Effect of Eccentric Gaze on Pursuit

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The effect of eccentric gaze on pursuit eye movements was studied with electro-oculography in normal human subjects and a patient with defective pursuit. Sinusoidal target trajectories were centered about the primary position of gaze and eccentric, horizontal positions of gaze. Eccentric gaze decreased pursuit gain (eye velocity/target velocity) when the eyes moved farther eccentrically in the orbits and increased pursuit gain when the eyes moved toward the centers of the orbits. The magnitude of these effects increased with increasing eccentricity of gaze, increasing peak target velocity, and decreasing pursuit gain during tracking of target trajectories centered about the primary position. These effects can be caused by the elastic forces of the extraocular muscles, globe and other orbital tissues. The pursuit subsystem cannot compensate for these factors at high target velocities, or when it is impaired by pathologic lesions. Invest Ophthalmol Vis Sci 24:1108–1114, 1983

Pursuit eye movements are smooth movements that track targets moving in smooth patterns. Pursuit movements are usually elicited in the laboratory by predictable patterns, such as target trajectories with sinusoidal and constant velocities. The pursuit movements maintain the image of the target on the fovea, and can precisely match the velocity of the target. The performance of the ocular motor pathways that generate pursuit is usually quantified by calculating a gain (eye velocity/target velocity). The pursuit gain is dependent on parameters of the target trajectory, such as velocity, frequency and acceleration. Previous studies have investigated the effects of target velocity, frequency, amplitude and acceleration on pursuit.[1-4] Pursuit gain is nearly one at target velocities up to 60 deg/sec and target frequencies up to 1 Hz.

The effect of eccentric gaze on small saccades has been studied in normal human subjects.[5] Centering saccades had higher peak velocities than eccentric saccades. However, the effect of eccentric positions of gaze on pursuit has not been reported. Tests of pursuit in normal human subjects and in patients who have lesions in the ocular motor pathways have used target trajectories that are centered about the primary position of gaze. Studies in animals[6] and humans[7-8] investigating the mechanical properties of the eye muscles, globe, and other orbital tissues have demonstrated that significant force is required to overcome viscoelastic forces in eccentric gaze. Therefore, the position of the eyes in the orbits might be expected to affect tracking. The purpose of this study was to demonstrate the effect of target trajectories that are centered about eccentric positions of gaze on pursuit in normal human subjects and in a patient with impaired pursuit.

Materials and Methods

Five normal, human subjects, who had no evidence of significant abnormalities on neuro-ophthalmic and neuro-otologic examinations were studied. When the subjects attempted to gaze 30° eccentrically in both horizontal directions in the dark, smooth eye movement drifts back to the center had velocities less than 5 deg/sec. A patient with a cerebellar atrophy syndrome and impaired pursuit was also studied. The patient did not have gaze-paretic nystagmus in the light in 30° of eccentric gaze. While attempting to maintain eccentric gaze in the dark, the patient demonstrated drifts toward the center of 2 to 4°/sec from both directions. All subjects were informed of the study, and their informed consent was obtained prior to testing.

Detailed descriptions of the eye movement recording and analysis systems have been reported previously,[3,9] but will be summarized and described briefly below. Summed, horizontal eye movements of both eyes were recorded with D-C electro-oculography using silver-silver chloride skin electrodes at the lateral canthi. All of the subjects had conjugate eye movements. The bandwidth of the recording system was 0–35 Hz (−3dB). The analog signal was digitized at 200 samples/sec by an online computer (DEC LSI-11). The instantaneous eye position and velocity were calculated. Saccades were identified by velocity and amplitude criteria and were removed from the data

by the computer. The average pursuit velocity was calculated for every 20 msec interval.

The peak velocities of saccades are much greater than those of pursuit movements on the same amplitudes. The velocity-amplitude relationships of saccades and smooth movements, such as pursuit, are markedly different.[10] Therefore, we chose velocity as the major criterion for saccade identification for the computer algorithm. The minimum velocity criterion for saccades is set at the maximum velocity of the pursuit target. The velocity of pursuit movements is not expected to exceed that of the target. The minimum *peak* velocity criterion for saccades is set at 70°/sec, since we wish to identify saccades of 1° amplitude or greater. Therefore, if the eye velocity exceeds that of the maximum target velocity for a minimum of 20 msec and has at least one velocity sample above 70°/sec, a saccade identified. In addition, we can easily identify small saccades missed by the computer by detecting them as high velocity discontinuities in the computer output of pursuit velocity vs time. Saccades are identified in other laboratories as similar discontinuities in an eye velocity channel of the polygraph, obtained by electronic differentiation of eye position. Therefore, we are confident that velocities of saccades were not included in our calculations of pursuit velocity.

Subjects were seated 1 meter from a white, featureless screen. Their heads were fixed with a forehead brace. An intense, 1 deg, red dot was projected from a helium-neon laser and mirror galvonometer (General Scanning) that were mounted above the subjects' heads. The target moved in sinusoidal, horizontal trajectories centered about the center of the screen. The peak-to-peak amplitude of the trajectories was 20°. The peak velocity of the target was varied from 6 to 78.5°/sec by increasing the target frequency from 0.095 to 1.25 Hz. To record pursuit centered about the primary position of gaze the subjects' heads were aligned with the center of the screen. To record pursuit centered about an eccentric position of gaze, the heads and bodies were aligned with an eccentric point on the screen and the eyes were directed back to the center of the screen. The heads were not rotated on the bodies to avoid stimulation of neck stretch receptors. For example, to record pursuit centered about 30° gaze to the right the heads and bodies were aligned with a point on the screen that was 30° to the left. Gaze back to the center of the screen placed the eyes 30° to the right in the orbits. Since the laser target trajectories were always centered on the screen, the peak target velocity occurred twice in a cycle, once as the target carried the eyes further eccentrically in the orbits and once as the target carried the eyes toward the center of the orbits. Pursuit gains (peak

eye velocity/peak target velocity) were calculated as the target and eyes moved to the right and left during each cycle, and mean gains to the right and left were calculated.

Results

Normal Subjects

Eccentric gaze had a significant and consistent effect on pursuit and pursuit gain at high target velocities in all of the normal subjects. Centering the target trajectory about an eccentric position of gaze impaired pursuit and decreased pursuit gain when the target was moving in the direction that carried the eyes further eccentrically in the orbits. For example, when the center point of the target trajectory was at 30° right gaze, pursuit gain to the right was less than the pursuit gain to the right measured when the target's trajectory was centered about the primary position of gaze. This effect increased as the target's trajectory was centered about more eccentrically located positions of gaze, and was greater at higher peak target velocities. Eccentric gaze also affected pursuit and pursuit gain measured when the target and eyes moved toward the center of the orbits. For example, when the target's trajectory was centered about 30° right gaze, pursuit gain to the left was greater than pursuit gain to the left measured when the target's trajectory was centered about the primary position of gaze. The effect of eccentric gaze on pursuit toward the primary position was almost always less than its effect on pursuit toward more eccentric positions of gaze.

Figure 1 illustrates pursuit in Subject 1. On the left side of the figure the target's sinusoidal trajectory had a peak velocity of 24°/sec. The top line depicts the target movement. When the target's trajectory was centered about the primary position of gaze (second line), pursuit movements were able to maintain the target's image on the foveas and the pursuit gain was nearly one in both directions. Centering the target's trajectory about 30° of eccentric gaze to the right (third line) and to the left (fourth line) did not significantly affect pursuit to the right. However, pursuit to the left was affected. When the target's trajectory was centered about 30° gaze to the right, the velocity of pursuit movements to the left that carried the eyes back toward the center of the orbits increased slightly. Pursuit gain to the left was 1.08; whereas, pursuit gain to the left when the target was centered about the primary position was 0.97. Eccentric gaze to the left was more effective in impairing pursuit to the left. When the target trajectory was centered about 30° left gaze, the eye velocity did not match the target velocity, the target image slipped from the foveas and
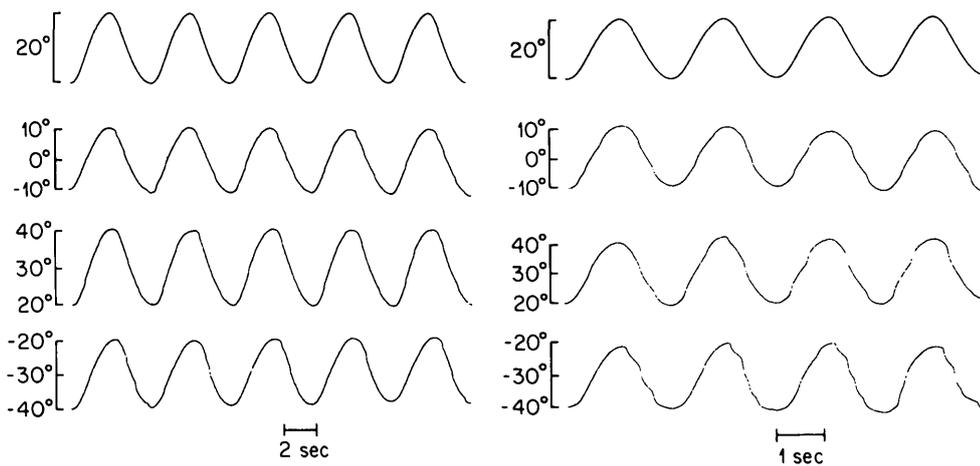
Fig. 1. Pursuit in subject 1. Left side-peak target velocity of 24 deg/sec; right side-peak target velocity of 47°/sec. Top line represents target trajectories, second line pursuit centered about primary position, third line pursuit centered about 30° right gaze, and fourth line pursuit centered about 30° left gaze. Deflections up are to the right, down to the left. Note impaired pursuit with catch-up saccades during tracking to left at peak target velocity of 47°/sec and 30° eccentric gaze to the left (right side, fourth line).

small amplitude catch-up saccades were used to re-foveate the target image. Pursuit gain to the left was decreased to 0.83.

On the right side of Figure 1 the peak target velocity was 47°/sec. When the target's trajectory was centered about the primary position of gaze, pursuit gain was only 0.85 and 0.80 to the right and left, respectively (second line). Catch-up saccades were made in both directions. Eccentric gaze 30° to the right had only slight effects on pursuit (third line). Pursuit to the right into more eccentric positions in the orbits
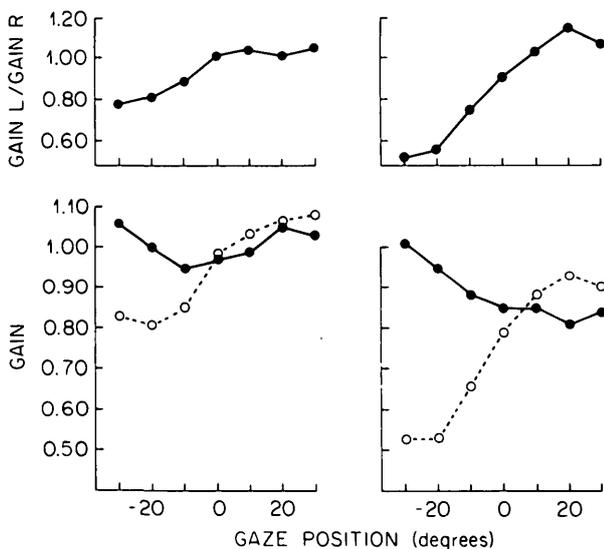

Fig. 2. Pursuit gain vs gaze position in subject 1. Left side-peak target velocity of 24°/sec; right side-peak target velocity of 47°/sec. In lower graphs open circles represent pursuit gains to the left, closed circles pursuit gains to the right. Note that eccentric gaze to the left (negative gaze position) has greater effects on pursuit than gaze to the right (positive gaze position). In top graphs the ratios of pursuit gain to the left-pursuit gain to the right are presented. Greater slope at 47°/sec than at 24°/sec indicates larger effects of eccentric gaze at the higher peak target velocity.

was not significantly affected, and pursuit gain to the left toward the center of the orbits was only slightly increased. Pursuit gain to the left was 0.90. However, eccentric gaze to the left had much greater effects on pursuit (fourth line). Pursuit to the right toward the center of the orbits improved, and catch-up saccades were no longer present. Pursuit gain to the right increased to 1.00. Pursuit to the left toward more eccentric positions in the orbits was further impaired, and larger amplitude catch-up saccades were made. Pursuit gain to the left decreased to 0.53.

Figure 2 presents the pursuit gains in Subject 1 graphically. Data obtained during peak target velocities of 24°/sec are shown on the left, and data obtained during peak velocities of 47°/sec are shown on the right. The lower graphs represent pursuit gains to the right (closed circles) and left (open circles) when target trajectories were centered about the primary and eccentric positions of gaze. Eccentric gaze to the left had greater effects on pursuit than did eccentric gaze to the right. Gaze to the left decreased pursuit gains to the left (the direction of further eccentric gaze) and increased gains to the right (the direction toward primary gaze). The upper graphs present the ratio of pursuit gain to the left/pursuit gain to the right vs the position of the target trajectories in the orbits. The slopes of these lines reflect the magnitude of the effects of eccentric gaze on pursuit. The effects of pursuit were clearly greater at the higher peak target velocities of 47°/sec. Several other findings that were observed in all of the subjects are demonstrated in the lower graphs. Eccentric gaze was more effective in decreasing pursuit gain than in increasing gain. During eccentric gaze to the left the decrease in gain to the left was greater than the increase in gain to the right. The effects of eccentric gaze increased with increasing eccentricity of gaze. Finally, eccentric gaze in one direction had a greater effect on pursuit at all
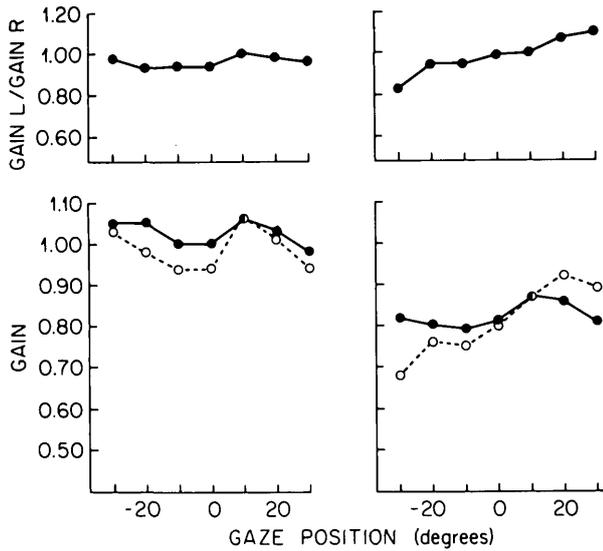
Fig. 3. Pursuit gain vs gaze position in subject 2. Left side-peak target velocity of 47°/sec; right side-peak target velocity of 63°/sec. In lower graphs open circles represent pursuit gains to the left, closed circles pursuit gains to the right. Note that eccentric gaze has little effect on pursuit at 47°/sec, in contrast to subject 1. At 63°/sec eccentric gaze to the left (negative gaze position) has greater effects on pursuit than gaze to the right (positive gaze position).

this target velocity was reached. Figure 3 graphically presents the pursuit gains in subject 2. Data during peak target velocities of 47°/sec and 63°/sec are shown on the left and right sides of the figure, respectively. At peak velocities of 47°/sec there was minimal effect of eccentric gaze, in contrast to subject 1 (right side of Fig. 2). However, marked effects were present at 63°/sec. In this subject pursuit to the left (open circles) was affected by eccentric gaze (decreased by gaze to the left, increased by gaze to the right), but pursuit to the right (closed circles) was not significantly affected.

The means of pursuit gains of the group of normal subjects tracking in eccentric gaze were compared to the means during tracking centered about the primary position. The Student's t-test for paired observations was used. The differences in means were statistically significant at the 5% level at gaze positions of 20 and 30° and at velocities of 36°/sec and greater. Differences were not significant at 10° at any target velocity or at target velocities lower than 36°/sec.

Figure 4 presents the pursuit gain to the left/pursuit gain to the right vs gaze position for all normal subjects at peak target velocities of 24 and 47°/sec on the left and ride sides of the figure, respectively. The best-fit lines to the data are shown. Despite the variations among subjects the correlation coefficients of the lines at 24°/sec (slope = 0.0018/deg) and at 47°/sec (slope = 0.0038/deg) were 0.46 and 0.60, respectively. The greater slope at 47°/sec indicates a greater effect of eccentric gaze at the higher target velocity.

target velocities than did gaze in the other direction. For example, gaze to the left had greater effects than gaze to the right in Figure 2.

A significant effect of eccentric gaze on pursuit was not observed in any of the normal subjects at peak target velocities less than 24°/sec. At 24°/sec the pursuit gains were 0.90 or greater when the target's trajectories were centered about the primary position. In subjects 2 and 3 the pursuit gains during tracking centered about the primary position did not decrease to less than 0.90 until peak target velocities were increased to 63°/sec. Significant effects of eccentric gaze on pursuit were not seen in these two subjects until

Eccentric gaze significantly affected pursuit in a 59-year-old man with a diffuse cerebellar atrophy syndrome with onset in adult-life. Pursuit was markedly impaired, and is shown in Figure 5. The patient had no pathologic nystagmus in the primary position or in eccentric gaze 30° to the right or left. Pursuit during peak target velocities of 12°/sec is shown on the

Fig. 4. Ratios of pursuit gain to the left/pursuit gain to the right vs gaze position in all normal subjects. Data from each subject are identified by different symbols. Right side-peak target velocity of 24 deg/sec; left side-peak target velocity of 47°/sec. Lines represent best-fit linear regression lines. Note that effect of eccentric gaze is greater at the higher target velocity.
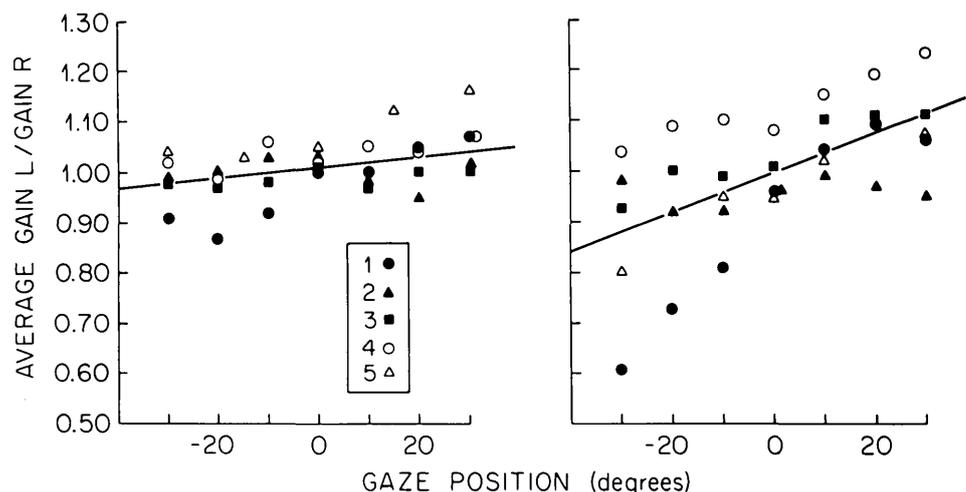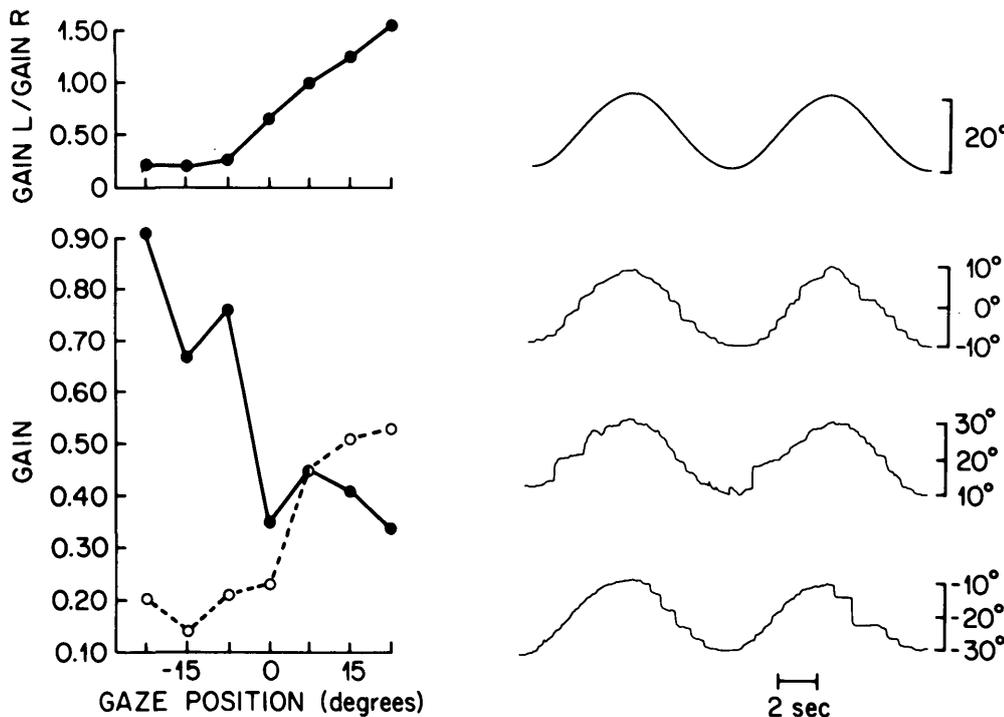
Fig. 5. Pursuit vs gaze position in a patient with cerebellar atrophy. Right side-pursuit movements at peak target velocity of 12 deg/sec. Top line represents target motion, second line tracking centered about primary position, third line tracking at 20° gaze to the right, and fourth line tracking at 20° gaze to the left. Note impaired pursuit at the primary position with numerous catch-up saccades in both directions (second line). Eccentric gaze to the left (fourth line) improves pursuit to the right. Left side-pursuit gain vs. gaze position. Note that eccentric gaze to the left (negative gaze position) has greater effects on pursuit than gaze to the right (positive gaze position).

right side of the figure. When the target trajectory was centered about the primary position (second line), pursuit was poor and numerous catch-up saccades were made in both directions. Pursuit gain to the right was only 0.34, and was 0.23 to the left. In the presence of such low pursuit gains, eccentric gaze had large effects on pursuit even at the low peak target velocities of 12°/sec. Eccentric gaze to the left (fourth line) markedly increased pursuit gain to the right to nearly one. Eccentric gaze to the right increased pursuit gain to the left to 0.52. Interestingly, eccentric gaze did not significantly decrease pursuit gains in this patient. Pursuit gains vs gaze positions are demonstrated on the left side of the figure.

Discussion

At high target velocities eccentric gaze can significantly affect pursuit in normal subjects. When the trajectory of the target is centered about the primary position of gaze, the peak velocities of pursuit eye movements are approximately equal to the right and left. However, when the trajectory is centered about an eccentric position in the orbit, velocities of pursuit moving more eccentrically are decreased; whereas, velocities of pursuit moving toward the center are increased. The causes of these effects are not specifically identified by the experiments in this study. Explanations must account for the following experimental observations: (1) asymmetry of effect, ie, decrease in velocity of eccentric movements and increase

in velocity of centering movements, (2) increasing effect with increasing eccentricity, (3) increasing effect with increasing target velocity, and (4) variability of effect between subjects.

We suggest that the effects of eccentric gaze on pursuit can be explained by interaction between the mechanical properties of the orbit and the smooth pursuit, ocular motor subsystem. The extraocular muscles, globe, and other orbital tissues have viscous and elastic properties that must be overcome during eye movements. Viscous forces counteract motion of the eye away from a stationary position, and are important factors to overcome during eye movements of high velocity, such as saccades. Collins[6] measured the viscous forces of detached extraocular muscles of anesthetized cats at low velocities of extension of the passive muscles (up to 30°/sec). The forces were of relatively low magnitude (up to 4 g) and varied linearly with muscle length and the velocity of extension. Viscous forces might affect the higher velocity eye movements of pursuit in our subjects, but would not be expected to result in an asymmetric effect, as we have observed.

Elastic forces counteract motion of the eye away from the center of the orbit. If the eye has been rotated to an eccentric position of gaze, elastic forces will cause the eye to drift back toward the center of the orbit unless they are opposed by active contraction of the agonist extraocular muscle. These forces increase with passive lengthening and increasing tension of the muscles. The agonist muscles can easily

overcome these forces in stationary eccentric gaze. However, elastic forces could account for the asymmetric effects of eccentric gaze on pursuit and the increasing effects with increasing eccentricity of gaze on pursuit observed in our subjects.

Collins[6] has studied these forces in the cat and in human patients undergoing strabismus surgery with general anesthesia. If the horizontal rectus muscles are removed, the globe is moved passively to an eccentric, horizontal position of 45° in the orbit and the globe is released, the eyeball moves toward the center of the orbit with smooth movements of two steps with time constants of 0.02 sec and 1 sec. The elastic forces of the globe, other extraocular muscles, and other orbital tissues are thought to cause the centering movements. Rosenbaum and co-workers[11] have measured the velocity of centering movements in human, strabismic patients under general anesthesia. Velocities up to or greater than 100°/sec were measured. The horizontal rectus muscles were not removed, and the centering movements reflected elastic forces of these rectus muscles and the other orbital tissues.

In an alert subject the eye is maintained in an eccentric position in the orbit primarily by contraction of the agonist muscle. Collins[6] measured the length-tension curves of an isolated, right lateral rectus muscle in a strabismic patient, who was anesthetized with only topical anesthetics. With the left eye fixating a stationary target at different gaze positions, the force generated by the right lateral rectus muscle that is required to hold the right globe at those positions can be estimated. About 50 g of force was generated by the right lateral rectus in 30 deg of gaze to the right. Forces of this magnitude can be generated easily by the agonist muscles. Forces of greater than twice this magnitude are produced by the agonist muscles during large saccades. Collins[8] has measured the in vivo forces generated by a right lateral rectus muscle during pursuit movements in a strabismic patient with topical anesthetics. Forces were measured with a small strain-gauge secured between the muscle insertion and muscle. The forces measured during pursuit of 10°/sec in the temporal direction were only slightly greater than those during fixation at eccentric positions of gaze.

The maximal forces that can be generated by the extraocular muscles and the maximal firing rates of the ocular motor neurons that produce contraction of the muscles are probably not the limiting factors during pursuit in our subjects. The limiting factor appears to be the function of the pursuit subsystem. Pursuit has been modeled as a closed-loop subsystem. If the velocity of the eye is less or greater than that of the target, a retinal slip velocity of the target's im-

age is produced. The visual afferent pathways perceive the slip velocity and adjustments in the motor signals occur that decrease the slip velocity. Recently, a difference in retinal positions of the target's image and fovea[12] and acceleration of the target[4] have been suggested as stimuli for pursuit. If the pursuit subsystem is able to generate eye movements whose velocities exactly match those of the target, the pursuit gain (peak eye velocity/peak target velocity for sinusoidal target trajectories) is 1.0. The pursuit gains in normal human subjects are nearly 1.0 until higher values of target velocity, frequency and acceleration are reached. At these higher target parameters the closed-loop pursuit subsystem can no longer effectively correct target-eye velocity errors, and the pursuit gains decrease.

We suggest that normal subjects show little or no effect of eccentric gaze on pursuit at relatively low peak target velocities since their pursuit subsystems can compensate for the effect of elastic forces, that can be thought of as a drift velocity toward the center of the orbit. At higher target velocities pursuit gain is significantly less than 1.0 in the primary position, even without the effect of elastic forces. In eccentric gaze pursuit cannot compensate for the effect of these forces, and eye velocity decreases as the eye moves eccentrically against the forces and increases as it moves centrally in the same direction as that of the forces.

Pursuit gain in the primary position decreases as peak target velocity increases. Therefore, we would expect that the changes in pursuit velocity in eccentric gaze will increase as the target velocity increases, as observed in our experiments. The variability of the effect of eccentric gaze on pursuit between normal subjects can be explained by differences in the function of the pursuit subsystem among subjects. Some subjects, such as subject 1, demonstrated effects of eccentric gaze at lower target velocities and greater effects at the same target velocity than other subjects, such as subject 2. As expected, the former subjects had lower pursuit gains in the primary position. Their pursuit subsystems were less able to compensate for the effects of the elastic forces. Observations in the patient with cerebellar dysfunction and impaired pursuit corroborate our suggestion that the function of the pursuit subsystem determines whether or not effects of eccentric gaze are observed. The patient demonstrated marked effects at target velocities much lower than those required in the normal subjects.

We cannot adequately account for two observations in our experiments. Eccentric gaze was less effective in increasing pursuit velocities than in decreasing velocities in most normal subjects. At high target velocities pursuit gain centered about the primary position was often well below 1.0. We would

have expected equal increases and decreases in gain, if the effects of the elastic forces simply summated with pursuit velocity. The effects of eccentric gaze to the right were often different from those of gaze to the left. Gaze-paretic nystagmus was not present in the light, and the velocities of drifts toward the center in the dark were similar from right and left gaze. Therefore, asymmetric function of neural intergrators maintaining eccentric gaze did not seem to be present.

In conclusion, the elastic, restoring forces of the globes, extraocular muscles and other orbital tissues can have a significant effect on pursuit centered about eccentric positions of gaze. The pursuit system can overcome the pertubations of pursuit that these effects would cause unless its function is sthologic lesions. In the future these observations might be useful in developing sensitive, clinical tests of pursuit.

Key words: eccentric gaze, pursuit eye movements, orbital mechanics, defective pursuit, electro-oculography, eye movement recording

References

1. Fender DH and Nye PW: An investigation of the mechanisms of eye movements. Kybernetik 1:81, 1962.
2. Engelken EJ and Wolfe JW: A modeling approach to the assessment of smooth pursuit eye movement. Aviat Space Environ Med 50:1102, 1979.
3. Baloh RW, Kumley WE, Sills AW, Honrubia V, and Konrad HR: Quantitative measurement of smooth pursuit eye movements. Ann Otol Rhinol Laryngol 85:111, 1976.
4. Lisberger SG, Evinger C, Johanson GW, and Fuchs AF: Relationship between eye acceleration and retinal image velocity during foveal smooth pursuit in man and monkey. J Neurophysiol 46:229, 1981.
5. Abel LA, Dell'Osso LF, Daroff RB, and Parker L: Saccades in extremes of lateral gaze. Invest Ophthalmol Vis Sci 18:324, 1979.
6. Collins CC: Orbital mechanics. In The Control of Eye Movements, Bach-y-Rita P and Collins CC, editors, New York, Academic Press, 1971, pp. 283-325.
7. Scott AB: Extraocular muscle forces in strabismus. In The Control of Eye Movements. Bach-y-Rita P and Collins CC, editors. New York, Academic Press, 1971, pp. 327-342.
8. Collins CC: The human oculomotor control system. In Basic Mechanisms of Ocular Motility and Their Clinical Implications, Lennerstrand G and Bach-y-Rita P, editors. New York, Pergamon Press, 1975, pp. 145-180.
9. Baloh RW, Langhofer L, Honrubia V, and Yee RD: On-line analysis of eye movements using a digital computer. Aviat Space Environ Med 51:563, 1980.
10. Bahill AT, Clark MR, and Stark L: The main sequence, a tool for studying human eye movements. Math Biosci 24:191, 1975.
11. Rosenbaum AL, Weiss SJ, Bateman JB, and Liu PY: Quantitative analysis of spring forces in esotropia and exotropia during surgery, J Pediatr Ophthalmol Strabismus 19:7, 1982.
12. Pola J and Wyatt HJ: Target position and velocity: The stimuli for smooth pursuit eye movements. Vision Res 20:523, 1980.