

Similarity in the Response of Smooth Pursuit and Manual Tracking to a Change in the Direction of Target Motion

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Engel, Kevin C., John H. Anderson, and John F. Soechting. Similarity in the response of smooth pursuit and manual tracking to a change in the direction of target motion. *J Neurophysiol* 84: 1149–1156, 2000. Subjects were asked to track, with their eyes or their hand, the movement of a target that maintained a constant speed and made a single, abrupt change in direction. The tracking speed and direction of motion after the step change in target direction were compared for the eyes and the hand. After removal of the saccades from the eye movement records, it was found that in both cases, there was a slow rotation from the initial direction to the new direction. For the eyes and the hand, it was found that this change in direction of movement occurred at a similar rate that was proportional to the magnitude of the abrupt change in target direction. This was further described by comparing the direction of pursuit tracking with the response of a second-order system to a step input. In addition, it was found that the speed of manual and pursuit tracking was modulated in a similar manner, with a reduction in tracking speed occurring before the change in tracking direction. This reduction in speed following the change in the direction of target motion was very similar for the hand and the eye, despite the large difference in the inertias of the two systems. Taken together, these data suggest that the neural mechanisms for smooth pursuit and manual tracking have common functional elements and that musculoskeletal dynamics do not appear to be a rate-limiting factor.

INTRODUCTION

Questions concerning the coordination of the hand and the eye have been the focus of neuroscientists and magicians alike. Clearly, there can be very precise coordination of eye and hand movements. For example, in a task involving grasping and transporting an object, the movement of the eyes precedes the movement of the hand in a stereotyped, well-coordinated manner (Flanagan and Johansson 1999). It has also been found that during open-loop pointing movements, the displacement of the hand is correlated with the amplitude of the corresponding saccade (van Donkelaar 1997). Furthermore, it has been known for a long time that the accuracy of smooth pursuit increases when the motion of the target is directly controlled by the subject's hand, again implying a link between pursuit eye movements and hand movements (Steinbach and Held 1968; Vercher and Gauthier 1992).

It is thought that the motion information that is present in the medial temporal visual area (MT) provides an initial, common neural substrate for manual and pursuit tracking. The neurons

in area MT are known to encode the speed as well as the direction of moving targets (Groh et al. 1997; Maunsell and Van Essen 1983). In monkeys and humans, lesions of this area produce a decrement in motion perception as well as ocular tracking deficits (Leigh and Zee 1991; Newsome et al. 1985; Zihl et al. 1983).

The anatomic pathway involved in smooth pursuit eye tracking has been worked out in some detail and is known to include areas such as the medial superior temporal area (MST), posterior parietal cortex, the frontal eye fields and the cerebellum (for a review, see Leigh and Zee 1991). In contrast, the anatomic substrate underlying manual tracking is less well defined. However, it has been shown that the simple spike discharge in cerebellar Purkinje cells encodes movement velocity during manual tracking (Coltz et al. 1999). During smooth pursuit of a circularly moving target, Purkinje cell firing is related to the eye velocity and position in two dimensions (Leung et al. 2000). Johnson et al. (1999) have recorded from premotor and primary motor cortical neurons during an instructed delay pursuit tracking task. They found evidence for a possible transformation of visual information into motor commands in the cue period of this task. In addition, the neural activity in a reach planning area of the posterior parietal cortex appears to be in eye-centered coordinates, suggesting that eye and hand movements are encoded in the same reference frame (Batista et al. 1999). If this were the case, hand-eye coordination would be facilitated.

We have been studying tracking movements in two dimensions during manual tracking tasks (Engel and Soechting 2000) as well as during ocular motor tracking tasks (Engel et al. 1999). In these experiments, we have used a paradigm based on the simplest two-dimensional (2-D) trajectory, that of a target moving at a constant speed and making a single, abrupt change in direction. In this paper we present a kinematic analysis of the smooth pursuit and manual tracking movements that follow this abrupt change. The similarities in the two movements suggest that there is a common element in the neural substrate that generates the motor commands for both systems.

METHODS

Eye tracking experiments

The methods for this study have been reported previously (Engel et al. 1999) and are briefly summarized here. Five subjects who either

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did not require corrective lenses or wore eyeglasses tracked a moving target binocularly. The magnetic search-coil technique (Robinson 1963) was used to monitor eye movements. The target, a red spot of light 0.5° diam, was produced by a 5-mW helium-neon laser that was rear-projected on a tangent screen in the frontal plane 150 cm in front of the subject. The motion of the target was controlled by a two-axis, servo-controlled galvanometer mirror system (General Scanning) with a dynamic range >300 Hz. The motion of the target and the sampling of eye position were controlled at a rate of 1,000 Hz/channel. Each trial began with the target being displaced from a center hold position directly in front of the subject's right eye to a position 20° upward. After 1.5 s, the target began moving downward at a constant speed, alternating between 15 and $30^\circ/\text{s}$ on successive trials. When the target reached a random position between 5° above and 10° below the horizontal plane, it changed direction abruptly to 1 of 11 directions spanning 360° at 30° increments. To reduce the number of trials, these directions excluded 180° (i.e., the target reversing on its path). After changing direction, the target would continue until it reached an angular displacement of either 20° to the left or right, or 20° above or below the center position of gaze. At all times during a trial, the target maintained a constant speed. Each session had 88 trials and lasted no longer than 45 min.

Data analysis

Eye movement records were analyzed off-line by means of custom software. The records were filtered digitally by means of a "notch"-type filter to remove 60 cycle noise. Eye velocity was computed by numerically differentiating the position data and digitally smoothed using a two-sided exponential filter with a cutoff frequency of 120 Hz. As all directional changes occurred close to the forward gaze position, the difference between this method and the exact derivation of eye velocity using quaternions is minimal ($<5\%$) (Tweed and Vilis 1987). In this paper, we describe the response of the smooth pursuit system in terms of speed (S_E) and direction (θ_E). Pursuit speed (S_E) was determined by the vector summation of velocities along the X (horizontal) and Y (vertical) axes

$$S_E = \sqrt{v_x^2 + v_y^2}$$

Pursuit direction (θ_E) was computed from the inverse tangent of the ratio of the X and Y velocities

$$\theta_E = \tan^{-1} \frac{v_x}{v_y}$$

Ocular tracking has smooth pursuit and saccadic components. To isolate and study the reaction of the smooth pursuit system to a change in target direction, we developed a procedure by which the entire time course of the smooth pursuit could be estimated. This was done by determining the time for the onset and end of saccades and interpolating through this region (Barnes 1982). Desaccading was performed independently for the X and Y components of velocity. For both components, a speed threshold, which was exceeded by all saccades in a given trial, was set. This threshold could be modified interactively for each component of the saccade. To define the beginning of a saccade, a 50-ms "baseline" window was delimited starting at a point 75 ms before the saccade crossed the threshold. The average and standard deviation of speed in the "baseline" period were then calculated. The beginning of the saccade was defined as the point 3 ms before the eye velocity crossed the 2 standard deviation limit of this interval. The end of a saccade was determined in a similar manner. Finally, a cubic spline was fit across the saccade using 4 points that included the defined beginning and ending points of the saccade as well as points 20 ms before saccade onset and 20 ms after saccade end. Trials were examined individually, and the times that were determined automatically could be adjusted manually via an interactive process if necessary.

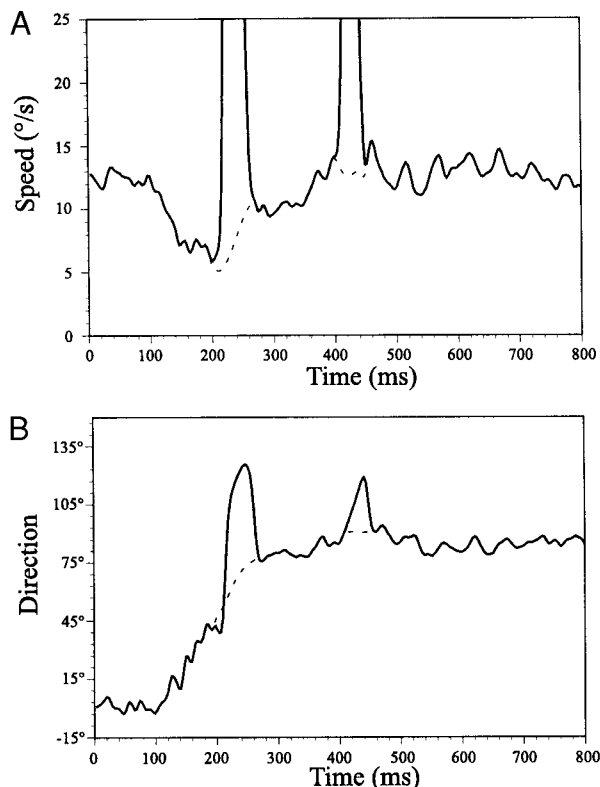


FIG. 1. An example of oculomotor tracking following a step change in the direction of target motion at time $t = 0$. *A*: the speed of the eye. *B*: the change in direction of the eye for the same trial. —, the original data; ---, the results of the desaccading procedure. Desaccading produced a curve that changes smoothly with time.

Figure 1 is an example from an individual trial illustrating the results of this procedure. Figure 1*A* shows the speed of the eye following a change in target direction. Solid lines indicate the speed of the eye before the saccades were removed. In this example there were two saccades. The dotted lines show the results of the desaccading procedure. Figure 1*B* displays the direction of eye movement for this same trial. Again, the dotted line segments indicate the resulting direction computed from the interpolated velocity data. Individual desaccaded eye movement records were averaged by aligning trials on the point in time at which the target changed direction.

To quantify the time course of the direction of smooth pursuit (θ_E), we modeled the data as the response of a second-order linear system to a step input

$$\ddot{\theta} + A\dot{\theta} + B\theta = 0$$

with A and B being the damping and stiffness coefficients. By using a root mean square error minimization algorithm (Nelder and Meade 1964), the values of A , B , and a time delay were found such that the errors between the modeled output and the actual data were minimized. The system described by this equation can be classified as under damped, critically damped, or over damped. To quantify this behavior, we report the damping factor, defined as

$$\xi = \frac{A}{2\sqrt{B}}$$

If $\xi < 1$, then the system is under damped. If $\xi > 1$, the system is over damped. Finally, if $\xi = 1$ the system is critically damped (Wylie 1960).

Hand tracking experiments

The methods used for the hand tracking experiments have also been reported (Engel and Soechting 2000) and are briefly summarized here. Six subjects participated in this experiment. Finger position was recorded using a touch-sensitive screen (Elo Touch Systems, TN) mounted over a standard, vertically mounted, 20-in. computer video monitor (Mitsubishi Diamond Scan 20M). The touch screen has a spatial resolution of 0.08 mm. The position of the finger was recorded at a rate of 100 Hz. Target location was updated at a rate of 60 Hz, equal to the refresh rate of the video monitor. Right-handed subjects, seated approximately 50 cm away from the touch screen, were asked to track, with their right index finger, the motion of a target 1.6 cm diam (1.8°) displayed on the video monitor. The motion of the target was similar to that used during the eye tracking experiments. The target appeared at the middle of the top edge of the screen and moved straight downward at a constant speed of 10.8 cm/s. Then, after the target had traveled a random distance, it made an abrupt change in direction to 1 of 12 randomly selected directions spanning 360 in 30° increments. Again, as was the case for the eye tracking experiments, the speed of the target remained constant throughout all trials.

In a second experiment, four subjects tracked a target that changed to one of six directions equally spaced around 360° . The speed of the target remained constant throughout any given trial but was varied randomly on a trial-by-trial basis. Four constant speeds (5.4, 10.8, 16.2, and 21.7 cm/s) were used. (These speeds roughly correspond to ocular angular rates of 6, 12, 18, and $23^\circ/\text{s}$, respectively).

Data were averaged by aligning the trials on the point at which the target changed direction. As there is symmetry in responses about the mid-line, and as the results are invariant under a rotation (see Engel and Soechting 2000), trials to the left and right were combined. The X and Y components of velocity were calculated by numerically differentiating the position data and digitally smoothed using a two-sided exponential filter with a cutoff frequency of 12 Hz. Direction (θ_M) and speed (S_M) of manual tracking were computed from the X and Y components of hand velocity.

For all experiments, subjects gave their informed consent to the experimental procedures, which were approved by the Institutional Review Board of the University of Minnesota.

RESULTS

Time course of the change in direction

The saccadic system is able to make rapid changes in eye position at very sharp angles with respect to the direction of smooth pursuit (Engel et al. 1999) (see also Fig. 1*B*). In contrast, it appears that the changes in tracking direction brought about by the smooth pursuit system occur in a smooth, continuous manner. Figure 1 displays the results obtained from one trial of eye tracking. In this trial, the subject tracked a target that abruptly changed direction from 0° (straight downward) to a new direction of 90° . Figure 1, *A* and *B*, respectively, show the speed and direction of eye movement as a function of time. The two traces begin at the point when the target changed direction. Solid lines indicate the complete motion of the eye, including the intervening saccades.¹ The dotted lines demonstrate the results obtained from interpolation through the saccade. While a portion of the actual response of smooth pursuit to the change in target direction is masked during the saccadic intervals, the interpolation produces curves

¹ In this example the latency before the first saccadic onset was 198 ms, while the time until saccade end was 270 ms. Across all subjects, the average time for saccade onset was 190 ± 28 (SD) ms and the average time for saccade end was 239 ± 28 ms.

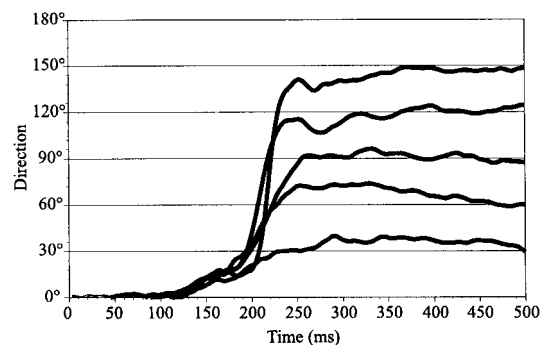


FIG. 2. The average direction of smooth pursuit eye movements for one subject. The straight horizontal lines indicate the 5 different target directions, with a step change from straight downward (0°) occurring at time $t = 0$. Each trace is the average of ~ 16 desaccaded trials, aligned at the time the target changed direction. Notice that for small angular changes of the target, the eye initially overshoots the final direction, whereas for large angular changes, the eye undershoots the ultimate direction.

for speed and direction that are continuous and change smoothly throughout the duration of the change in direction. From these traces, one can see that the speed of smooth pursuit decreases as direction changes, and then accelerates back to the target speed of $15^\circ/\text{s}$. From Fig. 1*B*, it is clear that the direction of smooth pursuit also changes in a smooth manner. As the speed and direction traces varied in a continuous manner after interpolation, it appears that the intervening saccades did not affect the underlying time course of the smooth pursuit.

Figure 2 shows the direction of smooth pursuit tracking for one subject, each trace being the average of about 16 desaccaded trials. In these trials, the target maintained a constant speed of $15^\circ/\text{s}$, changing direction randomly in increments of 30° to the left or the right for each trial. Target directions are depicted in the figure by horizontal lines. Notice that for small angular changes of the target (30 and 60°), the direction of smooth pursuit initially exceeded the direction of the target at 250–300 ms and then slowly returned to the direction of the target at approximately 450–500 ms. Furthermore, for large angular changes of the target (120 and 150°), the eye initially fell short of the target direction, then slowly approached it, and eventually matched the target direction at ~ 350 –400 ms. Finally, for 90° changes in the direction of the target, the eye appeared to rotate almost exactly to the target direction, matching the direction of the target at about 250 ms. The results illustrated in Fig. 2 are representative of those obtained for all subjects.

In addition, for this subject, it appears that the initial rate at which the smooth pursuit eye velocity changed direction did not depend on the amount by which the motion of the target changed direction. Up to about 180 ms, all of the traces are nearly superimposable. Thereafter, the rate of change of direction of smooth pursuit velocity clearly depends on the amount by which the target changed direction. This same trend was evident in four of the five subjects.

To quantify the time course of the direction of smooth pursuit velocity, we modeled the data as the response of a second-order system to a step input (see METHODS). In Fig. 3, the results of fitting the model to the data are presented for another subject. The bold lines show the model, while the thin lines show the experimental data. The thin solid lines denote results for target speeds of $15^\circ/\text{s}$, and the thin dashed lines

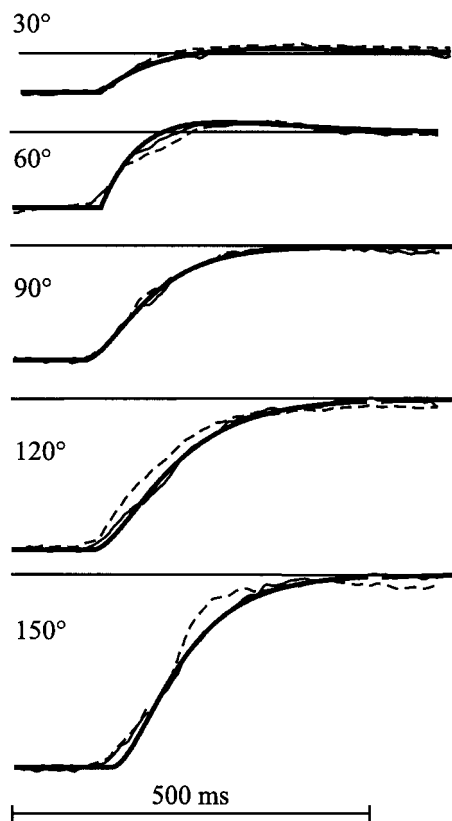


FIG. 3. Direction of smooth pursuit and the fit of a 2nd-order model. For each set of traces, the direction of the target is shown by the horizontal line. The thin solid lines represent the response at a target speed of 15°/s, and the thin dashed lines depict data for a target speed of 30°/s. The bold solid lines show the results of the model fit to the data for a target speed of 15°/s. Note that the response is under damped for small angular changes of target motion (30 and 60°) and over damped for larger angular changes (120 and 150°). Data are averages from 1 subject.

represent results for target speeds of 30°/s. From the comparison of the thin solid and dashed lines, it is clear that target speed, and hence, pursuit speed, had little, if any, effect on the direction of smooth pursuit velocity. For this subject, the 30 and 60° changes of the target direction were best fit with model parameters leading to an under-damped response, while the 90° change in target direction was best modeled by a critically damped system. Finally, for 120 and 150° changes in the direction of target motion, the change in smooth pursuit direction could best be fit by an over-damped response. This same progression from an under-damped response for small angular changes to an over-damped one for large angular changes in target direction was characteristic of all five subjects in this study. To quantify this behavior across all subjects, we report the damping factor for each change in target direction (see METHODS).

The damping factor increases in an amount proportional to the amount by which target motion changes direction. This is evident in Fig. 4 in which the mean and standard deviation of the damping factor are shown for increasing changes in target direction. Data are provided from the fit of the model to all five subjects. It is clear that for the two target speeds, as the change in the direction of the target increases, the response moves from an under-damped to an over-damped condition, passing

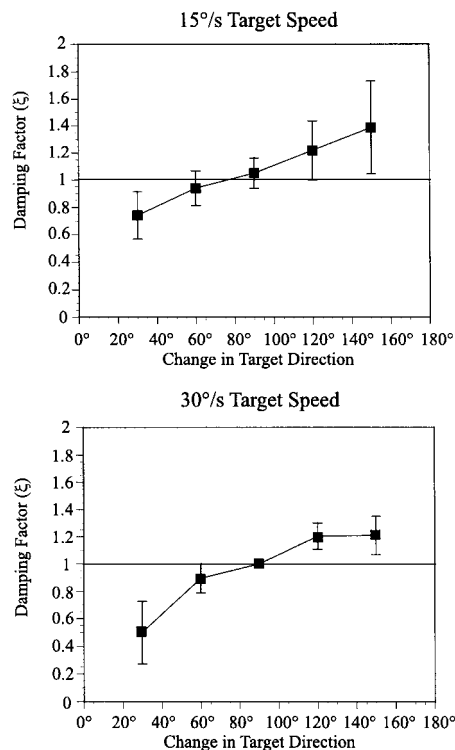


FIG. 4. Dependence of damping factor on the amplitude of the change in target direction. Data are averages (\pm SD) of results for all 5 subjects for target speeds of 15°/s (top panel) and 30°/s (bottom panel). Notice that in both cases, as the change in direction increases, the model fit moves from an under-damped (damping factor <1) to an over-damped (damping factor >1) condition, passing through the region of critical damping (damping factor = 1) at $\sim 90^\circ$.

through the region of critical damping at a directional excursion of about 90°.

The results for manual tracking showed similarities and differences with respect to smooth pursuit ocular tracking, as can be ascertained by inspection of Fig. 5. As was the case for ocular tracking, the direction of hand motion changed after a reaction time. However, for manual tracking, this direction exceeded the direction of the target motion for all angular excursions. This can be reconciled when one considers that ocular tracking involves a combination of the smooth pursuit and saccadic components of tracking, smooth pursuit eye

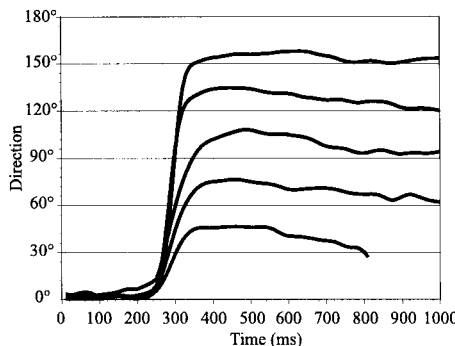


FIG. 5. Direction of manual tracking in response to a step change in direction of target motion. The horizontal lines indicate the 5 different target directions, with a step change from straight downward (0°) occurring at time $t = 0$. Each trace is the average of ~ 16 trials from one subject, aligned at the time the target changed direction. Note that in each case the direction of the finger overshoots the direction of the target during reacquisition of the target.

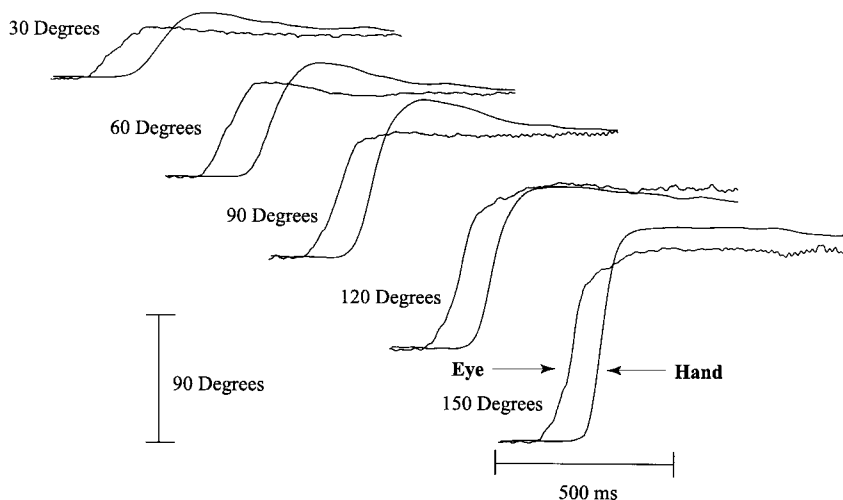


FIG. 6. A comparison of the time course of the direction of manual and smooth pursuit. The latency for the hand is approximately 100 ms longer than that for the eye. Notice that in each case, the rate at which direction changes for the eye and the hand is similar.

movements being driven primarily by the velocity of target motion, and the saccades reducing positional errors (Engel et al. 1999; Rashbass 1961). In contrast, both positional and velocity error signals are reflected in the hand trajectory (Engel and Soechting 2000).

The time course of the direction of hand velocity was also compared with the response of a second-order system to a step input. For all subjects, hand tracking could be modeled as an under-damped system for changes in target direction that were $<120^\circ$. Above this value, the responses were critically damped. A linear regression of the damping factor on the amount of angular change in target direction (over the interval between 0 and 120°) gave a slope of 7.5×10^{-3} with a y intercept of 0.053 ($R^2 = 0.84$). Thus there are similarities and differences in the directional responses of the eye and the hand. For both, the response is under damped for small changes in target direction and becomes progressively more damped as the change in target direction becomes larger. Hand tracking never exhibited an overdamped response, however. This is not surprising, as the direction of the hand must exceed the direction of the target if the positional error is to be reduced.

Rate of change in direction

A comparison of the rate of change in direction for manual and smooth pursuit tracking tasks demonstrates that they are equivalent across all the changes in target direction. This can be appreciated in Fig. 6, which shows data averaged over all subjects for hand and eye tracking. The latency of the eye is about 100 ms less than that of the hand. However, the slopes of the direction of eye and hand tracking not only increase with the magnitude of the change in target direction, but also do so to the same extent.

We quantified the rate of change in eye direction ($\dot{\theta}_E$) by fitting a regression line to θ_E for a 100-ms interval during the time in which θ_E was changing maximally. The rate of change in direction for the hand ($\dot{\theta}_M$) was computed in the same manner. The average results are shown in Fig. 7. For smooth pursuit tracking at $15^\circ/\text{s}$, as the amplitude of the change in target direction gets larger, the rate of change in smooth pursuit tracking direction ($\dot{\theta}_E$) increases as well. A comparison between the traces for target speeds of 15 and $30^\circ/\text{s}$ reveals that doubling the target speed had no apparent effect on the rate of change in direction for the eye.

For comparison, the rate of change in direction of the hand ($\dot{\theta}_M$) is also plotted in Fig. 7 (\blacktriangle). Again, the slope is essentially the same as that found for the eye. Regression analysis showed no significant ($P > 0.05$) difference between the slopes or intercepts obtained for pursuit tracking at 15 or at $30^\circ/\text{s}$, or between pursuit tracking at $15^\circ/\text{s}$ and manual tracking (see Table 1).

The rate of change in direction for smooth pursuit does not depend on the speed of target motion (Fig. 3). To determine whether this also holds true for manual tracking, we asked four subjects to track a target that changed to one of six directions at four constant speeds spanning a broad range (see METHODS). An ANOVA showed no effect of target speed on the rate of change in direction for any subject ($P > 0.05$).

Eye and hand velocity

In addition to the rate of change in direction, the modulation of tracking speed during a directional change of target motion is similar for ocular and manual tracking. In Fig. 8, the speeds of manual and smooth pursuit tracking are plotted for increasing

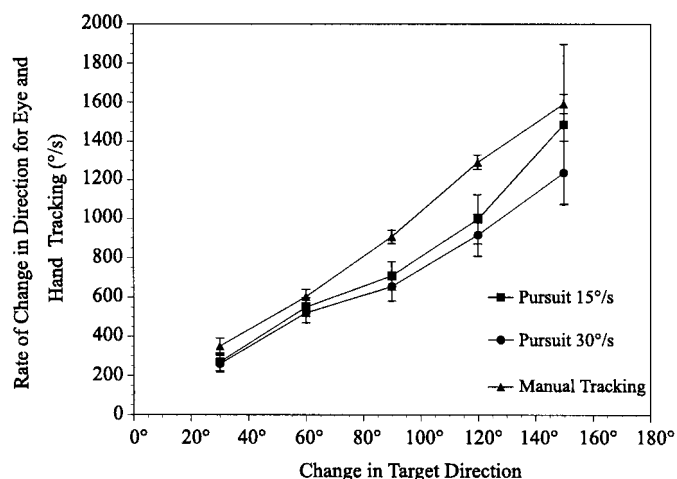


FIG. 7. Average rate of change in direction versus the change in target direction. \blacksquare , data from smooth pursuit following targets moving at $15^\circ/\text{s}$; \bullet , from smooth pursuit at $30^\circ/\text{s}$; \blacktriangle , data obtained from the manual tracking of a target moving at 10.8 cm/s ($\sim 12^\circ/\text{s}$). Error bars indicate SE. For both manual and oculomotor tracking, the rate of change in direction is similar across all changes in target direction.

TABLE 1. Slope and intercept values for the rate of change in direction versus the change in target direction

	Slope (1/s)	Intercept ($^{\circ}$ /s)	R^2
Pursuit (15 $^{\circ}$ /s)	9.4 \pm 1.7	-51.8 \pm 166.2	0.58
Pursuit (30 $^{\circ}$ /s)	7.8 \pm 0.9	17.7 \pm 91.0	0.76
Manual (10.8 cm/s)	10.6 \pm 0.42	-2.4 \pm 42.0	0.96

Values are means \pm SD in Slope and Intercept. Values are shown for pursuit tracking at 15 $^{\circ}$ and 30 $^{\circ}$ /s, and for manual tracking at 10.8 cm/s (\sim 12 $^{\circ}$ /s). For each value, the 95% confidence limits are shown.

angular changes of target motion. The two panels show averages across all subjects. In the two figures, the dashed line represents target speed. In Fig. 8A, one can see that before the reaction time, the speed of the finger was already slightly below the speed of the target, possibly because of anticipation. Then, after a latency in excess of 220 ms the hand slowed and reached a minimum speed proportional to the change in direction of the target ($R^2 = 0.98$). Finally, the hand accelerated well above target speed to intercept the target (see Engel and Soechting 2000). The modulation in the speed of ocular pursuit (Fig. 8B) showed a similar pattern. Again, the speed of the smooth pursuit tracking was slightly below the speed of the target at the time the target changed direction. Then, after a latency slightly in excess of 100 ms, the eye decelerated, again reaching a minimum speed proportional to the amount of angular excursion of the target ($R^2 = 0.94$). The eye then accelerated to target speed. Note that the smooth pursuit system did not accelerate to a level above target speed, as was the case for manual tracking. Rather, the positional errors between the eye and the target were reduced by the intervening saccades.

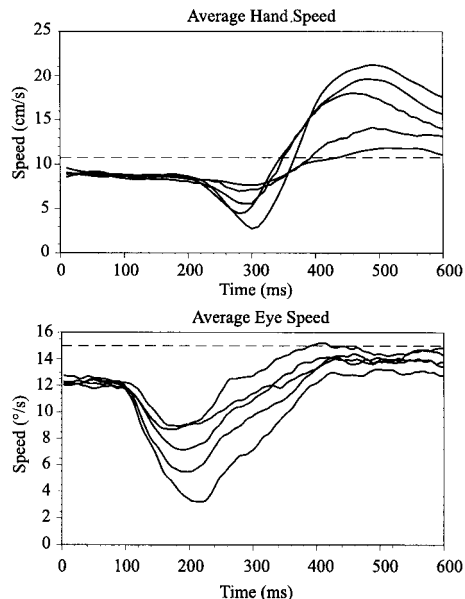


FIG. 8. Average speed of smooth pursuit and manual tracking during a change in direction. The top panel shows the average speed of 4 subjects during the change in direction of the finger. All traces begin at the point where the target changed direction ($t = 0$). Target speed was set at 10.8 cm/s. As the amount of angular change in direction increased, the minimum speed of the finger decreased in a proportional manner. The finger then accelerated well above target speed to reacquire the target. The bottom panel shows similar results for smooth pursuit tracking. Notice that the minimum speed of pursuit tracking was proportional to the amount of change in target direction. However, unlike manual tracking, pursuit speed accelerates back to target speed, without exceeding it.

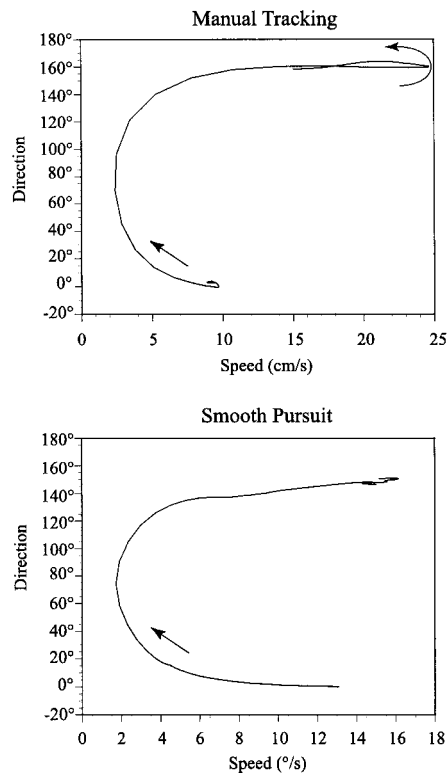


FIG. 9. Direction vs. speed for manual and pursuit tracking. The top panel in this figure shows the average relationship between direction and speed for one subject during manual tracking. In this example, the target changed direction by 150 $^{\circ}$ moving at 10.8 cm/s. During the change in direction, the progression of the movement is shown by the arrow with the subject slowing, changing direction and then accelerating above target speed to intercept the target. The bottom panel shows the same movement for a different subject during pursuit tracking. In this example, the subject was tracking a target moving at 15 $^{\circ}$ /s. Movement again progresses in the direction of the arrow, with the subject again slowing, changing direction, and finally accelerating back to target speed.

There are very strong similarities in the way in which direction and speed are modulated during ocular motor and manual tracking. It is therefore instructive to consider the temporal relationship between the two variables, speed and direction. For the eye and the hand, the latency for changes in speed was shorter than the latency for changes in direction. This can be appreciated in Fig. 9, which shows plots of direction versus speed for manual tracking in the top panel and for ocular motor tracking in the bottom panel. The two traces are averages from one subject. Traces begin at the time the target changed direction (direction, 0 $^{\circ}$). The movement progresses in the direction of the arrows. One can see that in each case, most of the reduction in speed occurred before the majority of the change in direction. After the change in target direction, the eye accelerated back to target speed (15 $^{\circ}$ /s). During manual tracking, however, the hand accelerated well above target speed (10.8 cm/s) then decelerated so that the finger could reacquire the target. This same pattern was seen in all subjects.

DISCUSSION

In the present paper we have described hand and smooth pursuit eye tracking based on two variables: speed and direction. We showed that the direction of smooth pursuit rotates smoothly from one direction to another in response to a step

change in the direction of target motion. We also found that the rate of this change in direction is similar to that found during manual tracking under similar conditions.

Removal of saccades

For smooth pursuit, an estimate of its time course required that the intervening saccades be removed (Fig. 1). Across all subjects, the latency for smooth pursuit was ~ 110 ms, and most of the modulation in direction was over by 250 ms. The latency of the saccadic system was ~ 190 ms, with a typical saccade duration of about 50 ms. We estimated the time course of smooth pursuit by interpolating across the saccades. In most cases, the first interpolation occurred just slightly after the beginning, and before the end of the rapid portion of the change in direction of smooth pursuit. However, there was some variability in the pursuit and saccadic latencies. In this manner, the average tends to be a more accurate representation of the overall time course than a single trial. In one subject, whose overall saccadic latency was slightly longer than the others, it was possible to capture almost the entire change in the direction of smooth pursuit before a saccade was generated. These individual trials appeared very similar to the desaccaded averages, with the direction of eye motion changing smoothly across time. Therefore the direction of smooth pursuit does not appear to be affected by the intervening saccades, and it seems appropriate to average across the desaccaded trials, producing a continuous time course of smooth pursuit activity.

Change in smooth pursuit direction

After an abrupt change in target direction, the direction of ocular pursuit rotates smoothly from one direction to another, passing through all intervening angles. We characterized this change in direction with a second-order system (Fig. 3). The direction of pursuit could thus be modeled by an under-damped system for small angular changes of the target, transitioning smoothly to an over-damped system for large angular changes. This is consistent with our previous results in which we described the direction of the pursuit interval after the first saccade (Engel et al. 1999). We reported that the direction of this segment of pursuit exceeded the target direction for small angular changes, and fell short of the target direction for large angular changes, transitioning at approximately 90° . These results can now be more easily appreciated in the context of the complete time course. It had previously been shown that the early phase of pursuit may show damped oscillations at frequencies of 3–4 Hz, with an initial velocity overshoot (Leigh and Zee 1991). The current study demonstrates that the output of the system changes dramatically with the size of the input, implying that the underlying controller is nonlinear (Krauzlis and Lisberger 1994).

Clearly, the characterization of pursuit eye movements using a second-order system is an oversimplification and is meant only as a descriptive tool. There are certain aspects of the data that could not be fitted. In particular, the data suggest that the response to a change in target direction consists of at least two phases: an early phase, which appears to be independent of the amplitude of the input, and a later phase, which is dependent on the extent of the target rotation (Fig. 2). This is similar to what has previously been shown for eye speed during pursuit initiation in response to a step change in target speed (Lisberger

and Westbrook 1985; Tychsen and Lisberger 1986). In those studies it was suggested that two separate cell populations could be providing the visual inputs for pursuit.

Comparing the speed and direction of smooth pursuit and manual tracking movements

While the characterization of the response of the pursuit system to a change in direction is interesting, it becomes considerably more exciting when it is compared with the results from manual tracking experiments. For the cases of manual tracking, one might argue that a gradual change in the direction of limb movement is not a consequence of the behavior of a central neural controller, but, rather a consequence of the mechanical and musculoskeletal properties of the limb (as discussed in Pellizzer 1997; Zajac 1989). In fact many models of limb movement have represented the limb and its musculature by a damped, second-order system (Stark 1968). However, we previously showed that the evolution of the direction of hand tracking could be accounted for by a model in which the desired direction was the vector sum of the target velocity and a positional error signal (Engel and Soechting 2000). That model would suggest that the observed behavior is a consequence of the properties of a central controller rather than of the peripheral plant.

The parallelism between the behavior of ocular tracking and manual tracking also suggests that these behaviors reflect the properties of a central controller, since the inertia of the eye is considerably less than the inertia of the arm. Furthermore, during oculomotor tracking, the direction of the interwoven saccades may rapidly depart from the current direction of pursuit at sharp angles. Therefore the relatively slow change in direction we report for smooth pursuit does not appear to be constrained by the mechanical factors of the eye such as inertia or the viscoelastic properties of the orbit, but, rather appears to be a consequence of the neural representation of pursuit tracking. A neural mechanism in which the central coding of pursuit direction continues to change smoothly throughout the saccadic interval would be consistent with our current results.

A comparison of manual and ocular motor tracking suggests that at least a portion of this neural mechanism may in fact be shared. The finding that the rates of change of direction are so strikingly similar (Fig. 6), given that the two systems are so mechanically different, supports the idea that this might be the result of a shared central planning mechanism. The rate of change in direction increased in a linear manner with the degree of angular change of the target motion for ocular motor as well as manual tracking. Furthermore, this rate was nearly identical in the two cases across the complete 0 – 180° range of target directions (Figs. 6 and 7). In addition, this rate appeared to be invariant for the eye and the hand over a broad range of target and tracking speeds. It has also been shown that, by using adaptation to modify the gain of ocular motor pursuit, one can subsequently influence manual tracking responses as well. This implies that the adaptation occurs at a level common to the two motor systems (van Donkelaar et al. 1994a).

Certainly there are major differences in the two responses. The latency for smooth pursuit is nearly 100 ms less than what has been found for limb tracking (Engel and Soechting 2000; Lisberger and Westbrook 1985). Furthermore, limb tracking must, by necessity, include position and velocity information with respect to trajectory planning, whereas positional errors

are relegated to the saccadic system during ocular motor tracking (Engel et al. 1999; Krauzlis and Lisberger 1994; Rashbass 1961). Van Donkelaar et al. (1994b) have demonstrated that during manual tracking without visual feedback of hand position, subjects were able to match target speed, but were *not* able to reduce positional error. This suggests two separate inputs for manual tracking, analogous to the smooth pursuit and saccadic inputs found in ocular tracking.

The speed of manual and pursuit tracking is modulated in response to a change in the direction of target motion. We found that during a change in direction, there was a reduction in speed that was proportional to the change in target direction (Fig. 8). The rate at which the eye changes direction is also proportional to the amount of change in target direction (Fig. 7). It therefore follows that the faster the eye changes pursuit direction, the slower the tracking speed. Again, the intervening saccades preclude the idea that this modulation of tracking speed during the change in direction is due to the mechanical properties of the orbit, as the saccades can rapidly change ocular direction without any prior reduction in speed. Previous research by other investigators has shown that during the tracking of a continuously changing curved trajectory, the error in smooth pursuit tracking was smaller when the target obeyed a power law relating curvature (the rate of change of direction) to target speed (de'Sperati and Viviani 1997). Considering manual tracking, this same modulation of speed during an abrupt directional change is observed.

Finally, the interaction between speed and direction is also remarkably similar for the two systems (Fig. 9), again suggesting that a portion of the central planning is shared by ocular motor and manual tracking. Recent studies of manual tracking tasks have shown that speed and direction may be encoded in the firing of neurons in the motor cortex and Purkinje cells in the cerebellum (Coltz et al. 1999; Johnson et al. 1999). In these two cases, there is a consistent temporal sequence in the neural representation of these two parameters, with the coding of speed occurring before the coding of direction. In a recent study of manual tracking in two dimensions (Engel and Soechting 2000), we proposed an analytical model of tracking. To most accurately fit the experimental data, the modeled reaction time for a change in speed was found to be much lower than the reaction time for the change in direction of finger motion. This is consistent with our present findings in which speed appears to change appreciably before a significant change occurs in the direction of hand or eye tracking.

In conclusion, we found that the rate at which the eye and the hand change direction after an abrupt change in target direction was remarkably similar. In both cases, the relation between speed and direction was comparable, with speed decreasing considerably before a change in direction. These similarities, despite the obvious inertial differences in the two systems, point to a common neural controller.

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