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RESEARCH ARTICLES

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Smooth pursuit tracking of an abrupt change in target direction: vector superposition of discrete responses

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Abstract The directional control of smooth pursuit eye movements was studied by presenting human subjects with targets that moved in a straight line at a constant speed and then changed direction abruptly and unpredictably. To minimize the probability of saccadic responses in the interval following the target's change in direction, target position was offset so as to eliminate position error after the reaction time. Smooth pursuit speed declined at a latency of 90 ms, whereas the direction of smooth pursuit began to change later (130 ms). The amplitude of the offset in target position did not affect the subsequent smooth pursuit response. In other experiments, the target's speed or acceleration was changed abruptly at the time of the change in direction. Step changes in speed elicited short-latency responses in smooth pursuit tracking but step changes in acceleration did not. In all instances, the earliest component of the response did not depend on the parameters of the stimulus. The data were fit with a model in which smooth pursuit resulted from the vector addition of two components, one representing a response to the arrest of the initial target motion and the other the response to the onset of target motion in the new direction. This model gave an excellent fit but further analysis revealed nonlinear interactions between the two vector components. These interactions represented directional anisotropies both in terms of the initial tracking direction (which was either vertical or 45°) and in terms of the cardinal directions (vertical and horizontal).

Keywords Eye movements · Human subjects · Target acceleration · Target velocity

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Introduction

During smooth pursuit, eye velocity is controlled so as to match the target's velocity (Keller and Heinen 1991; Lisberger et al. 1987; Rashbass 1961). Thus, the control signal is primarily related to the target's velocity, although signals related to target position and acceleration contribute to a lesser extent (Krauzlis and Lisberger 1994b; Pola and Wyatt 1980). Velocity is a vector quantity with a direction and magnitude and to date, most of the work has concerned how the magnitude of the velocity of the eye is related to that of the target. Less attention has been devoted to the directional control of smooth pursuit eye movements (Leung and Kettner 1997; Leung et al. 2000). If there is an uncertainty about the target's direction (as provided by two stimuli moving in different directions), the initial response of smooth pursuit reflects a vector average of the response to the individual target motions (Ferrera 2000; Gardner and Lisberger 2001, 2002; Lisberger and Ferrera 1997). Similarly, when a multifaceted object is tracked, the initial response reflects a vector average of the component motions, i.e., the motions of each side, rather than the actual motion of the target (Masson and Stone 2002).

These observations suggest that a model of smooth pursuit that treats the inputs and outputs as vectors (such as position, velocity and acceleration), rather than as scalars, would be an appropriate generalization. However, the results of a recent study of manual tracking suggest a different parameterization (Engel and Soechting 2000). We used a task in which the target initially moved at a constant speed and then unpredictably changed direction. We described the response in terms of the speed and direction of the finger motion, i.e., by two scalar quantities. After the target changed direction, hand speed initially declined, and this deceleration was graded with the amount by which the target changed direction. The direction of hand motion changed gradually and monotonically. The latency for the change in speed was less than the latency for the change in direction, suggesting that these parameters were controlled separately. In fact, a control model based on this assumption provided an excellent fit to the data.

We also studied ocular tracking of the same set of stimuli and found that the time course of smooth pursuit exhibited remarkable similarities to that of manual tracking (Engel and Soechting 2003; Engel et al. 1999, 2000). Specifically, as was the case for manual tracking, smooth pursuit declined in speed before it changed direction (Engel et al. 2000). However, since smooth pursuit was generally interrupted by a saccade to the target, we did not attempt to model these responses quantitatively. In the present study, we reexamined this issue by introducing a modification to the target motion (following Rashbass 1961) which decreases the probability of saccades around the time of the change in target direction. Thus, in the present experiments, the target underwent a step change in position coincident with the change in direction.

In agreement with our previous results, the latency for the change in smooth pursuit speed was less than the latency for the change in direction. However, in contrast to the results obtained for manual tracking, the initial deceleration in the direction of target motion did not depend on the amount by which the target changed direction. Accordingly, the experimental data could be explained by a model based on the vector superposition of a stereotypical response to the arrest of the initial target motion followed by a directional response to the onset of the new target motion. Although this simple two-component model fit the data well, an even better fit was obtained by including direction-dependent anisotropies in the gain of the response.

Methods

Subjects

Twelve subjects (seven males and five females) participated in these experiments. Their vision was normal or corrected to normal. All gave their informed consent to procedures that were reviewed and approved by the Institutional Review Board of the University of Minnesota.

Experimental overview

Experimental procedures and methods for data acquisition and analysis were similar to those described previously (Engel and Soechting 2003; Mrotek et al. 2004). Subjects tracked targets presented on a computer monitor (Mitsubishi Diamond Scan 20 M) with a resolution of 640×480 pixels (34.8×26.0 cm) and a 60-Hz refresh rate. They sat about 60 cm from the screen, placed at eye level in a dimly lit room. Eye movements were recorded binocularly at a sampling rate of 250 Hz with head-mounted infrared cameras (SMI Eye Link).

In most experiments, the target initially appeared at the top center of the screen and began moving downward (positive *y*-direction) at a speed of 240 pixels/s (12.6°/s). The target was a cyan circle, with a radius of 4 pixels (0.2° of visual angle). After the target had traveled between 5/12 and 2/3 of the distance to the bottom of the screen, it underwent a sudden change in direction. Thus, direction changed at a random time in a 1/2-s interval. The amount by which direction changed was also randomized and ranged from 0 to ±150° in 30° increments. At the start of each trial, a red fixation spot directed gaze to a point 2.1° below the top of the screen.

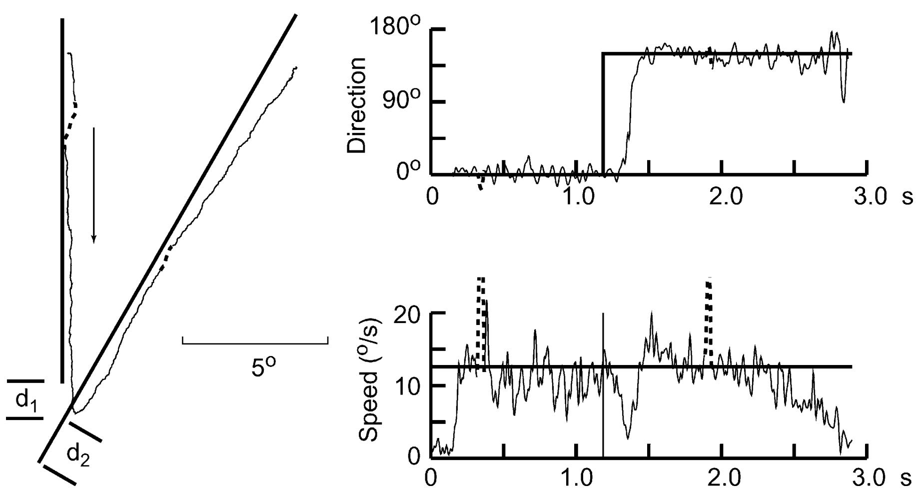

Fig. 1 Response to a step change in the direction of target motion. The *left panel* shows the motion of the target (*heavy trace*), which was initially downward and then changed abruptly by 150° upward and to the right. At the time that the direction changed, the target was also displaced so that the target's motion would ideally intercept the gaze trajectory. The *lighter trace* shows the gaze trajectory; *thicker dotted lines* indicate saccades. The *panels on the right* show target and gaze direction (*upper panel*) and speed (*lower panel*) for the same trial. The *vertical line* denotes the time when the target changed direction. The change in direction resulted in a transient decrease in the speed of smooth pursuit and a gradual change in its direction

Simultaneously with the change in direction, the target underwent a step change in position (see Fig. 1). The amplitude and the direction of the step were designed so that eye position and target position would coincide at the end of the smooth pursuit reaction time (120 ms, see de Brouwer et al. 2002b). Accordingly, the vertical position of the new target trajectory was displaced downward ($d_1$in Fig. 1) by the amount the eye would travel in 120 ms, assuming perfect tracking. Since pursuit speed initially decreases (Engel et al. 1999), we introduced an additional delay of 30 ms so that the target would intercept the *y*-axis 150 ms after the change in direction. Thus the target's new direction began with the offset labeled d_2 in Fig. 1.

We took care not to artificially introduce a discontinuity in speed. Let frame 0 correspond to the time at which direction changes. On the preceding frame (−1), we presented two targets: the first displaced according to the initial downward motion and the second appearing at the new position. On the subsequent frame (0), the first target disappeared and the second target was displaced in the new direction. Thus, in each frame, only one target was in motion: the first target in frame (−1) and the second target in frame (0). Accordingly, the target's speed was not influenced by the amplitude of the step displacement.

Experimental design

We studied four different experimental conditions, with four subjects participating in each experiment. One subject took part in three experiments, and two others took part in two experiments.

Experiment 1: effect of a step change in target direction

This experiment implemented the basic design described in the overview and examined the effect of the initial direction of target motion on the response. In one block of trials, the target initially traveled downward at 12.6°/s, and then underwent a step change in position and direction. In a second block of trials, the target initially traveled downward and to the right (45°) at the same speed. In each block, there were 11 directions of subsequent target

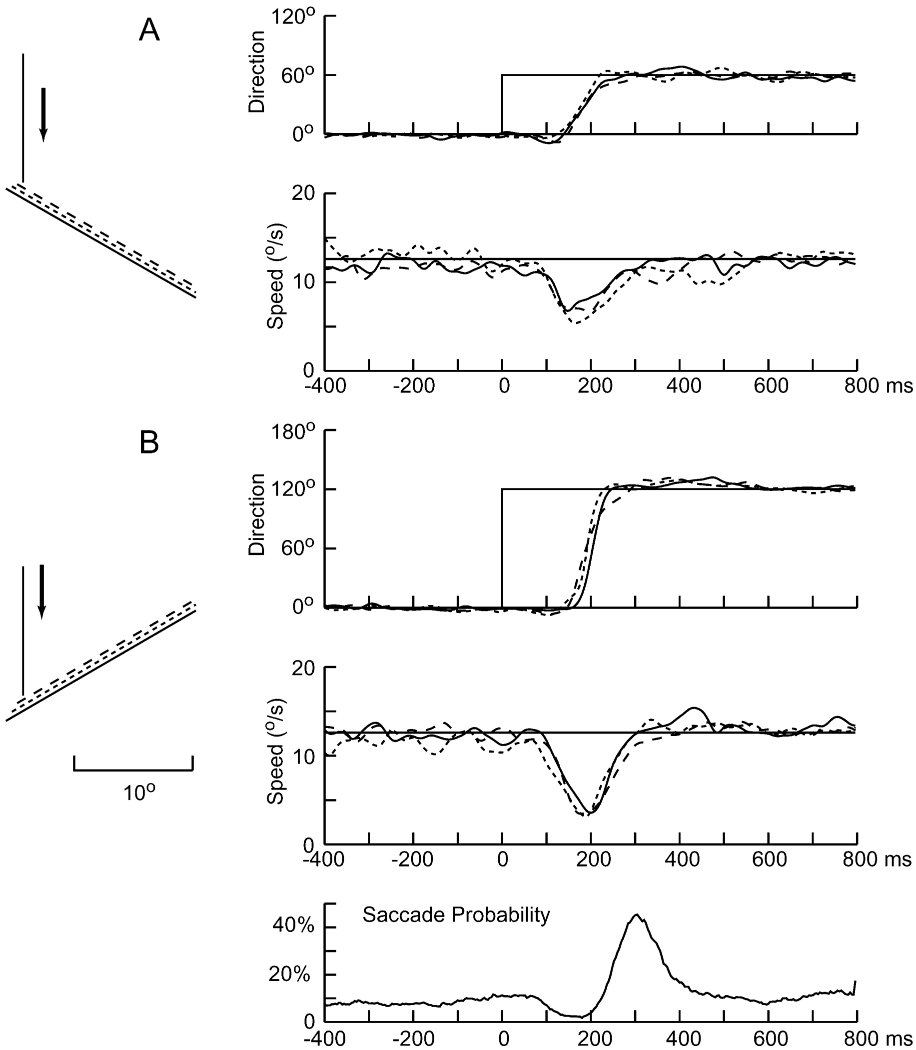

Fig. 2a, b Effect of varying the amplitude of the step change in target position. The target motions are indicated in the *left panels* (for a 60° change in direction in **a** and a 120° change in direction in **b**). The three line styles (*solid, dotted* and *dashed*) denote three different amplitudes of step change in target displacement. The *right panels* show averaged records of speed and direction for one subject in the three experimental conditions. The *bottom panel* shows the probability of the occurrence of a saccade at various times, using data for all subjects in Exps. 1 and 2 (largest step displacement). Note that this probability was low prior to the change in the direction of target motion, decreased almost to zero shortly after direction changed at time 0, and subsequently rose to a peak at about 300 ms motion, equally spaced in 30° increments and 12 repeats per condition. The new direction and the time at which it began were randomized from trial to trial.

Experiment 2: effect of the size of step displacement

In this experiment, we varied the size of the step displacement of the target by three different amounts: the nominal one used in Exp. 1, and ones that were 2/3 or 1/3 as large (see *left panels* of Fig. 2). In each instance, target speed was constant throughout the trial. There were seven trials for each experimental condition (direction and amount of offset), for a total of 231 trials (11 directions × 3 conditions × 7 repeats). Target direction, offset and the time of the change in target direction were randomized.

Experiment 3: effect of a step change in target speed

In this experiment, the target could undergo a step change in speed by ±50% at the time of the change in the target's direction. On one third of the trials, target speed did not change from its original value of 12.6°/s. The offset in the step change in target position ($d_1$and d_2) was adjusted for each speed to minimize tracking error. There were 11 directions × 3 speeds × 8 repeats for a total of 264 trials.

Experiment 4: effect of a step change in target acceleration

Immediately following the change in the direction of target motion, the target could accelerate or decelerate at a constant rate. Target acceleration (12.6°/s^2) was maintained for 0.5 s, such that target speed had changed by ±50% at the end of 0.5 s. Target acceleration was zero in one third of the trials. Since speed changed gradually, we did not vary the amount by which target position was offset.

Data analysis

Sampled data were calibrated using a procedure performed at the onset of each session, with drift compensation performed prior to each trial. The *x*- and *y*-position data were filtered (double-sided exponential filter with 4 ms time constant) and numerically differentiated. Saccades were removed by interpolating the velocity traces with a cubic spline and the desaccaded data were averaged, after aligning each trial on the time at which target motion changed (for additional details see Engel and Soechting 2003; Mrotek et al. 2004). The speed (*s*) and direction (θ) of smooth pursuit were computed from the *x*- and *y*-components of velocity:

$$s = \left(v_x^2 + v_y^2\right)^{1/2} \qquad \theta = \tan^{-1}\left(v_x/v_y\right) \tag{1}$$

The appropriate models were then fit to average speed, direction or velocity, in order to quantify the influence of the experimental variables.

Results

Smooth pursuit response to a step change in target direction

After the direction of target motion changed, the speed of smooth pursuit decreased transiently and its direction changed smoothly and gradually, in agreement with previous observations (Engel and Soechting 2003; Engel et al. 2000). This is evident in the results from the single trial illustrated in Fig. 1. The target initially traveled downward, and then underwent a step change in position, changing its course to move 150° upward and to the right from the vertical (*left panel*). The offset in the target position was chosen so that, at the time when smooth pursuit began to respond to the change in target motion, gaze position (indicated by the *light trace* in the left panel) would coincide with the position of the target. This experimental design minimized the probability of saccades interrupting smooth pursuit, particularly around the time at which the target changed direction. In this example, there was one saccade (indicated by *heavier, dashed lines*) early in the trial (around 0.4 s), and a second one about 600 ms after the target had changed direction.

Smooth pursuit speed (shown in the *lower right panel* of Fig. 1) on average was slightly less than target speed prior to the change in target direction (*vertical line* at 1.2 s). Over all trials, the average gain for this subject was 0.90, evaluated in the 100-ms interval prior to the target's change in direction. Average gain for all subjects in Exps. 1 and 2 was 0.73 in this interval. Shortly after the change in target direction, speed decreased transiently and then reacquired the target's speed. Pursuit gain after direction had changed was slightly larger (0.98 evaluated in the interval between 400 and 500 ms), a result that was typical (average 0.93 for Exps. 1 and 2). The latency for the change in the direction (*top right panel*) appeared to be somewhat greater than the latency for the decrease in speed.

The results illustrated in Fig. 1 were typical of the results obtained in this experimental condition, as can be ascertained from the averaged data shown in Fig. 2 for two other target directions (60° in Fig. 2a and 120° in Fig. 2b). In each panel, *three traces* are superposed, corresponding to the different amounts of target displacement (Exp. 2). The *solid traces* correspond to the nominal values of target displacement (the amount designed to minimize tracking error), while the *dotted* and *dashed traces* correspond to step displacements that were 1/3 and 2/3 less. In Fig. 2, the latency for the change in tracking speed is about 80 ms, and the latency for the change in direction is much longer

(~130 ms). Furthermore, the amount of the target displacement did not influence the speed or the direction of smooth pursuit in any consistent or significant way.

Statistical analysis supported this conclusion. For speed, we computed the time and the amplitude of the minimum in speed. Both parameters depended on the amount by which target direction changed, but they did not depend on the size of the step displacement (ANOVA, $F_{(2,99)}$=0.885 for amplitude, $F_{(2,99)}$=0.245 for time, p>0.05). The latency for the decline in speed (estimated by regression analysis of the initial transient) averaged 90±2 ms (SE), and did not depend on the target direction or on the size of the step displacement ($F_{(2,99)}$=1.183, p>0.05).

To characterize the time course of the change in smooth pursuit direction, we fitted the averaged data for each experimental condition with the logistic distribution function:

$$\theta(t) = \theta_f / \left(1 + e^{-(t-\tau)/\beta}\right) \tag{2}$$

where θ_f is the final direction of target motion. From this fit, we computed a latency, defined as the time at which θ exceeds 5% of θ_f, and a rise time, defined as the time from 5 to 95% of the final value. The results of this analysis gave a latency of 128±2 ms (SE) and a rise time of 94 ±4 ms. These values did not depend on the step size (p>0.05, $F_{(2,78)}$=0.770 for latency and $F_{(2,78)}$=0.759 for rise time).

Saccades

The *bottom trace* in Fig. 2 shows that the experimental design succeeded in reducing the probability of saccades around the time that the target changed direction. Prior to this time, there was an 8% probability of a saccade at any instant. At about 100 ms after the target step, this probability decreased dramatically and then increased, reaching a peak of 45% at 300 ms. (Note that by 300 ms, the direction of smooth pursuit had matched the new target direction and its speed had recovered from the transient decrease.) These results correspond to the instances in which the step displacement was designed to minimize the probability of saccades. Saccade probability increased and its latency decreased for smaller step displacements. When the step displacement was 2/3 of the optimal amount, the probability reached a maximum of 65% at 260 ms; when it was 1/3 of the optimal amount, the corresponding values were 75% at 236 ms.

In the few instances in which saccades were initiated in the interval 50–100 ms after the change in target direction, the saccade direction tended to reflect the step change in the target's position. An example is provided in Fig. 3a. In this example, the saccade initiated 68 ms after the target had changed direction was directed −27° from the vertical (down and to the left), compensating for the jump in the target's position. This behavior was characteristic of saccades that occurred in the interval between 50 and 100 ms, as shown in the plot of saccade direction in Fig. 3b. In this plot, the sign of the saccade direction (relative to initial target direction) is defined by the new direction of target motion, a negative angle corresponding to saccades that were in the direction of the step in target position (as in Fig. 3a). Statistically, for saccades starting before +56 ms (relative to the time at which target direction changed), saccade direction did not differ from 0 (t-test, Bonferroni correction for multiple comparisons, p>0.05). Thereafter, until +88 ms, saccade direction was consistently negative (−14.8°, p<0.01).

This range of times (56–88 ms) is less than the minimum interval for a step change in target position to influence saccade *amplitude* (~100 ms, Becker and Juergens 1979; de Brouwer et al. 2002a). However, it is identical to the value reported by Gellman and Carl (1991) at which saccade *direction* was first influenced.

Influence of previous trial

As demonstrated above, the experimental design eliminated most saccades just after the change in direction and allowed us to examine smooth pursuit. Although the main goal was to describe the influence of specific target parameters, it is known that expectations about target motion can influence smooth pursuit (Kowler 1989; Kowler et al. 1984). In our experimental design, the ultimate direction of target motion was unpredictable, as was the time at which the target changed direction. Nevertheless, it is possible that the stimulus and the tracking behavior on one trial influenced the response on the subsequent trial (cf. Thoroughman and Shadmehr 2000). We assessed this possibility by using the following model:

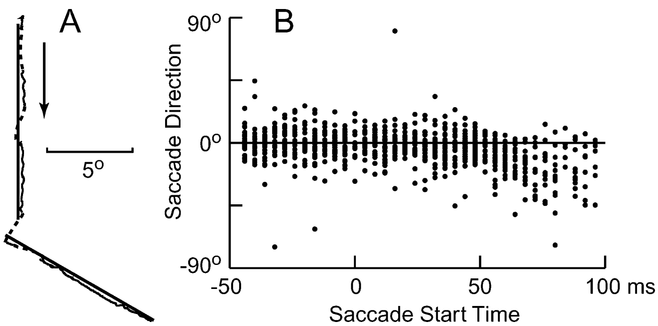

Fig. 3a, b Saccade direction related to target position. **a** Tracking of a target whose motion changed by 60° to the right. Smooth pursuit is indicated by *light, solid lines* and saccades are denoted by *heavier, dashed lines*. Note that the saccade initiated shortly (68 ms) after the change in the target's direction is directed 27° to the left, toward the target that was displaced to the left. **b** Saccade direction for all instances in which a saccade began in the interval −50 to +100 ms relative to the time at which target direction changed. Positive saccade directions are in the direction of the new target velocity, whereas negative saccade directions are in the direction of the target's position immediately after the change in direction

$$\begin{aligned} s_i^j(t) &= A_s(t)s_{i-l}(t) + B_s(t)\bar{s}^j(t) \\ \theta_i^j(t) &= A_\theta(t)\theta_{i-l}(t) + B_\theta(t)\bar{\theta}^j(t) \end{aligned} \quad (3)$$

where s and θ refer to speed and direction, the subscript i refers to the i^{th} trial and the superscript j refers to the j^{th} experimental condition (i.e., direction and step size in Exp. 2). $\bar{s}^j$ and $\bar{\theta}^j$ denote the averages of speed and direction for all trials for that particular condition. The weighting coefficients A and B were obtained from a least-squares fit of all of the data for each session. To decrease the amount of variability in the data, we assumed that these coefficients were constant over 40-ms intervals, and computed them every 20 ms (i.e., we used a moving average).

The outcome of this analysis is shown in Fig. 4, which depicts results from all 16 sessions in which the target initially moved downward. If the previous trial had no influence on the response, then the weighting coefficient for the average (Fig. 4b) should be 1.0, and that for the previous trial (Fig. 4a) should be 0.0. This was true beginning about 300 ms after the target had changed direction. However the response on the preceding trial did initially influence the speed and the direction of smooth pursuit on the present trial, with a positive weighting coefficient.

Statistically, the weighting coefficient of the previous trial for speed (A_s) differed from 0 in the interval from 0 to 220 ms (mean weight = 0.073, $p<0.05$, t-test, corrected for multiple comparisons). During this interval, the average speed was either constant or declining and this result most likely reflects slow fluctuations (over the course of several trials) in the gain of smooth pursuit tracking of the vertical motion. The weighting also differed from 0 in the interval from 700 to 780 ms, but with a much lower value (0.028).

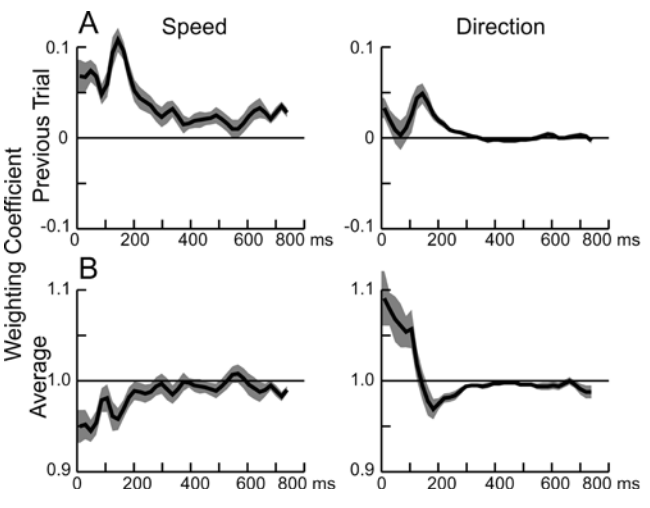

Fig. 4a, b Influence of the previous trial on the smooth pursuit response. The speed and direction of smooth pursuit were represented by a weighted sum of the average response to that direction of target motion (**b**) and of the response on the previous trial (**a**). The shaded area encompasses ± SE. Note that the weighting coefficient of the previous trial (**a**) was small (less than 10%) and positive, decreasing to zero about 200–300 ms after the target changed direction (which occurred at time 0)

The direction of smooth pursuit on any given trial was influenced by the direction on the previous trial in the interval from 160 to 300 ms ($p<0.05$), with an average weighting coefficient (A_θ) of 0.021 (Fig. 4a). Thus the time course of the transition from one direction to another was influenced by the previous trial. From 0 to 100 ms, the weighting coefficient of the average directional response B_θ was consistently greater than 1.0 (Fig. 4b), but these values did not reach the threshold for statistical significance.

In summary, the previous trial did have a small, but consistent influence on the tracking response. This influence contributed a small amount of variability to the averaged responses but it was too small to affect estimates of smooth pursuit responses obtained by averaging.

Initial velocity transient

In response to the change in the direction of the target's motion, the speed of smooth pursuit decreased with a latency and a slope that appeared to be the same, irrespective of whether direction changed by a large amount (as in Fig. 2b) or to a smaller degree (Fig. 2a). Furthermore, this slope did not depend on the size of the step displacement (Fig. 2), nor (as quantified below) on the target's speed after its direction had changed (Exps. 3 and 4).

Therefore, the initial velocity transient seemed to be independent of the stimulus parameters. This can be appreciated in Fig. 5, which shows overlays of all of the data for one session (Exp. 2 in Fig. 5a and Exp. 3 in Fig. 5b). Each plot depicts the average x- and y-components of smooth pursuit velocity for all 33 experimental conditions. In all instances, the target initially moved in the positive y-direction and changed direction at time 0. Because the final target motion could be either to the left or right and up or down, there is a wide divergence of the x- and y- gaze velocities by 400 ms. Nevertheless, the initial deceleration of the y-component of smooth pursuit velocity was consistent for all experimental conditions. This initial deceleration began at about 80 ms (compare with the *dashed reference line* at 100 ms). By contrast, the change in the horizontal component of the velocity began later, at about 120 ms, with a slope that appears to be graded, depending on the final speed in the x-direction at 400 ms.

The results in Fig. 5 suggest that initially (i.e., between 80 and 120 ms) the y-component of velocity is not graded with the stimulus parameters. Conversely, the x-component of the velocity (reflecting the new direction of target motion and having a longer latency) does appear to be graded with the stimulus. To assess this impression quantitatively, we computed the variance of the x- and the y-components of the smooth pursuit velocity over all experimental conditions for each subject, normalizing the variances by their mean values over the 200-ms interval prior to the change in target direction (Fig. 6a). As a second test, we correlated the x- and y-components of the

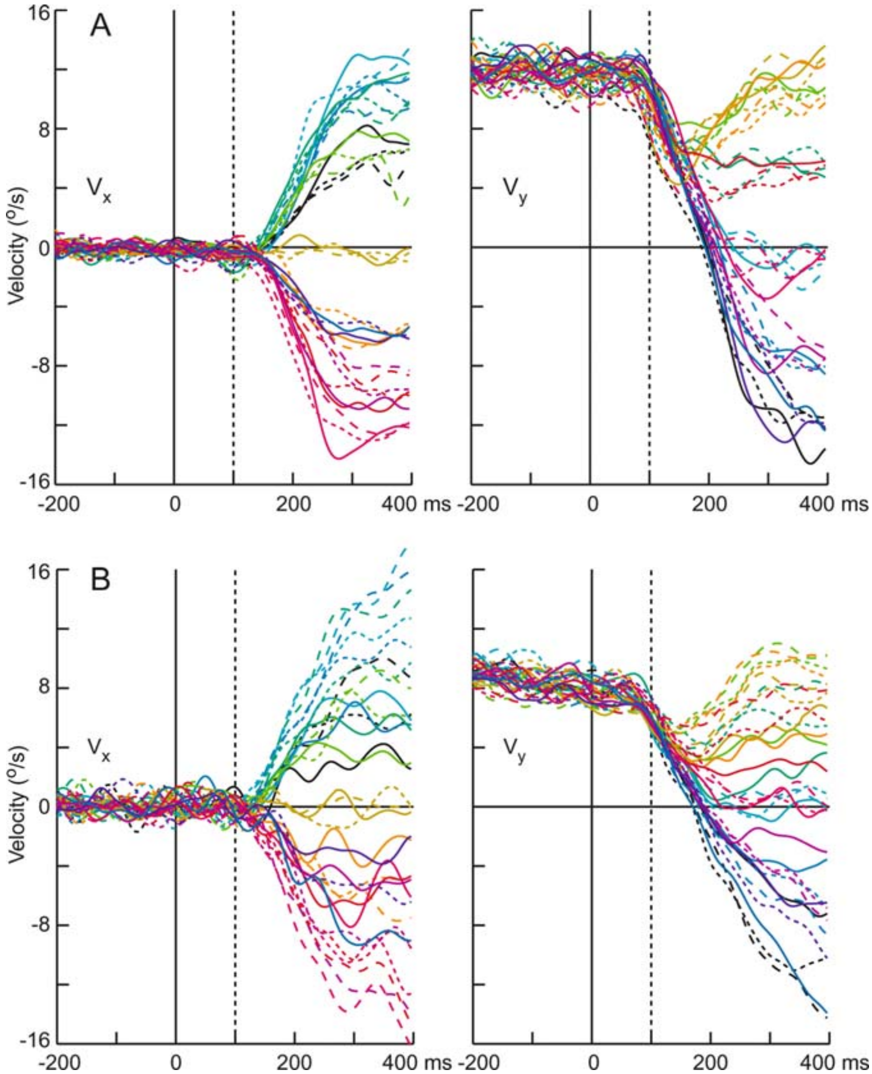

Fig. 5a, b Horizontal (V_x, *left panels*) and vertical (V_y, *right panels*) components of smooth pursuit velocity. The data represent all of the results for 11 directions of target motion from one session in which the amplitude of the target step was varied (**a**, three amplitudes, Exp. 2) and from a session in which target speed could change by ±50% (**b**, Exp. 3). *Traces* are color coded according to the final direction of target motion and the *solid, dotted and dashed lines* denote the three amplitudes of step displacement (**a**) or target velocity (**b**). Note that the initial vertical deceleration of smooth pursuit was consistent for all experimental conditions, and that the latency for the horizontal velocity component (V_x) was longer than that for V_y

velocity with their respective values at 400 ms (Fig. 6b). If the response was graded with the stimulus parameters, they should be positive and significant.

The two approaches gave results that were virtually identical. For the analysis of variance (Fig. 6a), the critical value (*horizontal dashed lines*) was $F_{(2,32)}>3.32$ ($p<0.05$). This value was first exceeded at 136 ms for v_x and then at 160 ms for v_y. For the second analysis (Fig. 6b), the critical value was $|r|>0.349$ ($p<0.05$), and this value was exceeded at 136 ms for v_x and at 156 ms for v_y. Thus, according to both analyses, the x-components of the velocity responses diverged earlier than did the y-components, even though the latency for v_y was greater than the latency for v_x (Fig. 5). This analysis supports the conclusion that the earliest part of the response did not depend on the amount by which the direction of target motion changed.

Vector superposition

These findings are consistent with the hypothesis that smooth pursuit results from the vector superposition of two responses at different latencies. The first of these responses would be the arrest of tracking in the initial target direction (*vertical* in Fig. 5). The second component, occurring at a longer latency, would be the initiation of tracking in the new direction of target motion. Accordingly, the initial deceleration of smooth pursuit should be invariant because it represents the arrest of tracking of the initial target motion. Furthermore, the gradual change in the direction of pursuit at a longer latency would result from such a control strategy. In this section we test the predictions of this model quantitatively.

According to this model, smooth pursuit velocity $\mathbf{v}_i(t)$ is the sum of two components:

$$\mathbf{v}_i(t) = v_0(t)\mathbf{j} + v_I(t)\mathbf{e}_i \quad (4)$$

where $\mathbf{j}$ is the unit vector in the initial (y) direction and $\mathbf{e_i}$ is the unit vector in the target's new direction. The function v_0 represents the time course of the response to the arrest of a target's motion, and v_I the response to the onset of the target's motion in the new direction. Furthermore, the

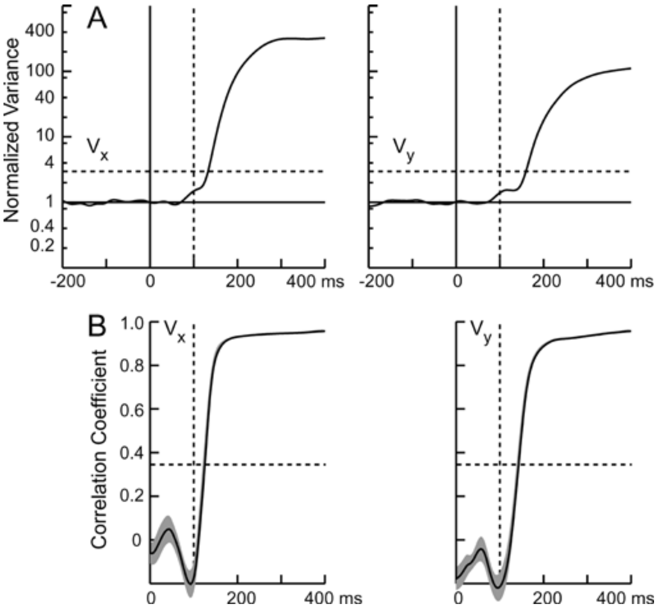

Fig. 6a, b Normalized variance (**a**) and coefficient of determination (**b**) for the horizontal (V_x, *left*) and vertical (V_y, *right*) components of smooth pursuit velocity. The *traces* represent average results obtained from the data for all 16 sessions. Normalized variance was obtained by computing the variance of the velocity components for all experimental conditions (direction, target offset, speed, acceleration), normalized by the mean value in the 200-ms interval prior to the time at which the direction of motion changed (time 0). The coefficient of determination was obtained by correlating the values of V_x and V_y at each point in time with the respective values 400 ms after the time at which the direction of motion changed. The coefficients of determination (*r*) were computed separately for each subject, and then averaged over the 16 sessions. The *horizontal lines* in **a** and **b** denote the 0.05 significance level and the *shaded area* in the *bottom panel* encompasses ±1 SE

shape of neither v_0 nor v_1 should depend on the final direction of target motion. The time courses of v_0(t) and v_1(t) were determined by a least-squares approach.

Representative results of this analysis are shown in Fig. 7 for one session in Exp. 2. The model gave a good fit to the data as can be seen by comparing the *heavy, solid traces* (modeled response) with the *lighter traces* which depict instances where the target's motion changed by ±90° (i.e., $v_0 = v_y$ and $v_1 = v_x$). A second assessment of the adequacy of the model is provided in Fig. 7b, which shows the standard deviation of the difference between the data and the model.

The off-response (v_0, Fig. 7a, *left panel*) caused velocity to decline at a latency of 75 ms, from an initial level that is 96% of the target's speed. The deceleration was close to constant (−67.0°/s^2), and there was a small overshoot and a gradual return to the baseline of zero. The on-response (v_1, *right panel*) showed a similar time course with a longer latency (147 ms) and a steeper slope (99.6°/s^2). These results were typical of the values obtained for all sessions (Table 1). Similar results were also obtained when the initial direction of target motion was at 45°, i.e., down and to the right. Neither the slopes nor the latencies of the

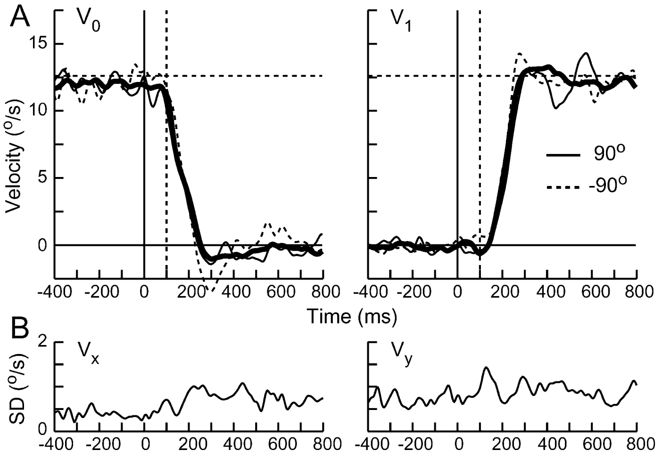

Fig. 7a, b Vector superposition of smooth pursuit responses. Smooth pursuit was modeled as the superposition of an off-response (V_0) in the initial, vertical direction of target motion and an on-response (V_1) in the new direction of target motion. The *heavy solid lines* in **a** denote the modeled responses obtained by a least-squares fit to the data for all directions of target motion. The *lighter, solid and dashed traces* depict experimental data obtained for conditions in which target direction changed by ±90° (conditions in which the on- and off-responses are perpendicular to each other). *Vertical lines* are provided for reference at time 0 and at 100 ms. The *bottom panels* (**b**) depict the standard deviation between the modeled and the experimental data for V_x (*left*) and for V_y (*right*). Data are for one subject in Exp. 2

on- and the off-responses differed for the two conditions of initial target motion (pairwise comparisons, *t*-test, $p>0.05$).

Effect of target speed and acceleration

Analogous results from sessions in which target speed could change instantaneously or gradually are shown in Fig. 8. In agreement with our observations on manual tracking (Engel and Soechting 2000), a step change in velocity evoked early and clear changes in the speed of smooth pursuit (Fig. 8a), but the sensitivity to step changes in acceleration was much lower (Fig. 8c).

When target speed changed instantaneously (Fig. 8a), the slopes of the on-responses for the three conditions differed significantly ($F_{(2,9)}$=81.1, $p<0.01$). When target speed was constant (*solid trace* in Fig. 8a), this slope averaged 70.6°/s^2. The effect of speed was asymmetrical; a 50% decrease in speed led to a 38% decrease in the slope, whereas a 50% increase in speed only led to 20% increase. There was no effect on the latency of the on-response, which averaged 123 ms. Averaged over all directions and sessions, the speed of smooth pursuit in response to step increases and decreases in target velocity diverged from each other with a latency of 132 ms (*t*-test, adjusting for multiple comparisons, $p<0.05$).

The effect of target acceleration (Fig. 8c) became apparent only after the initial rise in v_1. The on-response increased at a constant rate up to about 300 ms. Thereafter, the three traces diverged, v_1 increasing or decreasing depending on whether the target accelerated or decelerated. Target acceleration did not have a statistically

Table 1 Characteristics of off- and on-responses. Slopes and latencies of off- (V_0) and on-responses (V_1). Results are listed for each experimental session. In Exps. 3 and 4 (step changes in speed (*S*) and acceleration (*A*)), the off-response was fit to all of the data. Separate on-responses were computed for conditions in which speed or acceleration did not change (indicated by the suffix "0"), when it increased (+) and when it decreased (−). In Exp. 1, the suffix (0° or 45°) denotes the initial direction of target motion. For Exps. 3 and 4, averages (±SD) are reported only for the condition in which speed did not change

Experiment	V_0 - latency (ms)	V_0 - slope (°/s^2)	V_1 - latency (ms)	V_1 - slope (°/s^2)
1-1-0°	84	−41.3	134	64.6
1-1-45°	48	−42.2	129	57.5
1-2-0°	67	−58.9	126	70.7
1-2-45°	68	−58.2	133	69.1
1-3-0°	75	−66.0	129	78.7
1-3-45°	82	−68.3	138	86.7
1-4-0°	78	−53.4	109	76.5
1-4-45°	92	−71.5	113	67.7
2-1	85	−51.9	115	66.4
2-2	74	−50.6	130	70.4
2-3	75	−67.0	147	99.6
2-4	67	−46.4	136	74.5
Average (0°)	76±7	−54.4±9.0	128±12	75.2±11.0
3-1S−	66	−58.8	150	50.8
3-1S0	-	-	129	75.6
3-1S+	-	-	125	85.5
3-2S−	78	−56.1	111	37.1
3-2S0	-	-	109	66.9
3-2S+	-	-	115	89.7
3-3S−	68	−51.3	128	41.5
3-3S0	-	-	125	68.4
3-3S+	-	-	122	80.1
3-4S−	67	−62.6	124	45.3
3-4S0	-	-	122	71.4
3-4S+	-	-	121	83.7
Average (S0)	70±5	−57.2±4.1	121±7	70.6±3.3
4-1A−	98	−51.4	146	81.0
4-1A0	-	-	151	88.2
4-1A+	-	-	146	87.2
4-2A−	61	−61.5	119	82.9
4-2A0	-	-	120	89.2
4-2A+	-	-	119	84.8
4-3A−	61	−69.0	107	82.7
4-3A0	-	-	122	100.4
4-3A+	-	-	121	103.0
4-4A−	80	−58.2	141	80.1
4-4A0	-	-	149	100.8
4-4A+	-	-	148	109.6
Average (A0)	75±15	−60.0±6.3	135±15	94.6±6.0

significant effect on the on-response latency (132 ms on average) nor on its slope ($F_{(2,9)}$=3.90, p=0.06), although the mean value of the slope for accelerating targets (96.2°/s^2) was slightly larger than the mean (81.7°/s^2) for decelerating targets. Statistically, the speed traces of the

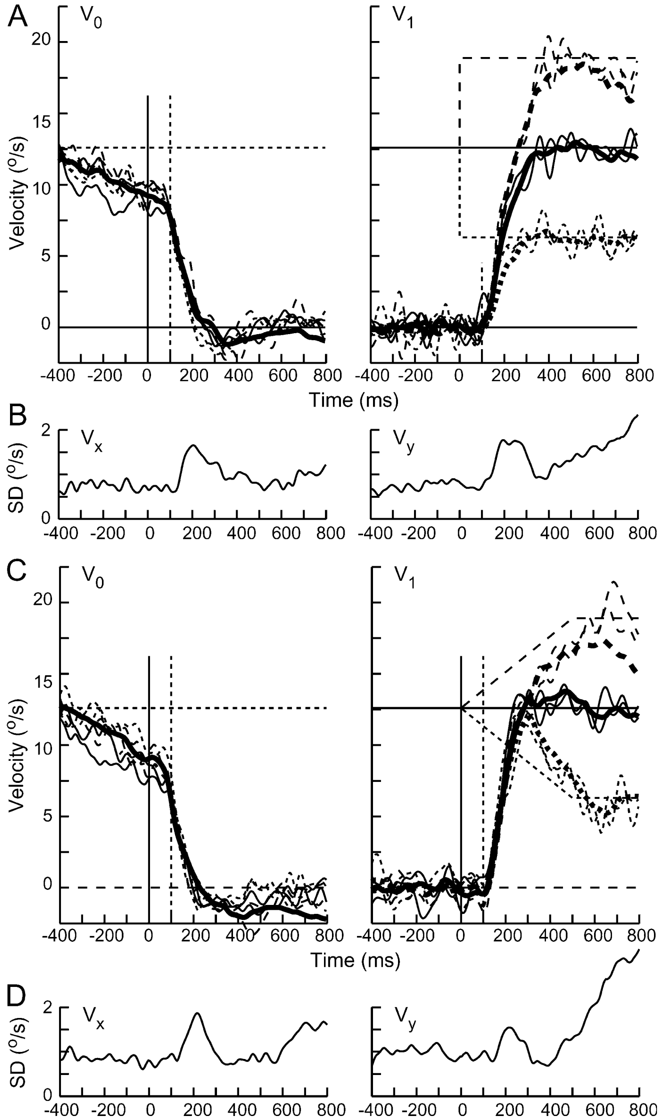

Fig. 8a–d Vector superposition of smooth pursuit responses to a step change in target speed (**a** and **b**, Exp. 3) or to a step change in target acceleration (**c** and **d**, Exp. 4). In this analysis, the on-response (V_1) was assumed to be different for each speed condition, but the same off-response (V_0) was used for all three conditions. Target velocities are also indicated. The results are presented in the same format as in Fig. 7. The large gradual increase in the SD (beginning at about 400 ms in **b** and **d**) reflects the fact that there was considerable variability in the pursuit gain at the highest target speed in these experimental conditions

smooth pursuit response to accelerating and decelerating targets diverged at 212 ms. These results are consistent with models of smooth pursuit in nonhuman primates in which the gain of an image acceleration component was much less than the gain of an image velocity component (Krauzlis and Lisberger 1994b).

Nonlinear interactions

Overall, the linear vector superposition model gave an excellent fit to the data. In the example shown in Fig. 7, the model accounted for 98.2% of the variance. In all but two of 20 sessions, this value exceeded 90%. Furthermore, in the example shown in Fig. 7, the variance not accounted for by the model was fairly uniform, with an SD that was generally less than 1°/s. However, in the other two examples (Figs. 8b, d), the SD's for v_x and v_y show a rapid increase beginning at about 120 ms, with a peak at about 200 ms. Thus, although the linear vector superposition model gave an excellent fit, there were often transient increases in the SD around the time of the onset of v_1.

The initial model assumed linear superposition of the on- and the off-responses and differences between the model and the data could arise from nonlinear interactions. To identify the errors more precisely, we computed separately for each direction the errors in the vertical and horizontal velocities (v_y and v_x). Figure 9 presents the results of this analysis for all sessions in which the target initially moved downwards. It is clear that the results were remarkably consistent from session to session, both in terms of the form of the off- and the on-responses (Fig. 9c) as well as in the nature of the errors in the linear model (Fig. 9a).

When the target continued to move downward (30 and 60°), the horizontal component of smooth pursuit velocity was greater than predicted. Conversely, when the target reversed direction (120 and 150°), the error in the horizontal component was small but the vertical component was more positive than predicted. In other words, for these latter directions, the amplitude of the vertical velocity was smaller than predicted. In all instances, the errors began to increase about 100 ms after the target changed direction and decayed to zero by about 400 ms.

The gain of smooth pursuit exhibits directional anisotropies when a small perturbation is imposed on an ongoing target motion (Schwartz and Lisberger 1994), the gain in the direction of the motion being greater than the gain in the perpendicular direction. We tested for such anisotropies in our data by using the following model (Nonlinear Model 1):

$$\begin{aligned} \mathbf{v}_i(t) &= v_0(t)\mathbf{j} + g_i(t)v_1(t)\mathbf{e}_i \\ g_i(t) &= \left[1 + g_i e^{-(t-\tau)/a}\right] \quad t > \tau \\ &= 1 \quad t < \tau \end{aligned} \tag{5}$$

where g_i is a scalar gain element. Because the errors in the

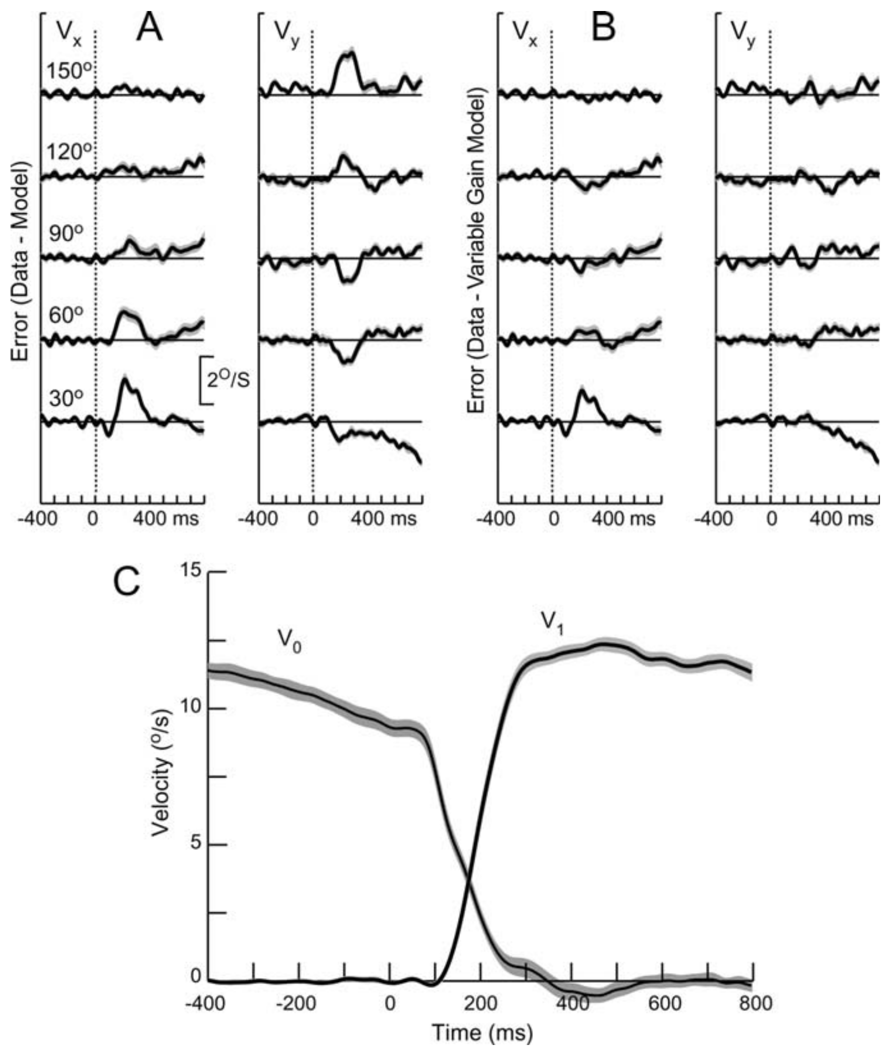

Fig. 9a Errors in the linear vector superposition model. The *traces* depict the mean difference between the horizontal (*x*) and vertical (*y*) components of smooth pursuit velocity and the vector addition of the two components of the model, v_0 and v_1 depicted in the l*ower panels*. Results from instances in which the target moved to the right or to the left by the same amount have been combined, after inverting the sign of the horizontal error. The *traces* represent the means and the *shaded area* encompasses ±1 SEM of data from all 16 sessions (Exps. 1–4) in which the target originally moved downward and for trials in which target speed did not change. **b** Errors in the superposition model, modified to incorporate directionally dependent time-varying gains (Nonlinear Model 2). **c** Average off- (V_0) and on-responses (V_1) for the same data set

linear model decayed to zero, we assumed the directional gain decayed exponentially with a time constant a. Thus, this model had six free parameters, five directional gains and one time constant. We assumed a value of 120 ms for τ, based on the time delay for v_1. The model parameters were identified using the simplex algorithm (Nelder and Mead 1964) and the waveforms v_0 and v_1 were obtained by linear regression, as before. The model gave only a 7% reduction in the variance not accounted for (VNAF), and did not substantially reduce the errors in the interval from 100 to 400 ms.

We then tried a second model (Nonlinear Model 2) in which we assumed that the gains along the vertical and horizontal components of the motion could differ:

$$\begin{aligned} & v_{xi}(t) = \left[1 + g_{horiz} e^{-(t-\tau)/a}\right] v_l(t) \sin\theta_i \\ & v_{yi}(t) = v_0(t) + \left[1 + g_{down} e^{-(t-\tau)/a}\right] v_l(t) \cos\theta_i \\ \text{or} \quad & v_{yi}(t) = v_0(t) + \left[1 + g_{up} e^{-(t-\tau)/a}\right] v_l(t) \cos\theta_i \end{aligned} \tag{6}$$

In this model, we assumed the gains for the up and the down direction of target motion (g_{up} and g_{down}) could differ. Because the pattern of errors in the linear model was the same for rightward and for leftward target motion, we assumed the same value for both (g_{horiz}). Even though this second model had fewer free parameters (4), it gave a substantially better fit to the data. VNAF was reduced by 17% and with the exception of the vertical component of pursuit velocity for the 30° direction, the remaining errors were largely uniform over time (Fig. 9b).

The parameter values that gave the best fit are reported in Table 2. The gain was most reduced transiently in the direction opposite to the initial motion of the target (g_{up}) and to a lesser extent in the downward direction. The gain in the horizontal direction was constant ($g_{horiz} = 0$). These results suggest there is a transient anisotropy in the gain of smooth pursuit. This anisotropy could be along the cardinal directions of eye motion (horizontal and vertical) or it could be defined by the original direction of target motion. Since the target motion was initially always in the downward direction, both interpretations are consistent with the data.

Table 2 Model parameters. Coefficients of the time varying gains for Model 2 (Eq. 6) fit to the data in which the target initially moved downward and for Model 3 (Eq. 7) fit to the data in which the target initially moved on a diagonal, down and to the right

Nonlinear Model 2	
g_{horiz}	0.0
g_{down}	−0.324
g_{up}	−1.068
τ(ms)	105
Nonlinear Model 3	
g_{right}	0.0
g_{left}	−0.693
g_{down}	−0.359
g_{up}	−1.067
τ(ms)	173

To resolve this ambiguity, we also analyzed the results from sessions in which the initial target motion was along a diagonal (Exp. 1). In this case, the linear model resulted in a different pattern of errors (Fig. 10). For small changes in direction (30 and 60°), the model underestimated the perpendicular component of pursuit velocity (V_{perp}, analogous to V_x in Fig. 9). However, for the larger changes in target direction, V_{perp} was too small. In contrast, errors along the tangent to the direction of the original target motion (V_{tan}, equivalent to V_y in Fig. 9) were much smaller. Therefore, it appears unlikely that a model in which directional anisotropies are solely defined by the initial motion of the target can account for the data. This was confirmed quantitatively. The second model (Eq. 6, substituting perp and tan for x and y) gave only a 4.4% decrease in VNAF, while the first model (Eq. 5) did slightly better (10.2%).

However, a model in which the anisotropies in gain were defined along horizontal and vertical directions was able to account for the errors depicted in Fig. 10:

$$\begin{aligned} & v_{xi}(t) = v_0(t)\sin\theta_0 + \left[1 + g_{right} e^{-(t-\tau)/a}\right] v_l(t) \sin\theta_i \\ \text{or} \quad & v_{xi}(t) = v_0(t)\sin\theta_0 + \left[1 + g_{left} e^{-(t-\tau)/a}\right] v_l(t) \sin\theta_i \\ \text{and} \quad & v_{yi}(t) = v_0(t)\cos\theta_0 + \left[1 + g_{down} e^{-(t-\tau)/a}\right] v_l(t) \cos\theta_i \\ \text{or} \quad & v_{yi}(t) = v_0(t)\cos\theta_0 + \left[1 + g_{up} e^{-(t-\tau)/a}\right] v_l(t) \cos\theta_i \end{aligned} \tag{7}$$

(θ_0 is the initial direction of target motion and θ_i the final direction.) This model gave a 22.9% reduction in VNAF and the parameter values are provided in Table 2.

The fit to these data (combined with the results in Fig. 9) suggests that the gain of smooth pursuit is transiently reduced in the direction opposite to the initial direction of target motion (up for Model 2, and up and to the left for Model 3). The results also suggest a second effect—the gain is transiently reduced more along the vertical direction than it is along the horizontal (compare g_{right} with g_{down} and g_{left} with g_{up}). The fitting procedure resulted in a time constant (173 ms) that was larger than that obtained for the other data (105 ms). However, fixing the time constant at value more comparable to the first (i.e., 125 ms) gave a fit that was almost as good (20.5% improvement vs. 22.9%).

Discussion

In this study, we examined smooth pursuit of target motion that underwent a sudden change in direction. We used an experimental design, patterned after the one used by Rashbass (1961), that was intended to minimize the chance that smooth pursuit would be interrupted by saccades shortly after the target changed direction. This was achieved by introducing a discontinuity in the position of the target at the time it changed direction. The analysis of the data suggested a simple interpretation: smooth pursuit could be described by the vector addition of a

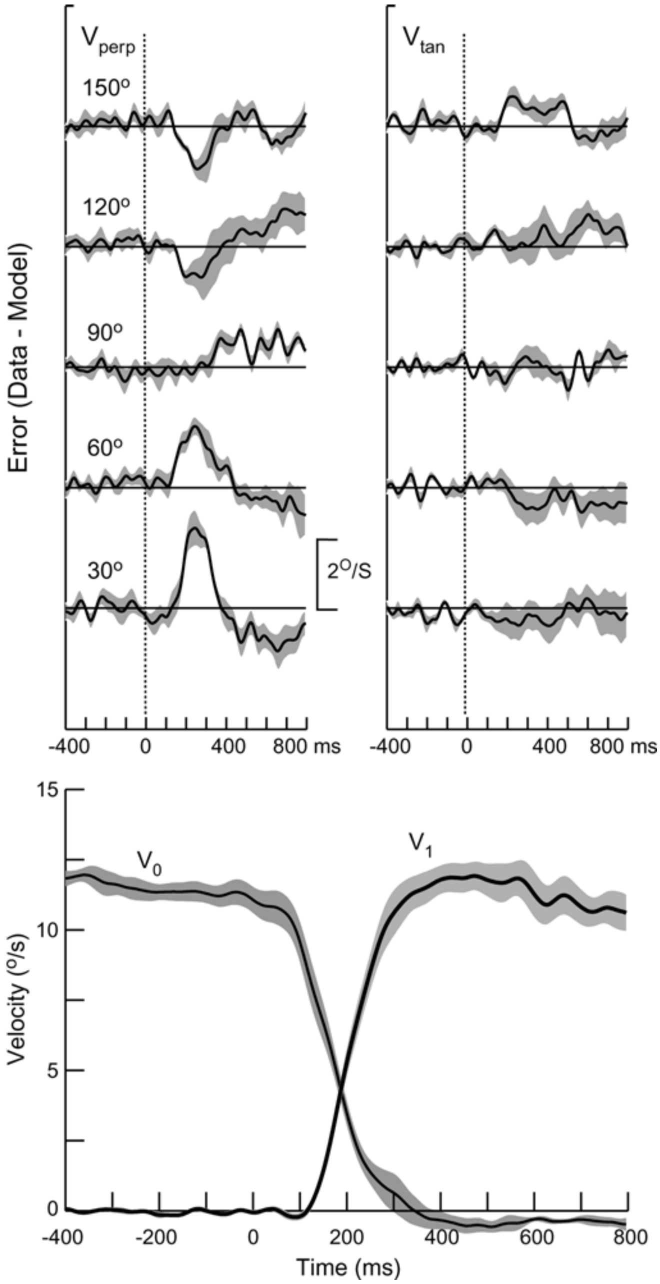

Fig. 10 Errors in the linear superposition model for sessions in which the target initially traveled at 45° down and to the left. The difference between the experimental data and the vector superposition of v_0 and v_1 shown below has been decomposed into components perpendicular and tangent to the initial direction of target motion. Results are the mean ±1 SEM for four sessions in Exp. 1

response to one target stopping and to a second target beginning to move in a new direction. The analysis also showed directional anisotropies in the gain of the response to the second target that decayed with a time constant of slightly more than 100 ms.

We first take up methodological issues related to the experimental design. Then we will discuss the evidence for a vector superposition of responses and the extent to which it is compatible with previous descriptions of smooth pursuit for rectilinear target motions. Finally, we will compare the current results with results from our previous investigation of manual tracking that led to an interpretation very different from the one we propose here.

In the present experiments, we introduced a discontinuity in target position at the time that the target changed direction, designed to minimize the probability of an intervening saccade while smooth pursuit velocity was changing. The experimental design was successful. For the optimal step size, saccade times were delayed and their probability was reduced substantially (Fig. 2). However, the size of the step displacement did not affect the smooth pursuit response. Therefore, it does not appear that the saccades influenced the gain of the subsequent smooth pursuit (Gardner and Lisberger 2001, 2002; Lisberger 1998).

In designing the stimulus presentation, we took care not to introduce spurious motion transients related to the target's step displacement; only one target was in motion at any instant. Nevertheless, it is possible that neurally mediated temporal filtering of the visual signal (Soechting et al. 2003) could have presented subjects with a situation in which two targets were in apparent motion simultaneously. Previous reports have shown that such a situation leads to a smooth pursuit response that represents the vector average of the two motion signals (Ferrera 2000; Lisberger and Ferrera 1997). We do not believe that this was the case in our experimental situation for two reasons. First, as already mentioned, the amplitude of the step had no influence on the response. Secondly, the present results do not differ from results we have reported previously in which the target also changed direction abruptly without undergoing a step displacement (Engel et al. 1999, 2000). Those results were obtained using a different method of stimulus presentation (mirror galvanometer and tangent screen) and a different method of recording eye movements (magnetic search coil). Thus, it is also unlikely that any of these factors influenced the results.

Vector superposition of two responses

Our vector-addition model emerged from the observation that the initial smooth pursuit deceleration in the original target direction did not depend on the final target speed or direction (Fig. 5). This qualitative observation was supported by several lines of analysis. We showed that variance of the velocity in the initial direction of target motion (v_y) only began to differ from its background level 160 ms after the target changed direction (Fig. 6a), much later than the latency of smooth pursuit deceleration (~80 ms, Table 1). The times at which the magnitudes of the velocity components began to be significantly correlated with those of the final steady state response (Fig. 6b) were also considerably longer than 80 ms. Finally, we showed (Figs. 7 and 8) that a model that assumed vector addition of two components could account for more than 90% of the variance in the data.

The time courses of these two components—one representing the response to the arrest of the motion of one target and the second representing the response to the onset of motion of another target—are in reasonable agreement with previous observations. Several investigators (Huebner et al. 1992; Krauzlis and Lisberger 1994a; Robinson et al. 1986) have reported that the response to the arrest of target motion can be described by an exponential decay with a single time constant. In contrast, the smooth pursuit response to the onset of target motion shows a transient overshoot with subsequent oscillations and has a longer latency. The off-response in our results also follows an approximately exponential decay, but its slope (−56.5°/s^2, Table 1) is somewhat less than the values reported previously (−95°/s^2, Robinson et al. 1986) as is the latency (74 ms on average).

The on-response began at a longer latency (120 ms on average) and showed an overshoot, in agreement with previous reports (Huebner et al. 1992; Krauzlis and Lisberger 1994a; Robinson et al. 1986). Its acceleration (78.9°/s^2 for a target speed of 12.6°/s) was slightly less than previous reports. The slope of the on-response decreased by about 38% for a 50% decrease in speed and it increased by 20% for a 50% increase. This is compatible with a component proportional to target velocity with a saturating non-linearity and a motion transient independent of the magnitude of the target's speed (Krauzlis and Lisberger 1994b).

The hypothesis that smooth pursuit could be represented by a linear vector summation of two components did not fully account for the data and the pattern of errors showed consistent trends that depended on the direction of the subsequent target motion (Figs. 9 and 10). Our analysis (Table 2) suggested that there were directional anisotropies in the gain of the smooth pursuit that decayed with a time constant somewhat greater than 100 ms. The results also suggested that these transient anisotropies were related to two separate factors: 1) the gain is reduced in the direction opposite to the original motion and 2) the gain differs along the horizontal and vertical directions.

The first factor is reminiscent of the directional anisotropies described by Schwartz and Lisberger (1994). For small perturbations during steady-state tracking, the gain was largest along the direction of steady-state motion and smallest in the orthogonal direction. They found the gain to be enhanced for transients in the direction of motion as well as in the opposite direction. Thus, our results are somewhat contradictory to theirs in that we found the greatest decrease in gain for transients in the opposite direction, a smaller decrease for transients in the same direction and none for the perpendicular. However, their small perturbations did not interrupt ongoing smooth pursuit, whereas we have suggested that our large perturbation (i.e., the abrupt change in target direction) led to a cessation of pursuit in the original direction. From this perspective, our results imply that the off-response depresses smooth pursuit gain selectively in its initial direction, especially when the on-response involves motion in the opposite direction.

Our results also suggest that the gain was transiently smaller for the vertical component than it was for the horizontal, irrespective of the initial direction of target motion. This interpretation is consistent with other reports finding lower vertical than horizontal gains for smooth pursuit tracking (Baloh et al. 1988; Collewijn and Tamminga 1984; Rottach et al. 1996).

Comparison with manual tracking

As mentioned in the Introduction, manual tracking of a target whose direction of motion changes abruptly has considerable similarities to the smooth pursuit response described here (Engel and Soechting 2000). For manual tracking, speed initially declines and follows a time course similar to the one for smooth pursuit (Fig. 2). Furthermore, the latency for changes in the direction of manual tracking is greater than the latency for changes in speed, as is also the case for smooth pursuit.

A model in which these two parameters (speed and direction) were controlled explicitly accounted for manual tracking behavior. This control model is fundamentally different from the one we propose here. Specifically, we proposed that the control of manual tracking was effected in local path coordinates, namely in directions tangent and perpendicular to the instantaneous motion of the hand (acceleration in the tangential direction is equal to the rate of change in speed, while acceleration in the perpendicular direction is proportional to the rate of change in direction.) Thus, control along these two dimensions was viewed as representing the control of speed and direction. A different model, based on a control in Cartesian coordinates was rejected, because it could not account for the fact that the latencies for speed and direction of manual pursuit were different. It also could not account for the observation that a horizontal perturbation in velocity evoked a response in the vertical as well as horizontal directions.

The question thus arises: given the apparent similarities in ocular and manual tracking, could a model based on the control of speed and direction account for the present data? While we have not formally tested such a model, there are two aspects of the present data that are incompatible with it. First of all, the initial deceleration in smooth pursuit was not graded with the amplitude of the change in target direction (Fig. 5). By contrast, during manual tracking, the initial deceleration of the hand following the change of direction does depend on the magnitude of the change in direction (see Fig. 8 of Engel et al. 2000). This feature was an essential characteristic of the speed-direction model because the rate of change in speed was driven by an error signal in the present direction of motion (see also Roitman et al. 2004) and the amplitude of this error signal depends on the amount by which the direction of target motion changes. Furthermore, the speed-direction model predicts a response that is invariant under a rotation. Accordingly, the response to targets initially moving at 45°should be the same as the response to targets moving at 0°. This was found to be true for manual tracking (Engel and Soechting 2000) but it was not the case in the present experiments (Figs. 9 and 10).

Thus, despite considerable similarities in the time courses of manual and ocular tracking (Engel et al. 2000), the present results suggest that there may be fundamental differences in the manner in which the hand and the eye are controlled.

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