



Comparison of Horizontal, Vertical and Diagonal Smooth Pursuit Eye Movements in Normal Human Subjects

KLAUS G. ROTTACH,* ARI Z. ZIVOTOFSKY,† VALLABH E. DAS,† LEA AVERBUCH-HELLER,*
 ALFRED O. DISCENNA,* ANUCHIT POONYATHALANG,* R. JOHN LEIGH*†‡§

Received 19 July 1995; in revised form 1 November 1995

We compared horizontal and vertical smooth pursuit eye movements in five healthy human subjects. When maintenance of pursuit was tested using predictable waveforms (sinusoidal or triangular target motion), the gain of horizontal pursuit was greater, in all subjects, than that of vertical pursuit; this was also the case for the horizontal and vertical components of diagonal and circular tracking. When initiation of pursuit was tested, four subjects tended to show larger eye accelerations for vertical as opposed to horizontal pursuit; this trend became a consistent finding during diagonal tracking. These findings support the view that different mechanisms govern the onset of smooth pursuit, and its subsequent maintenance when the target moves in a predictable waveform. Since the properties of these two aspects of pursuit differ for horizontal and vertical movements, our findings also point to separate control of horizontal and vertical pursuit. Copyright © 1996 Elsevier Science Ltd.

Smooth pursuit Eye movements Step-ramps Human

INTRODUCTION

Smooth pursuit eye movements “keep the line of regard congruent with the line of interest” (Dodge, 1903), so that the image of a moving object is held close to the fovea. Most studies of smooth pursuit have dwelt on various aspects of horizontal tracking, defining its dynamic properties either in response to predictable target motion (e.g. sine waves), or the onset of pursuit as subjects attempt to track an object that suddenly begins to move. A few studies have compared smooth pursuit of sinusoidal target motion in the horizontal and vertical planes, and have found better tracking for horizontal target motion (Collewijn & Tamminga, 1984; Baloh *et al.*, 1988; Grant *et al.*, 1992). On the other hand, differences between the *onset* of horizontal and vertical smooth pursuit have not received as much attention. Using step-ramp stimuli (Rashbass, 1961), Tychsens and

Lisberger (1986) studied pursuit initiation in response to horizontal and vertical target motion. They found that horizontal responses were greater when the target moved towards the vertical meridian, and that vertical responses were greater when target motion started in the lower field and moved up or down. They did not systematically compare horizontal or vertical responses, but they provided evidence that, in some subjects, vertical eye acceleration may be higher than horizontal acceleration (their Fig. 3). Under natural conditions, we may visually follow the motion of objects (e.g. birds) that travel in oblique trajectories; however, little information is presently available on how smooth pursuit behaves under these conditions, and how the horizontal and vertical components interact.

The purpose of this study was to compare horizontal and vertical smooth pursuit, using sinusoidal, triangular and step-ramp stimuli, in normal human subjects. We wanted to know whether horizontal–vertical differences in each individual were similar for each type of smooth pursuit response. In addition, we investigated these horizontal–vertical differences during diagonal smooth pursuit, and during tracking of a target moving in a circle.

METHODS

We studied five healthy subjects (age range 29–48 yr); three were male, all were emmetropes, and none was taking medication. Two (subjects 2 and 5) had no prior

*Department of Neurology, Department of Veterans Affairs Medical Center and University Hospitals, Case Western Reserve University, Cleveland, OH 44106, U.S.A.

†Department of Biomedical Engineering, Department of Veterans Affairs Medical Center and University Hospitals, Case Western Reserve University, Cleveland, OH 44106, U.S.A.

‡Department of Neuroscience, Department of Veterans Affairs Medical Center and University Hospitals, Case Western Reserve University, Cleveland, OH 44106, U.S.A.

§To whom all correspondence should be addressed [Email: rjl4@po.cwru.edu].

experience as subjects. All subjects gave informed consent in accordance with the Declaration of Helsinki.

Eye movement measurements

During the recording sessions, horizontal and vertical rotations of the dominant eye were measured, using the magnetic search coil technique with 6 ft field coils (CNC Engineering, Seattle, WA); subjects viewed monocularly with this eye. The system was 98.5% linear over an operating range of ± 20 deg in both planes, cross-talk between horizontal and vertical channels was $< 2.5\%$ and the standard deviation (SD) of system noise of < 0.02 deg. Search coils were calibrated prior to each experimental session using a protractor device. Coil signals were passed through 4-pole Butterworth filters (Krohn-Hite Corporation, Avon, MA, model 3321) with bandwidth 0–25 Hz prior to digitization at 333 Hz (for step-ramp stimuli) or 200 Hz (for sinusoidal stimuli).

Experimental stimuli

The visual stimulus was a red He–Ne laser spot that was rear-projected onto a semitranslucent tangent screen 1.2 m in front of the subjects; it subtended 0.1 deg with a luminance of 10 cd/m² against a background luminance of < 1.0 cd/m². The position of the laser spot was determined by an X–Y mirror galvanometer (General Scanning DX2003) under the control of a 80486 computer. *Sine waves* had an amplitude of ± 20 deg and a frequency of 0.4 Hz (peak velocity of 50.26 deg/sec). The target moved horizontally, vertically, diagonally, or circularly. Diagonal movements were in two directions: upper-left to lower-right (“backslash”) and upper-right to lower-left (“slash”). *Triangular-waveform* target motion, ± 20 deg at 35.5 deg/sec, was also presented. *Step-ramps* always started with the target stationary at the central fixation point (“zero”) and moved in various centrifugal directions. The step was directed opposite to the subsequent ramp, and we adjusted the step size so that the target moved back through zero 200 msec after the step; in preliminary experiments, we found this to be an optimal arrangement to avoid saccades. The following stimuli were presented: purely horizontal and purely vertical step-ramps with velocities of 10.0, 14.14, 20.0 and 28.28 deg/sec, diagonal step-ramps with identical velocities of the horizontal and vertical component of 10.0 and 20.0 deg/sec (resulting in angular velocities of 14.14 and 28.28 deg/sec, respectively); each trial contained six step-ramps at one velocity and lasted 30 sec. The step-ramp stimuli were randomized in direction, duration (0.4–1.5 sec) and in the time the target was stationary at zero (1.0–2.25 sec) before the onset of motion.

Data analysis

For data analysis we used interactive programs written in the ASYST language.

Responses to sine waves. Using velocity signals, we applied an interactive desaccading procedure modified from Barnes (1982) and measured the pursuit gain from

linear regression of remaining points (typically 2000–2500) of desaccaded eye velocity and target velocity; we also calculated the standard error of the regression slope (Glanz, 1992). We calculated the phase shift between target and gaze velocity using a fast Fourier transform. For diagonal and circular stimuli, horizontal and vertical signals were analyzed separately. For triangular target motion, we measured the gain from four segments (each at least 750 msec, two in each direction) of the best pursuit in each plane, avoiding transients corresponding to turn-around points.

Responses to step-ramp stimuli. In order to determine the onset of the smooth pursuit movement we employed a regression technique (Carl & Gellman, 1987; Morrow & Sharpe, 1993). The digitized gaze position signals were filtered using a Blackman window with bandwidth 0–15 Hz (Oppenheim & Schaffer, 1989) and then differentiated to obtain the gaze velocity signal. Both this digital filtering and the analog filtering of signals prior to digitization provided a pass-band much above that required for adequate resolution of pursuit eye movements (Martins *et al.*, 1985). A first regression line was fit along the baseline (zero velocity), calculated from the data points of 220 msec; a second regression line was fit along the velocity signal of the smooth pursuit response to the target ramp movement. The calculation was based on at least 60 msec of recording time, beginning 5 msec before gaze velocity exceeded three standard deviations above the baseline and ending where gaze acceleration exceeded the limit for saccades (500 deg/sec²). Onset of the presaccadic smooth pursuit was determined at the point where these two regression lines intersected. Responses with < 60 msec of smooth pursuit before the first catch-up saccade occurred were not analyzed. If the presaccadic smooth pursuit lasted > 100 msec, we used only the first 100 msec for the analysis in order to stay within the temporal bound of the open-loop response (Robinson, Gordon & Gordon, 1986); average eye acceleration was determined within this segment as described by Tychsen and Lisberger (1986). We also measured the maximum smooth pursuit eye velocity from the mean of three points: the highest value, and the points preceding and following it. When data were normal in distribution, we used a *t*-test for statistical comparisons; when data were not normal, we used the Mann–Whitney rank sum test or signed rank-sum test.

RESULTS

Sinusoidal, circular and triangular stimulus motion

All five subjects had lower mean gains for vertical pursuit of sinusoidal and triangular target motion compared to horizontal pursuit. This was also generally true when vertical and horizontal components of diagonal, sinusoidal and circular pursuit were compared, although the differences were generally less evident for the circular pursuit. Mean gain values are summarized in Table 1; standard error values were always < 0.02 . Representative responses are shown in Fig. 1(a) and

TABLE 1. Summary of gain values during sinusoidal, circular and triangular pursuit

S	PURE HOR	PURE VER	SL HOR	SL VER	B/SL HOR	B/SL VER	CW HOR	CW VER	CCW HOR	CCW VER	TRI HOR	TRI VER
1	0.98	0.91	1.00	0.91	1.02	0.97	1.03	1.02	1.00	0.98	1.02	0.92
2	0.99	0.87	1.01	0.92	0.98	0.89	0.99	0.89	0.97	0.85	1.00	0.71
3	0.97	0.82	0.99	0.86	0.90	0.78	0.99	0.90	0.99	0.79	0.99	0.86
4	0.95	0.85	0.95	0.87	0.94	0.90	0.96	0.92	0.94	0.94	1.01	0.96
5	0.89	0.52	0.79	0.65	0.87	0.76	0.86	0.74	0.83	0.83	0.88	0.65

S, subject; PURE HOR, purely horizontal target motion; PURE VER, purely vertical target motion; SL, "slash" diagonal motion; B/SL, "back-slash" diagonal motion; CW, clockwise circular target motion; CCW, counter-clockwise circular target motion; TRI, triangular target motion. Values given are means. SEM never exceeded 0.02 for any subject or test. Comparison of the group of subjects, using paired *t*-test, for corresponding tests (e.g. PURE HOR and PURE VER) was significant for all cases ($P < 0.05$) except CCW HOR and CCW VER.

(b). We used paired *t*-tests to compare, for the group of subjects as a whole, horizontal and vertical gain values for corresponding tasks (e.g. pure horizontal vs vertical tracking; horizontal and vertical components of "slash" diagonal tracking). We found that horizontal gain was significantly ($P < 0.05$) greater than vertical gain for all comparisons except for counter-clockwise target motion. When we compared the gains of up pursuit with down pursuit for each subject, differences were $<10\%$ with no directional preponderance, except for subject 3 (0.93 up; 0.77 down) and subject 5 (0.74 up; 0.43 down). Phase lags were generally small (median: 2.1 deg; range -4.0 – 5.8) during horizontal, vertical and diagonal pursuit, and there were no consistent differences between horizontal and vertical values. During circular pursuit, phase lags were larger (median: 5.5 deg; range 0.2–9.7) and, for all subjects, were greater for the horizontal component during clockwise tracking and for the vertical component during counter-clockwise tracking.

Step-ramp stimuli

We recorded a total of 1788 step-ramps, 1415 (79.1%) of which fulfilled our criteria for analysis of smooth pursuit initiation; the percentage of step-ramps that could be analyzed from each subject varied between 53.0 and 97.6%. Anticipatory responses (Kowler & Steinman, 1981) were encountered in $<5\%$ of trials and these were discarded. The majority of initial responses consisted of a smooth movement directed towards the step (Carl & Gellman, 1987); this response was of low velocity, occurred 110–150 msec after the step and soon reversed its direction, so that it was always in the direction of the ramp as the target passed through zero. Nevertheless, we always measured the latency of onset of the pursuit response to the ramp motion of the target, and this may account for our measured values (overall median latency of 207 msec) being larger than reported by others (e.g. Robinson *et al.*, 1986; Tychsen & Lisberger, 1986). For all responses to horizontal target motion, the median latency to onset of the pursuit response was 203 msec (range 189–213), and for vertical target motion, median latency was 207 msec (range 189–227); these results were not significantly different. For responses to diagonal target motion, the median latency of the overall response was 215 msec (range 195–263); differences between the time of onset of horizontal and vertical components were

undetectable in half the trials (overall, vertical components were later by a median of 2.5 msec, range 0–10). Thus, no significant differences were evident between horizontal and vertical latency values. Furthermore, no individual subject showed consistent differences between the latencies of horizontal and vertical pursuit responses.

We searched for individual left–right and up–down asymmetries of eye acceleration, as described by Tychsen and Lisberger (1986). All subjects showed differences for some of the stimulus velocities, but there was never a consistent pattern for all conditions and statistical significance ($P < 0.05$) was reached only for two or less of the four stimulus velocities for each subject. Furthermore, of the two subjects who showed better upward tracking of sinusoidal target motions, only subject 5 showed significant asymmetry for the 10 deg/sec stimulus ($P < 0.001$), with higher gain downwards. Thus, we pooled up and down as well as left and right responses, and only separated responses by stimulus velocity and main direction (horizontal, vertical, diagonal). The results of analyzing eye acceleration in response to step-ramps are summarized in Table 2; values given are medians and 25th–75th percentile ranges. When the eye acceleration responses to horizontal and vertical step-ramps of similar speeds were compared, four of the five subjects had higher vertical than horizontal accelerations at most stimulus speeds; this tendency was greater at higher stimulus speeds that were similar to those employed by Tychsen and Lisberger (1986). However, this difference was not consistent or significant for all four velocities. One subject had significantly higher horizontal accelerations at all four velocities. When the eye acceleration responses to diagonal step-ramps were compared, four subjects showed significantly higher vertical component acceleration for both 10 and 20 deg/sec diagonal stimuli. The subject with higher horizontal acceleration also had higher acceleration of the horizontal component of diagonal step-ramps (significant for the 20 deg/sec stimulus). In general, eye accelerations were lower for horizontal and vertical components of oblique pursuit than during purely horizontal or vertical tracking at similar velocities. An example is shown in Fig. 1(c).

We also compared the peak velocities of horizontal and vertical responses. Subject 2, who showed consistently higher accelerations for horizontal movements, also

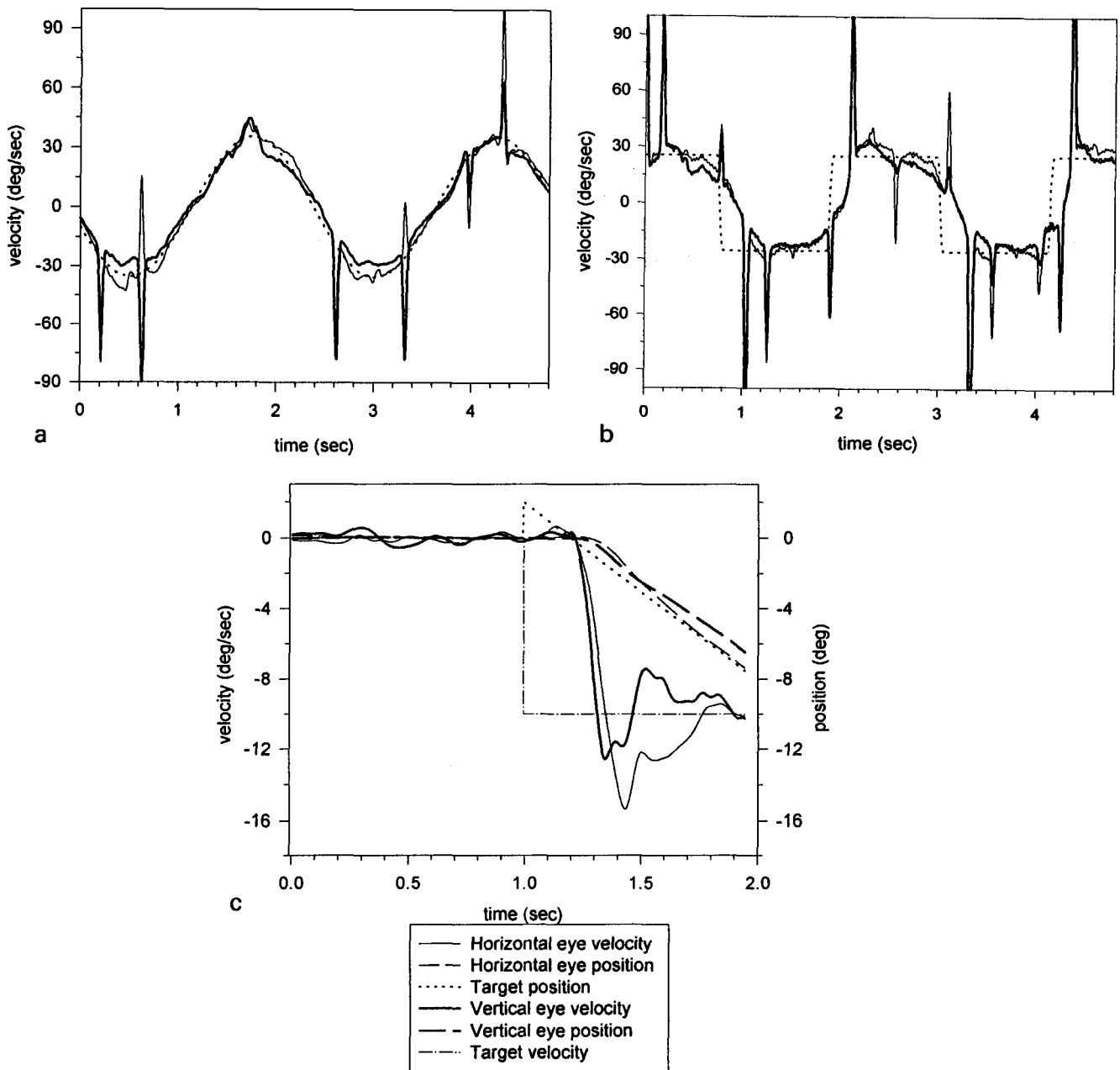


FIGURE 1. Representative data from subject 3. (a) Response to a sinusoidal stimulus moving diagonally (between upper-right and lower-left) ± 20 deg at a frequency of 0.4 Hz. The velocity of the horizontal component of smooth pursuit is higher than the velocity of the vertical component. (b) Response to triangular target moving diagonally ± 20 deg at 35.5 deg/sec. Again, the velocity of the horizontal component is greater than that of the vertical (gain being estimated from four segments of the best pursuit in each plane for the entire record, avoiding transients corresponding to turn-around points). (c) Response to diagonal (in 45 deg direction) step-ramp stimulus. Note that the velocity of the vertical eye component increases faster (higher acceleration of smooth pursuit initiation), although the horizontal component has a greater maximal velocity. Note that in each panel, movement of the horizontal (or vertical) *component* of diagonal target motion is shown. Positive values correspond to rightward and upward movements.

always showed greater horizontal peak velocities in response to purely horizontal or diagonal target motion. However, the other subjects showed no consistent pattern. The group mean peak velocity (\pm SD) for 10 deg/sec stimuli horizontally was 14.04 (\pm 1.24) deg/sec and vertically was 14.62 (\pm 0.85) deg/sec. The group mean peak velocity for 20 deg/sec stimuli horizontally was 22.08 (\pm 1.08) deg/sec and vertically was 22.04 (\pm 1.55) deg/sec.

We also estimated the average frequency of oscilla-

tions during the onset of smooth pursuit (Robinson *et al.*, 1986). Reliable estimates were only possible from the 10 deg/sec responses, and although all subjects showed "ringing", saccades made it only possible to make reliable estimates from about 10 records in some subjects. We found that the median frequency of oscillations horizontally was 2.7 Hz (range 2.27–3.01) and vertically was 2.63 Hz (range 2.04–3.43). Ringing was also evident, at approximately similar frequencies, in horizontal and

TABLE 2. Eye acceleration during pursuit onset

S/D	Cardinal		Directions		Diagonal	
	10 deg/sec	14.1 deg/sec	20 deg/sec	28.3 deg/sec	10 deg/sec	20 deg/sec
1/H	91.7 (80.5–104.3)	105.1 (89.5–117.6)	121.1 (111.1–137.4)	151.3 (126.6–166.9)	76.2 (65.6–87.8)	107.3 (91.3–124.5)
V	89.0 (79.8–104.3)	121.9* (103.9–137.3)	132.7 (113.2–157.6)	138.3 (116.4–161.3)	84.7*** (77.5–98.7)	111.2* (100.1–135.9)
2/H	111.5** (104.9–121.3)	130.4** (108.9–146.2)	154.5*** (145.3–168.8)	173.4*** (152.2–193.3)	89.5 (69.1–102.6)	122.7*** (106.0–143.1)
V	98.6 (82.7–104.7)	110.9 (97.9–119.6)	122.2 (115.0–144.6)	136.5 (126.4–156.6)	87.4 (76.9–96.3)	108.9 (95.1–124.5)
3/H	76.5 (59.2–83.6)	82.8 (73.5–91.1)	101.4 (84.74–116.9)	109.5 (93.2–127.5)	73.4 (67.4–81.4)	83.6 (73.3–96.5)
V	74.9 (60.9–86.6)	93.6* (78.6–111.0)	108.8 (90.5–113.3)	119.0 (87.4–143.0)	85.8*** (71.9–96.1)	97.3** (80.5–113.5)
4/H	76.2 (71.3–90.7)	100.0 (92.0–104.9)	116.4 (106.6–131.5)	135.6 (121.6–140.1)	72.9 (65.1–79.4)	93.3 (88.1–99.8)
V	89.3* (77.8–103.6)	113.3* (96.7–134.3)	151.3* (114.4–164.3)	126.4 (110.3–165.9)	91.1*** (80.7–101.7)	108.4*** (89.3–122.6)
5/H	60.6 (51.4–76.0)	71.8 (61.5–88.3)	75.4 (59.6–86.3)	84.4 (76.8–93.8)	45.2 (38.0–51.88)	64.7 (47.3–87.5)
V	65.7 (43.5–73.2)	80.4 (57.9–113.8)	87.0 (66.6–121.4)	108.8* (75.6–146.3)	65.7*** (51.5–86.4)	101.6*** (67.3–130.6)

S/D, Subject and direction of pursuit; H, horizontal; V, vertical. Significant difference between horizontal and vertical: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Values are medians (25th–75th percentile ranges).

vertical components during diagonal responses [Fig. 1(c)].

DISCUSSION

We have compared smooth pursuit in the horizontal and vertical planes using predictable sinusoidal and triangular target motions, and randomized step-ramp stimuli. We confirmed previous reports that, for predictable target motions, most normal subjects show higher gain values during horizontal than during vertical tracking (Baloh *et al.*, 1988; Collewijn & Tamminga, 1984; Grant *et al.*, 1992). However, four of our five subjects showed greater eye acceleration in response to vertical than to horizontal step-ramp stimuli. Although this difference was not consistent with purely horizontal and vertical stimuli, it did become so when horizontal and vertical components of diagonal responses were compared. In one subject, horizontal tracking was always better than vertical, irrespective of the stimulus. Differences for diagonal step-ramp responses were more consistent, probably because the horizontal and vertical components were generated synchronously, and each pair of responses could be directly compared. On the other hand, the pure horizontal and vertical responses were generated at different times, so that comparisons were not paired and were more subject to the known variability of eye acceleration at the onset of pursuit (Carl & Gellman, 1987; Morrow & Sharpe, 1993).

Tychsen & Lisberger (1986) systematically studied the initiation of pursuit in response to stimulation at different retinal locations. They found greater vertical responses when the stimulus was presented in the lower visual field, irrespective of whether it moved up or down. We found that pursuit initiation was the same when the stimulus started to move in the lower field as when it started to move in the upper. Baloh and colleagues (1988) showed no up–down asymmetries during pursuit of sinusoidal target motion. In our subjects, gain was generally <1.0 for sinusoidal tracking, and thus, during downward pursuit the target would tend to be in the lower visual field. However, our two subjects who showed asymmetries of

vertical sinusoidal tracking had greater gains for upward than downward movement; furthermore, in both subjects, the gain for upward tracking was less than for horizontal pursuit. Two points emerge from these results.

The first point is that when the initiation and maintenance of pursuit are compared, at least some subjects show better initiation of pursuit vertically, but better maintenance of pursuit horizontally. This finding provides additional evidence to support the view that different mechanisms contribute to the onset of the pursuit when target motion cannot be predicted, and to the maintenance of pursuit when target motion is predictable. If the onset of target motion is predictable, then anticipatory responses can be generated (Kowler & Steinman, 1981; Kao & Morrow, 1994). However, we randomized the timing and direction of target motion and encountered few such anticipatory responses in our study. In the absence of anticipatory eye movements, the onset of smooth pursuit is largely dependent on latencies dictated by the visuomotor response, and for small stimuli, these exceed 100 msec (Carl & Gellman, 1987). If, however, target motion is smooth and “predictable”, as in a sine wave, pursuit eye movements can be generated that track the target with a gain of close to 1.0, and with minimal phase lag—properties that exceed expectations of a tracking system encumbered with delays exceeding 100 msec (Dallos & Jones, 1963; Robinson *et al.*, 1986; Pavel, 1990; Barnes, 1993). Thus, it seems likely that at least two separate mechanisms—one that generates eye movements in response to visual motion, and the other that produces eye movements which predict target motion—contribute to the overall properties of smooth pursuit.

The onset of pursuit depends on cortical areas concerned with moving visual stimuli; in the rhesus monkey the middle temporal (MT-V5) and medial superior temporal (MST) visual areas have been shown to be important for deriving signals encoding the speed and direction of moving targets [reviewed in Lisberger *et al.*, 1987; Keller & Heinen, 1991], and experimental lesions in these areas impair both saccades and smooth

pursuit made to moving targets (Dürsteler & Wurtz, 1988). Probable human homologs of these areas have been identified based on studies of lesions (Zihl *et al.*, 1983; Thurston *et al.*, 1988) and functional imaging (Corbetta *et al.*, 1990; Zeki *et al.*, 1991). Such information on target motion may then be passed to pontine nuclei and cerebellum (Keller & Heinen, 1991). Relatively little is known concerning the neural substrate responsible for pursuit of predictable target motions. Lesion studies have indicated that the frontal eye fields contribute to the generation of predictive sinusoidal target motion (Keating, 1991; Gottlieb *et al.*, 1994), and Heinen (1994) has demonstrated cells in the dorsomedial frontal cortex (supplementary eye fields) that seem to encode signals for predictive smooth tracking of sinusoidal target motion. Whether the frontal eye fields or their caudal projections account for better tracking of horizontal sinusoidal target motions remains to be determined.

A second point supported by our findings is that different circuits govern horizontal and vertical pursuit. Cells in cortical area MT show all directions of motion preference (Maunsell & Van Essen, 1983). Moreover, Krauzlis and Lisberger (1994) have recently demonstrated that Purkinje cells in the flocculus encode the neural signal necessary to initiate either horizontal or vertical smooth pursuit. The Purkinje cells that encode vertical pursuit signals may project through the y-group nucleus (Chubb & Fuchs, 1982; Partsalis *et al.*, 1995) or the superior vestibular nucleus (Zhang *et al.*, 1995) to the ocular motoneurons. This pathway is probably different from that mediating horizontal smooth pursuit, which projects via vestibular nucleus neurons to the abducens nucleus (Keller & Heinen, 1991).

Collewijn and Tamminga (1984) suggested that horizontal smooth pursuit may be superior to vertical pursuit because of more extensive use in following the everyday motion of objects, which tend to be horizontal, and that vertical pursuit might be improved with practice. It is curious, however, that vertical pursuit tends to be initiated with greater eye accelerations. Perhaps this relates to the larger retinal slip velocities that may occur during locomotion if the vestibulo-ocular reflex does not fully compensate for pitch head movements, which tend to be of higher velocity (Grossman *et al.*, 1989). It would, therefore, be of interest to compare horizontal and vertical smooth tracking movements when subjects are stationary or in motion.

REFERENCES

- Baloh, R. W., Yee, R. D., Honrubia, V. & Jacobson, K. (1988). A comparison of the dynamics of horizontal and vertical smooth pursuit in normal human subjects. *Aviation Space and Environmental Medicine*, *59*, 121–124.
- Barnes, G. R. (1982). A procedure for the analysis of nystagmus and other eye movements. *Aviation Space and Environmental Medicine*, *53*, 676–682.
- Barnes, G. R. (1993). Visual-vestibular interaction in the control of head and eye movement: The role of visual feedback and predictive mechanisms. *Progress in Neurobiology*, *41*, 435–472.
- Carl, J. R. & Gellman, R. S. (1987). Human smooth pursuit: Stimulus dependent responses. *Journal of Neurophysiology*, *57*, 1446–1463.
- Chubb, M. C. & Fuchs, A. F. (1982). Contribution of y group of vestibular nuclei and dentate nucleus of cerebellum to generation of vertical smooth eye movements. *Journal of Neurophysiology*, *48*, 75–99.
- Collewijn, H. & Tamminga, E. P. (1984). Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds. *Journal of Physiology (London)*, *351*, 217–250.
- Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L. & Petersen, S. E. (1990). Attentional modulation of neural processing of shape, color and velocity in humans. *Science*, *248*, 1556–1559.
- Dallos, P. J. & Jones, R. W. (1963). Learning behavior of the eye fixation control system. *IEEE Transactions on Automatic Control*, *AC-8*, 218–227.
- Dodge, R. (1903). Five types of eye movement in the horizontal meridian plane of the field of regard. *American Journal of Physiology*, *8*, 307–329.
- Dürsteler, M. R. & Wurtz, R. H. (1988). Pursuit and optokinetic deficits following chemical lesions of cortical areas MT and MST. *Journal of Neurophysiology*, *60*, 940–965.
- Glanz, S. A. (1992). *Primer of biostatistics*. (3rd edn, pp. 233–235). New York: McGraw-Hill.
- Gottlieb, J. P., MacAvoy, M. G. & Bruce, C. J. (1994). Neural responses related to smooth-pursuit eye movements and their correspondence with electrically elicited smooth eye movements in the primate frontal eye field. *Journal of Neurophysiology*, *72*, 1634–1653.
- Grant, M. P., Leigh, R. J., Seidman, S. H., Riley, D. E. & Hanna, J. P. (1992). Comparison of predictable smooth ocular and combined eye-head tracking behavior in patients with lesions affecting the brain stem and cerebellum. *Brain*, *115*, 1323–1342.
- Grossman, G. E., Leigh, R. J., Bruce, R. J., Huebner, W. P. & Lanska, D. J. (1989). Performance of the human vestibuloocular reflex during locomotion. *Journal of Neurophysiology*, *62*, 264–272.
- Heinen, S. J. (1994). Evidence of a timing mechanism for predictive smooth pursuit in frontal cortex. In: Fuchs, A. F., Brandt, Th., Buttner, U. & Zee, D. S. (Eds) *Contemporary ocular motor and vestibular research: A tribute to David A. Robinson* (pp. 408–410). Stuttgart: Thieme.
- Kao, G. W. & Morrow, M. J. (1994). The relationship of anticipatory smooth eye movement to smooth pursuit initiation. *Vision Research*, *34*, 3027–3036.
- Keating, E. G. (1991). Frontal eye field lesions impair predictive and visually guided pursuit eye movements. *Experimental Brain Research*, *86*, 311–323.
- Keller, E. L. & Heinen, S. J. (1991). Generation of smooth-pursuit eye movements: Neuronal mechanisms and pathways. *Neuroscience Research*, *11*, 79–107.
- Kowler, E. & Steinman, R. M. (1981). The effect of expectations on slow oculomotor control—III. Guessing unpredictable target displacements. *Vision Research*, *21*, 191–203.
- Krauzlis, R. J. & Lisberger, S. G. (1994). Simple spike responses of gaze velocity Purkinje cells in the floccular lobe of the monkey during onset and offset of pursuit eye movements. *Journal of Neurophysiology*, *72*, 2045–2050.
- Lisberger, S. G., Morris, E. & Tychsen, L. (1987). Visual motion processing and sensory-motor integration for smooth pursuit eye movements. *Annual Review of Neuroscience*, *10*, 97–129.
- Martins, A. J., Kowler, E. & Palmer, C. (1985). Smooth pursuit of small-amplitude sinusoidal motion. *Journal of the Optical Society of America*, *A*, *2*, 234–242.
- Maunsell, J. H. R. & Van Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *Journal of Neurophysiology*, *49*, 1127–1147.
- Morrow, M. J. & Sharpe, J. A. (1993). Smooth pursuit initiation in young and elderly subjects. *Vision Research*, *33*, 203–210.
- Oppenheim, A. V. & Schaffer, R. W. (1989). *Discrete-time signal processing* (pp. 447–448). Englewood Cliffs, NJ: Prentice Hall.

- Partsalis, A. M., Zhang, Y. & Highstein, S. M. (1995). Dorsal Y group in the squirrel monkey I. Neuronal responses during rapid and long-term modifications of the vertical VOR. *Journal of Neurophysiology*, *73*, 615–631.
- Pavel, M. (1990). Predictive control of eye movements. In Kowler, E. (Ed.), *Eye movements and their role in visual and cognitive processes* (pp. 307–348). Amsterdam: Elsevier.
- Rashbass, C. (1961). The relationship between saccadic and smooth tracking eye movements. *Journal of Physiology (London)*, *159*, 326–338.
- Robinson, D. A., Gordon, J. L. & Gordon, S. E. (1986). A model of the smooth pursuit eye movement system. *Biological Cybernetics*, *55*, 43–57.
- Thurston, S. E., Leigh, R. J., Crawford, T., Thompson, A. & Kennard, C. (1988). Two distinct deficits of visual tracking caused by unilateral lesions of cerebral cortex in humans. *Annals of Neurology*, *23*, 266–273.
- Tychsen, L. & Lisberger, S. G. (1986). Visual motion processing for the initiation of smooth-pursuit eye movements in humans. *Journal of Neurophysiology*, *56*, 953–968.
- Zeki, S., Watson, J. D. G., Lueck, C. J., Friston, K. J., Kennard, C. & Frackowiak, R. S. I. (1991). A direct demonstration of functional specialization in human visual cortex. *Journal of Neuroscience*, *11*, 641–649.
- Zhang, Y., Partsalis, A. M. & Highstein, S. M. (1995). Properties of superior vestibular nucleus flocculus target neurons in the squirrel monkey. I. General properties in comparison with flocculus projecting neurons. *Journal of Neurophysiology*, *73*, 2261–2278.
- Zihl, J., von Cramon, D. & Mai, N. (1983). Selective disturbance of movement vision after bilateral brain damage. *Brain*, *106*, 313–340.

Acknowledgements—Supported by USPHS Grant EY06717, the Department of Veterans Affairs, the Evenor Armington Fund (to Dr Leigh), and Deutsche Forschungsgemeinschaft (to Dr Rottach).