

Human Smooth Pursuit: Stimulus-Dependent Responses

J. R. CARL AND R. S. GELLMAN

Laboratory of Sensorimotor Research and Neuro-ophthalmology Section, Clinical Branch, National Eye Institute, National Institutes of Health, Bethesda, Maryland 20892

SUMMARY AND CONCLUSIONS

1. We studied pursuit eye movements in seven normal human subjects with the scleral search-coil technique. The initial eye movements in response to unpredictable changes in target motion were analyzed to determine the effect of target velocity and position on the latency and acceleration of the response. By restricting our analysis to the presaccadic portion of the response we were able to eliminate any saccadic interactions, and the randomized stimulus presentation minimized anticipatory responses. This approach has allowed us to characterize a part of the smooth-pursuit system that is dependent primarily on retinal image properties.

2. The latency of the smooth-pursuit response was very consistent, with a mean of 100 ± 5 ms to targets moving $5^\circ/\text{s}$ or faster. The responses were the same whether the velocity step was presented when the target was initially stationary or after tracking was established. The latency did increase for lower velocity targets; this increase was well described by a latency model requiring a minimum target movement of 0.028° , in addition to a fixed processing time of 98 ms.

3. The presaccadic accelerations were fairly low, and increased with target velocity until an acceleration of about $50^\circ/\text{s}^2$ was reached for target velocities of $10^\circ/\text{s}$. Higher velocities produced only a slight increase in eye acceleration. When the target motion was adjusted so that the retinal image slip occurred at increasing distances from the fovea, the accelerations declined until no presaccadic response was measurable when the image slip started 15° from the fovea.

4. The smooth-pursuit response to a step of target position was a brief acceleration; this response occurred even when an oppositely directed velocity stimulus was present. The latency of the pursuit response to such a step was also ~ 100 ms. This result seems consistent with the idea that sensory pathways act as a low-pass spatiotemporal filter of the retinal input, effectively converting position steps into briefly moving stimuli.

5. There was a large asymmetry in the responses to position steps: the accelerations were much greater when the position step of the target was away from the direction of tracking, compared with steps in the direction of tracking. The asymmetry may be due to the addition of a fixed slowing of the eyes whenever the target image disappears from the foveal region.

6. When saccades were delayed by step-ramp stimuli, eye accelerations increased markedly ~ 200 ms after stimulus onset. For both closed-loop and open-loop stimuli, the waveform of this later response was not consistent with a simple velocity feedback system with a 100-ms time delay; we suggest that this may represent a response to an internally generated estimate of target velocity.

INTRODUCTION

The smooth-pursuit system is the oculomotor control mechanism that attempts to move the eyes, in order to stabilize the retinal image of a target moving in space. The system has usually been characterized as a negative feedback controller, where motion of the retinal image is the stimulus that drives the smooth eye movement. Since an image must

both be still on the retina and near the fovea for highest acuity, both the velocity and the position of the retinal image have to be controlled when a subject visually tracks a moving target. The hypothesis that retinal image motion is the stimulus parameter that drives smooth pursuit, leaving position errors to be corrected by the saccadic system, was first supported in an experiment by Rashbass (29). He showed that a target moving smoothly toward the fovea produced a tracking movement away from the *position* of the target and in the direction of the *movement* of the target. Using similar step-ramp target motions, Robinson (31) noted a 26-ms increase in latency compared with simple target ramps and pointed out that this implies that the target position had not gone unnoticed by the pursuit system. Experiments using stabilized images such as perifoveal afterimages (12, 14) have demonstrated that target position may be utilized by the pursuit system in some conditions, but the relationship between motion and position has not been quantified and may be quite variable (8). More recently, Pola and Wyatt (27, 28) have suggested an even more prominent role for position errors in the generation of smooth-pursuit eye movements.

In addition to these pursuit movements, which may be directly driven by retinal images, Westheimer (37) noted that when a simple repetitive stimulus waveform is used, the eyes may, in fact, change direction before the target. In this case the retinal images could not be directly responsible for the response, but some form of prediction must take place. Although most investigations of human pursuit have used predictable target motions using sinusoidal or triangular waveforms, complex target motions that were judged to be unpredictable have also been used in attempts to describe the pursuit response (2, 6, 19, 21, 32, 34, 38). Even when the target motion cannot be predicted at all, human subjects will produce some anticipatory smooth eye movements, albeit very slow ones (16, 18). This diversity of predictive and cognitive effects on human tracking has made it difficult to identify stimulus parameters that are used to generate pursuit movements (40).

The present study was undertaken to examine and quantify pursuit system responses that were as free as possible from the mental processing necessary for predictive pursuit re-

sponses. We wanted to know if it was possible to describe smooth-pursuit responses that were directly dependent on retinal images and to characterize the input-output relationships. Toward these ends we used target motions consisting of changes in target velocity, changes in target position where no retinal image slip was present, and combinations of the two. A small bright target was used and there was never more than one stimulus present at a time, to decrease anticipatory effects due to target selection. Positions, velocities, and time of onset were pseudorandomly varied by computer so that the initial changes were not predictable by the subjects. We restricted our analysis to the portion of the smooth-pursuit response before the usual saccade to eliminate the possible effect of saccade-pursuit interactions. We also used a very low noise recording system and objective computerized analysis methods. These methods allowed us to describe a stereotyped response with well-defined relationships to the stimulus parameters.

METHODS

Seven men, including the authors, served as subjects, although not all of them participated in each experiment. The subjects were familiar with the experimental environment, and four had had experience with similar oculomotor tasks. All eye movement recording was done with the electromagnetic search-coil technique (7, 30) in six foot field coils (CNC Engineering, Seattle, WA). A topical anesthetic was used in the eye wearing the eye coil, and the coil was on the eye no more than 0.5 h, once a day. An eye velocity signal was obtained by analog differentiation over a 0–100 Hz (–3 dB) bandwidth, then digitized, and stored at 500 Hz. Eye and target position were sampled at 250 Hz.

Head movements were minimized by the use of chin and forehead supports. The subjects were orthophoric and viewed the target binocularly unless otherwise noted, and two subjects wore their normal glasses for most experiments. The target was a spot of white light 0.1° in diameter, whose luminance was more than 3 log units above threshold, as measured in two subjects. A larger spot of 0.5° was used in some experiments; there were no differences detected in the responses. We used a single bright target spot to reduce variability due to luminance (38, 39), background effects (6, 15), or anticipatory effects of target selection when multiple stimuli are present (1). The target spot was backprojected on a tangent screen 110 cm from the subject and moved by means of servo-controlled mirror gal-

vanometers (General Scanning) in the projector beam. The room was dark except for the target spot. The subjects were instructed to follow the target as best they could, and were "reinforced" for good performance by a brief tone. Stimulus presentation and data collection were directed by REX, a UNIX-based software system developed for real-time experiments in the laboratory (11) and run on a PDP 11/73 microcomputer.

We used a large number of different combinations of changes in target velocity and position as stimuli. We presented these under two conditions: when the target was initially stationary and the response was initiation of tracking, and when the subject was following a target moving at 5 or 10°/s. In the latter case, the target movement generated a tracking error, which the eye response corrected. We report only on experiments in which targets moved in a single plane; unless we indicate otherwise we refer to the horizontal plane. Position steps were produced in two ways: the light spot was blanked for 10 ms while the mirror galvanometer moved to a new position, or two separately controlled spots were used with only one visible at a time. In the latter case only 1 ms was required to switch between them. The two methods appeared to yield identical results. In the trials starting from zero velocity, the spot would come on in the center of the screen and the computer program would require the subject to maintain fixation within 1.5°. The target started to move (stimulus onset) after a random delay period of 500–1,100 ms and remained visible for 700 ms longer. The next trial commenced after an intertrial interval of 1 s. For those trials in which the stimulus was presented as the subject was tracking, the target spot was initially placed eccentrically on the screen and then moved toward the center at 5 or 10°/s. The stimulus onset occurred after a delay of 1,250–1,750 ms, when the target was within 2.5° of the center of the screen. All subjects were able to reach a steady tracking velocity, usually within 5% of target velocity, within this delay.

In order to minimize responses due to anticipatory and predictive behavior, we used 12–18 different stimuli in each experimental run. We combined several different types of target motions in each experiment, including two or more amplitudes of position or velocity changes, and provided an equal number of trials with stimulus motion rightward and leftward. As additional conditions, the target motion was either not modified or the target disappeared after a pseudorandom interval. Each stimulus was presented 15–20 times, and each experiment lasted <30 min.

Data analysis

The data were analyzed by an off-line computer program that eliminated the need for subjective

judgements. Eye acceleration was determined by digital differentiation of the eye velocity with a finite impulse response filter (0–50 Hz bandwidth, linear phase) to permit the identification of saccades by acceleration criteria. Eye velocity was then filtered with a low-pass (0–50 Hz bandwidth) digital filter, and the saccades were removed along with 10 ms of data before and after to ensure complete deletion. A mean response was generated by computing the average eye velocity for each point in time, aligned on stimulus onset. Due to the deletion of saccades, the number of values used in the average varied for some points, and no magnitude was assigned to the mean when there were fewer than five values available. This mean eye velocity response was used to calculate the latency and acceleration and is the response used in all figures unless otherwise noted. We made no attempt to interpolate data for the saccades, and we restrict our quantitative analysis throughout this paper to presaccadic events.

Two quantitative parameters were of particular interest, namely the latency of the response and the initial acceleration. The method used for determining these values is demonstrated in Fig. 1*D*. Briefly, we defined the latency of the response by the point at which a regression line along the base line intersected a regression line along the response. The prereponse base line was defined as the period beginning 100 ms before the stimulus was presented and ending 80 ms after the stimulus onset. We calculated a regression line over this 180-ms interval and then found the time at which the amplitude of the eye velocity was more than three standard deviations from this line. Starting from this time, the regression line fitted to the next 40 ms of eye velocity was defined as the response, and the acceleration as the slope of this line. Because this method of calculating the latency does not depend on the earliest time that the average deviates from the base line, it does not bias the result in favor of the shortest latency, as a method based on an acceleration or velocity threshold would. We do note, however, that the use of a zero-phase digital low-pass filter theoretically smears the response over several milliseconds. When we compared several sets of data analyzed with and without this filter, we found that the filter had no net effect on the latency measurement. This is presumably because our method of latency measurement is largely insensitive to small changes around the onset of the response.

RESULTS

Pursuit initiation

The 14 individual responses of one subject to a 10°/s velocity step (0–10°/s, ramp stimulus) are shown in Fig. 1*A* as eye position and in Fig. 1*B* as eye velocity. The mean eye ve-

locity of the 14 responses is shown in Fig. 1C (dotted lines indicate 1 SD). The overlapping responses and small standard deviation emphasize the consistent “machinelike” nature of the response. All of the remaining eye movement traces used in this paper are averaged in this fashion. The only individual trial data are in Fig. 1, *A* and *B*. The regression lines shown in Fig. 1D were used to determine the response latency (99 ms) and acceleration ($38.2^\circ/\text{s}^2$), as described in METHODS. There was no drift apparent in the preresponse pe-

riod. Anticipatory drifts of the eyes before the onset of some stimuli have been reported (17), but these drifts were extremely small before a ramp in an unpredictable direction ($0.05^\circ/\text{s}$ or less), well below our ability to resolve.

The averaged eye velocity trace shown in Fig. 1D forms a nearly straight line for ~ 60 ms after the response onset, indicated with an arrow, until the trace ends due to the presence of saccades. The close fit of the response and the regression line indicates that the slope of the regression line is an adequate measure of

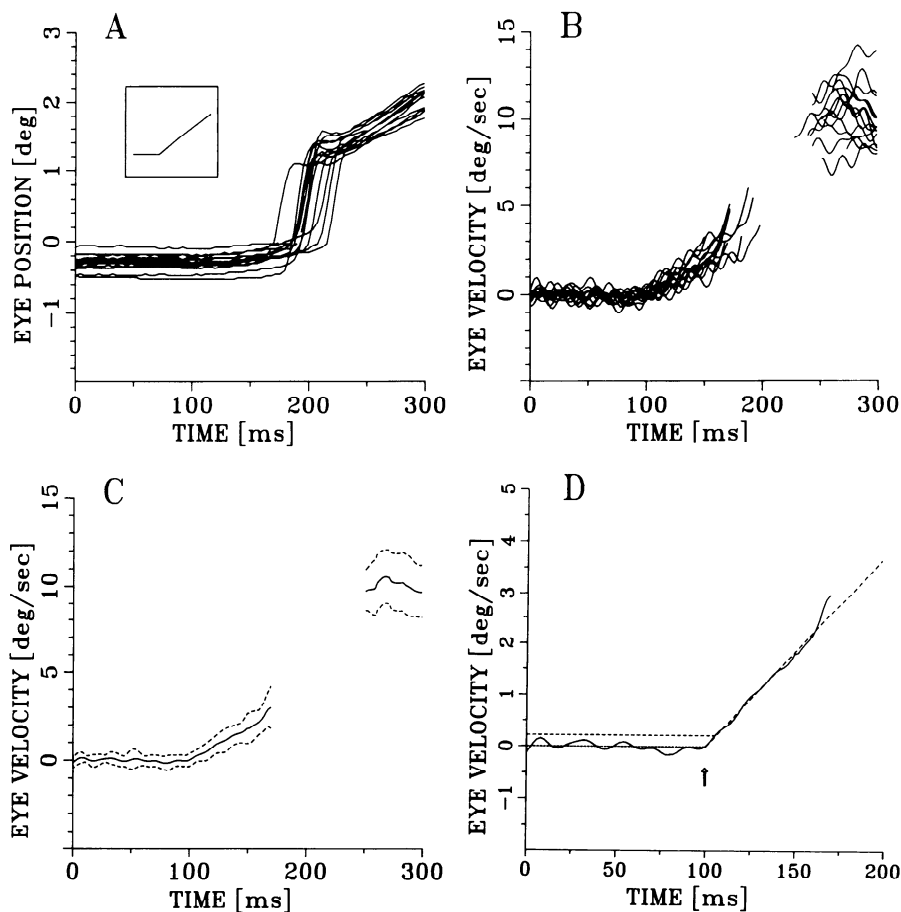


FIG. 1. Data from 14 trials in which the target moved to the right at $10^\circ/\text{s}$. The target motion is shown in a schematic diagram in *A*. In all plots of eye movement, rightward motion is plotted upward. *A*: the eye position for each individual trial (note the variability in saccadic latency). *B*: the eye velocity on each trial. The gap in each velocity trace reflects the occurrence of a saccade during that period. Note the consistency of the response up to the saccade. *C*: the point-by-point mean of the velocity traces in *B*, with the dashed lines indicating ± 1 SD from the mean. In *D* we illustrate the algorithm for determining the latency of the response and its presaccadic acceleration. The lower of the nearly horizontal lines is the regression line over the preresponse period, and the upper is drawn at 3 SD above this base line. The line slanting upward is a regression line fitted to the first 40 ms (20 points) of the response after it crossed the 3 SD line. The slope of this regression line is the acceleration calculated for these data ($38^\circ/\text{s}^2$). The latency (99 ms) is the time of the intersection of the regression line with the base-line response, indicated by the arrow.

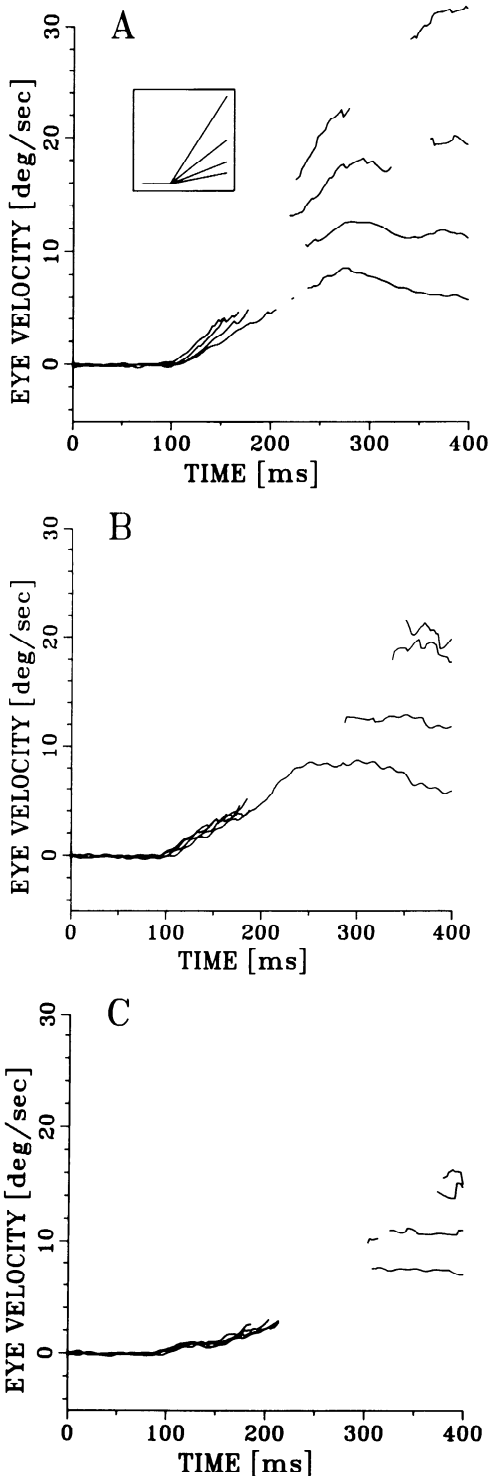


FIG. 2. Mean responses of 3 subjects to ramps of 5, 10, 20, and 40°/s. Each panel shows the responses of a different subject. The subject of *A* is able to attain a velocity of over 30°/s in the short time displayed, whereas the sub-

ject of *B* hardly exceeds 20°/s in the time shown. The subject of *C* has an idiosyncratic, but consistent, dip at ~140 ms in the velocity profile of his response to all target velocities. The latencies of the subjects increased slightly to the lowest velocities. The subject of *A* produces slightly greater acceleration for higher target velocities, whereas the other two subjects show little change in acceleration over this target velocity range.

the response acceleration during the presaccadic period. The averaged responses of three subjects to a series of velocity steps (5–40°/s) are shown in Fig. 2, in which each panel shows the response of one subject. Although these subjects showed some differences in their responses, particularly to the higher velocities, they illustrate features common to all subjects. The latency of the pursuit response varied slightly with target velocity, with longer latencies present for lower velocities, best seen in the responses in Fig. 2*A*. The remarkable consistency of latencies from subject to subject can be seen in the small standard deviations of Fig. 3*A*, where the mean latencies are shown for each stimulus velocity. The mean response latency for target velocities of 5°/s and above was 100 ± 5 ms, increasing to 125 ms for a 1°/s target.

The initial eye acceleration was more variable from subject to subject than the latency. Each individual subject, however, generated a characteristic acceleration that was fairly constant over the period evaluated. Two of the subjects showed a small stereotyped dip in the presaccadic velocity waveform that was not affected by target velocity. The responses of one of the two are shown in Fig. 2*C*. In general, the accelerations increased only slightly with velocity for target velocities in excess of 5°/s, and in some subjects there was a striking similarity of responses in this velocity range, demonstrated by the subject of Fig. 2*B*. The dependence of initial eye acceleration on target velocity for all seven subjects is depicted in Fig. 3*B*. Most of the variability in response occurred in the low target velocity range and there was a near saturation of response at $\sim 50^\circ/\text{s}^2$ for stimuli moving 10°/s and faster. For any one target velocity, there was some variation in eye acceleration that depended on the range of velocities used in an experiment. The accelerations to 5 and 10°/s targets were about 12% greater (mean of 4 subjects) when

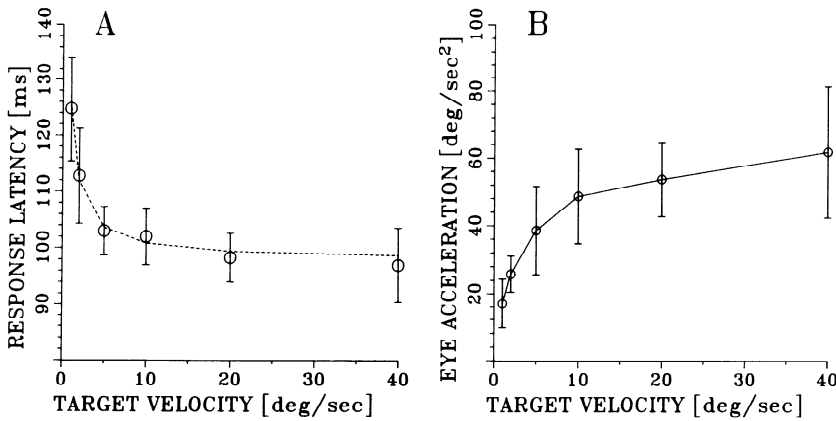


FIG. 3. *A*: the relationship between target velocity and mean response latency for all 7 subjects. Only 4 subjects were tested on targets of 1 and 2°/s. In this and all subsequent figures the vertical bars represent ± 1 SD. Since there was only 1 measurement for each subject, namely his mean, the SD represents the intersubject variability. The dashed line connects latencies predicted by a model where $\text{latency} = 98 \text{ ms} + (0.028^\circ / \text{target velocity})$ (see DISCUSSION). *B*: the dependence of presaccadic acceleration on target velocity for the same subjects. Note that there is only $\sim 10^\circ/\text{s}^2$ increase in acceleration for a fourfold increase in target velocity above 10°/s.

the range of velocities was 5–40°/s, compared with experiments where the range of velocities was 1–10°/s. Similar findings have been reported for pursuit in monkeys (20). An analogous effect in the saccadic system (13) has been termed the range effect.

Most of the subjects showed a small asymmetry between leftward and rightward accelerations that was idiosyncratic and present when tested with binocular viewing of the stimulus. Although there was some degradation of visual acuity in the eye with the coil, monocular control experiments showed no statistically significant differences in latencies or accelerations between the viewing eye and the nonviewing eye. In addition, there were no statistically significant differences between nasally and temporally directed responses during monocular testing.

Responses to velocity steps introduced during tracking

All our subjects were able to accurately track targets moving at 5 and 10°/s. As the postsaccadic velocities of Fig. 2 indicate, 20°/s stimuli appeared to be too great a challenge for some, and none were able to accurately follow a 40°/s target in this brief interval. The 5 and 10°/s stimuli were therefore selected as initial velocities in those experiments in which a velocity or position step was introduced when the subject was already tracking. The ability

of the subjects to track a 5°/s target accurately is indicated by the mean eye velocity attained by the subjects before the change in target mo-

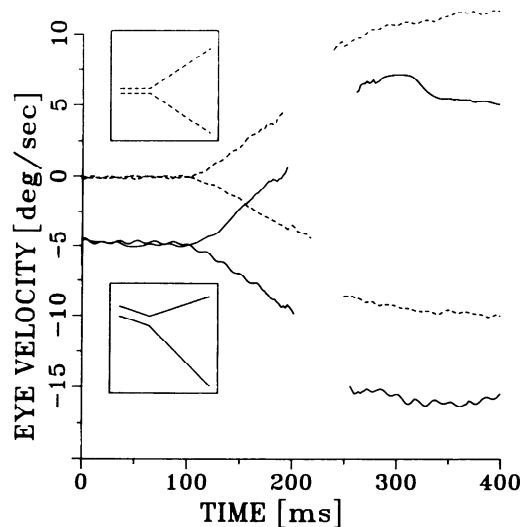


FIG. 4. The mean responses of 1 subject to velocity steps of 10°/s presented under two conditions. The dashed lines show the responses to velocity steps (ramps) to the left and right. The solid lines show the responses to equal-sized velocity steps (ramp-ramps) presented while the subject was tracking a target moving at 5°/s to the left. In this case the target either increased its speed to 15°/s to the left or underwent a change in direction, moving at 5°/s to the right. Note that the latencies under all 4 stimulus conditions appear identical and the accelerations are comparable.

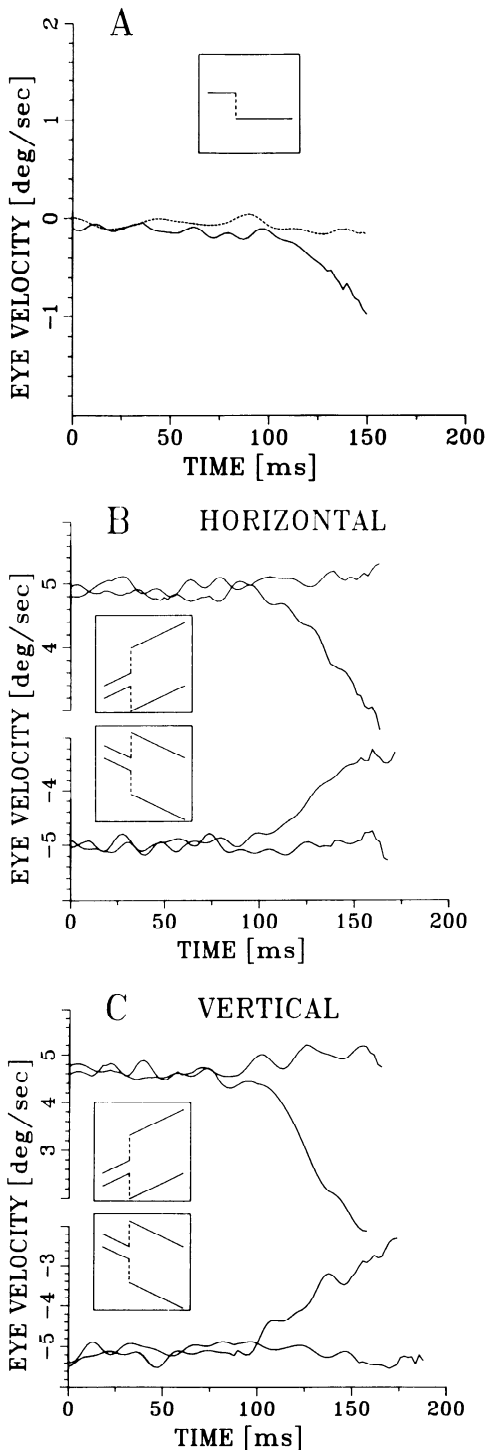


FIG. 5. *A*: small presaccadic responses may be present when infrequent position steps are presented in an experiment consisting primarily of ramp stimuli. The *solid line* is an averaged response of 1 subject to steps of 2° presented

tion was presented: $4.94 \pm 0.22^\circ/\text{s}$, averaged over 262 separate stimulus conditions in six subjects.

The latency of the response induced by a step change in target velocity presented while a subject was already tracking was the same as for initiation of tracking. Figure 4 compares the averaged responses of one subject to velocity steps of $10^\circ/\text{s}$, from fixation (dashed line) with tracking $5^\circ/\text{s}$ to the left (solid line). The mean difference in the response latencies for these two situations was not significant for six subjects (2.4 ms , $P = 0.166$). The eye accelerations were generally the same in both directions when initiating tracking, but when the same velocity step size occurred during tracking, some subjects showed a small asymmetry. When the velocity step created a reversal of target direction the initial response was a slowing down of the eyes. Some subjects showed a slightly higher acceleration when slowing down than when the velocity step was in the same direction as the tracking, and the response was a speeding up of the eyes. This small difference may be due to mechanical factors associated with the orbital contents and the asymmetric final eye velocity. However, for most subjects, the responses were almost the same whether the target was moving or stationary prior to the step. Likewise, the response was similar if the velocity step was one which stopped the target. This suggests that the basic response mechanisms were the same for initiating a response and for correcting errors present during tracking.

The response to position steps

The stimuli described above produced smooth image motion across some region of

in the ratio of 1 step to 3 ramps. No discernible response was present in an experiment where all the stimuli were steps (*dashed line*), *B*: asymmetric responses were generated by all our subjects when the target suddenly changed position without changing its velocity. In the *upper traces* the subject was tracking a rightward moving target; a 4° step to the left, i.e., a backward step, caused an acceleration of the eye to the left at 100 ms, whereas a similar step to the right (an onward step) produced no measurable presaccadic acceleration. When the subject was tracking to the left (*lower traces*) the converse was true. *C*: a similar onward-backward asymmetry was present when the target motion and steps were vertical, for upward (*top traces*) and downward (*lower traces*) tracking. Upward velocities are plotted upward.

the retina. We also investigated the tracking responses to target images that did not produce any retinal image slip, but rather stepped from one location to another on the retina. When a position step was presented while the subject was fixating a stationary target, the response depended on the context. That is, if all the stimuli presented were position steps, the responses were pure saccadic eye movements with no detectable presaccadic accelerations (dashed line, Fig. 5A). If, however, the stimuli were primarily velocity steps, the response to a position step presented in one out of four trials consisted of a small presaccadic pursuit response with a latency of ~ 100 ms (solid line, Fig. 5A). These responses were not anticipatory, as they were always in the direction of the unpredictable target step and they occurred 100 ms after the stimulus. The pursuit response to a position step was much greater, however, when the step was introduced while the subject was already tracking. Sample responses to onward and backward 4° position steps presented during tracking are shown in Fig. 5B. The response to the backward step was vigorous; the onward step generated either a small response (barely noticeable in this figure), no measurable response, or a response directed opposite to the direction of the step. This onward-backward asymmetry held whether the subject was initially tracking to the left or to the right.

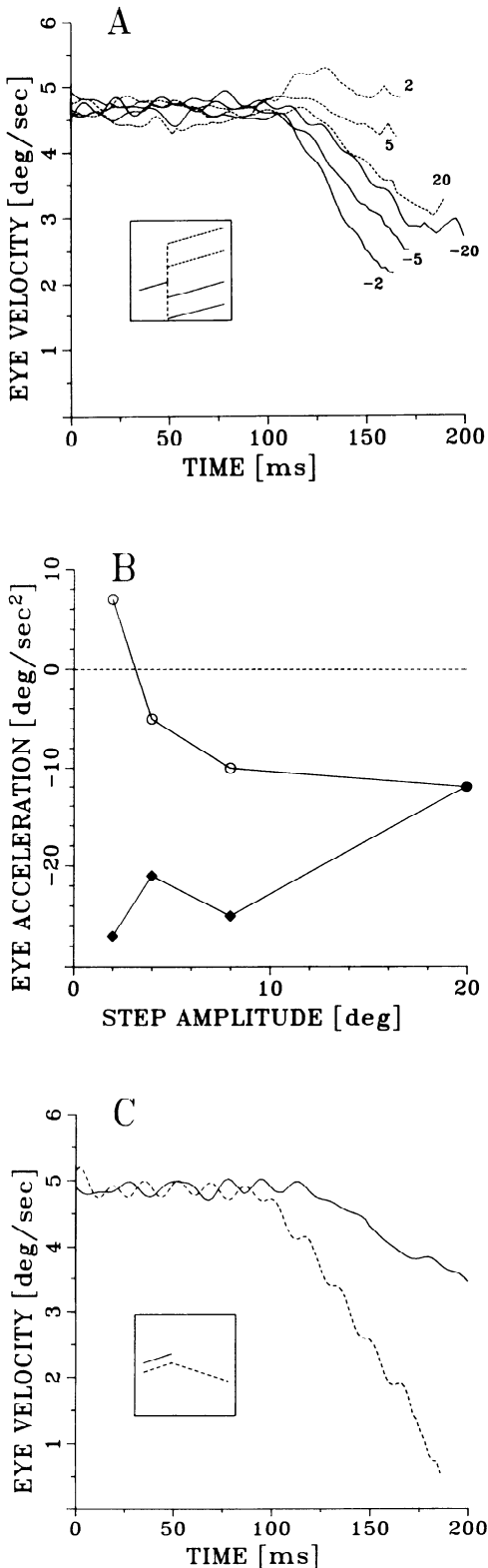
Subjects were generally slightly behind the target when tracking, so that a backward step would usually move the target to the opposite side of the fovea and therefore project it to the opposite hemisphere. We wanted to know if this might be the reason for the asymmetry, so we used position steps when a subject was tracking vertically, a situation that should not involve a switch in the hemispheric projection of the target. Figure 5C demonstrates that a similar asymmetry was present in the vertical plane as well.

In addition to the asymmetry, the responses to steps of position depended on the size of the step. A series of averaged eye velocities in response to different size onward and backward steps is shown for one subject in Fig. 6A. The acceleration of the responses to the backward steps can be seen to decrease as the step size increases. As previously noted, the response to small onward steps usually showed

little, if any, acceleration in the direction of the target. As the size of the onward step increased, the subjects all showed a slowing of the eyes, so the acceleration was away from the direction of the step. This result can be seen in the dashed lines of the figure, where most of the responses to onward steps are in the same direction as to the backward steps. The response to a large onward step was nearly the same as to a large backward step. Figure 6B summarizes this dependence of eye acceleration on the amplitude and direction of the step for two subjects. In this figure, onward accelerations are plotted as positive and backward accelerations as negative. The magnitude of the acceleration in response to backward steps decreased as the step size increased, until the response to large steps in either direction was identical. Thus changes in acceleration were roughly symmetrical about a line corresponding to a slowing down at $15^\circ/\text{s}^2$.

We expected that the response to a very large step should be similar to the response to a disappearing target, so we tested that hypothesis by blanking the target at an unpredictable time, so that it disappeared while the subject was tracking at a constant velocity. The response, shown in Fig. 6C, was always a slowing down of the eyes with a latency slightly > 100 ms and an acceleration ($15^\circ/\text{s}^2$) that was similar to that seen in response to large onward or backward steps. These results suggested that the asymmetry might be due to an addition of the disappearing response to a symmetric position response, creating the apparent offset seen in Fig. 6B.

In a pilot study we had created position steps without blanking the stimulus light and noted that there was often a visible streak as the mirror galvanometer moved to a new position. We tested the effect of this stimulus in a control experiment where position steps were produced with the target randomly either blanked or not blanked during the step. In the latter case the visible spot moved across the screen to the new location at velocities of up to $5,000^\circ/\text{s}$ during the ~ 5 -ms sweep time of the galvanometers. There were no significant differences in the response acceleration or latency for the two methods when the steps were $< 4^\circ$. For larger steps, however, the two methods produced different results: when the target was not blanked, the accelerations to steps up to



30° in both directions remained constant, in contrast to the results for the blanked method shown in Fig. 6. This result indicates that the tracking system was able to use the brief extremely high-velocity information produced by the target image.

Combined position and velocity steps

(A) SAME DIRECTION. When position and velocity steps were combined (step-ramps), the velocity step moved the target image across the retina and the position step placed that image motion on different regions of the retina. When the step and ramp motions of the target were both away from fixation, in the same direction, the initial acceleration of the eyes depended on the size of the step. This effect is demonstrated in Fig. 7, which shows that the mean accelerations of three subjects to 10°/s velocity steps declined with eccentricity of the retinal image slip, becoming unmeasurable by our methods by ~15°. Because the accelerations were so low for eccentrically presented velocities, we were unable to determine latencies accurately. Even though the presaccadic acceleration diminished, the immediate postsaccadic pursuit velocities were

FIG. 6. *A*: the asymmetric response to steps is affected by the step size. Averaged responses of 1 subject to steps of increasing size are shown together to demonstrate the trend for the accelerations to both onward and backward steps to become similar. Step amplitudes are shown by inset numbers. As the onward step size increased, the responses (*dashed lines*) changed from a small onward acceleration to an acceleration opposite to the direction of the step, i.e., to a slowing down. This subject also showed some increase in latency to larger steps. *B*: the nature of this dependence of the response on the step amplitude is demonstrated by plotting the mean initial acceleration of 2 subjects against the size of the step. Positive accelerations are those in the same direction as the tracking and indicate that the response was a speeding up of the eyes, whereas negative accelerations indicate a slowing down of the eyes. The responses to onward steps, shown by *open circles*, changed from a small onward acceleration when the step was small to a backward acceleration for larger steps. The larger backward acceleration seen in response to a backward step (*filled diamonds*) can be seen to lessen gradually as the step size increased. Note that the accelerations were the same for large (20°) onward or backward steps and that the accelerations were roughly symmetrical about this value. *C*: the response (*solid line*) to a target that suddenly disappeared while the subject was tracking it. This is compared with the response to a 10°/s velocity step (*dashed line*), which has a higher acceleration.

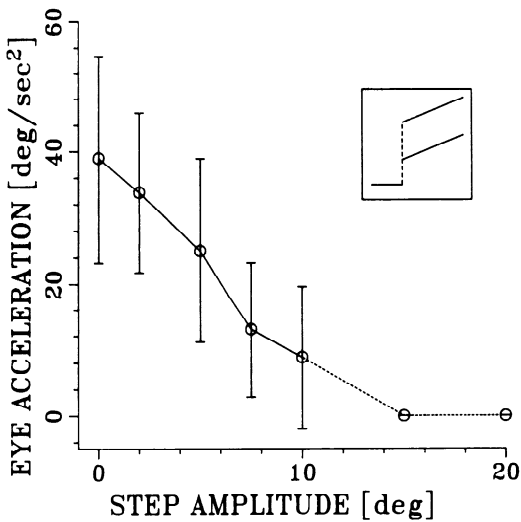


FIG. 7. The dependence of response acceleration on the retinal eccentricity at which the image movement was presented. The *ordinate* values are the initial accelerations of the eye to the $10^\circ/s$ target, and the *abscissa* values indicate the distance of the target image from the fovea at the onset of the ramp. The acceleration declined monotonically and became unmeasurable for eccentricities $>10^\circ$.

only slightly affected and were higher for the 20° step than for the 2° step (13.7 vs. $10.4^\circ/s$). Since these velocities were present within 10 ms of the end of the saccade, the information about target velocity must have come from the more peripheral part of the retina. This result suggests that the earliest part of the response uses only the perifoveal region, whereas longer-latency pursuit mechanisms may utilize a much larger region of the retina.

Combined position and velocity steps

(B) OPPOSITE DIRECTIONS. An initially stationary target, that suddenly steps away from and then moves back toward fixation, presents a conflict to the smooth-pursuit system: the response direction that would reduce the retinal image slip is opposite to the direction that would reduce position error. We observed a consistent and complex pattern of eye movement response to these stimuli (Fig. 8). The first component of the ensuing tracking response was a brief acceleration in the direction of the position step. This initial acceleration was seen in the response of all seven subjects. This first component has a latency of ~ 100

ms, which is the usual latency for responses to both velocity and position steps, as we have described above. Eye movement in the direction of the velocity step does not become evident until ~ 50 ms later. The change in direction of response can easily be seen in Fig. 8, in which the averaged responses for one subject to stimuli in opposite directions cross over. These stimuli were generated with the step size adjusted so that the target passed through its original location at ~ 240 ms; the retinal image of the target was still moving toward the fovea, and the potential conflict over response direction persisted until this time. During this period of conflicting inputs the eye movement is initially in the direction of the target position and later in the direction of target velocity. Figure 8 also includes a response to a ramp stimulus for comparison. Although the latencies are nearly identical, the

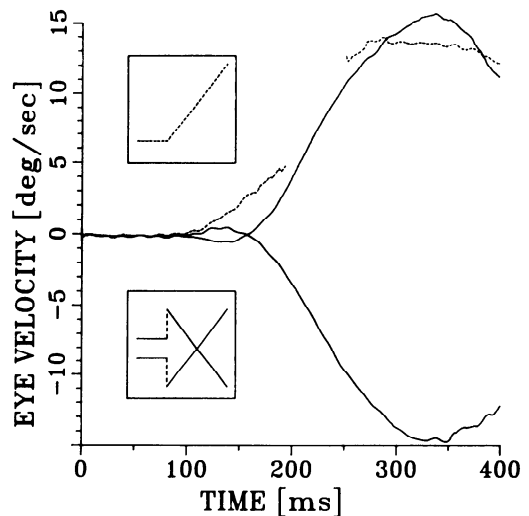


FIG. 8. The response to oppositely directed step-ramps where the target image stepped 2.4° in one direction and then moved back toward the fovea at $10^\circ/s$. The response to a simple ramp at the same velocity is shown by the *dashed line* for comparison. Note that the step-ramps elicited a response at the same latency (~ 100 ms) as the simple ramp, but the initial response to the step-ramps was in the direction of the position step. The response in the direction of the velocity did not become evident until ~ 150 ms. The response to the simple ramp had a velocity immediately after the saccade (gap) that was higher than that projected by extrapolating the presaccadic acceleration to the end of the saccade. Effective acceleration during the saccade is similar to the acceleration present at the same time in the step-ramp response.

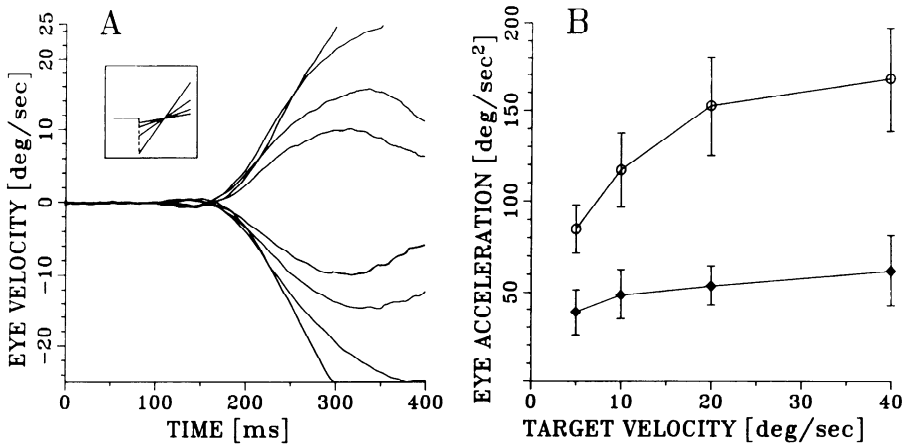


FIG. 9. *A*: the responses to a series of step-ramps (5, 10, 20, and 40°/s, left and right) are shown superimposed. Note that the velocities were very similar up to ~ 180 ms and that the peak accelerations occurred shortly after 200 ms. *B*: the relationship between target velocity and peak eye accelerations (measured from 200 to 240 ms) for step-ramp stimuli (*open circles*). For comparison, the initial accelerations to simple ramps (*filled diamonds*) over the same range of target velocities has been repeated from Fig. 3*B*. The values are means of all 7 subjects, and the bars indicate ± 1 SD.

early portion of the response is quite different and demonstrates the difficulty in comparing the accelerations for stimuli moving away from the fovea (ramp—dashed line) and for stimuli moving toward the fovea (step-ramp—solid lines).

The responses to a series of step-ramp stimuli with ramp velocities of 5–40° had nearly identical initial components and only varied in the later part of the response (Fig. 9*A*). These stimuli all caused delays in the initial saccade, so we were able to evaluate a much longer presaccadic interval. The peak accelerations in the direction of the velocity step did not occur until ~ 200 ms after stimulus onset. In Fig. 9*B*, the velocity dependence of acceleration measured at 200 ms for the step-ramps is compared with the initial accelerations of simple ramps (repeated from Fig. 3*B*). The accelerations to the step-ramps are much higher, and there is less apparent saturation. It is interesting to note, however, that the responses to the ramp and step-ramp are similar after ~ 200 ms: the effective acceleration of smooth pursuit during the saccade (for the ramp stimulus; open part of dashed line in Fig. 8) is clearly very similar to the acceleration to the step-ramp measured at the same time. The step-ramp stimulus thus allows one to examine the pursuit response at a time that this re-

sponse would normally be occluded by the presence of saccades.

Combined position and velocity steps

(C) OPPOSITE DIRECTIONS DURING TRACKING. The preceding results demonstrate that the response to an image moving toward the fovea (as in the conflicting step-ramp) was quite different from that elicited by an image moving away from the fovea (as in the simple ramp). These differences were even more striking when a conflicting step-ramp stimulus was presented when the subject was already tracking. The initial components of the responses, shown in Fig. 10*A*, were similar to the responses to position steps presented during tracking, i.e., there was a marked asymmetry with the onward position step generating little if any acceleration (see Fig. 5*B*).

Does this response to combined position and velocity steps depend on the simultaneous occurrence of the two stimuli? In an experiment designed to answer this question, the position step was shifted in time with respect to the velocity step in 40-ms increments, from -40 to 80 ms. Figure 10*B* shows that the responses to the two components are clearly separable in time, with a brief response in the direction of the position step present at all temporal separations.

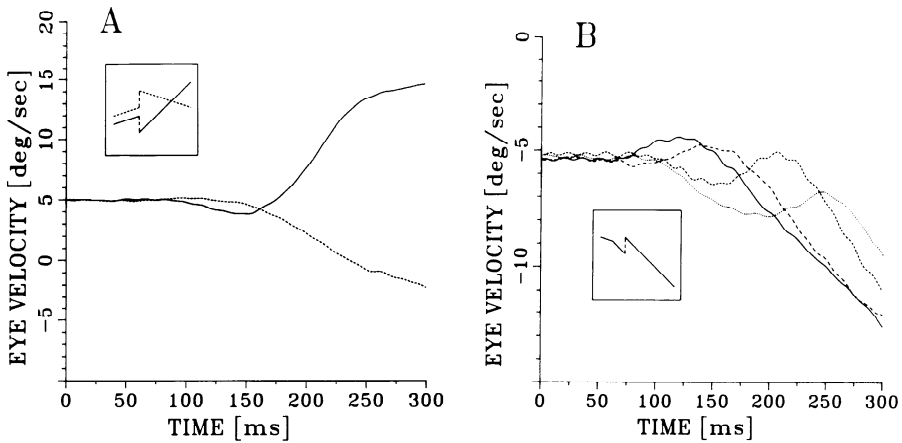


FIG. 10. *A*: the averaged responses of one subject to ramp-step-ramps, where the target stepped 2.4° either onward (*dashed line*) or backward (*solid line*) and then changed velocity by $10^\circ/\text{s}$ in the opposite direction. There is a large asymmetry in the initial segment with the onward step generating very little response (compare with symmetric responses from fixation in Fig. 8). This asymmetry in the earliest part of the response is similar to that seen to ramp-steps, illustrated in Fig. 5*B*. *B*: averaged responses of 1 subject to a series of ramp-step-ramps where the position and velocity steps were not simultaneous. The position step was shifted in time in 40-ms increments, from 40 ms before the velocity step to 80 ms after it. The *hump* seen in each waveform indicates the brief response to the position step.

Open-loop responses

In experiments using simple ramps from stationary fixation or from tracking, the entire response that we measure—that is, the pre-saccadic response—is effectively an open-loop response, generated in the absence of feedback.

This conclusion stems from the consistent observation that it takes ~ 100 ms, under all conditions, for any stimulus to produce a measurable response. In the case of a step-ramp stimulus we were able to record several hundred milliseconds of saccade-free response

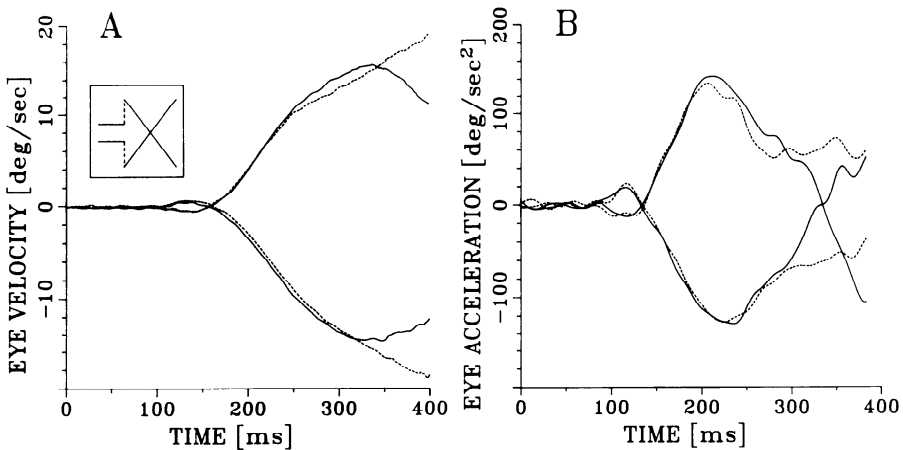


FIG. 11. The responses to step-ramps under normal and open-loop conditions. In the open-loop case, the eye position was added to the target ramp of $10^\circ/\text{s}$, so that the velocity of the retinal image was kept constant. *A*: an overlay of the normal (*solid*) and open-loop (*dashed*) response velocities. They are clearly quite similar up to ~ 300 ms. *B*: the accelerations of the same traces (digitally differentiated). The identical decline in acceleration starting at ~ 225 ms is now evident, as is the point at which the two types of response diverge. Note that the acceleration began to decline earlier than could be expected from velocity feedback with the 100-ms delay seen in other responses (see DISCUSSION).

and examine a later part of the response that should not be open-loop and could be influenced by feedback. We wanted to determine if feedback was affecting the response with the expected delay of 100 ms, so we performed some experiments in which we opened the feedback loop artificially. This was done by having the computer add the eye position to the target ramp, thus canceling the effect of the increasing eye velocity. The velocity of the retinal image of the target was then constant, regardless of the eye velocity. In Fig. 11, the averaged eye accelerations and velocities in response to these stimuli (dashed lines) are compared with those obtained in the normal closed-loop condition (solid lines). The responses are almost identical up to nearly 300 ms; at this point they diverge. The very low eye velocities generated in the first 200 ms are probably insufficient to produce a noticeable difference between the open- and closed-loop responses. The eye velocity after 200 ms is great enough to reduce retinal image velocity in the closed-loop experiment, so the divergence seen at 300 ms is still consistent with the hypothesis of a 100-ms delay in the feedback loop. Interestingly, in both responses there is a *decrease* in acceleration at ~ 225 ms. In the open-loop experiment the retinal image velocity was constant, so there was no change in retinal image velocity that could account for this part of the response. In the case of the closed-loop responses, 100 ms before the decrease in acceleration occurred there was negligible eye velocity, so velocity feedback cannot be the cause of this observation. Thus, in both cases, there is a component of the response present by ~ 200 ms that has markedly different characteristics from the first 100 ms of the response.

DISCUSSION

In these experiments we have attempted to examine pursuit responses that are primarily dependent on the retinal image of the stimulus and as free as possible from cognitive processes of the subject. We have focused particularly on two input parameters, target position and velocity, and described primarily two output parameters, response latency and acceleration. The principal findings were that 1) the initiation of pursuit is remarkably machinelike, both with regard to the constancy of latency

and the waveform of the response; 2) both the velocity of the target and step changes in the position of the target are determinants of the response; 3) the latencies and initial accelerations of responses are nearly identical for velocity and position steps; and 4) much higher accelerations become evident later in the response.

One complication in the interpretation of these results stems from the apparently complex interactions of position and velocity information. Clearly, retinal image *velocity* alone cannot account for the acceleration in the direction of position steps (e.g., Figs. 5 and 6). Conversely, retinal image *position* alone cannot account for our observation that the eye response reverses direction, to that of the target velocity, at a time when target position and velocity are still in conflicting directions (e.g., Figs. 8 and 10). In this discussion we propose an hypothesis about the interactions of position and velocity information that allows all of our results to be described by a few simple mechanisms.

Smooth-pursuit inputs are filtered

We were initially surprised by our observation that position steps usually evoke responses very similar to those of velocity steps. Although it has been observed previously that position errors produced by stabilized images are capable of producing tracking movements (12, 14, 27, 28), the onset of these tracking movements had not been quantified. In our experiments, all target position errors were produced as sudden displacements occurring at the stimulus onset. Since we followed the response for only a few hundred milliseconds, we cannot address the role of *sustained* position errors in the generation of smooth-pursuit eye movements. The responses to the position displacements, however, appeared very similar to the responses to velocity steps, suggesting that these stimuli might be processed by the same pathway.

The smooth-pursuit responses to position steps and step-ramps become more readily understood if one assumes that the input to the smooth-pursuit system is a filtered version of the physical stimulus. A similar suggestion has been made for the saccadic system (10). The effect of a low-pass filter on a position step input would be to convert the nearly in-

stantaneous change in position into one perceived more gradually and with a finite velocity. The responses to steps and to step-ramps could therefore be generated by a single pathway that is sensitive to stimulus velocity alone. The precise temporal sequence of the response would depend on the filter characteristics. A low-pass filtering of a step of position creates an apparent smooth movement of the stimulus between the two positions with a corresponding brief velocity that could be used by the pursuit system to generate the acceleration seen in response to a step stimulus. Filtering of a step-ramp stimulus would similarly create an apparent smooth movement first in the direction of the step and then following the oppositely directed target velocity: the velocity profile of the filtered waveform then has the same sequence of direction reversals as the eye acceleration to a step-ramp. This idea of filtering explains the effectively identical latencies of responses to position and velocity steps: whatever the *physical* stimulus, it is treated by the pursuit system as a continuous *physiological* stimulus. Such a filtering process would account for the ability of the pursuit system to generate smooth eye movements in response to a variety of discontinuous stimuli, such as that generating the phi phenomenon. The latter is the observation that a series of position steps, spaced appropriately in time and space, is treated as a continually moving stimulus by both the perceptual and motor systems (3, 24, 25). A neurophysiological correlate of this form of motion processing was investigated by Mikami, Newsome, and Wurtz (22, 23). They found that motion-sensitive neurons in cortical area MT could respond to phi stimuli as they did to a true moving target.

We used a single small spot of light as a stimulus, so there was always an instantaneous "position error" present when the target image was not on the fovea. The stimulus therefore always had both position and velocity characteristics before the image was foveated and steady-state tracking was established. Because both aspects of the stimulus were present together, one cannot completely separate out the respective roles that position and velocity play in generating tracking responses. The hypothesis of a temporal filtering of stimulus position can, however, completely account for our responses to position displacements.

In addition to the apparent temporal filtering of the target position, there are also spatial effects present in the responses to both velocity and position steps (Figs. 6B and 7) such that the acceleration decreases as the target motion is projected onto retinal regions further from the fovea. This represents yet another type of position sensitivity, although one that only decreases the pursuit response.

The mechanism underlying the response latency

One striking feature of the response was the machinelike character of the latency. The latencies were not only similar among subjects, but they were also very repeatable from day to day for individuals. Although our values for smooth-pursuit initiation were ~ 25 ms less than those measured directly in some earlier studies, estimates of time delays from phase measurements (9, 33) were less than our values. Recent direct latency measurements are in close agreement with values of ~ 100 ms (3).

Although response latencies were very consistent, they were significantly increased for low target velocities ($< 5^\circ/\text{s}$). A detection model, which assumes that the target must move some threshold distance before it is recognized as a stimulus for the pursuit system, can account for this dependency. The overall response latency can be calculated as a sum of this "detection time" and a fixed processing delay. A similar model has been proposed for the optokinetic nystagmus of the rabbit by Collewyn (5). We have plotted the latencies predicted by a model with a fixed processing time of 98 ms and a threshold distance of 0.028° in Fig. 3A (dashed line); the agreement with our observations is remarkably good. Applying our model to data derived from psychophysical reaction time experiments studying conditions for the detection of movement (36), we calculate a threshold distance of 0.027° , supporting the idea that this detection delay may be a part of motion processing in humans.

The acceleration of the response

EARLY PHASE OF THE ACCELERATION. The response accelerations to simple ramps, although more variable among subjects than the latency, nonetheless showed a stereotyped waveform for each individual. For five of the

seven subjects, the acceleration was nearly constant from the onset of the response until the intervening saccade. In the other two subjects, there was a small stereotyped dip in the acceleration at ~ 40 ms, and then a resumption of the initial acceleration.

The magnitude of the acceleration was unexpectedly low, considering the much higher values of smooth-pursuit accelerations that have been recorded for different types of target motions, particularly periodic waveforms (19). We too have recorded much higher accelerations at a later time in the response (Fig. 9B) and conclude that these low values seen in the initial segment of the response cannot be due to either mechanical factors in the orbit or to limitations inherent in the smooth-pursuit system.

What might be the utility of this low acceleration? Clearly, the purpose of the pursuit system is to improve acuity by minimizing retinal image slip. In attempting to achieve this goal, the pursuit system is confronted with two conflicting concerns. On the one hand, it should minimize the time during which retinal image slip occurs; this calls for a high acceleration. On the other hand, the 100-ms delay in the feedback loop presents a formidable problem, namely the danger of significant overshoot and oscillation, which increases as higher accelerations are employed. The velocity mismatch and oscillation resulting from an increase in smooth-pursuit accelerations were well demonstrated by Optican, Zee, and Chu (26) in a study of adaptation to extraocular muscle weakness. We suggest that the relatively low accelerations represent a compromise by the pursuit system. This attempt to balance conflicting needs may also explain the range effect that we have noted. In this effect the acceleration to a given velocity step increases with the range of velocity steps present in a given experiment. Since the accelerations are nearly constant, the velocity achieved by the end of the presaccadic period of ~ 80 ms is fixed by the acceleration, at about $4\text{--}5^\circ/\text{s}$ for our subjects. If all the experimental velocities are much higher than this velocity, the subject can improve the dynamics of his response by increasing the initial accelerations without increasing overshoot.

LATER PHASE OF THE ACCELERATION. Two characteristic features of the responses de-

scribed thus far are a latency of ~ 100 ms and a low constant acceleration in the presaccadic period. Later accelerations cannot normally be measured, since saccades occur starting at ~ 160 ms. To avoid this problem, we used "Rashbass"-type step ramps, which substantially delay or eliminate saccades (29). The saccade-free responses measured at 200 ms had a much greater acceleration, ($\sim 150^\circ/\text{s}^2$, Fig. 9) and show a dependence on target velocities up to $20^\circ/\text{s}$ or more. A study of pursuit in monkeys also demonstrated a change in acceleration during the response; although the times were shorter in the monkey, this may represent a common feature of pursuit response (20).

Close examination of the acceleration profiles at these later times (Fig. 11) reveals features that cannot be generated by a simple velocity feedback system with a 100-ms delay. In both the open- and closed-loop experiments, the acceleration began to decline at ~ 225 ms. In the case of the open-loop condition, where the velocity of the retinal image was stabilized, this decline in acceleration cannot be attributed to a change in image velocity. Since all of our experiments suggest a minimum delay of 100 ms between stimulus change and eye response, the acceleration decline in the closed-loop condition cannot be due to feedback, because 100 ms earlier the eye velocity was negligible. Even later in the response, a steady state was achieved that was far more stable than expected in the presence of feedback delays, best illustrated by the pre-response portions when tracking had been established (Fig. 10A).

Related experiments of ours demonstrated another feature of these later responses that indicates that they are generated by separate mechanisms (4). We used paradigms designed to encourage subjects to increase or decrease their tracking responses by optical feedback methods. The accelerations and velocities in the presaccadic period were unchanged by these paradigms, whereas the velocities measured after 200 ms were altered by up to 60%. This result supports the idea that the early portion of the response is dependent only on the retinal image velocity present 100 ms earlier, whereas the later response is dependent on a mechanism that is subject to adaptation.

These observations on the high acceleration,

stability, adaptability, and lack of correlation with stimulus properties lead us to suggest that by 200 ms it is no longer retinal image slip that is primarily responsible for the acceleration, but rather an internally generated estimate of the target velocity. Such a motor program would effectively eliminate the 100-ms delay and its attendant instabilities, allow the eyes to catch up with the target rapidly, and permit stable eye velocities without significant oscillation.

The asymmetry in the response to position errors

An additional result of our study that warrants explanation is the onward-backward asymmetry observed in the accelerations to position steps, best seen in Figs. 5B and 10A. One possible mechanism for this finding is suggested by Fig. 6, in which the onward and backward accelerations appear to be generally symmetric about a backward acceleration (slowing down) that is the same as that in response to disappearing targets. We propose a simple mechanism that considers the response to a position step as consisting of the sum of two components: 1) a response to the position step that is symmetrical and due to the effect of the spatiotemporal filter generating a brief effective stimulus velocity as an input; and 2) a response to the sudden disappearance of the stimulus from the foveal region, such as that in Fig. 6C. When the position step is backward, the responses produced by the two components are in the same direction, namely backward. When the step is onward the direction of the two responses conflict and the sum of the accelerations is near zero. The response to the change in target position, *component 1*, decreases as the step size increases, possibly because the effective velocity created by filtering is interpreted as occurring at the end of the step (compare with Fig. 7). Thus, when the step is very large—either onward or backward—only *component 2*, the disappearing response, is evident.

A conceptual model of the pursuit system

The mechanisms for smooth-pursuit responses that we have proposed can be combined in a relatively simple fashion to form a description of the smooth-pursuit system. Visual inputs are effectively low-pass filtered so that instantaneous changes in target location

are endowed with a finite velocity. The pursuit system is initially responsive only to target motion in the filtered input, and detection requires movement over a distance of 0.028° . Image motion occurring near the fovea is most effective in generating a response, with decreased sensitivity present in more peripheral retinal areas. After a processing delay of ~ 98 ms, an eye acceleration is generated with a soft saturation at $\sim 50^\circ/s^2$. A programmed slowing of the eyes occurs with a comparable latency when the target disappears from the foveal region, and the responses are added together. A later mechanism becomes active by 200 ms, is responsible for much higher accelerations, and is sensitive to adaptation. This later phase of the pursuit response might be related to the development of an internal estimate of target velocity. The sensory input is continuously evaluated and the responses are the same for initiation and maintenance of pursuit.

This characterization of pursuit has attempted only to describe mechanisms that seem to depend on retinal images, and as such cannot address pursuit eye motion seen before the stimulus onset or after predictive mechanisms become active. The variability of pursuit in these other modes has made general models of pursuit subject to criticism (35). The inclusion of cognitive factors in pursuit models will have to await a more quantifiable database, which is not likely to be available for some time.

This description of smooth pursuit has several important consequences for studies of human subjects. Measurements of pursuit accelerations and velocities occurring more than 200 ms after stimulus onset cannot be assumed to be dependent on stimulus properties in a simple fashion. Stimulus waveforms that include a disappearance of the target from the foveal region may introduce asymmetries in the response if the subject is already tracking. The accelerations to stimulus motion presented on the peripheral retina decrease with eccentricity so that measurable presaccadic tracking should not be expected when image motion occurs more than 10° from the fovea. Finally, although the response latencies are the same for ramp and step-ramp stimuli, the initial accelerations to a conflicting step-ramp may be too small to reliably describe.

These results should be of benefit to models of smooth pursuit in humans, as many aspects of the response have been quantified for the first time. The description of consistent responses across subjects should allow tracking deficits in humans to be examined in a quantitative fashion, and the suggestion of multiple independent mechanisms may lead to the

identification of deficits associated with individual response segments.

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