterized

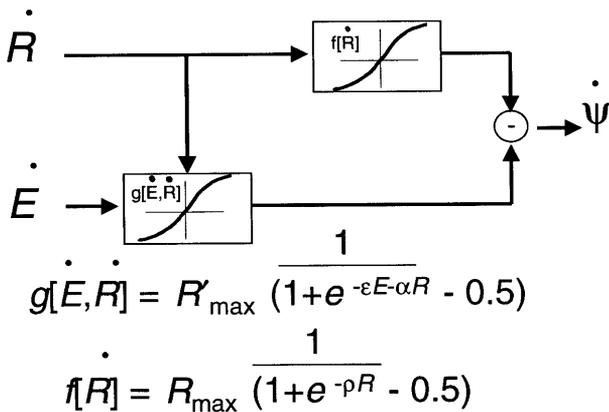


Fig. 7. A schematic of the present nonlinear compensation model. Perceived velocity, $\dot{\psi}$, is the difference between $f[\dot{R}]$, a saturating nonlinear function relating estimated retinal velocity to actual retinal velocity, and $g[\dot{E}, \dot{R}]$, a saturating nonlinear function estimating the compensating signal from the inputs, retinal velocity (\dot{R}) and eye velocity (\dot{E}).

linear model (with three free parameters) shows a better fit to the data, which has a RMSE of 0.65, compared to the modified traditional linear model (with one free parameter), which has a RMSE of 0.71. The simple nonlinear model, which also has three free parameters has a high RMSE, 0.93, reflecting its poor fit to the data. The model that best fits the data is the simple nonlinear model with the interaction term (four free parameters). This model has a RMSE of 0.46. The difference between the fits of the two nonlinear models and the ad hoc parameterized linear model demonstrates the importance of the interaction term, i.e. the retinal velocity in the compensation signal to determine perceived velocity. Simply adding degrees of freedom with the nonlinearity is not sufficient to describe the trends in the data.

9. Discussion

The results of Experiment 1 provided direct evidence for the existence of an extra-retinal signal that is generated by pursuit eye movements. With a stationary stimulus whose retinal image was slaved to the subject's eye movements we were able to isolate the motion percept that was generated by an extra-retinal motion signal during pursuit eye movements. We demonstrated that the motion percept is in the same direction as the eye movement and can perceptually match the motion that is generated from retinal image motion. A comparison of the motion percepts generated from eye movements and from retinal image motion indicates that the eye has to move at a speed approximately 1.25 times that of the retinal image motion to produce equivalent motion percepts.

In Experiment 2 we tested the hypothesis that an extra-retinal signal combines with retinal velocity in a linear manner as described by existing models to determine perceived velocity. The results showed that the linear models cannot explain the present data. Linear models, such as the modified traditional model or even an ad hoc parameterized linear model, failed to fit the data, suggesting the existence of nonlinearities, particularly for fast eye speeds.

A model that was successful in explaining the data was one that takes the difference between two simple saturating nonlinear functions, g and f , each symmetric about the origin, but one having an interaction term. That is, the function g has two arguments: retinal velocity, \dot{R} , and eye velocity, \dot{E} . The only argument to f is retinal velocity, \dot{R} . Each argument has a scaling parameter. The difference in goodness of fits between the two nonlinear models demonstrates that the success of the model is the interaction term, i.e. the modification of the compensating eye velocity signal by the retinal velocity prior to combination.

9.1. Comparison to Wertheim's model

In our model the compensating signal, $g[\dot{E}, \dot{R}]$, contains a visual (retinal) component in addition to an eye-velocity component. In this sense our model is similar to the one proposed by Wertheim (1994). In Wertheim's model the reference signal is a combination of visual, extra-retinal, and vestibular signals. In our experiments the head was steadied with a bitebar and headrest maintaining constant vestibular signals throughout the experiment. Therefore the issue of a vestibular input to the compensating signal was not addressed in our model. The two models do differ with respect to the functions relating estimates of eye and retinal velocities and their actual values. In the Wertheim model the estimators were related to the actual values by a scalar, whereas in our model the functions are saturating nonlinearities.

9.2. Localization of the compensation for pursuit eye-movements

Motion processing is thought to occur in a hierarchical fashion. Neurophysiological studies with the monkey have shown that the spatio-temporal components of the retinal velocity are first processed in striate cortex (V1). The components are then integrated in the middle temporal (MT) area of the superior temporal sulcus to compute two-dimensional pattern velocity (object motion) (Movshon, Adelson, Gizzi, & Newsome, 1986; Rodman & Albright, 1989). Some evidence suggests that the two-dimensional components are then combined in the medial superior temporal (MST) area of the superior sulcus to compute three-dimensional motion (Saito et al., 1986; Tanaka, Fukada & Saito, 1989; Tanaka and Saito, 1989; Duffy & Wurtz, 1991), e.g. optic flow. It had been traditionally thought that compensation for eye movements occurs at a low level of visual processing (von Holst, 1954; Wertheim, 1994), where the visual motion signal represents the spatio-temporal components of the retinal velocity.

Recent studies (Duffy & Wurtz, 1993; Haarmeier & Thier, 1996, 1998) suggest that eye movements may be compensated at a higher level, after the visual system has integrated the spatio-temporal information into an object-motion signal. (As studies call into question the level of visual processing at which the compensation occurs, we may also need to redefine the nature of the visual-motion signal, which we have referred to as retinal velocity, for the compensation process.) The later stages of the hierarchy (MT and MST) have been shown by single unit recording, electrical stimulation, and ablation studies with the monkey to be involved in both motion perception (Newsome & Pare, 1988; Salzman, Britten, & Newsome, 1990; Britten, Shadlen, Newsome, & Movshon, 1992; Salzman, Murasugi Brit-

ten, & Newsome, 1992; Celebrini & Newsome, 1994; Pasternak & Merigan, 1994) and smooth pursuit eye movements (Sakata, Shibutani, & Kawano, 1983; Kawano, Sasaki, & Yamashita, 1984; Newsome, Wurtz, Dursteler, & Mikami, 1985; Komatsu & Wurtz, 1988, 1989). MST is the first cortical area in the visual motion pathway that manifests both visual motion and extra-retinal signals during smooth pursuit eye movements (Sakata et al., 1983; Newsome & Pare, 1988). MST may be the area where the compensating signal combines with the visual motion signal to compensate for pursuit eye movements. If so, lesions to MST would prevent the recovery of head-centric velocity during eye movements.

The parieto-occipital cortex is an area speculated to involve cortex homologous to monkey area MST. Support for identifying this area as the site of eye-movement compensation comes from a person with bilateral lesions located in the parieto-occipital lobe. This patient was unable to compensate for eye movements (Haarmeier et al., 1997). When presented with a stationary scene, the patient perceived motion at a velocity that corresponded to his eye movements.

Further support for identifying the parieto-occipital cortex as the site of eye-movement compensation comes from discovering an electrophysiological correlate for the Filehne illusion (Haarmeier & Thier, 1998). The Filehne illusion is the perception of a stationary background moving in the direction opposite a smooth pursuit eye movement (Gibson, 1968; Mack & Herman, 1973). The illusion is believed to reveal the lack of complete compensation for eye movements. The amplitudes of the N300 and the P300 components of the event-related potential correlated with the modulation of the Filehne illusion.

In summary, recent studies have revealed the inadequacies of the traditional views on the compensation process for pursuit eye movements. Studies have shown that the visual system does not fully discount the velocity field in the retinal image motion due to smooth pursuit eye movements. In this study we used a perceptual matching paradigm and a stabilized stimulus display to demonstrate that the attempts that have been made to save the traditional models, by introducing gains for the extra-retinal and retinal-velocity signals, are unable to account for the perceived velocity data. Our results showed that an extra-retinal signal does exist but it does not combine in a linear manner with retinal velocity to determine perceived velocity. To fit the data it was necessary to introduce saturating non-linear functions and a retinal-velocity input to the compensating signal to determine perceived velocity. At present, neurophysiological evidence points to area MST as a possible cite for the combination of the compensating signal and the visual motion signal.

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