Smooth pursuit of small-amplitude sinusoidal motion

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Subjects used smooth eye movements to track small-amplitude sinusoidal target motions. Target frequencies (0.05 to 5 Hz) and amplitudes (1.9 to 30 min of arc) were in the range of those found in the retinal image during fixation of a stationary target while the head is not artificially supported. Smooth pursuit was poor at high target frequencies in several ways: (1) Large uncompensated drifts were observed for target frequencies between 1 and 4 Hz. The drifts were superimposed upon oscillations of the eye in response to the target motion. (2) Mean retinal-image speeds were higher than retinal-image speeds during slow control (smooth eye movements with stationary targets) for target frequencies above 0.5 Hz. Mean retinal-image speeds were as high as target speed for target frequencies above 3 Hz. (3) The ratio of eye speed to target speed decreased as target frequency and amplitude increased. The dependence on amplitude could be reduced and often eliminated by computing an adjusted ratio in which a constant (approximately equal to the mean speed of slow control) was subtracted from eye speed before dividing by target speed. Adjusted ratios declined for frequencies above 0.5 to 1 Hz and did not depend on amplitude. These results show that the response of the smooth-pursuit subsystem to target motion above 0.5 Hz is poor, even though the velocity and the acceleration of th motions are low. Models of smooth pursuit in which the response of the eye depends exclusively on the velocity, acceleration, or position of the target do not account for our results. Head oscillations above 0.5 Hz uncompensated by the vestibulo-ocular response will result in image motions that the pursuit subsystem cannot track during viewing of stationary targets with an unstabilized head.

INTRODUCTION

Previous research has shown that natural head rotation leads to more retinal image motion than is observed when the head is supported artificially. For example, Skavenski *et al.*[1] asked subjects to sit or stand, as still as possible, while fixating a distant stationary target. They found that the head oscillated at frequencies ranging from 0 to 7 Hz, with amplitudes typically less than 30 min of arc. The average speed of the retinal image during these head oscillations was about 20 to 40 min of arc/sec (about twice as fast as the average retinal-image speed observed in the same subjects when natural head rotations were prevented by a bite board).

Skavenski *et al.*[1] showed that the high retinal-image speeds occurred because the vestibulo-ocular response (VOR) does not compensate perfectly for the small-amplitude rotations characteristic of natural head movements. Compensation is typically much better for large-amplitude head rotations. Skavenski *et al.*[1] suggested that imperfect compensation of small rotations occurs because the compensatory systems adjust their response to ensure that the retinal-image speed is sufficiently high for clear vision. This suggestion is plausible for the VOR. The VOR rapidly adjusts to compensate for changes in retinal-image speed produced by magnifying or minifying spectacles.[2] But poor compensation by the VOR does not explain the failure of visually guided smooth-pursuit eye movements to reduce image speeds. The retinal-image speeds measured when the head was free were low enough so that accurate tracking would be expected, based on previous studies of smooth pursuit of low-frequency, periodic motion.[3,4] Perhaps natural retinal-image speeds were not reduced by smooth pursuit because the smooth-pursuit subsystem does not respond to image motion created by moving the head as well as it responds to image motion created by moving a target in space. Or, alternatively, perhaps the frequencies of image motion created by the head movements were too high to be tracked even though the amplitude of the motions was small, and, as a result, velocity and acceleration were low.

Previous studies[3–10] of smooth pursuit cannot choose between these alternatives, because the response to small-amplitude motions in the frequency range of natural head movements has not been studied. The target frequencies employed in previous studies were at the low end of the natural-head-movement range, and the target amplitudes were much larger than those found in the head rotations of subjects attempting to keep their heads as still as possible. Large amplitudes also meant that effects of increasing target frequency could not be unambiguously determined because detrimental effects of increasing target frequency were confounded with detrimental effects of increasing target velocity. We therefore studied smooth pursuit of target motions whose frequencies ranged from 0 to 5 Hz and whose amplitudes ranged from 1.9 to 30 min of arc, while the head was supported artificially.

METHODS

Eye-Movement Recording

Two-dimensional movements of the right eye were recorded by a Generation III SRI Double Purkinje Image Eye Tracker.[11] The left eye was covered and the head stabilized by a dental bite board. The voltage output of the tracker was fed on line through a 50-Hz low-pass filter to a 12-bit analog-to-digital converter (ADC) controlled by a computer. The

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ADC sampled eye position every 10 msec. Digitized voltages were stored for later analysis. Tracker noise on the horizontal and vertical meridians was measured with an artificial eye after the tracker had been adjusted so as to have the same first- and fourth-image reflections as the average subject's eye. The filtering and sampling rates were the same as those used in the experiments. Noise level, expressed as a standard deviation of position samples, was 0.65 min of arc.

Subjects

Two highly experienced eye-movement subjects (RS and EK) served in the complete series of experiments. A portion of the results was confirmed with a third experienced subject (GH).

Stimulus

The target, viewed through a collimating lens, was a well-focused point displayed on a cathode-ray tube (CRT) (Tektronix Model 604 with P4 phosphor). The intensity of the target was 2 log units above light-adapted foveal threshold. Two of the subjects (EK and GH) were myopic, and suitable negative lenses were placed between the tracker's dichroic mirror and the collimating lens to provide them with a well-focused image of the target. The target was viewed in complete darkness. All stray light was blocked by curtains and baffles.

The target was either stationary or moved horizontally sinusoidally at frequencies of 0.05, 0.1, 0.25, 0.5, 1, 2, 3, 4 and 5 Hz, with amplitudes of 1.9, 3.8, 7.5, 15, and 30 min of arc. The sinusoidal motions were produced by a signal generator (Tektronix Model 503). The voltage sent to the CRT was also sent to a channel of the ADC. This allowed eye and stimulus channels to be sampled at the same time so that a digital sample of stimulus position was obtained for each digital sample of eye position.

Procedure

The target was set in motion before the trial began. The subjects started the trial by pushing a button when they believed that they were pursuing the target well. This procedure was used to increase the likelihood of sampling the best possible tracking performance. Subjects were asked to avoid saccades and blinks during trials. Trials lasted 6 sec for target frequencies between 0.5 and 5 Hz, 9 sec for 0.25 Hz, 11 sec for 0.1 Hz, and 21 sec for 0.05 Hz.

Types of Sessions and Trials

Nine experimental sessions were run, one for each of the nine frequencies of target motion. Each session consisted of 20 trials. Three trials were run for each of the five amplitudes, which were tested in sequence from the largest (30 min of arc) to the smallest amplitude (1.9 min of arc). Following these trials with moving targets, two trials were run in which the target was stationary and the subject was asked to use smooth eye movements to maintain the line of sight on the target. Then, three trials were run in which the target was removed and the subject was asked to avoid making saccades while she remained in total darkness.

Data Analyses

Digitized eye- and target-position samples were analyzed by computer programs, which calculated mean 50-msec velocities of both the target and the eye. Fifty-millisecond samples were used because this duration was short enough to permit a sufficient number of velocity samples/cycle (at least four) to describe the response accurately at even the highest target frequency used (5 Hz). Fifty-millisecond eye-velocity samples containing saccades or containing portions of saccades were removed from analyses. Saccades were detected by means of a computer algorithm based on a velocity criterion. The accuracy of the algorithm was confirmed by visual inspection of analog eye-movement records in which flags marked the occurrence of saccades. Relatively few samples were removed because of saccades. For RS, 1,491 samples were removed out of a total of 25,870 samples; for EK, 1,115 samples were removed out of a total of 27,950 samples; for GH, 3,040 samples were removed out of a total of 20,430 samples.

RESULTS

Pursuit of High-Frequency, Small-Amplitude Target Motions Was Poor

Smooth pursuit was most prominent at target frequencies of less than 3 Hz. At 4 Hz, smooth pursuit was evident only

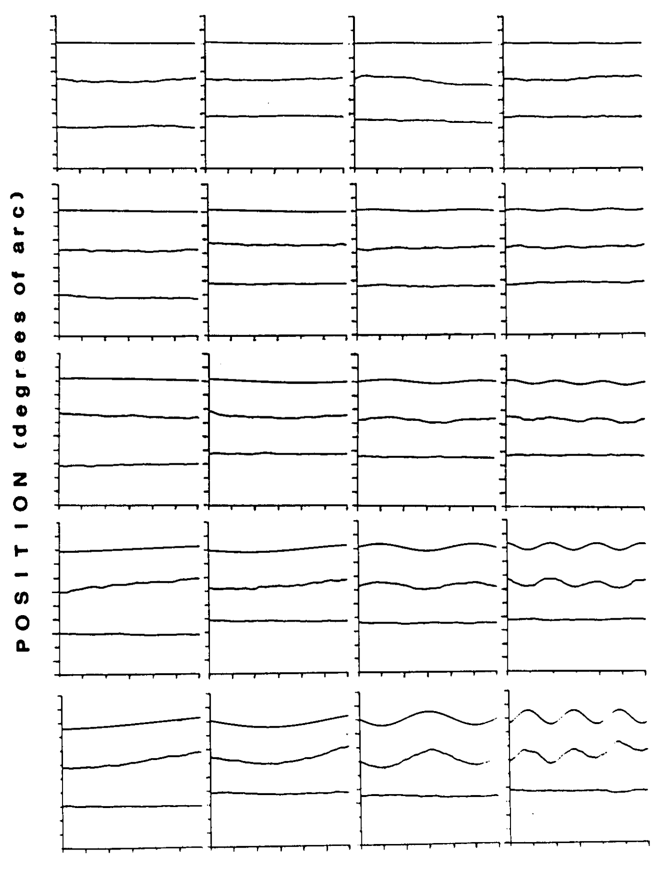

Fig. 1. Representative records of subject RS smoothly pursuing horizontal target motion. Frequencies were, from left to right, 0.05, 0.1, 0.25, and 0.5 Hz. Amplitudes were, from top to bottom, 1.9, 3.8, 7.5, 15, and 30 min of arc. The time scale shows 1-sec intervals and the position scale 1-deg rotations. Upper traces in each graph show the motion of the target, middle traces show horizontal eye movement, and lower traces show vertical eye movement. Upward changes in the traces signify rightward or upward motion. Trials at the three lower frequencies were longer than 6 sec, and only the first 6 sec are shown.

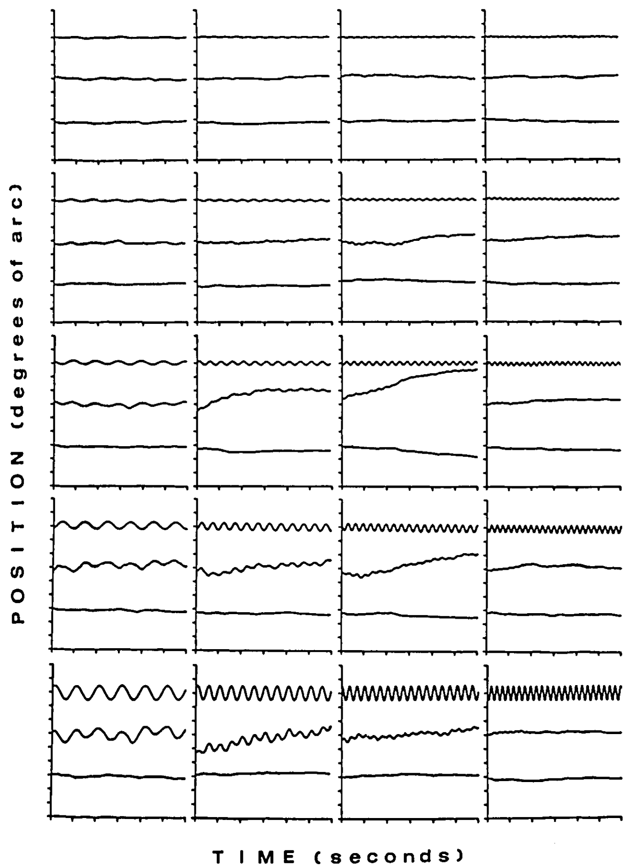

Fig. 2. Representative records of subject RS smoothly pursuing horizontal target motion. Frequencies were, from left to right, 1, 2, 3, and 4 Hz. Amplitudes were, from top to bottom, 1.9, 3.8, 7.5, 15, and 30 min of arc. The time scale shows 1-sec intervals and the position scale 1-deg rotations. Upper traces in each graph show the motion of the target, middle traces show horizontal eye movement, and lower traces show vertical eye movement. Upward changes in the traces signify rightward or upward motion.

during the initial seconds of the trial. After that, the smooth eye movements were barely distinguishable from the smooth eye movements observed when the target was stationary. At 5 Hz, smooth eye movements were always indistinguishable from smooth eye movements with stationary targets. These results are illustrated by eye-movement records of subject RS reproduced in Figs. 1 and 2.

Systematic Drifts Occurred during Smooth Pursuit

Smooth pursuit of target frequencies between 1 and 4 Hz was poor in that large systematic drifts of the eye away from its mean position were prominent. These systematic drifts were idiosyncratic in direction. RS drifted to the right. EK drifted to the left. Systematic drift is summarized by the mean 50-msec eye velocities shown in Fig. 3. A mean eye velocity of 0 min of arc/sec indicates that no systematic drift occurred, i.e., eye velocities to the right occurred about as often as eye velocities to left. Systematic drifts did not occur at frequencies below 1 Hz. Above 1 Hz, drift velocities could be as high as 27 min of arc/sec.

Because the subjects were instructed to avoid making saccades, the systematic drifts were not corrected during the trial, and the error between the eye and the target became quite large. For example, RS drifted as much as 2 deg to the right during the 6-sec trial at 3-Hz and 30-min-of-arc amplitude, reproduced in Fig. 2. EK's largest drift was 1.5 deg to the left at 4-Hz and at 15-min-of-arc amplitude. These errors were not corrected by smooth eye movements, i.e., the eye never turned around and drifted back toward the target.

Systematic drifts are known to occur when the fixation target is removed and the eye left in total darkness.[12] These drifts in the dark have been theoretically useful in the past. They have been used to show that there is a smooth oculomotor-control subsystem (slow control), which uses a visible target to maintain fixation position—a position from which the eye drifts when the target is removed.[13,14] The systematic drifts observed with a moving target suggested the possibility that particular frequencies and amplitudes of target motion inactivated slow control in much the same manner as it is inactivated by removing a stationary fixation target. This is not what is going on, however, because we found that systematic drifts produced by a target motion are not like drifts in the dark. Specifically, the idiosyncratic direction of motion-induced systematic drift was different from the idiosyncratic direction of dark drifts. In the dark, RS drifted down and to the right, and EK drifted up and to the left. The horizontal component of both subjects' drift in the dark was in the same direction as their systematic drift caused by horizontal target oscillation. This correspondence, however, did not occur between the vertical component of drift in the dark and the systematic drift caused by the vertical target oscillation (see Fig. 4).

We conclude that the systematic drifts observed with target motions from about 1 to 4 Hz did not arise from a failure to respond to a target moving at particular frequencies and amplitudes. Instead, the drifts arose from characteristics of the smooth-pursuit subsystem's response to visual properties of the target, for example, differences in the gain of the response as a function of the direction of target motion.

Smooth Pursuit Did Not Always Reduce Retinal-Image Speed

The results described up to this point show two ways in which smooth pursuit of high-frequency motion is poor. First, oscillations of the eye in response to high-frequency target motion are small relative to the amplitude of the target motion

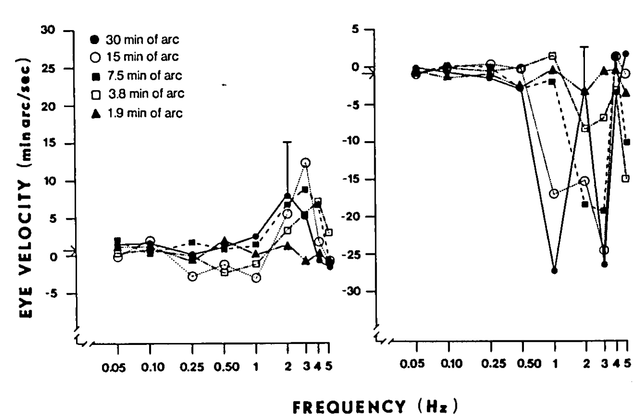

Fig. 3. Mean 50-msec smooth-pursuit velocity as a function of target frequency for subjects RS (left) and EK (right) for the five target amplitudes. Each mean velocity is based on about 300–600 samples. The largest standard error is shown by the vertical bar. The arrow on the ordinate shows mean 50-msec eye velocity measured when the target was stationary.

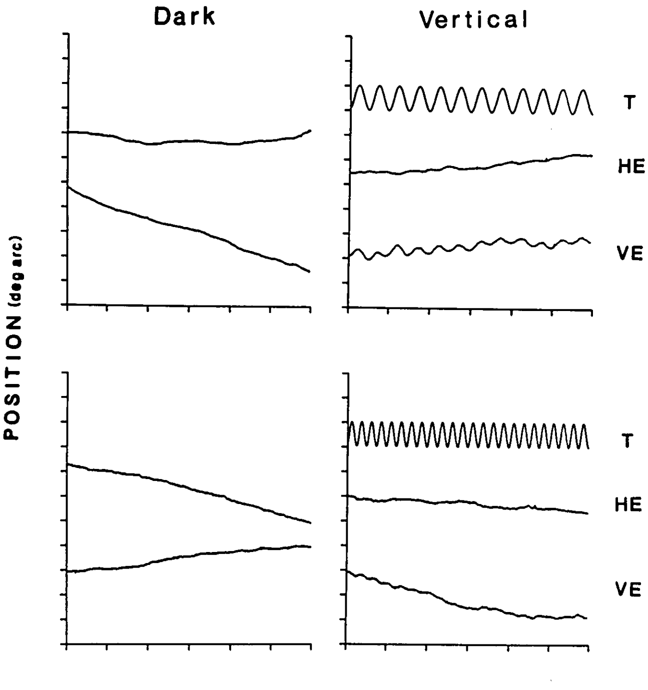

Fig. 4. Left graphs: Representative eye-movement records of subjects RS (top) and EK (bottom) showing horizontal (top traces) and vertical (bottom traces) eye movements made in the absence of a visual target (Dark). Right graphs: representative eye-movement records of RS (top) and EK (bottom) smoothly pursuing vertical target motion (top traces). Target amplitude was 30 min of arc for both subjects. Target frequency was 2 Hz for RS and 4 Hz for EK. Horizontal eye movements are shown in the middle traces, vertical in the lower traces. The time scale shows 1-sec intervals and the position scale 1-deg rotations. Upward changes in the traces signify rightward or upward motion.

(see Fig. 2). Second, systematic drifts away from the target are prominent (Figs. 2 and 3). These two characteristics imply that retinal-image speed with these high-frequency target motions will be high. Retinal-image speed was measured to verify this assertion and to provide a quantitative description of the smooth-pursuit response. Retinal-image speed was computed in the following way: Eye position was subtracted from target position at the same point in time to obtain a record of retinal-image position. Fifty-millisecond retinal-image speeds (absolute velocities) were then computed from the retinal-image positions. Speed samples containing saccades were detected and removed by the procedure described in the section entitled Methods. Mean retinal-image speeds are shown in Fig. 5.

Realize that the mean retinal-image speeds shown in Fig. 5 provide a measure of smooth-pursuit performance, which incorporates effects of both the speed and the direction of the pursuit. Retinal-image speed is zero when the movement of the eye perfectly matches the movement of the target. Retinal-image speed is greater than zero when the eye tracks slower or faster than the target or when the eye does not move in the same direction as the target.

Mean retinal-image speed was never zero. In fact, it was never less than the mean eye speed observed during slow control when the target was stationary. This was true even when the mean speed of the target was slower than the mean speed of slow control. For example, at 0.05 Hz, the mean 50-msec speed of the target ranged from 0.4 to 6 min of arc sec depending on target amplitude. Subject RS's mean retinal-image speed was 14 min of arc sec. EK's was 22 min of arc sec. Their mean retinal-image speeds were about the same as mean retinal-image speeds during slow control shown by the arrow on the ordinate in Fig. 5.

Retinal-image speed increased to values greater than the speed of slow control for target frequencies above 0.25 Hz. Nevertheless, smooth pursuit was at least partially effective in that retinal-image speed was less than target speed at frequencies from 0.5 to 2 Hz. At higher frequencies (3–5 Hz for RS and 4–5 Hz for EK), smooth pursuit was totally ineffective. Retinal-image speed was the same as target speed. Note that, at 3 Hz, although retinal-image speed was equal to target speed for RS, the eye nevertheless oscillated at target frequency, as can be seen in the analog eye-movement records reproduced in Fig. 2. These oscillations of the eye were not effective in reducing retinal-image speed because the eye did not always move in the same direction as the target.

The ineffective tracking observed for high target frequencies was not due to high target speeds. Peak target speeds were low enough for effective tracking to be expected, based on previous measurements[3] of smooth-pursuit velocity with large-amplitude (7–10-deg), low-frequency (<0.52-Hz), periodic (sinusoidal or triangular) target motions.[3] Consider, for example, the speeds of our 4-Hz target motion. Peak speeds were 0.8, 1.6, 3.1, 6.3, and 12.6 deg/sec for the five target amplitudes. Collewijn[3] and Tamminga reported smooth-pursuit gains greater than 0.9 for target speeds less than 5 deg/sec. Gain fell to only about 0.8 when target speeds increased to about 10 deg/sec (see their Fig. 7). The effective pursuit that Collewijn and Tamminga observed for low-frequency, large-amplitude motions was not observed for the high-frequency, small-amplitude motions that we studied in the same velocity range. Instead, we found totally ineffective pursuit. Retinal-image speeds were the same as target speeds.

The tracking observed for the intermediate target frequencies (0.5, 1, and 2 Hz) was partially effective: Retinal-image speeds were less than target speed but greater than the speed of slow control. Did the effectiveness of tracking at these frequencies depend on the speed of the target? If

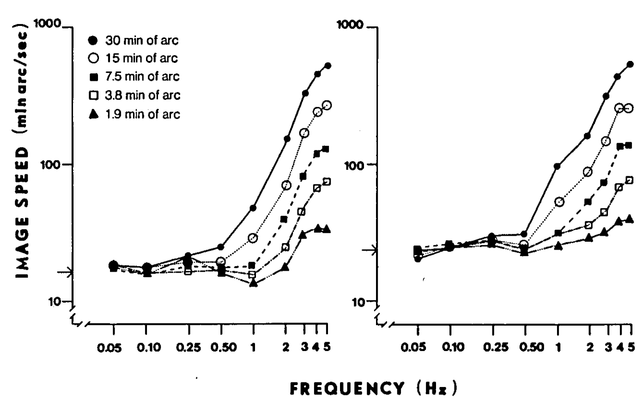

Fig. 5. Mean 50-msec retinal-image speed as a function of target frequency for subjects RS (left) and EK (right) for the five target amplitudes. Each mean speed is based on about 300–600 samples. The standard errors are smaller than the plotting symbols. The arrow on the ordinate shows mean 50-msec retinal-image speed measured when the target was stationary.

target speed alone determined tracking effectiveness, then retinal-image speed should vary as a function of target speed regardless of target frequency. This, however, was not what we observed. For RS, increasing target frequency above 1 Hz increased retinal-image speed, even when mean target speed remained the same. For EK, increasing target frequency from 0.5 to 1 Hz and from 2 to 3 Hz increased retinal-image speed when target frequency remained the same. Increasing frequency was not always detrimental, however. Increasing frequency from 0.5 to 1 Hz for RS and from 1 to 2 Hz for EK had no effect on retinal image speed.[15] These results are shown in Fig. 6.

The peak acceleration of the target did not determine tracking effectiveness. Families of target motions with the same peak accelerations had different retinal-image speeds (see, for example, the retinal speeds for the 1-Hz, 30-min-of-arc, the 2-Hz, 7.5-min-of-arc, and the 4-Hz, 1.9-min-of-arc motions shown in Fig. 5). This result does not support previous claims that peak acceleration, rather than target velocity or frequency, best predicts the response of the eye.[9]

In summary, our results show that increasing target frequency produced considerable retinal-image motion, which could not be attributed to effects of target speed or acceleration.

Smooth Eye Speed Contains a Constant and a Variable Component

The response of the eye to the motion of the target was summarized quantitatively by the mean 50-msec eye speed (absolute value of eye velocity). We believed that mean eye speed would provide a useful description of the response to the target motion for two reasons. First, mean eye speed, unlike mean retinal-image speed, provides a measure of tracking performance that should be unaffected by the large systematic drifts that were observed at target frequencies between 1 and 4 Hz (see Fig. 3). Such drifts should not affect eye speed because the relative increase in eye speed for movements in the direction of the systematic drift will be canceled by the relative decrease in eye speed for movements in the opposite direction. Second, mean eye speed has been used previously to describe the response of the eye to retinal motion produced by the natural oscillations of the head.[1] Analysis of mean eye speed in the present experiment, when retinal motions were produced by oscillations of a visual target in the same frequency and amplitude range, facilitates comparison with previous research. Note, however, that mean eye speed, unlike mean retinal-image speed described in the previous section, contains information about how fast the eye traveled relative to the target and not about the direction of the eye relative to the target.

Mean 50-msec eye speeds are shown in Fig. 7. Mean eye speeds never fell below the value observed during slow control when the target was stationary.

Figures 8 and 9 (left-hand graphs) show the ratio of mean eye speed to mean target speed as a function of target frequency. Ratios ranged from about 0.03 (for 5-Hz, 30-min-of-arc amplitude) to about 60 (for 0.05-Hz, 1.9-min-of-arc amplitude), indicating that the eye traveled much faster than the target at the low frequencies.

Why did the eye travel so much faster than the target? Recall that we found that eye speed during smooth pursuit never fell below a minimum value that was approximately equal to the speed of the subjects' slow control when targets were stationary (see Fig. 7). Suppose that the oscillations of the eye seen during slow control persist during smooth pursuit, when targets are in motion. The response of the eye to the target motion, then, would consist of a constant eye speed approximately equal to the speed of slow control and a variable eye speed proportional to the speed of the target. The suggestion that the oscillations of the eye seen during fixation of a stationary target also appear during smooth pursuit of a moving target is not new. Rashbass[16] and Yarbus[17] both described the presence of these oscillations during smooth pursuit. We will extend their observations by determining how taking these oscillations into account affects the quantitative description of the response of the eye to motion of the target.

We took oscillations into account in the following way. An adjusted speed ratio ($R'_{a,f}$) was calculated for each target frequency (f) and each amplitude (a) by subtracting the mean speed of the subject's slow control (S_f), measured in the trials following testing at each target frequency, from his mean eye speed ($E_{a,f}$) before dividing by mean target speed ($T_{a,f}$). That is,

$$R'_{a,f} = \frac{E_{a,f} - S_f}{T_{a,f}}. \qquad (1)$$

We found that the adjusted speed ratios differed from the

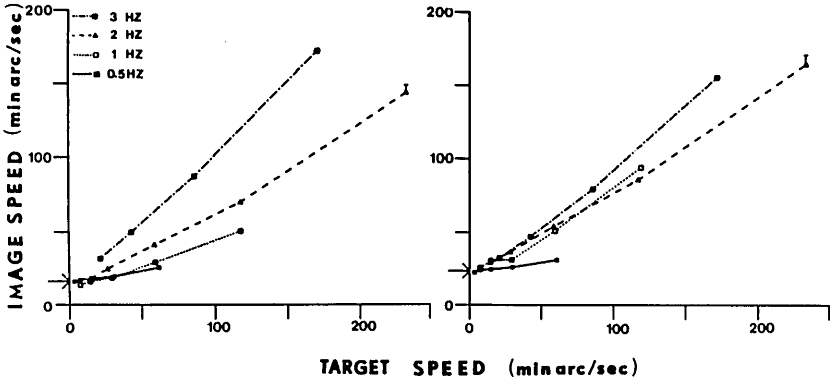

Fig. 6. Mean 50-msec retinal-image speed as a function of target speed for subjects RS (left) and EK (right) for four target frequencies. In each function, target speed was increased by increasing target amplitude. The mean retinal-image speed for the 3-Hz, 30-min-of-arc amplitude motion is not shown. Each mean speed is based on about 300–600 samples. The standard errors, when not shown, are smaller than the plotting symbols. The arrow on the ordinate shows mean 50-msec retinal-image speed measured when the target was stationary.

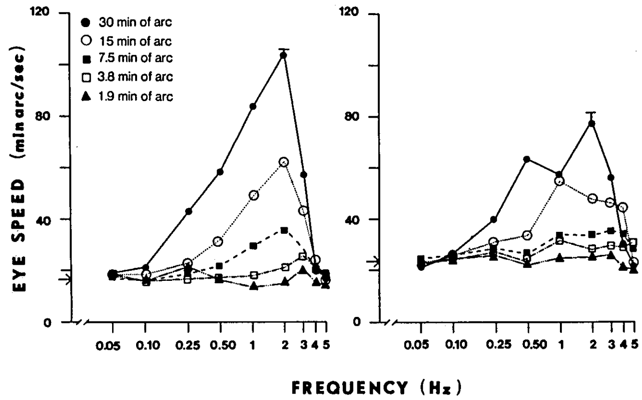

Fig. 7. Mean 50-msec smooth-pursuit speed (absolute velocity) as a function of target frequency for subjects RS (left) and EK (right) for the five target amplitudes. Each man velocity is based on about 300–600 samples. The largest standard error is shown by the vertical bar. Most standard errors were smaller than the plotting symbols. The arrow on the ordinate shows mean 50-msec eye speed measured when the target was stationary.

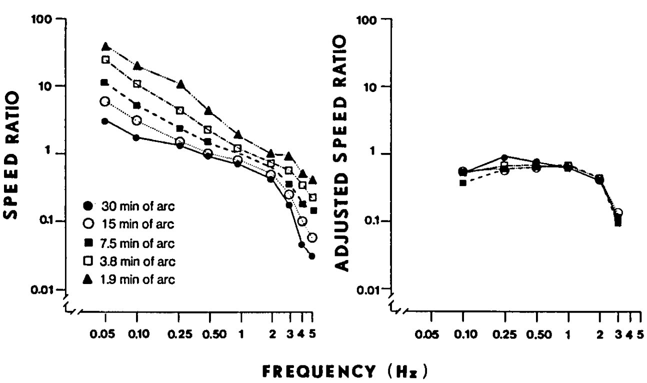

Fig. 8. Left graph: speed ratio (mean 50-msec eye speed/mean 50-msec target speed) for subject RS as a function of target frequency for the five target amplitudes. Right graph: adjusted speed ratio $R''_{a,f}$ [see Eq. (2)] as a function of target frequency for four target amplitudes (30, 15, 7.5, and 3.8 min of arc).

original speed ratios ($E_{a,f}/T_{a,f}$) in a surprising way: The effect of target amplitude on the ratio was reduced and, in some cases, eliminated.

These results showed that subtracting a constant from mean eye speed reduced the effect of target amplitude on the speed ratio. The effect of amplitude might be reduced further by choosing a different constant. To test this possibility, we computed an adjusted speed ratio ($R''_{a,f}$) in a different way. Instead of subtracting the mean speed of slow control from mean eye speed we subtracted the constant (K_f) that minimized differences among the speed ratios at each target frequency. Thus

$$R''_{a,f} = \frac{E_{a,f} - K_f}{T_{a,f}}; \tag{2}$$

K_f was determined separately for each target frequency by use of a computerized search procedure.[18,19] We expected K_f to be similar, but not necessarily equal, to the mean speed of slow control.

Adjusted speed ratios were computed only when mean eye speed reliably exceeded the speed of slow control (see Fig. 7). Thus adjusted speed ratios were computed for frequencies from 0.10 to 3 Hz for RS and from 0.25 to 3 Hz for EK at amplitudes between 3.8 and 30 min of arc.

Adjusted speed ratios ($R''_{a,f}$) are shown in the right-hand graphs of Figs. 8 and 9. Adjusted speed ratios were always less than 1 and did not depend on the amplitude of the target motion. These results were confirmed with a third subject, GH. Her performance is summarized in Fig. 10.

Adjusted speed ratios did not differ appreciably as a function of target frequency when frequency was low. RS's and GH's ratios, for example, were about the same for target frequencies up to about 1 Hz and decreased for higher frequencies. EK's ratios began to decrease when frequency exceeded 0.5 Hz, except that her ratios for the 1- and 2-Hz frequencies were about the same. The same idiosyncratic pattern of effects of target frequency on pursuit were described earlier for the mean retinal-image speeds of RS and EK (see Fig. 6). The correspondence of the results from these two measures supports the suggestion that the minimum constant eye speed must be taken into account before evaluating the ratio of eye and target speed. When this constant is taken into account, smooth pursuit of high-frequency, small-amplitude motions is shown to vary most prominently as a function of target frequency. Effects of target amplitude are small.

The constants (K_f) used to compute the adjusted speed

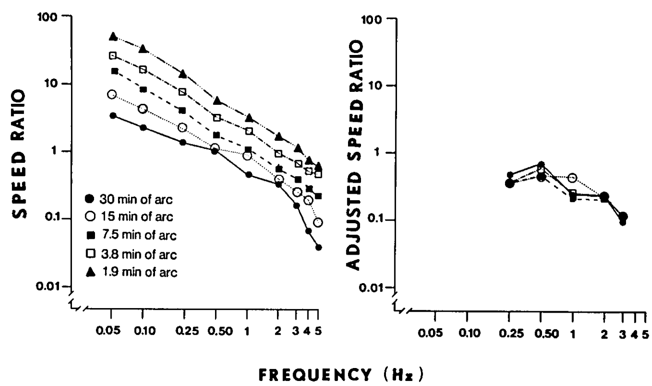

Fig. 9. Left graph: speed ratio (mean 50-msec eye speed/mean 50-msec target speed) for subject EK as a function of target frequency for the five target amplitudes. Right graph: adjusted speed ratio $R''_{a,f}$ [see Eq. (2)] as a function of target frequency for four target amplitudes (30, 15, 7.5, and 3.8 min of arc).

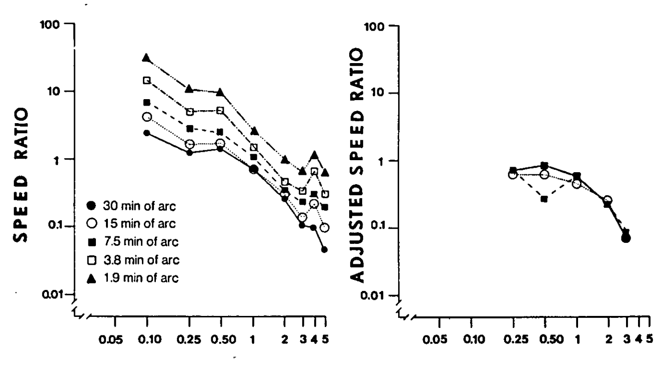

Fig. 10. Left graph: speed ratio (mean 50-msec eye speed/mean 50-msec target speed) for subject GH as a function of target frequency for the five target amplitudes. Right graph: adjusted speed ratio R'',a,f [see Eq. (2)] as a function of target frequency for four target amplitudes (30, 15, 7.5, and 3.8 min of arc).

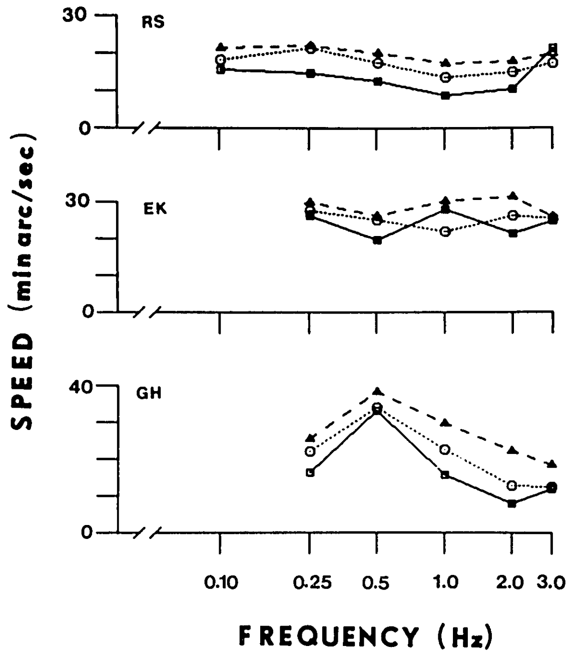

Fig. 11. The value of the constant (K_f) that minimized the differences among adjusted speed ratios at each target frequency (solid line), the mean speed of slow control for the trials following testing at each target frequency (dotted line), and the mean eye speed in darkness measured in trials following testing at each target frequency (dashed line) as a function of target frequency for three subjects (RS, EK, and GH).

ratios ($R''_{a,f}$) for each target frequency were, as expected, similar to the mean speed of slow control measured in the trials following testing at each target frequency. This result is shown in Fig. 11. Note that K_f, the mean speed of slow control, and the mean speed of the eye in the dark all varied in the same way with target frequency. Note well that K_f was not identical to the speed of slow control. K_f was almost always (in 15 out of 16 cases) less than the speed of slow control. The differences, however, were small. The mean speed of slow control was usually about 3 min of arc/sec faster than K_f.

Summary of Results

There were three main findings:

(1) The effectiveness of smooth pursuit (the reduction of retinal-image speed) varied with target frequency. At the lowest frequencies (0.05–0.25 Hz), smooth pursuit was most effective, i.e., retinal-image speed during smooth pursuit was about the same as retinal-image speed during slow control. At higher target frequencies (0.5–2 Hz), smooth pursuit was less effective. Retinal-image speed was greater than the retinal-image speed of slow control. At the highest frequencies (3–5 Hz), smooth pursuit was totally ineffective. Retinal-image speed was equal to the speed of the target.

(2) Smooth pursuit at intermediate target frequencies (1–4 Hz) was characterized by a systematic drift in idiosyncratic directions away from the target's mean position. Position errors as large as 2 deg, created by these drifts, were never corrected by smooth eye movements.

(3) The ratio of mean eye speed to mean target speed decreased as target frequency increased, and it decreased as target amplitude increased for each target frequency. Ratios, when eye speed exceeded the speed of slow control, ranged from about 0.03 to 3. The dependence of the ratios on amplitude could be reduced and often eliminated by subtracting a constant eye speed from the mean eye speed before dividing by mean target speed. The resulting speed ratios ranged from about 0.1 to 0.85. The constant eye speed was approximately equal to the mean eye speed of slow control.

DISCUSSION

The Functional Significance of the Constant Eye Speed

The constant eye speed (K_f) might represent the goal of smooth pursuit, viz., it guarantees a small amount of retinal-image slip, which might be beneficial to vision while fixating a stationary target or while tracking a moving target. If this were the case, then the contribution of the constant eye speed would have appeared only when the target was stationary or when all target motion was corrected by effective smooth pursuit. This cannot be its purpose, however, because we found that the constant eye speed was present even when there was appreciable retinal-image slip during smooth pursuit.

More likely, the constant eye speed represents noise in the smooth pursuit subsystem—a response uncorrelated with target motion or even with the presence of a visible target. Previous researchers have noted such noisy oscillations superimposed upon the smooth-pursuit response of both rabbits[20] and humans.[16,17] One note of caution: The noisy oscillations, which are uncorrelated with the motion of the target, contribute to the smooth-eye-movement response to a stationary target. But the smooth-eye-movement response to a stationary target does not consist entirely of noise, contrary to Cornsweet's[21] original proposal. It has been known since 1959 that smooth eye movements can maintain the line of sight on a stationary target.[13] This field-holding reflex has been referred to as slow control.[14]

We suspect that the response of the eye to the stationary target is superimposed upon the noisy oscillations in the same way that the response of the eye to moving targets is superimposed upon the oscillations. Our finding that the constant was a few minutes of arc per second slower than the mean speed of slow control in all three subjects supports this conclusion.

The Stimulus for Smooth Pursuit

A frequent goal of studies of smooth eye movements has been to search for the stimulus for smooth pursuit, that is, the particular characteristic of target motion that best predicts the effectiveness of pursuit. Various candidate stimuli have been proposed, including the position of the target on the retina relative to the fovea,[22] the velocity of the target,[3,23,24] and the acceleration of the target.[9,16] Our results show that none of these is exclusively responsible for pursuit.

Our results argue against retinal position as the stimulus for smooth pursuit for the following reason: We found pronounced systematic drifts during pursuit of target frequencies between 1 and 4 Hz. As the eye drifted, the difference between the position of the eye and the position of the target steadily increased. But the smooth oscillations in response to target motion continued in the presence of these steadily increasing position errors. This result shows that smooth-pursuit eye movements are made in response to the target motion and not to its retinal position. We found that smooth eye movements *created* large position errors while continuing to reduce retinal-slip velocity.

Our results also show that neither target velocity nor target acceleration can be exclusively responsible for pursuit. We found that pursuit of high-frequency (3-Hz or greater), small-amplitude (30-min-of-arc or less) motions was totally ineffective (i.e., retinal-image speed was the same as target speed), even though both target velocity and acceleration were sufficiently low that good pursuit would be expected based on previous studies with low-frequency, large-amplitude motions.[3,9] Our results show that high-frequency target motion is not tracked accurately, regardless of target speed or acceleration.

Realize that we are not suggesting that target frequency alone determines pursuit but rather that high target frequencies are detrimental. Recent experiments by Collewijn and Tamminga[3] (employing large-amplitude, low-frequency motions) have firmly rejected target frequency as the only stimulus. They found, for example, that smooth-pursuit gain decreased with increasing frequency when pure sinusoidal motion was tracked. But when pseudorandom motion was tracked (sums of sinusoids), the gain of the response to the sinusoidal components was generally lower than the gain with single sinusoids, and the gain increased with increasing target frequency.

The reason that high-frequency motions are hard to track is not that the eye cannot oscillate at high frequencies. High-frequency oscillations are present in slow control and, also, in response to high-frequency head rotations. The failure to track high-frequency motions accurately is likely to arise from the slow processing of information about changes in the direction of retinal motion or from the inability to change expectations quickly about the direction of future target motion.[25–28] These limitations should apply even to the tracking of complex patterns of motion containing high-frequency components.

Implications for Natural Retinal-Image Motion

The frequencies and the amplitudes of the sinusoidal target motions used were physiological in the sense that they contain retinal-image motions observed when a subject sits as still as possible with an unsupported head. We found that the smooth pursuit of targets oscillating in this frequency–amplitude range, in the absence of the VOR, reduced retinal-image oscillations in the range of 0.5–2 Hz only modestly. At higher frequencies, retinal motion was not reduced at all. These results clarify the role of visually guided smooth eye movements in determining retinal-image speed when the head is not artificially supported. The high retinal-image speeds observed when subjects try to hold their heads as still as possible is likely to arise from two sources: The first is the failure of the VOR to compensate fully for the head rotations.[1] The second is the failure of smooth pursuit to follow components of motion accurately with frequencies greater than about 0.5 Hz. There is no need to propose that the response of visually guided smooth eye movements to retinal motion created by moving a target in space is any different from the response of visually guided smooth eye movements to retinal motion created by rotation of the head. It would now be of interest to find out whether small-amplitude retinal-image motions between 0.5 and 5 Hz, which our results have shown will not be removed by smooth-pursuit eye movements, are particularly beneficial for vision.

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REFERENCES

1. A. A. Skavenski, R. Hansen, R. M. Steinman, and B. J. Winterson, "Quality of retinal image stabilization during small natural and artificial body rotations in man," Vision Res. **19**, 675–683 (1979).
2. H. Collewijn, A. J. Martins, and R. M. Steinman, "Compensatory eye movements during active and passive head movements: fast adaptation to changes in visual magnification," J. Physiol. **340**, 259–286 (1983).
3. H. Collewijn and E. P. Tamminga, "Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds," J. Physiol. **351**, 217–250 (1984).
4. E. Kowler, B. J. Murphy, and R. M. Steinman, "Velocity matching during smooth pursuit of different targets on different backgrounds," Vision Res. **18**, 603–605 (1978).
5. D. H. Fender and P. W. Nye, "An investigation of the mechanisms of eye movement control," Kybernetik **1**, 81–88 (1961).
6. L. Stark, G. Vossius, and L. R. Young, "Predictive control of eye tracking movements," IRE Trans. Hun. Factors Electron. **HFE-3**, 52–57 (1962).
7. P. J. Dallos and R. W. Jones, "Learning behavior of the eye fixation control system," IRE Trans. Autom. Control **AC-8**, 216–227 (1963).
8. B. J. Winterson and R. M. Steinman, "The effects of luminance on human smooth pursuit of perifoveal and foveal targets," Vision Res. **18**, 1165–1172 (1978).
9. S. G. Lisberger, C. Evinger, G. W. Johanson, and A. F. Fuchs, "Relationship between eye acceleration and retinal image velocity during foveal smooth pursuit in man and monkey," J. Neurophysiol. **46**, 229–249 (1981).
10. J. A. Michael and G. Melvill Jones, "Dependence of visual tracking capabilities upon stimulus properties," Vision Res. **6**, 707–716 (1966).
11. T. N. Cornsweet and H. D. Crane, "An accurate eye tracker using first and fourth Purkinje images," J. Opt. Soc. Am. **63**, 921–928 (1973).
12. A. A. Skavenski and R. M. Steinman, "Control of eye position in the dark," Vision Res. **10**, 193–203 (1970).
13. J. Nachmias, "Two-dimensional motion of the retinal image during monocular fixation," J. Opt. Soc. Am. **49**, 901–908 (1959).
14. R. M. Steinman, G. M. Haddad, A. A. Skavenski, and D. Wyman, "Miniature eye movement," Science **181**, 810–819 (1973).
15. An increase in retinal-image speed with target speed, such as that shown in Fig. 6, need not mean that the quality of the pursuit response gets worse with increasing target speed. A linear increase of retinal-image speed as a function of target speed would be expected if pursuit gain (eye speed/target speed) was constant and less than 1 across target speeds.

16. C. Rashbass, "The relationship between saccadic and smooth tracking eye movements," J. Physiol. **159,** 326–338 (1961).
17. A. L. Yarbus, *Eye Movements and Vision* (Plenum, New York, 1967), p. 162.
18. J. P. Chandler, "STEPIT: Finds local minima of a smooth function of several parameters," Behav. Sci. **14,** 81–82 (1969).
19. The constant K_f was determined to be that which minimized the sum of the pairwise differences of the speed ratios $R''_{a,f}$. Other methods of computing K_f, such as minimizing the standard deviation of the mean of the speed ratios for a given frequency, produced the same results.
20. H. Collweijn, "Latency and gain of the rabbit's optokinetic reactions to small movements," Brain Res. **36,** 59–70 (1972).
21. T. N. Cornsweet, "Determination of the stimulus for involuntary drifts and saccadic eye movements," J. Opt. Soc. Am. **46,** 987–993 (1956).
22. H. J. Wyatt and J. Pola "Slow eye movements to eccentric targets," Invest. Ophthalmol. Vis. Sci. **21,** 477–483 (1981).
23. H. Collewijn, "Optokinetic eye movements in the rabbit: input and output relations," Vision Res. **9,** 117–132 (1969).
24. J. de W. Puckett and R. M. Steinman, "Tracking eye movements with and without saccadic correction," Vision Res. **9,** 695–703 (1969).
25. E. Kowler and R. M. Steinman," "The effect of expectations on slow oculomotor control—I. Periodic target steps," Vision Res. **19,** 619–632 (1979).
26. E. Kowler and R. M. Steinman, "The effect of expectations on slow oculomotor control—II. Single target displacements," Vision Res. **19,** 633–646 (1979).
27. E. Kowler and R. M. Steinman, "The effect of expectations on slow oculomotor control—III. Guessing unpredictable target displacements," Vision Res. **21,** 191–203 (1981).
28. E. Kowler, A. J. Martins, and M. Pavel, "The effect of expectations on slow oculomotor control—IV. Anticipatory smooth eye movements depend on prior target motion," Vision Res. **24,** 197–210 (1984).