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Foveation dynamics in congenital nystagmus II: Smooth pursuit

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Abstract. It has been shown that, during 5 seconds of fixation, an individual with congenital nystagmus (CN) can repeatedly (beat-to-beat) foveate (SD = 12.87 minarc) and maintain low retinal slip velocities (SD = 118.36 minarc/sec). Smooth pursuit data from several CN subjects showed that eye velocities during these foveation intervals approximated target velocity. Despite some claims that CN is caused by absent or "reversed" smooth pursuit, those with CN hardly ever experience oscillopsia or exhibit any accompanying symptoms of such deficits in pursuit; they are able to master sports requiring tracking of rapidly moving small objects (e.g. racquetball or handball). We developed and describe several new methods to accurately assess the function of smooth pursuit in an individual with typical idiopathic CN. We investigated the dynamics of CN foveation periods during smooth pursuit to test the hypothesis that eye velocities would match target velocities during these periods. Unity or near-unity instantaneous (beat-to-beat) pursuit gains of both experimenter-moved and subject-moved targets at peak velocities ranging from only a few deg/sec up to 210°/sec were measured. The dynamic neutral zone was found to shift oppositely to target direction by amounts proportional to the increase in target speed. Our methods proved that eye velocity is made to match target velocity during the foveation intervals and support the conclusion that smooth pursuit in individuals with CN is functioning normally in the presence of the CN oscillation. In addition, we hypothesize that the same fixation mechanism that prevents oscillopsia during fixation of stationary targets, also does so during pursuit.

Introduction

During fixation of a stationary target by an individual with congenital nystagmus (CN), the oscillation carries the eyes away from and back to that target [1]; there is a period of time during each cycle of CN, called the foveation period, when the image of the target is on the fovea. The primary objective of the fixation mechanism in CN, analogous to normal fixation, is to prolong this foveation period and thereby maximize visual acuity [2]. High-acuity foveation periods require that eye position and target position coincide and retinal slip velocity be near zero. Eye movement records of a group of 7 subjects with CN (representative of the 400 such subjects we had recorded) pursuing a moving target showed that during the foveation periods of their waveforms, eye position and velocity approximated those of the target [3]. Two methods of properly calculating smooth pursuit gain were suggested. One could either form the ratio of eye velocity during foveation periods to target velocity (instantaneous, beat-to-beat gain) or the ratio of average eye velocity to average target velocity (average gain). Graphically, the latter could be approximated by joining the foveation periods on an eye position record with a straight line and comparing it's slope to that of the target position record [3]. Other measures of smooth pursuit are the extent to which retinal error position and velocity (or phase plane) mimic those measured during fixation. Means and standard deviations (SD's) of foveation-period retinal errors can also be compared to fixation values. *Each* of these methods were developed for, and employed in, this study; their implications are discussed in this paper.

Studies of smooth pursuit using groups of CN subjects have demonstrated that pursuit gain appears to be normal [3, 4]. In fact, the many examples presented in the first study within the theoretical framework for evaluation of pursuit in the presence of nystagmus showed that pursuit was normal in these subjects despite the direction of their CN slow phases. What had not been done prior to this study is to accurately calculate pursuit gain during foveation periods to prove that it is, indeed, within normal limits. The literature also contains statements, made either without proof or based on faulty evaluation of pursuit in CN, that the smooth pursuit mechanism is somehow defective or even, 'reversed'. Given the above information and using an accurate, high-resolution method of recording eye movements, we asked the following questions concerning the smooth pursuit of individuals with idiopathic CN:

What are the instantaneous gains during the foveation periods?
What are the average gains?
How do these gains compare to those of normals?
How do the means and SD's of retinal position during foveation periods compare with those measured during fixation?

In an effort to answer the above question, we developed several unrelated methods by which accurately taken foveation-period data could be analyzed to yield measures of pursuit performance of all subjects with CN. To demonstrate these methods, we used the responses of a subject whose CN is representative of the population of idiopathic CN and whose fixation we have studied in detail; the latter is necessary since some of the methods we developed to evaluate pursuit require comparison of the foveation during pursuit to that during fixation.

The major findings of this paper are the several new methods of evaluation of pursuit in CN that, based on their foundations, are generalizable to the analysis of other CN subjects. Also presented is the first quantitative measure of the neutral-zone shift accompanying smooth pursuit at different velocities in both directions. The methods used in this paper demonstrate calculation of the true gain of smooth pursuit in CN and provide future investigators with several approaches to its evaluation. The demonstration, by accurate methods, of normal pursuit in the subject used herein serves as the counter-example to refute the hypothesis that defective pursuit is either the cause of, or necessary result of, CN; less accurate methods have already demonstrated normal pursuit in the two different groups of CN subjects referred to above.

We measured both target and eye position for a subject with CN during smooth pursuit of a moving target with a fixed head; pursuit of both experimenter- and subject-moved targets was analyzed.

Methods

Recording. Eye and target rotations with respect to an earth-fixed framework were recorded by means of a phase-detecting, revolving magnetic field technique. The sensor coils consisted of 9 turns of fine copper wire imbedded in an annulus of silicone rubber molded to adhere to the eye by suction [5]. The signals were digitized at 488 samples per second yielding a bandwidth of 244 Hz. The system's sensitivity was less than one minute of arc, linearity was 1 part in 14,014, drift was 0.2–0.3 minarc per hour, noise was less that two minarc and eye-position data were stored to the nearest minarc. Further details on the recording system may be found elsewhere [6–8].

Protocol. The subject, with sensor coils attached to one eye, sat near the center of the revolving magnetic field using a bite board. The room was dimly illuminated. The target to study smooth pursuit was an LED, at a distance of 35.6 cm from the subject's eye, attached to a wheel whose center of rotation was above the center of rotation of the eye being tested. The stimulus was either rotated by the experimenter (passive motion) or by the subject himself (active motion). Target rotations were effected over large angles (up to 90°) and over a range of peak velocities up to 170°/sec for passive motion and 210°/sec for active motion.

Analysis. It has been shown previously [3] that only during foveation periods could eye velocity match target velocity and, for CN waveforms without such motionless foveation periods, eye velocity could *never* equal target velocity, even when pursuit was perfect. Thus, the formulation of the ratio of eye velocity to target velocity when evaluating subjects with spontaneous nystagmus does *not* yield a number that reflects the gain of smooth pursuit. The gain of any system is the ratio of its output to its input *only* when that output is produced by the input (causality); in CN the major component of the eye-movement measured, the CN oscillation, is *not* caused by target velocity but is present whenever the subject attempts to fixate or actively direct his eyes. During pursuit, the slow phases of CN consist of the CN itself plus the pursuit response. It is a *fundamental error* to equate them with pursuit alone and the inference that their usually reversed direction implies a sign reversal in the smooth pursuit pathway, only compounds that error. True pursuit gain can *only* be assessed when the CN component is zero. This usually occurs during the foveation periods if they are present in an individual's waveform.

For the analysis of pursuit, speeds were calculated from the digitized position arrays using a sliding window technique that took the central difference of each sample point and its two adjacent sample points. Due to the quality of the instrumentation, no further filtering was applied. We determined instantaneous, beat-to-beat pursuit gain by forming the array, eye velocity divided by target velocity for *non-zero* values of target velocity, using interactive graphics to identify the CN foveation periods and measuring gains during these periods. We refer to this as foveation-period gain (G_{fp}). This was done for two-12-second trials at each of six different target speeds for the passive-motion trials; for the active-motion trials, selected intervals of pursuit were analyzed to demonstrate both differences in response and better pursuit resulting from this condition of multisensory feedback and increased predictability of target motion. To eliminate the effects of the subject anticipating the target direction reversals (in both the passive- and active-motion trials), only data from the central 40–60° (±20° or ±30°) were used. The average target speeds ranged from 350 minarc/sec (≃6°/sec) to 6600 minarc/sec (110°/sec). Leftward and rightward values of G_{fp} were calculated independently and also averaged together for each target speed. We also calculated average gains (G_{av}) by forming the ratios of the averages of eye-velocity (nystagmus plus pursuit) and target-velocity arrays for each pursuit interval. This was done to assess its usefulness as a more easily calculated approximation to G_{fp}.

The quality of smooth pursuit was also assessed by other methods not involving the calculation of gain. We reasoned that, if the pursuit by an individual with CN was truly normal, we might expect that the resulting retinal error signals would approximate those measured during fixation; they were not expected to be better since fixation can be maintained more accurately on stationary rather than moving targets. We computed retinal error position by taking the difference between eye and target positions. The phase-plane portraits of retinal error velocity were constructed for comparison to those resulting from fixation. To facilitate the comparison between retinal error position during pursuit and eye position during fixation, the signs of error position and velocity were inverted.

The mean of retinal foveation position (RER_{fp}) and its SD were measured at each target velocity using interactive graphics and SD's were compared to the average value obtained during fixation at each gaze angle (15.02 minarc) [9]. Foveation-period means and SD's were calculated in two ways: (1) To facilitate direct comparison to the 5-second records of fixation previously reported [9], the RER_{fp}'s and SD's for all pursuit intervals in each 5-second record (combining pursuit in both directions) were averaged for each target velocity; (2) To preserve possible directional differences, RER_{fp}'s and SD's in each pursuit direction were calculated separately for each target velocity. Initial analysis was done on a PDP 11/73 computer and more extensive later analysis on an IBM PS/2 using the ASYST software for scientific computing [10] and SigmaPlot for plotting and curve-fitting data.

Results

Pursuit (passive motion). Two 12-second records of smooth pursuit of an experimenter-moved target at each of six target speeds were made. Fig. 1 contains typical 5-second records of pursuit of (a) a slowly moving target (6°/sec average speed) and (b) a rapidly moving target (110°/sec average speed). Target, eye and retinal error position are shown, the latter shifted to place zero-error at 36 and 42° right gaze respectively for the two records. In both records, the eye position during foveation periods is at or near the target position (retinal error is at or near zero); the accuracy of this coincidence during foveation periods decreased with increasing target velocity. Fig. 2a is a 1-second interval of target and eye position for the high-gain (gain near 1.0) pursuit of the 6°/sec target and Fig. 2b shows the 'gain' function 'eye velocity/target velocity' for that 1-second interval. The measurements of foveation-period (G_{fp}) were made from such plots using interactive graphics *after* first identifying the foveation periods from plots of retinal error position (Fig. 3a). To compare target foveation during pursuit with that during fixation, retinal error phase-plane plots were made and the pre-defined foveation window (0 ± 30 minarc and 0 ± 240 minarc/sec) superimposed on them. This is the *same* foveation window defined in our study of CN fixation; it is the foundation for both high visual acuity and oscillopsia suppression [9]. The phase plane of Fig. 3b shows repeated target foveation with the foveation period occupying the center of the foveation window.

The Figs. 4 and 5 contain similar data for lower gain pursuit (gain less than 1.0 requiring catch-up saccades) of the 110°/sec target. The interval shown in Fig. 4a is virtually indistinguishable from that of a normal subject pursuing a rapidly moving target with gain less than one (i.e. a series of pursuit segments, where eye velocity is less than target velocity, interspaced by catch-up saccades). Normal pursuit is illustrated by dashed lines for two

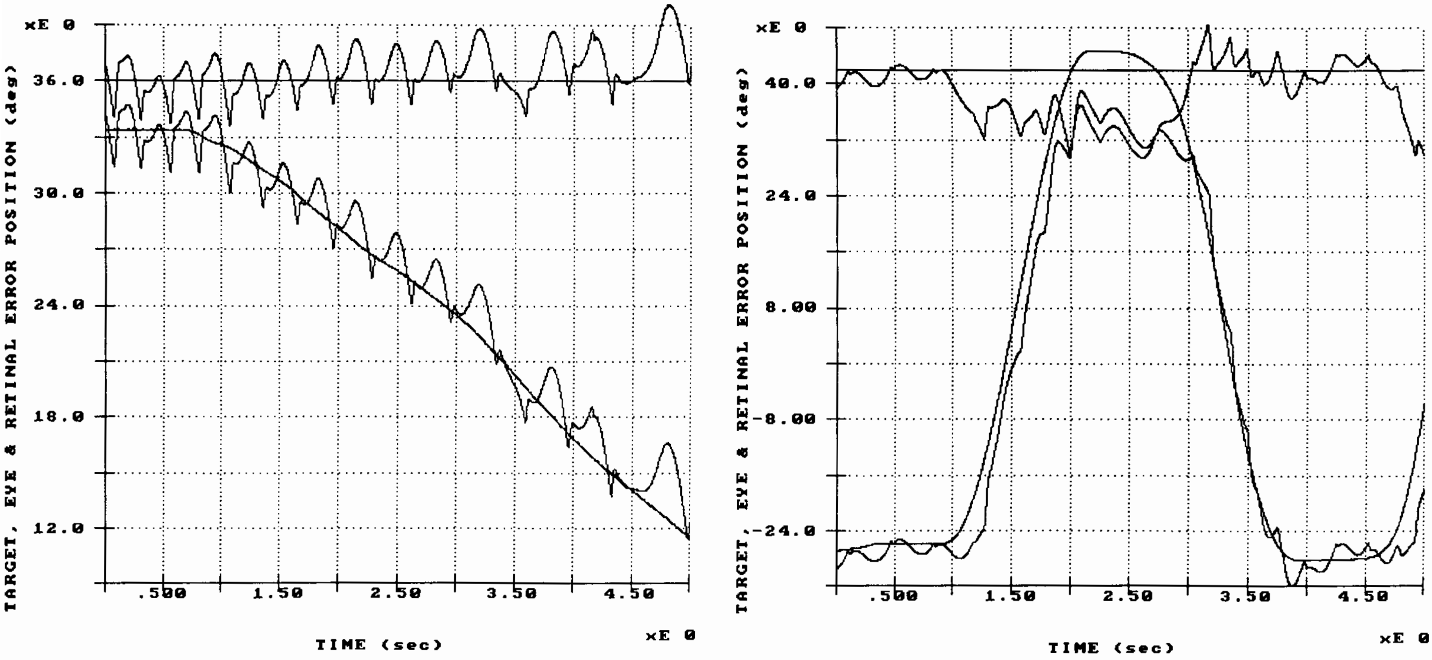

Fig. 1. (a) A 5-second record of smooth pursuit of a slowly moving target showing target, eye and retinal error (eye-target) positions. (b) A 5-second record of smooth pursuit of a rapidly moving target showing target, eye and retinal error (eye-target) positions. For clarity, the retinal error signals have been shifted upwards. Both records were the result of passive motion pursuit. In this and other Figures of eye movements, both axes include scientific notation containing the appropriate exponents; except for Figures 5a and 5b, they are 0.

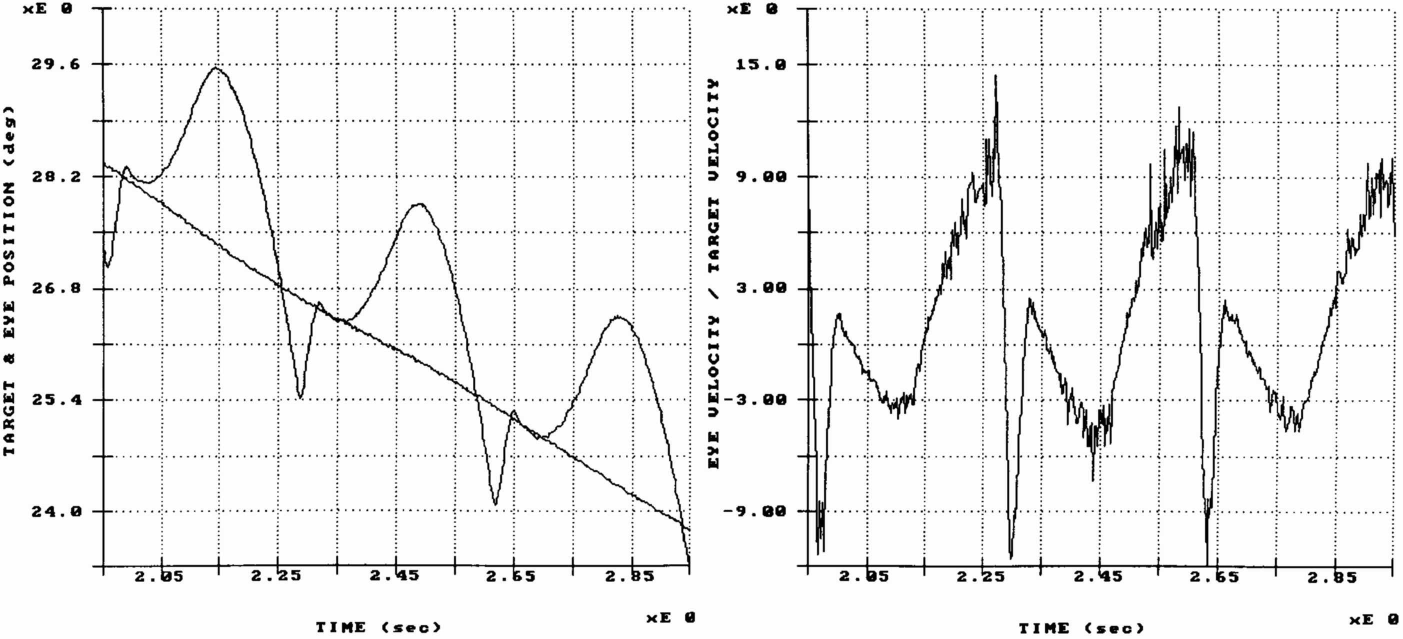

Fig. 2. (a) A 1-second record of target and eye position during pursuit of a slowly moving target. (b) The 'gain' (eye velocity/target velocity) record during the pursuit shown in (a). These records were the result of passive motion pursuit.

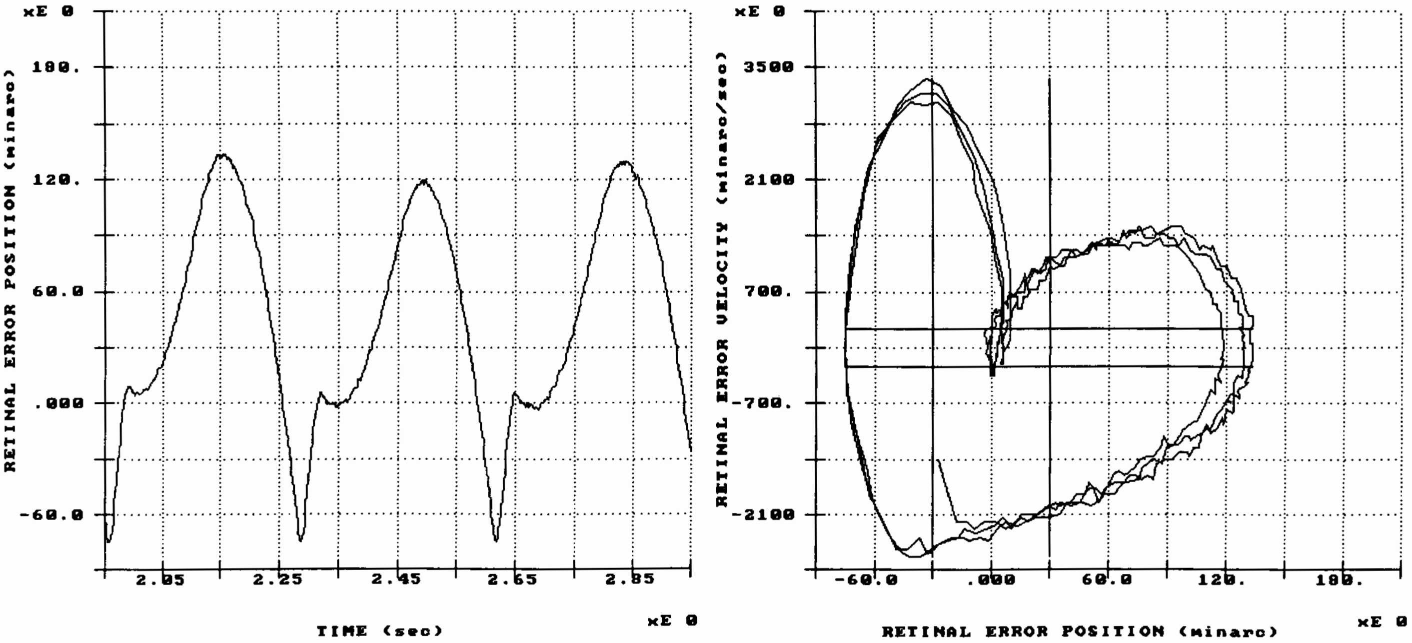

Fig. 3. (a) The retinal error position (eye-target) record of the 1-second record of pursuit of a slowly moving target shown in Fig. 2. (b) The phase plane or retinal error motion during this 1 second of pursuit. The foveation window defined for accurate foveation during fixation is shown on this and other Figures showing phase planes.

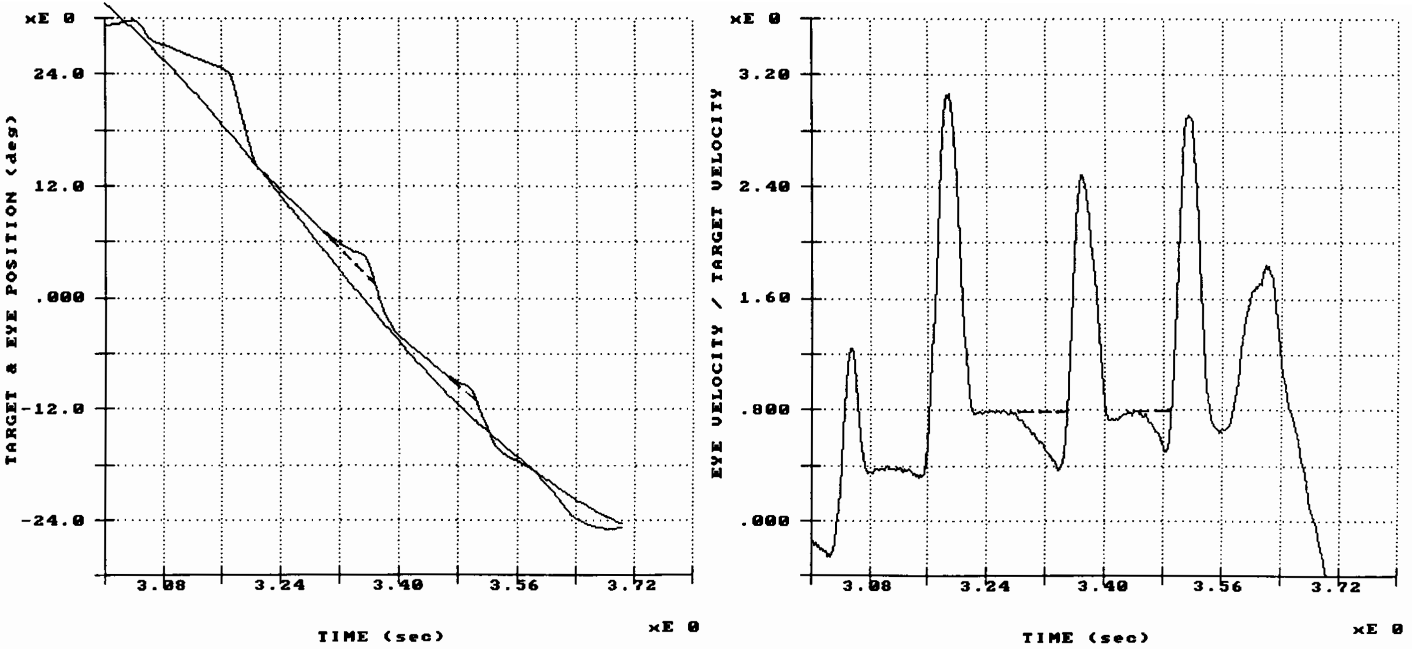

Fig. 4. (a) A 1-second record of target and eye position during pursuit of a rapidly moving target. (b) The ‘gain’ (eye velocity/target velocity) record during the pursuit shown in (a). The dashed lines illustrate normal pursuit (a) and gain (b). These records were the result of passive motion pursuit.

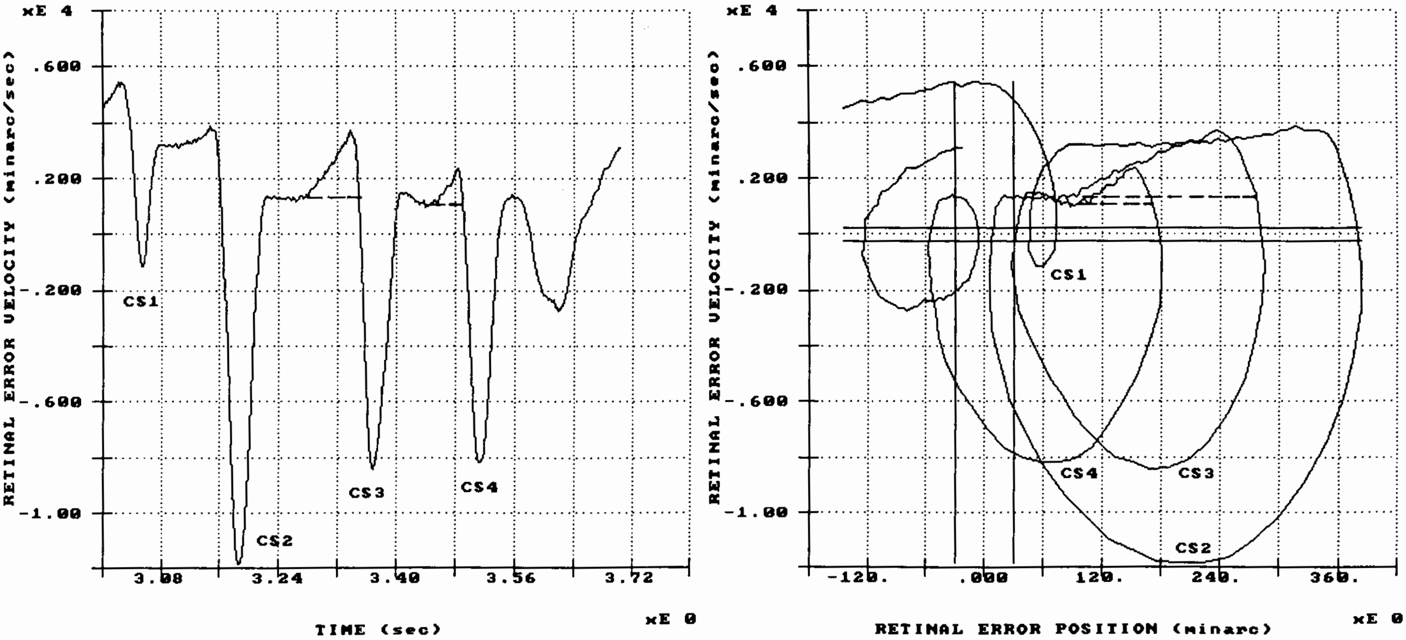

Fig. 5. (a) The retinal error position (eye-target) record of the 1-second record of pursuit of a rapidly moving target shown in Fig. 4. (b) The phase plane of retinal error motion during this 1 second of pursuit. Catch-up saccades (CS1–CS4) are shown in both Figures and the dashed lines illustrate normal pursuit. Note the exponents of '4' on the 'Retinal Error Velocity' axes of (a) and (b).

pursuit segments in Fig. 4. Fig. 4b is the 'gain' function of this interval of pursuit.

To aid in reading the phase-plane plot, Fig. 5a shows retinal error velocity with the catch-up saccades identified (CS1–CS4). In Fig. 5b are the same identifying labels; after each catch-up saccade there are both velocity and position errors. The pursuit movements are the horizontal segments beginning at the end of the catch-up saccades (outside the foveation window) and going to the right. This is essentially the phase-plane plot that would result from normal tracking of a high-velocity target (shown dashed for the pursuit segments following CS2 and CS3 in Fig. 5); the only difference is the presence of an accelerating tail on the pursuit segments of the CN subject's response. Note that after CS4 the subject managed to image the target on the fovea with minimal error velocity (i.e., the phase plane shows a pursuit movement through the foveation window).

Fig. 6 is the graphical result of calculating, for all foveation periods during pursuit segments of non-zero target speeds, the foveation-period gains (G_{fp}) for pursuit in each direction and for both directions combined. These are *normal gain values* for smooth pursuit through the range of target velocities tested. Also shown are the average gains (G_{av}) for pursuit at each of the six target speeds tested. Fig. 7 is the retinal error measured for rightward and leftward pursuit at each of the target speeds. At low target speeds, the error remained within the ±30 minarc foveation window but as target speed increased, larger retinal errors resulted. In Fig. 8, plots of both the means and SD's of retinal error during the foveation periods are shown as evaluated by the two different methods discussed in the METHODS'

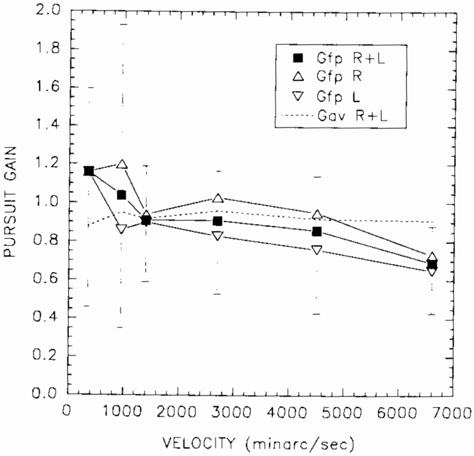

Fig. 6. Plots of foveation-period gains (Gfp) of pursuit to the right (R), left (L) and in both directions (R + L) for the range of target velocities tested. For comparison, the average gains (Gav R + L) are also plotted. The standard deviations of the R and L pursuit gains are shown.

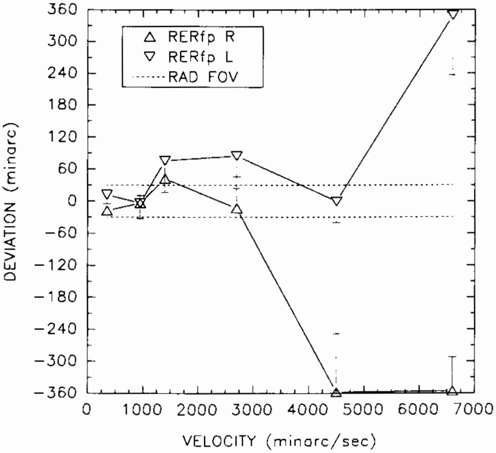

Fig. 7. Plots of the retinal error (RERfp) measured for rightward (R) and leftward (L) pursuit at each of the target velocities tested. The radius of the fovea (RAD FOV) is shown to aid in the evaluation of the retinal errors. The standard deviations of the retinal errors during R and L pursuit are shown

Analysis section. Also indicated are the SD of fixation and radius of the foveation window. both methods of evaluation yielded essentially the same results.

Table 1 contains the CN waveforms recorded at various gaze angles for

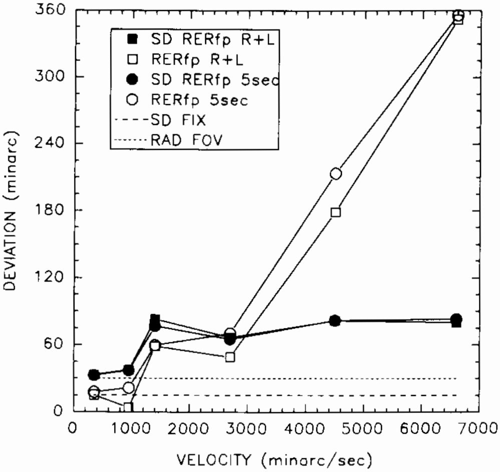

Fig. 8. Plots of the means and standard deviations (SD) of retinal error (RERfp) measured for rightward and leftward (R + L) pursuit at each of the target velocities tested. Both the means and SD were calculated by each of the two methods discussed in the METHODS section. For comparison, the radius of the fovea (RAD FOV) and the SD of fixation (SD FIX) are shown.

Table 1. Pursuit-induced shifts in CN waveforms and dynamic neutral zones.

Average target velocity (deg/sec)	Gaze angles (deg) −40	−30	−20	−10	0	10	20	20
110		JR	JR	JR	JR	JR	JR	JR
75		JR_{ef}	JR_{ef}	JR_{ef}	JR	JR	JR	JR
45		LPC	P_{lfs}/PP_{rfs} DNZ	JR_{ef}	RPC	RPC	RPC	RPC
23		LPC	PP_{rfs}	PP_{rfs}	PP_{rfs}	PP_{rfs}	P_{rfs}/RPC	RPC
			← – – – – –	– – – – – –	DNZ – – – –	– – – – →		
16		P_{lfs}	PP_{rfs}	PP_{rfs}	PP_{rfs}	PP_{rfs}	JR_{ef}	RPC
			← – – – – –	– – – – – –	DNZ – – – –	– – – – →		
6		P_{lfs}	P_{lfs}	PP_{rfs}	PP_{rfs}	PP_{rfs}/P_{rfs}	P_{rfs}	P_{rfs}
				← – – – –	DNZ – – – –	– – – →		
0	LPC	P_{lfs}	P_{lfs}	PP_{rfs}	PP_{rfs}	PP_{rfs}/P_{rfs}	P_{rfs}	P_{rfs}
				← – – – –	SNZ – – – –	– – – →		
− 6		LPC	P_{lfs}	PP_{rfs}	PP^{*}_{rfs}	PP_{rfs}	P_{rfs}	P_{rfs}
				← – – – –	DNZ – – – –	– – – →		
− 16			P_{lfs}	PP_{rfs}	PP^{*}_{rfs}	PP_{rfs}	P_{rfs}	
				← – – – –	DNZ – – – –	– – – →		
− 23			LPC	LPC	PP_{rfs}	PP^{*}_{rfs}	PP_{rfs}	PP_{rfs}
					← – – – –	– – – – – –	DNZ – – – –	– – – →
− 45			LPC	JL_{ef}	JL_{ef}	JL_{ef}	JL_{ef}	PP_{rfs} ←DNZ→
− 75			JL_{ef}	JL_{ef}	JL_{ef}	JL_{ef}	JL_{ef}	JL_{ef}
−110			JL	JL	JL	JL	JL	JL

* Single beats of JR or RPC.

D(S)NZ	Dynamic (static) neutral zone.
JR(L)	Jerk right (left).
$JR(L)_{ef}$	Jerk right (left) with extended foveation.
R(L)PC	Right (left) pseudopsycloid.
$P_{l(r)fs}$	Pendular with left (right) foveating saccades.
PP_{rfs}	Pseudopendular with right foveating saccades.

each target speed and direction along with those recorded during fixation at different gaze angles. During pursuit, specific waveforms shifted from their static (fixation) positions to their dynamic (pursuit) positions. The dynamic positions were shifted oppositely to the direction of pursuit in proportion to target speed. The neutral zone is that region of gaze angles containing pendular or bidirectional jerk waveforms and lying between the regions of unidirectional jerk waveforms (jerk left to the left and jerk right to the right) [11]. For this subject, the static neutral zone (SNZ), measured during fixation, contained pseudopendular with rightward foveating saccades (PP_{rfs}) waveforms. As Table 1 shows, the dynamic neutral zone (DNZ), measured during pursuit [3], shifted oppositely to target velocity proportional to the increase in target speed. Within the neutral zones and for the pendular waveforms to the right of the neutral zones, the foveating saccades were rightward; to the left of the neutral zones, they were leftward. Rightward foveating saccades occurred when the waveforms were biased to the right of the target; leftward foveating saccades occurred when they were biased to the left. Thus, when pursuing a target that was lateral to the DNZ, the subject's pendular waveforms were biased eccentrically to the target with foveation achieved by centrifugal saccades. At gave angles farther away from the DNZ (or for high-velocity targets), unidirectional jerk waveforms with centrifugal fast phases were found. At the highest velocities, the DNZ shift was so great that only unidirectional jerk waveforms were present during pursuit across the total ±30° range tested. Also at these high velocities, there were less data in far lateral gaze due to the subject's anticipation of the target's direction reversals; this resulted in a failure to fully pursue out to the farthest lateral extent of target motion and to anticipatory reversals of eye motion. At some gaze angles (shown with asterisks in Table 1) an occasional bias reversal of the CN waveform occurred, resulting in a unidirectional jerk waveform where PP waveform predominated; bias reversals have been documented during pursuit in other CN subjects [3] and commonly occur during fixation [2, 12].

Pursuit (active motion). A has been observed in normal subjects [13, 14], the quality of pursuit resulting from the active-motion trials at all target speeds was as good or better than that from the passive-motion trials. A type of response seen during several of the active-motion trials (less than 20% of the high-speed trials with a preference for pursuit to the right) consisted of complete suppression of the CN waveform for periods of up to 600 msec; only pursuit movements were present during these intervals. Fig. 9 is a 5-second record of pursuit of a 110°/sec target; both target and eye position (9a) and velocity (9b) traces are shown. Of particular interest is the rightward pursuit interval between 3.5 and 4 seconds. Fig. 9b reveals a complete absence of the CN waveform for 600 msec; also, *no* saccades were present. Fig. 10 is an expanded view of target, eye and error position (10a)

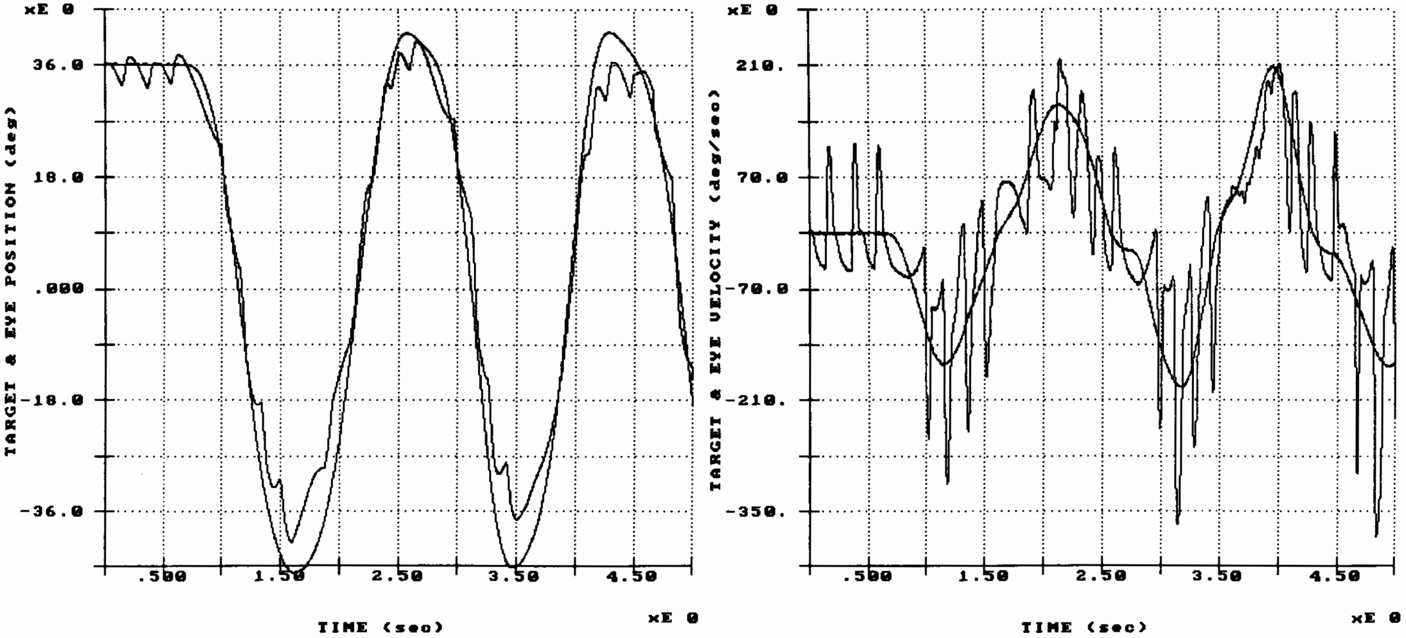

Fig. 9. (a) A 5-second record of smooth pursuit of a rapidly moving target showing target and eye positions. (b) The target and cye velocities of this period of active-motion pursuit.

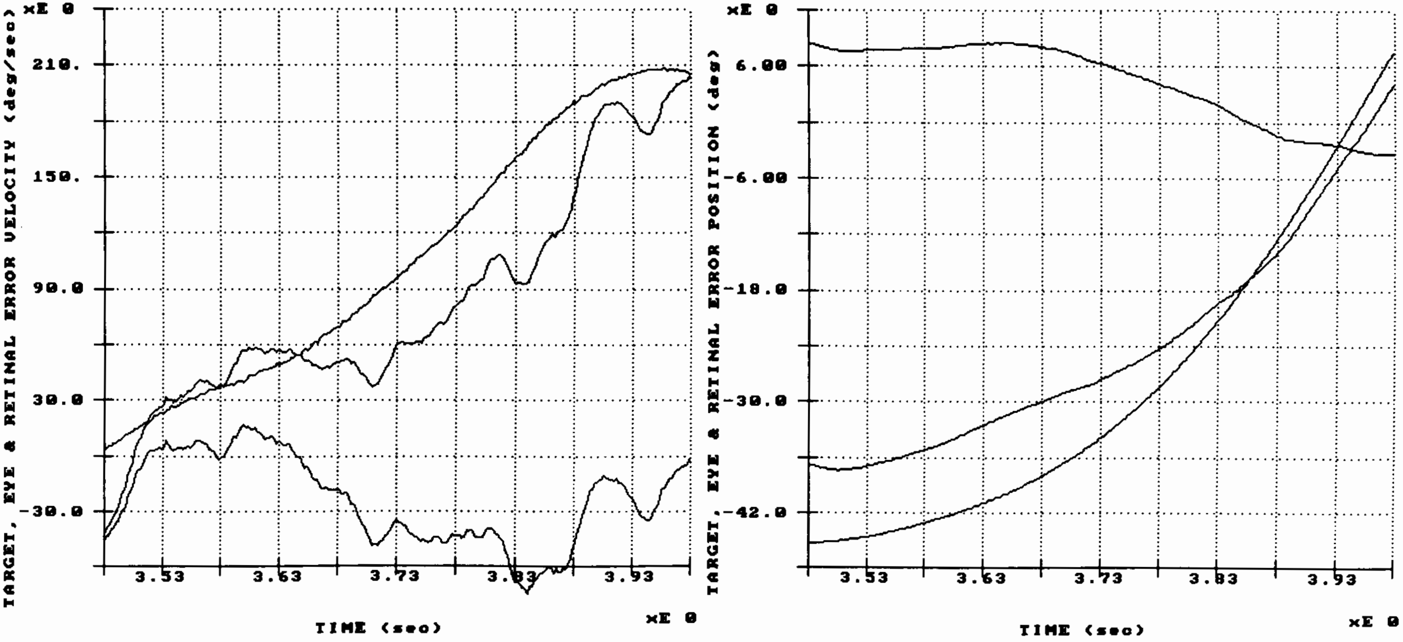

Fig. 10. (a) An expanded view of 500 msec of smooth pursuit taken from the record of Fig. 9. Target, eye and retinal error positions are shown. (b) Target, eye and retinal error velocities of the pursuit in (a).

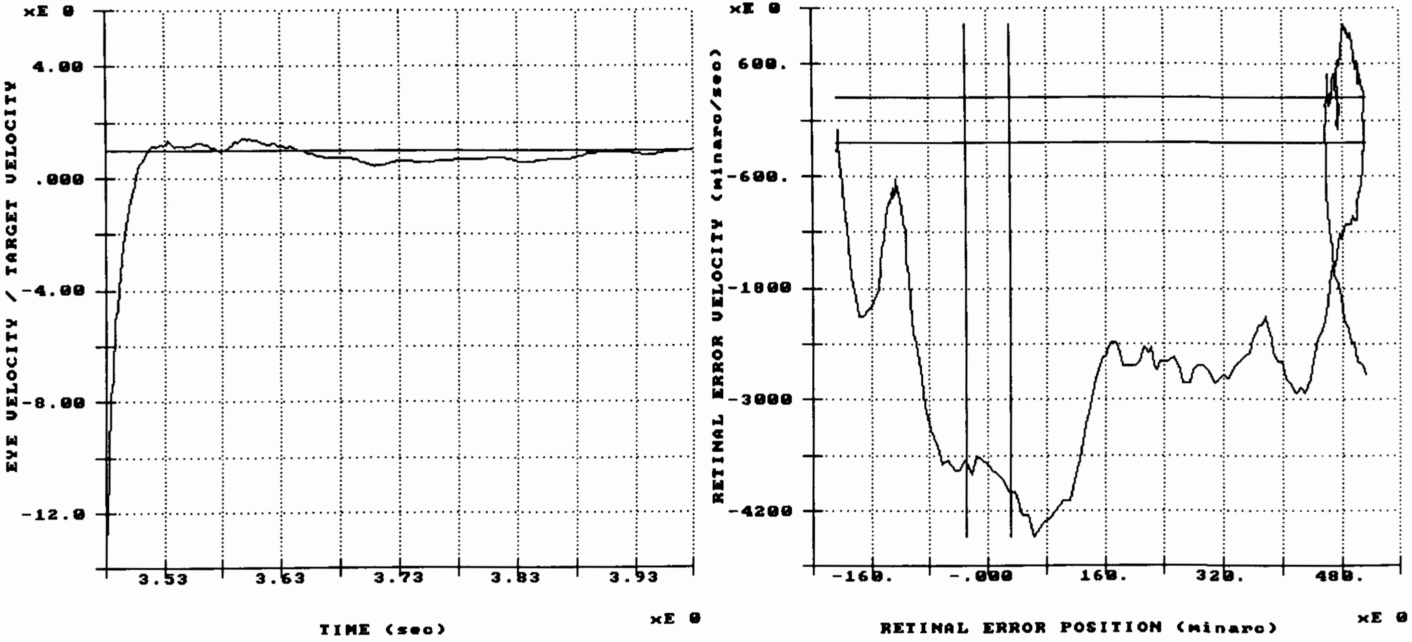

Fig. 11. (a) The pursuit 'gain' (eye velocity/target velocity) from the record of Fig. 9; the value of unity gain is shown for comparison. (b) The phase plane of this active-motion, high velocity pursuit.

and velocity (10b) during this pursuit interval. Initially, the subject led the target, due to prediction of target direction reversal. As the target accelerated to a peak velocity of 210°/sec, so did the subject's response, smoothly and without either catch-up or foveating saccades. In Fig. 11a, the 'gain' function reveals a fluctuation about unity gain and achievement of unity gain as the target speed reached its peak of 210°/sec. The phase plane in Fig. 11b shows that the intervals of low retinal error ($\leqslant$30 minarc) and low slip velocity ($\leqslant$240 minarc/sec) did not coincide and, therefore, fell outside the foveation window.

Discussion

In the past it was difficult to evaluate smooth pursuit in a subject with spontaneous nystagmus because the eye movements measured are not those of pursuit alone. In subjects with CN, the problem is compounded by the idiosyncratic changes in CN waveform and shift in neutral zone induced by the very attempt to pursue a moving target [3]. An eye-movement record of smooth pursuit obtained from a CN subject bears little resemblance to that of a normal, especially when only jerk waveforms with little or no extended foveation are present. It is not surprising, therefore, that this lack of correspondence has been misconstrued in such cases as a deficit in smooth pursuit [15, 16] and that the commonly recorded slow phases taking the eyes in an increasing-velocity movement opposite to target motion has led to the mistaken postulation that CN itself was caused by a smooth pursuit 'reversal' [17]. An understanding of the foveation dynamics operating in CN during fixation is a necessary precondition to the study of smooth pursuit and to its evaluation in CN. We endeavored to develop and employ several methods of smooth pursuit evaluation in an effort to measure the true pursuit output when the eye movement output is contaminated by a changing and confounding noise signal, the CN waveform. Earlier studies clearly identified a strong smooth pursuit component to the eye movement output and concluded that there was no deficit in smooth pursuit [3, 4, 18, 19].

Methodology. The foveation-period gain method of evaluating pursuit in CN is based on our knowledge of CN waveforms and their foveation periods [2]. If smooth pursuit is to help an individual with CN to see a moving target clearly, it must do so during these foveation periods. The velocity gain of smooth pursuit should be unity when the position error is at or near zero. Evaluation of gain during foveation periods, although time consuming (each 5-second segment required roughly 3.5 hours of analysis) is the most accurate measure of pursuit function. The variation in gains from one period to the next requires multiple samples at each velocity. The source of variation includes errors in accurate identification of foveation periods from the derived retinal error signal as well as any inherent variation in the actual gains on a beat-to-beat basis. The use of foveation-period gains preserves directional asymmetries that may be present due to the particular CN waveform present during pursuit. Although the calculation of gain is only accurate during foveation periods when eye velocity would otherwise be zero, this does not mean that pursuit (target) velocity is only part of the measured eye velocity signal during those periods. Rather, it is *always* present and the slow phase velocity is the sum of the nystagmus and pursuit velocities for the whole cycle of the waveform. If the pursuit was 'saccadic' (as has been claimed by some), a staircase would have to be subtracted from the eye signal to yield a retinal error waveform that equaled the eye waveform during fixation. That would produce a distorted error signal since subtracting the true target signal from the eye signal resulted in an error signal that matched the eye signal measured during fixation.

Average gain calculations are the least accurate and most affected by CN waveform. They fail to take into account the importance of the foveation periods and instead, are based on equally weighting the whole CN waveform. Average gain represents a highly filtered version of the eye-movement output velocity divided by the target velocity. As such, the average gain is only an approximation of the true pursuit function.

Comparison of the phase planes of retinal error during pursuit with those during fixation is a more accurate method than average gain despite the fact that the result is not a 'number' (e.g. gain). The means and SD's of retinal error position during pursuit at each velocity can be compared to each other as well as to those values measured during fixation; a descriptive picture of smooth pursuit function and the effect of target velocity emerges from this type of analysis. During fixation, the eye position signal contains only one component, the CN. The eye position signal during pursuit contains two components, CN and smooth pursuit. The retinal error signal (eye-target) also contains two components, CN and pursuit error. Thus, the retinal error signal is equal to the eye signal during fixation when pursuit error is zero. The more accurate the pursuit, the more closely will these values and their corresponding phase planes match those measured during fixation. This method was employed in two ways: (1) we computed the variables for pursuit in each direction separately at the target speeds used, and (2) we computed the variables for pursuit during each 5-second interval, combining both directions at the target speeds used. Both methods gave the same results (see Fig. 8) when the pursuit direction-specific figures of the first method were combined and then compared to those of the second method.

Pursuit (passive motion). The records shown in Fig. 1 revealed that for both slowly and rapidly moving targets there was a significant pursuit component in the eye movement response; this is clear prior to any analysis. There was a continuous, non-saccadic movement of the eyes in the direction of the target that could *only* be the result of pursuit. Subtraction of the target-position from the eye-position signal yielded an error-position signal that closely resembled that of the subject's eye-position signal during fixation. In Fig. 1b, it is hard to distinguish this subject's pursuit from normal pursuit of a high-speed target. The response consisted of pursuit segments interspaced with catch-up saccades. The records from a one-second interval of pursuit at low velocity resulted in an error-position signal and phase-plane portrait that are almost identical to those from similar intervals of fixation [9]. We conclude from this that pursuit was virtually perfect. For very fast target motions, we found pursuit gain to decrease as expected. Fig. 4a illustrates lower gain pursuit (gain ≃0.8 from Fig. 4b) and Fig. 5b shows the phase-plane portrait of this lower gain pursuit with the catch-up saccades labeled. Each saccade brought the eye to the target but with an error velocity due to the lower gain. If this were a normal rather than a CN subject, the pursuit segments would be horizontal on the phase plane without the accelerating tail preceding the next catch-up saccade; the dashed lines drawn on two pursuit segments illustrate this.

The data in Fig. 6 show the beat-to-beat foveation-period gain variation found and a slight directional asymmetry, with rightward pursuit slightly better than leftward. The gain vs. target speed profile is well within *normal limits* and shows high gain even at very rapid target speeds [20, 21]. The average gain profile is less indicative of gain variation with target speed. The mean retinal error position remained within the foveation window during pursuit at low velocities (Fig. 7) but increased with target speed. The small directional asymmetry seen may be a function of this subject's waveform rather than reflecting a true pursuit directional asymmetry. The data of Fig. 8 combine mean foveal error position and SD vs. target speed for the two methods employed. The SD's are greater during pursuit than fixation, even at low speeds, and increase to a higher level that is maintained from mid-range to fast speeds.

During smooth pursuit, the neutral zone exhibited by many individuals with CN shifts in a direction opposite to target by an amount proportional to target velocity [3, 4]. As a result, the CN waveforms measured during pursuit do not conform to those measured during fixation at each gaze angle. When this shift is great enough, the CN direction during pursuit is opposite that during fixation and may be opposite to target motion throughout the range of pursuit angles tested. The subject of this study had a broad SNZ (≃20°) that allowed us to document the DNZ shift more easily than for a narrow SNZ with little or no pendular waveforms. As Table 1 shows, during rightward pursuit CN waveforms and DNZ's were shifted to the left when compared to those measured during fixation; leftward pursuit produced a rightward shift. The amount of these shifts grew with increasing target speed. Fig. 12 is a plot of the shifts of the centers of the the DNZ's calculated by subtracting the SNZ from the DNZ's measured at each target velocity; at zero velocity, the DNZ equals the SNZ and the shift is shown as zero. The data points from each of seven target velocities (4 rightward and 3 leftward) were curve-fitted by a quadratic function for leftward shifts (rightward pursuit) and a cubic function for rightward shifts (leftward pursuit). These functions gave good fits of the data (easily determined by eye) and indicate that, for this subject, the DNZ shift was asymmetric; it was greater during leftward than rightward pursuit. At average target velocities higher than −23°/sec and +45°/sec, the DNZ's shifted so much that no DNZ waveforms (PP_{rfs}) were found within the ±30° range of pursuit tested; an exception to this occurred during pursuit at −45°/sec where PP_{rfs} waveforms were found at +30° but without data at more lateral gaze angles to calculate the center of this DNZ, we could not include it in Fig. 12.

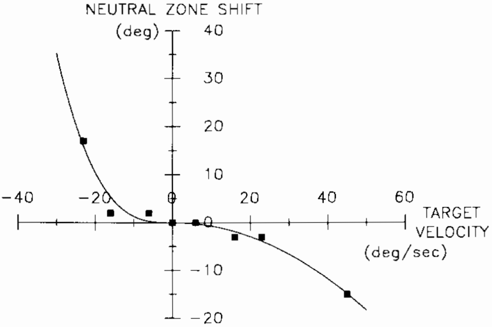

Fig. 12. A plot of the neutral zone shifts measured at each target velocity by subtracting the center of the static neutral zone from those of the dynamic neutral zones.

Pursuit (active motion). For both passive and active motion, the role of prediction ('expectations') confounds the concept of pursuit gain [22–24]; It is difficult to clearly define just what the 'input' to smooth pursuit really is and the definition of 'gain' loses its precision under these conditions of high predictability and multisensory inputs, even when considering only the pursuit of normals. Therefore, we restricted analysis to segments of active-moment pursuit showing a difference in response compared to passive motion. These differences were most obvious at high target speeds. Occasional periods of total suppression of the CN waveform for as long as 600 msec occurred for this subject during which time *only smooth pursuit* was evident (see Figs. 9 and 10). Although such CN suppression was not seen in this CN subject during passive-motion trials, it has been reported for other CN subjects at both high and low target speeds [3]. Active-motion trials allowed pursuit velocities to equal target velocities at higher speeds than during passive-motion trials. These pursuit velocities met or exceeded those reported for normals under both fixed-head [14, 25] and free-head [26] conditions.

We have analyzed the smooth pursuit of a subject with CN using several different methods (numerical and graphical), all of which provided strong evidence of normal smooth pursuit function; it was neither defective nor was it 'reversed' by any reasonable definition of the latter, erroneous concept. Pursuit during passive-motion trials was at normal gains for all the target speeds tested. Additionally, our active-motion trials revealed pursuit at velocities as high or higher than those reported in studies of normals.

Conclusions. The concept that CN is the direct result of deficient or even 'reversed' pursuit is one that has neither published supporting data nor associated symptoms in CN subjects. It was put forth based on the erroneous assumptions that the eye-movement responses of a CN subject were only pursuit responses and that, during the first 100 msec, these responses represented open-loop pursuit; *they do not.* In the CN subject, where there is an ongoing oscillation, the assumption is flawed and cannot be justified. Merely examining the whole pursuit record (beyond the first 100 msec) reveals the pursuit component carrying the eyes in the same direction as target motion. We have demonstrated, by *different* and *unrelated* methods, that pursuit in the individual with CN is normal and that a shift in the DNZ is the sole cause for CN reversal. Therefore, it can no longer be reasonably argued that CN is caused by defective or 'reversed' pursuit. The further coupling of this model of 'reversed' pursuit with a putative afferent misrouting is also without foundation. Apkarian et al. have shown conclusively that individuals with CN who are not albinos had *no* misrouting [27, 28]. Since these papers, Dr. Apkarian has studied at least 14 additional non-albino CN subjects and found *no misrouting* in any of them (personal communication). Thus, the existence of CN in non-albinos with no misrouting (by far, the great majority of individuals with CN) negates the hypothesis of misrouting and 'reversed' pursuit as a causal mechanism for CN.

As has already been suggested [3], the methods developed in this study also apply to the nystagmus responses to optokinetic stimuli (OKN). Here also, DNZ shifts result in a reversal of CN slow phases that have been mistakenly identified in the past as 'reversed' OKN [4, 29–32].

The suppression of oscillopsia during fixation of stationary targets has been related to the ability of an individual with CN to produce and maintain foveation periods [33–36]. Our data show that during smooth pursuit, foveation periods are maintained and thereby allow the same mechanism of oscillopsia suppression to operate as during fixation.

Based on the data presented in this and the accompanying study of CN fixation [9], we offer the following observations and hypotheses about the interaction between fixation, pursuit and the occurrence of the CN instability: (1) the individual with CN has strong fixation reflexes that maintain retinal image stability within tolerable limits during both fixation of a stationary target and smooth pursuit; (2) fixation prolongs target foveation in the presence of some, but not all, types of nystagmus; (3) we hypothesize that the ability to prolong target foveation is related to the suppression of oscillopsia [34]; (4) fixation is possible only when the target image falls within some foveation window defined by retinal error position and velocity; and (5) the smooth pursuit of individuals with CN is normal [3, 4].

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Glossary

General terms

CN	Congenital nystagmus
CS	Catch-up saccade
DNZ	Dynamic neutral zone
SNZ	Static neutral zone
SD	Standard deviation

CN waveforms

Jef	Jerk with extended foveation
JR(L)	Jerk right (left)
JR(L)ef	Jerk right (left) with extended foveation
Pfs	Pendular with foveating saccades
Pfl(r)s	Pendular with left (right) foveating saccades
PPrfs	Pseudopendular with right foveating saccades
R(L)PC	Right (left) pseudocycloid

Calculated (statistical) terms

Gav	Average gain
Gfp	Gain calculated during the foveation period
RERfp	Mean retinal error position during foveation period

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