THE PROCESSING OF VELOCITY INFORMATION BY THE PURSUIT OCULOMOTOR SYSTEM

Thesis by
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ABSTRACT

A study of human smooth pursuit eye movements has been performed in order to clarify the velocity information processing capabilities of the visual system.

A set of stimuli were designed which, when presented in motion to the visual system, contained no position information. Thus, the velocity sensitive pursuit system was stimulated in isolation from the saccadic system, which is position sensitive.

The smooth eye movements which were elicited by step increases in target velocity from zero velocity were analyzed in detail by a nonlinear least squares curve fitting procedure. Eye velocity was found not to exactly match stimulus velocity, the differences being unsystematic with velocity amplitude or direction. Response latency and the duration of eye acceleration were found to vary about average values of 150 and 300 msec, respectively.

Averaged velocity and acceleration responses were computed from first and second derivatives of the position responses to repeated presentions of the step velocity target motion. Response average acceleration pulse amplitude did not vary linearly with stimulus acceleration pulse amplitude. Increases in stimulus pulse amplitude were met with changes in amplitude, shape, and duration of the response pulse.

Averaged acceleration responses to two consecutive stimulus velocity steps were shown not to correspond with the response predicted by the linear superposition to two single pulse responses. The departure of the actual double pulse response from the predicted response was discussed in terms of possible sources of a such a nonlinearity.

The results of the single and double pulse experiments were used to design a pseudo-random stimulus acceleration signal which was subsequently used in a white-noise type of nonlinear analysis of the pursuit system. The first and second order pursuit system kernels which were obtained from the analysis showed that the technique could be used to study interactions within the pursuit-perceptual system. The results were not reliable to the extent that a mathematical model could be constructed. However, several suggestions for improving the pseudo-random input analysis technique were included in the conclusion chapter.

Finally, the experimental results were discussed in terms of the relationship between visual perception and the control of smooth pursuit eye movements.

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I. INTRODUCTION

In most situations, the human visual system is forced to function within a frame of reference in which the external environment is in constant motion. Movements of the eyes, head and body act to produce retinal image motions which usually are totally unrelated to the visual scene. Voluntary eye movements are the exception, in that their function is to bring the object of regard onto the portion of the retina with a high concentration of photoreceptors. It seems that the brain's task is to determine which retinal image motions are important to its processing of the visual scene. It would be interesting to find out how the brain performs such a complex task, but that project is probably beyond our reach at this time. We must first look at the more basic, and therefore more important, question of how is motion sensed by the visual system?

Other such questions in vision have been posed and are currently under study. For example, how are luminance, color, contrast sensed by the visual system? The concepts of motion and temporal frequency sensitivity are two more of the basic areas of vision research which are crucial to our understanding of the visual information processing flow, because they are basic attributes of the light input to the system. Luminance, color, and contrast are the spatial attributes; motion and time are the temporal attributes from which a visual percept is constructed by the brain. Thus it is of utmost importance to understand how each of these is measured by the visual system.

The significance of our understanding of motion information processing in vision thus established, how does one begin to study motion sensitivity? The complexity of the problem dictates some simplifying procedures and assumptions. Let us first restrict the sources of motion input to the system by securing the head. Now only two sources of retinal image movement remain, that produced by eye movements and that induced by external movement of the viewed target. (In some cases, further restriction of image motion may be desired. Either the target can be held stationary or eye movement-induced motion can be eliminated by the technique of retinal image stabilization.)

Secondly, let us assume that the perceptual system has access to information concerning the control signals sent to the extraocular muscles. That this assumption is reasonable for the case of the pursuit system and motion perception is demonstrated as follows. The percept of motion is generated from two sources of information. One is the motion of the target image on the retina. The other source is the orientation of the retina with respect to the visual scene. The latter source is easily revealed using an afterimage placed parafoveally. If one attempts to pursue the afterimage target, the percept is that the target is moving away from the fovea. This trivial observation is indicative of the interaction between eye movements and perception. Apparently the perceptual system receives motion information from the oculomotor system independent of motion of the retinal image. Furthermore, there is evidence (Yasui, 1973) that the oculomotor system receives control information not only from retinal signals but also by efferent pathways from perception. This close reciprocal relation between perception and the pursuit system will be explored in this thesis. The following paragraphs describe the bases upon which this work was undertaken.

The function of most voluntary eye movements is to bring the image of an object of regard onto the fovea, where the neural apparatus for spatial perception is highly developed. Tracking eye movements are elicited when one is asked to follow a moving target. If the target position changes in a step-like fashion, high velocity, short duration eye rotations called saccades are elicited. If the target movement is smooth and continuous in position, the eyes will respond with smooth pursuit eye movements upon which saccades are usually superimposed. The two types of eye movements work together to keep the target on the fovea. It is generally accepted that the input to the saccadic eye movement system is a position error signal calculated from the distance of the target from the fovea. Where and how the saccade amplitude and direction calculation is made is still under investigation. (The controversy arises from the observation that peripheral acuity as measured clinically is too poor to account for the highly accurate calculation of saccade magnitude.) The input to the pursuit system, however, is not as easily defined.

Let us assume that the pursuit system also is sensitive to position error, defined as the angular distance of the target from the fovea. In a typical smooth tracking task then, the eye should begin a smooth movement with some latency after the target begins to move away from the fovea. In a closed loop system the response is usually proportional to the unput magnitude. In this case it is reasonable to assume that the system responds to position error with a change in eye velocity. So at onset of stimulus motion, the error is increasing and the velocity of eye rotation also increases. If the stimulus velocity is constant, the eye should continue its acceleration until the position error ceases to increase. At that point eye velocity is equal to target velocity and yet a position error still exists. Such a position error triggers a saccade of appropriate magnitude to bring the target onto the fovea. Results of position ramp experiments show just such an eye movement response, one to several saccades superimposed upon a smooth pursuit eye movement. The closed loop system now operates to maintain eye velocity equal to stimulus velocity by minimizing the position error.

Apparently, the assumption of position error as input to pursuit does not lead to any glaring contradictions. There is, however, the unsettling observation that the function of the pursuit system is to match eye velocity to target velocity. Wouldn't it therefore be more reasonable for the system to respond to velocity input with a velocity change, i.e. acceleration? Of course Rashbass (1961) proposed just this model from his observations of ramp and step-ramp input experiments. When a velocity error between target and eye is detected, the pursuit system responds with a change in velocity in the direction of decreasing velocity error, even though the eye may be moving away from the target. If a velocity error still exists, the system responds with another acceleration and so on until velocity error is reduced to zero. At some time during the velocity matching process, the saccadic system responds to the relative positon error between fovea and target. Rashbass (1964) recordings point out this independence of the saccadic and pursuit systems (see his fig. 2). Apparently, the error sensing mechanisms for the two systems are also independent, since the saccadic system is able to respond to the position error at any time during the acceleration phase of the pursuit movement. This point provides some support for the notion that velocity error is the input to the pursuit system. However, considerably more evidence is needed to make a definite statement.

It is at this point where previous research on the pursuit oculomotor system fails to give clear answers. The background section of this thesis will review the relevant work. It will become obvious from that analysis that many questions crucial to an understanding of the pursuit system remain unanswered. Not only is the question of the unput to the system unanswered, but also the dynamics of the response have not been sufficiently defined. For example, Yasui (1973) proposed a closed loop model for pursuit, based upon perceived velocity as the relevant input, rather than retinal velocity. Many other models have been proposed which account for some of the first order dynamics of pursuit, but the second order effects have usually been ignored or experiments have been designed in such a way as to linearize the system. Some thought about second order effects reveals their relative importance to our understanding of pursuit. The basic question is, how does the past affect the response to the present input? Quantification of these second order nonlinearities will be one of the major contributions of this thesis. The results of the experiments also should shed some light on the problem of position vs. velocity input.

An easily demonstrable property of pursuit eye movements is that they cannot be voluntarily initiated. Motion of a visual target is a necessary condition for the generation of pursuit. Foveal stimulation is also a necessary condition in most cases. These simple observations indicate that the perceptual system must play an important role in the input pathway to the pursuit system. In primates, motion detection is believed to be a non-retinal event (Hubel and Wiesel 1960, 1968). The more complicated neural networks found in the superior colliculus and visual cortex are organized into motion detection systems. Furthermore, the perceptual mechanisms associated with foveal viewing probably play a large role in the control of pursuit eye movements. Thus, in order to see the complete picture of pursuit oculomotor control, the motion sensitivity of the perceptual system must also be defined.

In the background section of this thesis, work will be reviewed which attempts to elucidate some of the properties of perceptual motion sensitivity. The problem we face is that most of these studies do not consider eye movements as a possible source of motion information. It is this deficiency in the existing literature which this thesis will attempt to correct. The psychophysical experiments to be described have been designed around such problems as the relationship between velocity and temporal frequency sensitivity.

Of course, the real goal, for most scientists studying vision, is to understand how the collection of nerve cells making up the visual system interact to produce the visual percept. It is important, therefore, in the context here to be aware of what the neurophysiologists know about motion sensitivity and its relation to eye movements. In the next chapter the neurophysiology of motion perception and pursuit will be reviewed as it applies to this work.

Finally, when the relevant background material has been presented and the experiments and results described, the discussion section will center around the possible interaction between perceptual and oculomotor control processes.

II. VELOCITY SENSITIVITY IN VISION: BACKGROUND

A moving target when imaged on the retina by the optics of the eye initiates a host of neurophysiological events, which in turn generate the perceptual and oculomotor responses to motion. In the human, the neurophysiology of motion senstivity must be inferred from the results of psychophysical experiments. The psychophysics of motion perception are presently foremost in the minds of investigators studying spatio-temporal visual sensitivity (see for example, Levinson and Sekuler, 1976). The oculomotor response to motion has also received a share of the attention of vision researchers. It has become apparent from recent work that the oculomotor and perceptual responses to movement are intricately related (Yasui, 1973; Matin, 1972).

It is the intent of this dissertation to elucidate some properties of the smooth component of the oculomotor motion response which previously have received insufficient attention due to methodological limitations. The first section of this chapter will be devoted to bringing together results of previous investigations of smooth pursuit eye movements in order to form a theoretical framework around the present research. The second section will briefly consider the psychophysical evidence for the involvement of perception in the smooth pursuit response. Section 2.3 will then consider the neurophysiological basis for oculomotor and perceptual velocity sensitivity as treated in this thesis.

2.1 The Pursuit Oculomotor System

2.1.1 General Description of the Pursuit System

Human smooth pursuit eye movements were described as early as Dodge (1903) and have been the subject of considerable study since that time. Most of the work has been devoted to quantifying the response of the system to various types of input. Frequency response analyses were carried out using pure sinusoidal motion, usually in the horizontal orientation (Fender and Nye, 1961; Stark, Vossius and Young, 1962). Also pseudo-random inputs (both sum of sinusoids and band-limited Gaussian white noise) were employed to study the oculomotor response to non-predictable target motion (Stark et al., 1962; Dallos and Jones, 1963; Michael and Jones, 1966; St-Cyr and Fender, 1969a, b). The result of these studies was a series of gain and phase vs. frequency relationships whose individual characteristics depended upon the specific input used. In general, the gain of the tracking system was found to be greater for pure sinusoidal stimuli than for band-limited Gaussian signals at most frequencies. The phase relationship followed a similar trend, showing smaller phase lag for sinusoidal stimuli than for random stimuli. These data led to conclusions regarding the ability of the oculomotor system to predict future target motion and adjust its gain and phase accordingly. A different theory, put forth by St-Cyr and Fender (1969a), was that system performance was determined by the statistics of the input waveform. In any case, it is obvious that the system under scrutiny is nonlinear. The response of a linear system to any input can be generated from the superposition of its responses to the components of the input. A system whose plant parameters depend upon input characteristics cannot be defined as linear.

In fact, another way of demonstrating the departure from linearity is to study the response of the tracking system to a spot stimulus which is made to "move horizontally with uniform velocity from an initially stationary position" as described by Rashbass himself. This was done in several labs (Rashbass, 1961; Robinson, 1965) and produced some interesting results. The Rashbass study showed that the response waveform elicited by the so-called position ramp stimulus depended upon the final velocity of the motion. As velocity was increased beyond about 2 deg/sec, the eye movement response consisted of one to several saccades superimposed upon the smooth component. Of course, just this behavior had been observed in the continuous input experiments. The saccades were usually in the direction of the target movement and tended to decrease the position error between target image and fovea. This observation led to the proposal that image <u>movement</u> on the retina was the stimulus for smooth pursuit. Rashbass then performed the crucial step-ramp experiment in which the target spot first rapidly jumped a specified distance then commenced its smooth velocity traverse in the opposite direction. The smooth pursuit response to such a stimulus indeed contained no saccades for initial steps of a certain magnitude (e.g. 1 deg step followed by 3.5 deg/sec ramp). The eye initially moved in a direction opposite to the position error but correcting for the velocity error. In this case, it seems that the nonlinearity of the response is introduced in the form of a saccadic component, while the smooth component is linearly related to input velocity. Whether or not this is a general characteristic of the composite tracking system (saccadic and smooth eye movements working together) will be considered later.

2.1.2 Classification of the Input Signal to Pursuit

The work of Rashbass has shown that the tracking system is primarily concerned with movement of the image across the retina, and in situations where image movement conflicts with the position error signal, the latter is ignored. Is this characteristic of the smooth pursuit system, and if so, what parameters of image movement are used in programming an eye movement response? As discussed in Chapter I, position, velocity or acceleration could be the relevant stimulus for pursuit. Existing evidence indicates that position is a relatively unimportant parameter for the control of smooth pursuit eye movements (Rashbass, 1961; Robinson, 1965). However, the distinction between velocity and acceleration as input parameters is more difficult to make. Rashbass suggests that the eye responds to retinal image movement with an acceleration. Thus when retinal image movement has been eliminated, the eye should travel with uniform velocity. This may be the case under normal tracking conditions, but when the retinal image is stabilized by eliminating the negative visual feedback pathway artificially, the hypothesis fails to predict the outcome. Yasui (1973) created a situation in which the subject perceived pseudo-random motion in the absence of retinal image motion. The eye responded to the perceived motion as if it were generated by retinal image motion. Apparently, perceived velocity also plays some part in the control of pursuit (see Sec. 2.2.1). Furthermore, the perceptual system is thought to be sensitive to the efferent signals controlling eye movements

(Helmholtz, 1924). Thus, although Rashbass' hypothesis is elegant in its simplicity, it does not tell the whole story.

Another possibility for pursuit control is that a true velocity match is attempted but never achieved. That is, image velocity is measured and compared to eye velocity and the result of the comparison drives the oculomotor plant. In such a system, output can never be exactly equal to input or the system would not respond. This hypothesis, a reasonable theory of pursuit control, surprisingly has never been tested and therefore remains a viable possibility. The function of pursuit eye movements may be just to keep the target image in motion within the foveal region, not to exactly stabilize the image. An accurate comparison of target and eye velocity would constitute a strong test of this possibility.

A third hypothesis is that image acceleration is measured and used to program an eye acceleration during smooth pursuit. This situation seems to be the simplest mode of operation to conceptualize. In the time domain, a step change of velocity is equivalent to an impulse of acceleration. The acceleration response of the tracking system to such an impulse is a measure of the transient properties of the system, the impulse response. Since differention is a linear transformation, the analysis of the pursuit system could be carried out in terms of acceleration, even though the system may actually be responding to position or velocity. In this thesis acceleration will be adopted as the domain in which to analyze pursuit responses.

2. 1. 3 Smooth Pursuit Response Dynamics

As discussed in Section 2. 1. 1, the response of the human oculomotor tracking system to both periodic and aperiodic position signals has been extensively studied. The results are usually presented in the form of frequency response functions, gain and phase plotted as functions of input frequency. For a linear system this type of engineering analysis completely describes the system. However, the major result produced by the frequency response analysis of the tracking system is that system characteristics are not independent of input statistics. Both gain and phase behavior change as the input statistics are changed e. g. from pure sinusoid, to sum of sinusoids, to bandlimited Gaussian noise (Fender and Nye, 1961; Stark, Vossius and Young, 1962; Dallos and Jones, 1963). These published results show that as the frequency content of the input signal is increased, gain decreases and phase lag increases over the entire frequency range. Thus, in strict engineering analytical terms, the system cannot be described as linear.

In Fig. 2. 1 the data from previous studies of the frequency response of the tracking system have been plotted on a single graph. The most surprising characteristic of these data is that gain begins to drop very rapidly above about 1. 5 hz. This is not consistent with Robinson's (1965) observation that the system can respond to velocity changes separated by about 75 msec, which would correspond to a frequency of about 6. 5 hz. Apparently the system response has significant power at higher frequencies than indicated by published frequency response functions. It is this apparent anomaly which has in part provided the stimulus for the undertaking of the present research project. For I contend that the roll off in gain curves

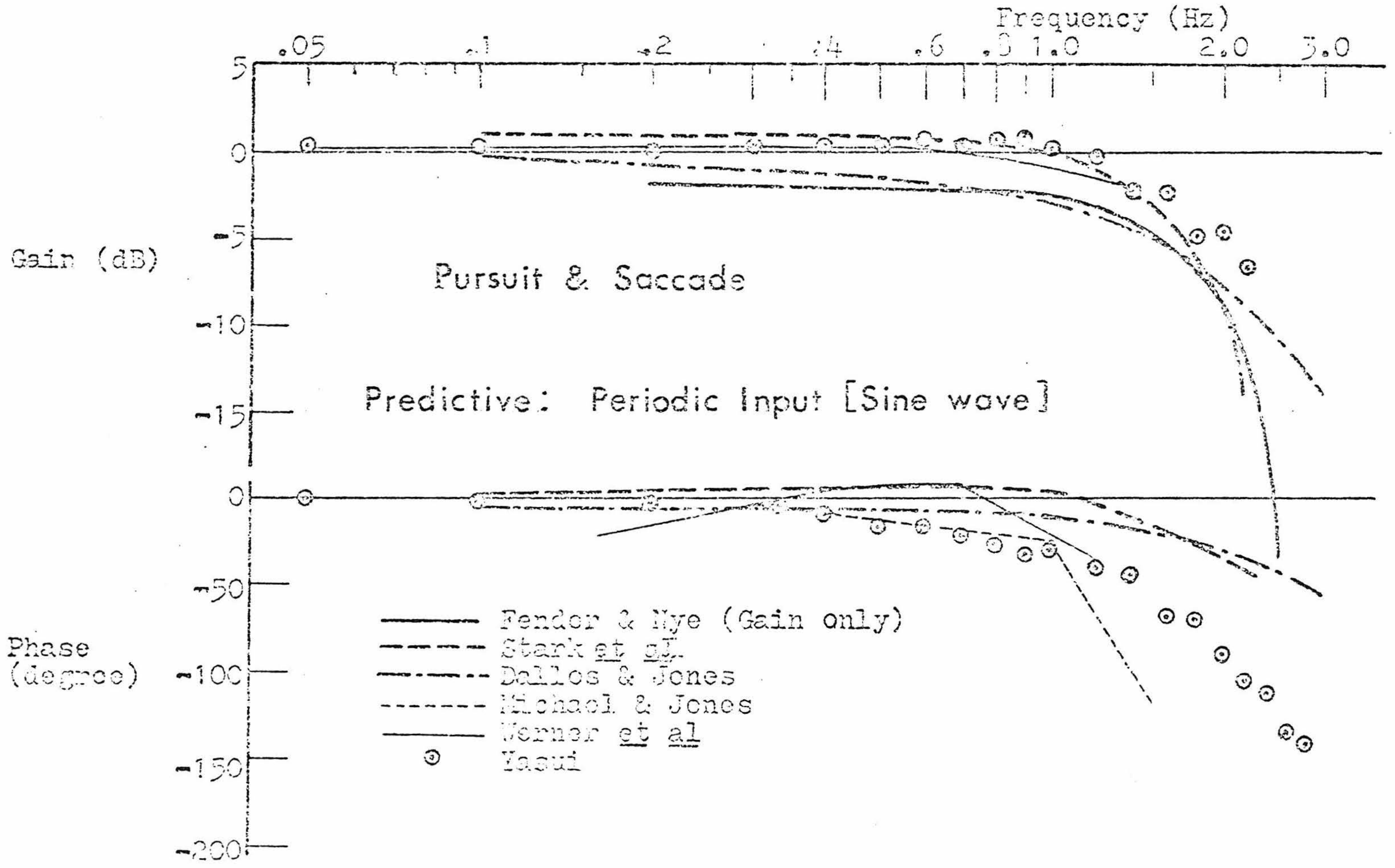


Fig. 2.1 Periodic-input composite frequency response from previously published results. (Redrawn from Yasui, 1973).

published to date occurs at such low frequencies because i) gain has been measured by comparing eye position to target position rather than eye velocity to target velocity, ii) stimulus motion has been generated in terms of position.

The latter point is especially significant in the case of a random position signal input to a velocity or acceleration sensitive system. The power spectrum of a white noise signal is flat from DC to infinite frequency. If such a signal is low pass filtered and subsequently used to control the position of a spot stimulus, the eye movements elicited by the target motion invariably bear little resemblance to the input signal unless the cutoff frequency of the filter is below 3 hz. The reason behind the attenuated high frequency behavior of the eye movements becomes apparent upon the assumption of a velocity (or acceleration) sensitive smooth pursuit system. For when the band-limited white noise signal is differentiated, the high frequency components are amplified while low frequencies become attentuated, the result being a shift of signal power to the high end of the frequency band. The situation for the second derivative, acceleration, is even worse. Thus it is no surprise that the velocity sensitive mechanisms of the oculomotor system become swamped even at relatively low frequencies (gain curves begin to drop above 1.5 hz) and the eye movement response correspondingly attenuated. In Chapter 5, the aperiodic stimulus motion used in the present experiments will be analyzed for its frequency content in both the position and velocity domains to illustrate the suitability of the velocity signal to oculomotor research.

The fact that frequency response analysis of the oculomotor tracking system has met with relative success in describing system behavior implies that the system under investigation is somewhat linear. It seems that as long as the input statistics are held constant the system responds in a linear fashion. Fender and St-Cyr (1969a) came to a similar conclusion based upon their results of tracking responses to two dimensional stimuli whose motion was the sum of several non-harmonically related sinusoids. They found that on the average the gain of the system behaved as a low-pass filter, decreasing with increasing frequency. However, within a narrow frequency band gain increased with frequency, the system responding preferentially to the highest frequency present. The latter observation constitutes a gross nonlinearity. The system, however, also showed linear properties in that it did not generate harmonics or sum and difference frequencies of the sinusoids present in the input. Thus the system produces no lumped nonlinearities. The conclusion presented was that the oculomotor tracking system is indistinguishable from a linear system in its response to a given input, but system parameters are dependent upon input statistics.

The above discussion has shown that the oculomotor system is a nonlinear system exhibiting many linear properties. There is a need for an anaylsis which could separate the linear and nonlinear properties and provide a quantitative description of each. The experiments and data analysis described in this thesis are an attempt to satisfy that need.

2.1.4 The Isolated Smooth Pursuit System

In most previous studies of oculomotor tracking of smooth motion, the eye movements analyzed have consisted of both smooth pursuit movements and saccades. Gain and phase curves and power spectral analyses have been computed from the composite eye movement response. Consider the fact that the two types of eye movement, saccade and pursuit, are functionally distinct. The former movement is elicited when an error exists between target retinal position and fovea. Smooth movements seem to be elicited only by movement of an image across the retina (or perceived image movement). Evidence also exists that the two systems are under independent oculomotor control (Rashbass, 1961; Robinson, 1968). Would it not be more rational then to study the response of each system separately rather than their combination? It is trivial to elicit a pure saccadic response by using discrete motion of the target. It is more difficult to produce pure pursuit motion. As the velocity of the target is increased, invariably saccades are generated when the target becomes displaced from the fovea. If it is assumed that the saccadic portion of the composite response has no effect on the smooth component, the saccades can be removed from eye movement signals by appropriate computer data processing techniques. (The validity of this assumption will be discussed in the methods section of this thesis.)

Yasui (1973) has used this technique to answer the question of whether the pusuit system exhibits predictive behavior when saccades are excluded from the analysis. The exclusion was achieved by a hybrid computer program which output an analogue signal proportional to the cumulative smooth pursuit eye position and it was this output which was analyzed. Both periodic and non-periodic stimulus motion were included in the study and frequency response functions were presented for both composite and the computed pursuit signal. For the periodic case, pursuit gain (relative to composite) was decreased at all frequencies (about 1 db from .05 to 1.0 hz, 5 to 10 db from 1.0 to 3.0 hz) since the saccadic portion had been subtracted from the position data. The phase plots were, however, almost indistinguishable for the composite eye movements and for the pursuit system alone. The interesting result was produced when Bode's theorem was applied to the straight-line approximation of the gain plots for the composite eye movements and for the pursuit system alone. The composite phase data points tended to show minimum phase behavior, a result at variance with previous published results. On the other hand, the pursuit phase characteristic, as in previous published data, showed less phase lag than predicted by Bode's theorem, implying an over-compensation for neuromuscular delays in the pursuit case.

The non-periodic composite frequency response obtained by Yasui (1973) was comparable to previously published results (Michael and Jones, 1966), showing the characteristic high frequency peak in the gain curve resulting from increasing saccade frequency at the high end of the band. The phase curves showed the general trend of increasing phase lag with increased input bandwidth. The frequency response data for pursuit alone showed relatively more gain attenuation as bandwidth was increased indicating the overall importance of saccades in tracking high frequency motion. The phase data for the non-periodic pursuit case showed a surprising phase lead at low frequencies, a zero phase error point at some intermediate frequency, and phase lag at the high frequency end. Furthermore, the frequency at which zero phase error occurred increased as input bandwidth was increased.

The main result achieved by Yasui (1973) in these experiments was that the pursuit system showed input adaptive behavior in its response to periodic motion (less-than-minimum phase lag). This conclusion is further supported by the non-periodic input phase behavior of the pursuit system. The predictive mechanism seems to function even when the input is random by attempting to cancel some average phase lag over the entire frequency spectrum, thus the phase lead at low frequencies. The system compensates for phase lag at high frequencies but must pay the cost of phase lead at low frequencies (Yasui, 1973).

2.1.5 The Need for Further Analysis

The previous discussion has shown that valuable new insight into the oculomotor system can be generated by an analysis of the saccade-free cumulative smooth pursuit signal. The smooth pursuit system shows input-adaptive characteristics of its own, independent of prediction by the saccadic system. This thesis is concerned with the analysis of some characteristics of the pursuit system which have not been previously studied in the isolated system, e.g. response to velocity input, linear and nonlinear response dynamics, and interaction with perceptual motion.

Most investigations of the tracking system have employed periodic or random signals applied to the position of a light spot. However, the pursuit tracking system seems to be interested only in velocity.

Smooth eye movements are generated only by the perception of continuous movement of a target. Discrete position changes are handled by the saccadic system. Therefore, in the analyses to be reported in this thesis, the oculomotor system will be stimulated by targets containing a minimal amount of position information. The stimuli have been designed so that residual position information, that could stimulate the saccadic system, will not contribute to the response of the pursuit system. When saccades are removed from the eye movement recordings, the cumulative smooth pursuit response can be analyzed in terms of the motion input to the system alone. Thus no reduction of gain will be observed due to loss of saccadic postion changes, since that position information was not available in the input.

The second innovation to be used in the present study is to analyze pursuit oculomotor responses in terms of velocity rather than position. Previous published results have described gain and phase characteristics in terms of eye position relative to target position. In the case of a system that attempts to match eye velocity with input target velocity, it seems intuitively more obvious to analyze the system in its own domain. However, frequency response analysis implies an assumption about linearity of the system of interest. The purpose in this study is to separate and quantify non linear and linear characteristics. Therefore, time domain analyses will be used to investigate step and impulse responses of the pursuit system. Also, the white noise method of nonlinear system analysis (developed in this laboratory by Marmarelis, 1972) will be used to achieve a quantitative description of the system linearities and nonlinearities.

One thing that will become obvious as the experimental results are presented is that thinking in terms of pure pursuit velocity response to input velocity adds new meaning to this analysis of oculomotor dynamics. This continuity of the analysis will be offered as evidence that the pursuit system performs a differentiation of the input position information and determines its response from that measure of velocity.

In Chapter V we will describe in detail the non-linear analysis techniques to be used in this work. This method for quantitative analysis of nonlinear systems has been applied to other biological systems (catfish retina, Naka, Marmarelis and Chan, 1975; fly visual system, Marmarelis and McCann, 1973) with successful results. However, in the case of the oculomotor tracking system, attempts at applying the analysis to the eye position signals elicited in response to a random position stimulus have not been very successful. The failure has been blamed upon the intelligence which drives the eye movement system of humans and refuses to respond to a wide band Gaussian random position stimulus.

As we have seen (Sec. 2. 1. 3), a more likely explanation of the previous results is that the input was not suitably matched to the system under investigation. The output of the oculomotor velocity sensing mechanisms saturated the neuromuscular mechanisms responsible for the control of tracking eye movements.

As a solution to this problem consider the nature of a band-limited white noise velocity signal. The power spectrum of such a signal is flat from dc to the corner frequency beyond which signal power drops monotonically. However, in this case the power spectrum represents signal energy in terms of velocity. If we integrate the random velocity signal and then compute the position power spectrum, we would find signal power shifted toward low frequencies, the high frequency components being averaged together by the integration process. The correlate of this principle in the time domain may clarify the situation. At any instant in time the white noise velocity signal can take on any value consistent with the amplitude probability distribution of the process used to generate the signal. In the position domain, the integrated random velocity signal, at any time instant, can take on only a value determined by the past history of the signal, i.e. successive position samples will be correlated. The latter property is a defining characteristic of a random walk, that is each sample of the time series is determined by the value of the previous sample according to some pre-defined conditional probability.

When the motion of a target takes on the characteristics of a random walk process, the probability of large changes in position over short periods of time is small, even for a relatively high bandwidth signal. Therefore, significant eye movement responses can be obtained using a velocity random stimulus containing power at higher frequencies than previously thought applicable in eye tracking experiments. System dynamics can now be studied at frequencies which produced only a small eye position response using conventional random position stimuli and at which most of the interesting interactions occur in tracking tasks (cancellation, re-programming, facilitation).

It is for these reasons that another engineering analysis of the pursuit system has been undertaken. Significant results have been obtained in areas of oculomotor research previously unexplored.

2.2 Psychophysics of Motion Sensitivity as Related to Pursuit Eye Movements

2.2.1 Retinal and Perceived Motion

The percept of motion is apparently generated not only from movement of an image across the retina but also from movement of the eyes. For example, an after-image appears to move as the eyes move. Smooth eye movement produces the appearance of a drifting image, and saccadic movement generates the percept of discrete jumps of the image. In the present study of the pursuit system, the question has been posed, what is the input to the system, position or velocity? Perceived velocity could be added as another possible input. To go even further, we could ask what is the relative contribution of perceived velocity and retinal image velocity to the eye movement response? In the experiments to be presented herein, one of the tasks of the subject is to respond to a step input of velocity. The target starts from rest and quickly accelerates to a constant velocity. As the motion begins, the target begins to slip across the stationary retina. But as the eye velocity begins to approach stimulus velocity the retinal image velocity decreases. At some point the velocity of the eye may exactly match target velocity so that retinal image information input to the pursuit system is eliminated. And yet the eye maintains its velocity match with the target and the motion percept remains. Perhaps then it is perceived velocity that drives smooth following eye movements in the absence of retinal image motion. The perceived velocity signal could be generated from some combination of retinal slip and oculomotor information. The latter source may be available to the perceptual system in the form of inflow from the extraocular muscles (Sherrington, 1918) or as the efference copy or corollary discharge of the command signal sent to the oculomotor system (Helmholtz, 1866; von Holst, 1950, 1954, 1957). Although Helmholtz' corollary discharge theory is widely accepted, Skavenski (1972) has recently claimed the existence of an inflow signal from passive ocular loading experiments performed in the dark.

Yasui (1973) has proposed a model for smooth pursuit control based upon what he calls the "perceptual feedback hypothesis". Fig. 2.2 shows the model presented by Yasui for the pursuit tracking system. In this model corollary discharge is summed with the retinal velocity to produce a perceived velocity signal which is fed back to the oculomotor system to generate the pursuit efferent command. To test the hypothesis an experiment was performed in which the subject was instructed to track the apparent motion of an after-image target. The percept of motion was generated through the vestibular system by applying a rotation to the subject's head. Eye movements with no after-image (vestibular nystagmus) were compared to eye movements elicited during active tracking of the "stabilized image". For sinusoidal head rotation, after-image tracking showed increased gain and a phase advance compared to vestibular nystagmus with "no vision". This result was taken as positive evidence that subjective motion produced an oculomotor command signal which altered the nystagmus response, i.e. the perceptual feedback hypothesis for oculomotor control was confirmed.

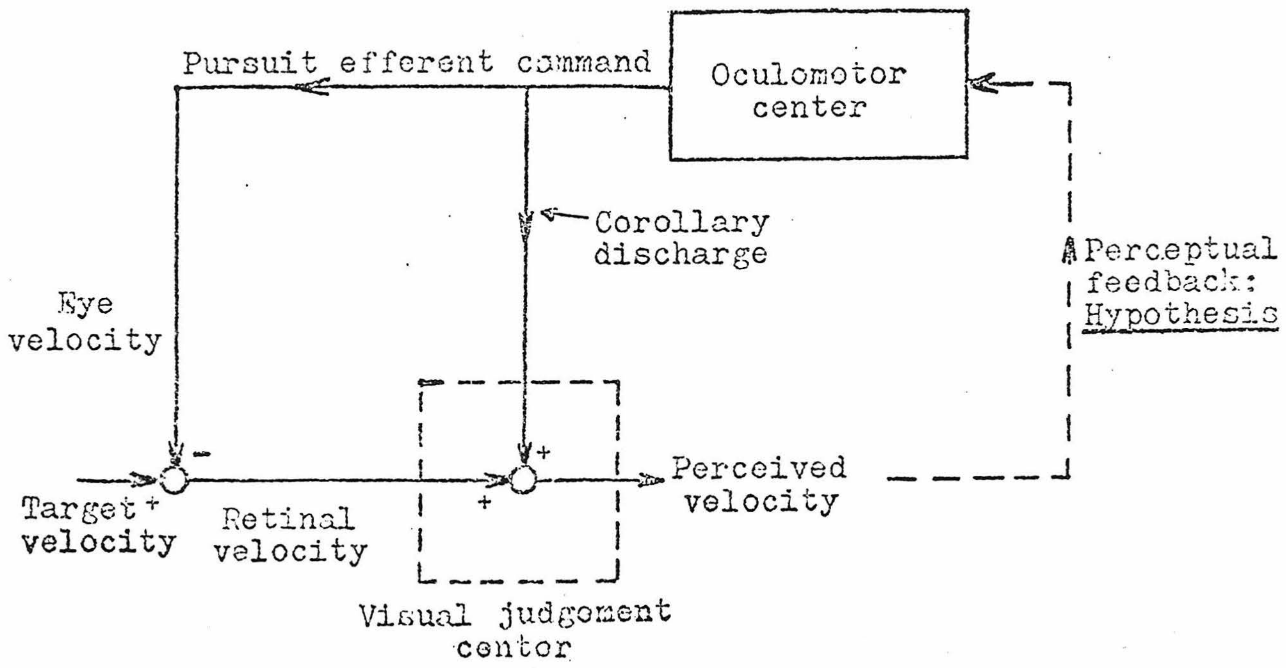


Fig. 2.2 Skeleton model for the pursuit tracking system based on corollary discharge theory and perceptual feedback hypothesis. (Redrawn from Yasui, 1973).

It appears then that retinal image motion and perceived motion interact in an additive way to generate the pursuit command signal. Thus in a study of pursuit dynamics the input to the system must be considered in terms of both retinal and perceptual signals. In the experiments constituting this thesis work, some consideration will be given the mechanism of retinal-perceptual interaction in pursuit control in the form of interpretation of results.

2.2.2 Further Examples of the Interaction of Motion Perception with the Oculomotor System

The approach taken in this thesis to study the processing of motion information by the oculomotor system, will be one of pure input-output relations. Thus movement of the target will be correlated with the eye motion generated by the command to the subject to follow the target. In this general context the concern over retinal or perceptual input is minimal. However, the relative effects of perceptual mechanisms in the smooth following task should not be underestimated when one attempts to interpret results say in the form of first and second order kernels generated by white noise analysis techniques. These mathematical functions are meaningless until they are considered in light of the biological system of which they are a description. For example, it is known that smooth following eye movements can be elicited without monocular cues. Tracking of motion produced by dynamic random dot stereo pairs shows similar properties as eye movement responses to conventional monocular stimuli. However, in the case of random dot stereo pairs, the motion information is not available on either retina alone, but only to the cyclopean retina (Julesz, personal communication; Julesz, 1971). So any theory or model proposed to explain oculomotor tracking phenomena must include a binocular stage at which information from the two eyes is correlated. The oculomotor command signals for tracking must be generated at a stage in the visual pathway at least as high as area 17 of the visual cortex where the first binocular interaction occurs. Of course other areas of the brain are probably also involved (e.g. superior colliculus, pretectal nuclei, vestibular nuclei). (Fig. 2.2 (from Robinson, 1968)).

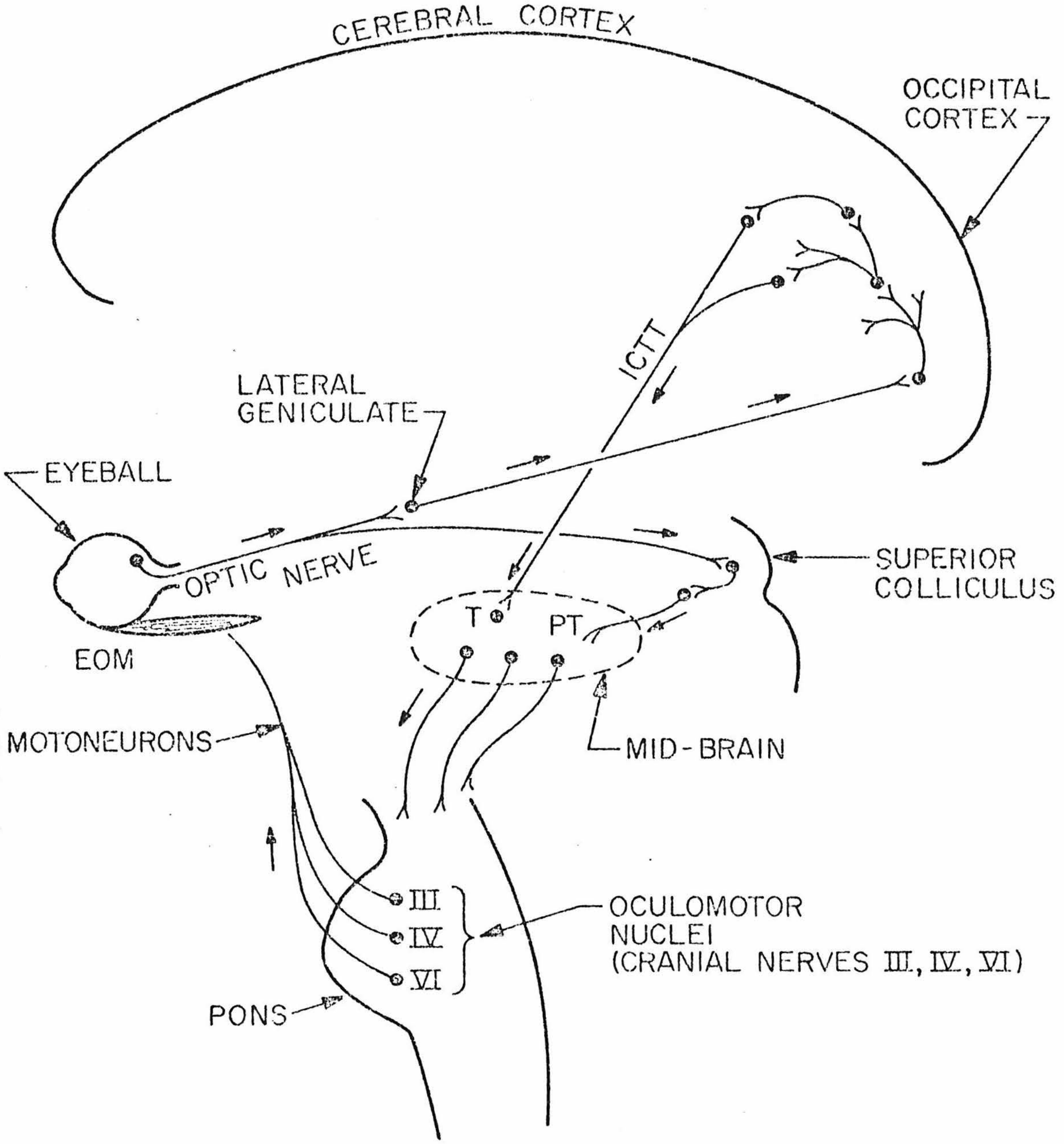
To summarize this discussion of perceptual aspects of oculomotor smooth tracking, one might say that the retinal image velocity is the primary signal, to which is added a corollary discharge signaling eye velocity, the result being perceived velocity. Experiments could be designed to tease out the relative importance of each type of signal to the oculomotor system. For example, if the retinal and perceptual velocities were made to conflict, to which would the system respond? The importance of the topic dictates a careful and detailed study of the many possible combinations of retinal and perceptual signals. The above discussion has been included merely to stimulate awareness of the problem of input to the "black box" in the case of the smooth following system. The discussion will be continued after the results have been presented.

2.3 Pursuit Oculomotor Neurophysiology

2.3.1 Pursuit Neurophysiology

The assumption that the smooth pursuit and saccadic systems are functionally and structurally distinct is valid for most applications. The rapid changes in smooth eye velocity which sometimes accompany saccades are examples of instances where the assumption fails. However, there is evidence (Robinson, 1968) that such interaction may be introduced at a peripheral level, where inhibition of the antagonist muscle during a saccade may augment the smooth component of an eye movement in the same direction as the saccade. Therefore, in this sub-section the known neurophysiological relationships which govern smooth following eye movements alone will be considered. For if a quantitative description of the dynamics of the system is to be derived, some effort should be made to relate that description to the physical reality of eye movement control. A review of the background on this topic will be presented here while the discussion of the relation of mathematical descriptions to neurophysiology will be delayed until experimental results have been presented.

Figure 2.3 shows the major known neurophysiological pathways involved in eye movements. It is generally accepted that the occipital eye fields are associated with involuntary smooth pursuit eye movements (Robinson, 1968). From the previous discussion on perceived velocity, it is not unreasonable that the visual cortical areas should be involved in smooth pursuit control. The mechanism of the association is, however, unknown. The superior colliculus is also believed to be involved in the control of visually guided eye movements. In the monkey, collicular cells have been shown to be sensitive both to eye movement input (inhibition of background rate during spontaneous eye movements)



EOM = EXTRAOCULAR MUSCLES
T = TEGMENTUM
PT = PRETECTAL NUCLEI
ICTT = INTERNAL CORTICOTECTAL TRACT

Fig. 2.3 Basic nerve pathways of the oculomotor svstem. (Redrawn from St-Cyr, 1969).

and retinal input (pandirectional and directionally selective cells). Furthermore, most collicular cells are binocularly activated. Goldberg and Wurtz (1972) who produced the results cited above, suggest that superior collicular cells may be useful for visual orientation. The relationship of the superior colliculus to smooth pursuit is not well understood, but its involvement in the guidance of fixations and saccadic eye movements seems to be its main concern. The semicircular canals and the cerebellum influence eye movements through the oculomotor nuclei. The mesencephalic and pontine reticular formations receive inputs from many sources (visual cortex, frontal eye fields, superior colliculus, cerebellum, vestibular nuclei, optic tract) and somehow process the data for use in oculomotor control. This brief review of the general neurophysiological pathways involved in eye movement control has shown that the system is complex, that much work has been devoted to it and still more remains to be done before the complete system is understood. The pursuit system seems to be the least studied of the various types of eye movement. Robinson (1965) has studied the mechanics of smooth pursuit eye movements. He found that the system is able to overcome the sluggishness of the physical plant in a short period of time by applying an excess rate of change of muscle force utilizing the overpowering action of a negative feedback system. Also the smooth following system is capable of responding to changes in target velocity spaced 75 msec apart, suggesting a continuous (as opposed to sampled) control system. This question is still unresolved, the distinction between a continuous system and one that is sampled at a very high rate being unclear.

Apparently it is the mechanics of the smooth pursuit system to which the results of the present study may be applied. For example, the first and second order impulse responses of the system will give an indication of response time and integration time of the system. The response to a double pulse of acceleration, two velocity changes separated by a variable time, reveals the interaction between past and present inputs. Questions of cancellation of one pulse by a second, or facilitation of the second pulse by the first, can be intelligently considered with knowledge of first and second order kernels in hand. Perhaps then neurophysiological questions can also be attacked using these types of results (e. g. , refractory periods, duration of pre-ephasis).

2. 3. 2 Neurophysiology of Velocity Sensitivity

One of the basic premises of this thesis is that the smooth pursuit system measures target velocity and is relatively unconcerned with position information. One might ask then what type of motion sensitive mechanisms are present in the human visual system and where are they anatomically located? A number of observations point to the visual cortex as the locus for initiation of smooth pursuit command signals (random dot stereo tracking, the need for perception of velocity to elicit smooth pursuit). The lower stages of the primate visual pathway, retina and lateral geniculate nucleus, exhibit no single unit velocity measuring capabilities. The concentric organization of retinal ganglion cell receptive fields is not suitable for the measurement of target velocity (Enroth-Cugell and Robson, 1966).

Although there exist two types of ganglion cells in the vertebrate retina, X-type (signal sustained luminance) and Y-type (signaling transient events), no directionally selective units have been found. Y cells could be regarded as motion sensitive in that a response would be elicited by movement of a light spot into and out of the receptive field. However, the continuity and velocity of the motion could not be determined by monitoring the output of that single unit. The association of the signals generated by the traverse of the light spot across a series of adjacent receptive fields would be needed in order to measure velocity. Lateral geniculate receptive fields are also concentric, exhibiting antagonistic center and surround regions, and thus also velocity insensitive. However, the visual cortex of cat and monkey exhibits several types of cells capable of measuring velocity of a target moving across the receptive field. Both complex and hypercomplex cells show modulation of firing rate only when the appropriate size target image at specific orientations is made to move across the receptive field. Furthermore, many of these types of cells appear to be selective for the direction of motion (Hubel and Wiesel, 1968).

Thus areas 17, 18, and 19 of primate visual cortex contain mechanisms sufficiently sensitive to target movement to enable an accurate measure of target image velocity on the retina. Now if both the corollary discharge signalling eye velocity and the cortical signals measuring retinal image velocity can be combined by some other neurophysiological mechanism, then the neural machinery is certainly available for the sensitive measure of perceived target velocity necessary to drive smooth pursuit eye movements. In Chapter III the perceptual feedback model for smooth pursuit control (Yasui, 1973) will be analyzed for evidence of nonlinear components. It will become evident from that discussion that corollary discharge and retinal velocity signals are combined using an asymmetrical weighting factor which tends to favor the negative feedback retinal information. How and where this perceptual summing operation is performed is not known. For present purposes, the evidence for velocity sensitivity is sufficient for an analysis of pursuit velocty response dynamics.

2.4 Summary

1. Up until now investigators of the oculomotor tracking system have applied frequency response analysis techniques to the eye movements elicited by periodic and aperiodic movements of a spot target. These studies have revealed a nonlinearity which seems to be characteristic of the eye tracking system, namely system parameters are not independent of input statistics.

2. Existing evidence indicates that the smooth pursuit system responds to movement of a target, its position being a relatively unimportant parameter. Therefore in this thesis, pure pursuit velocity responses to target velocity will be analyzed.

3. The pursuit system is reasonably linear in its response to a given input, but when the input statistics are altered to include a number of frequency components, the higher frequencies are preferentially tracked.

4. Although the saccadic and pursuit systems are not completely independent, they are certainly functionally distinct, allowing individual analysis of each system. Analysis of the isolated smooth pursuit response yields heretofore unobserved results.

5. Perceived motion, derived from retinal image slip and eye velocity, seems to be the relevant input to the smooth following system. Awareness of this distinction is important to those who model the oculomotorsystem as a closed loop feedback system.

6. Psychophysical and neurophysiological evidence points to visual cortical areas as the center for control of smooth pursuit eye movements.

7. A new study of smooth pursuit eye movements has been undertaken which attempts to overcome some of the stumbling blocks encountered in previous work. Unique stimulus conditions and innovations in data analysis provide a strong base upon which to construct a theoretical model capable of explaining many properties previously observed in oculomotor studies.

III. PROBLEM DEFINITION: OCULOMOTOR PROCESSING OF MOTION INFORMATION BY THE ISOLATED PURSUIT SYSTEM

3.1 General Description of Present Approach

3.1.1 Summary of shortcomings noted in previsous studies

In the last chapter what is known at present about smooth pursuit eye movements was reviewd. In the course of the discussion certain shortcomings of previous investigations were noted:

i. The stimuli used have invariably been generated in terms of position, a parameter with which the smooth pursuit system is relatively unconcerned.

ii. The frequency response analysis to such stimuli have also been calculated by considering eye position as a function of stimulus position. The combined effect of i and ii is the surprisingly-low frequency fall off of the gain curves as compared to known system transient response characteristics.

iii. The composite system, consisting of both saccadic and smooth components, has been stimulated and the response analyzed (except in the case of Yasui (1973)). The results have then been used to describe the smooth pursuit system without considering the possible contributions of the saccadic response.

iv. Linear analysis techniques have been applied to a system which shows gross nonlinearities under certain conditions. The nonlinearities have either been ignored or attempts were made to suppress their effects on data analyses.

3.1.2 Proposed Solutions

These shortcomings have provided a base upon which to construct a new investigation of the smooth pursuit system. The following general innovations have been adopted in an attempt to bypass difficulties encountered in previous work on this topic:

i. New stimuli have been generated which, when presented in motion to the visual system, contain a minimal amount of position information. Thus the smooth pursuit system alone can be stimulated without the contaminating effects of a saccadic response.

ii. System performance will be evaluated in terms of both velocity and acceleration. Comparison of the results of the two analyses should give some indication of the preferred input domain of the smooth pursuit system. When that determination has been made, the true system response bandwidth will be revealed.

iii. Since the smooth pursuit system alone is being stimulated, spurious saccadic responses, which are not related to the input signal, can be removed from the eye movement recordings without significantly affecting the calculated system response. The only effect will be to reduce the amount of noise present in the eye movement responses, and a cleaner picture of pursuit characteristics will be the result.

iv. A relatively new system identification technique (white-noise cross-correlation analysis) will be applied to the isolated smooth pursuit system. The advantage of the technique over linear frequency response analyses is that linear and nonlinear effects are quantified separately.

3.2 Specific Problem Definition

3.2.1 Velocity Step Response (Acceleration impulse response)

A standard analysis technique used by engineers is to apply a step change in the relevant input to the system in question. The step response of a linear system completely characterizes the system properties. For a system suspected of having nonlinear properties, the response to a step change in input contains contributions from linear and nonlinear system elements.

In the case of the smooth pursuit system a step change in velocity can be applied to a target (i.e. a position ramp stimulus). Responses elicited by repeated presentations of the same velocity step will be averaged to determine the characteristic shape of the pursuit system response to a particular velocity input. Also the relationship between averaged eye velocity response and input velocity will be examined for linear trends.

A step change in velocity could be considered a pulse of acceleration. Since differention is a linear transformation, the velocity step responses can be differentiated to obtain the system "impulse response" in terms of acceleration. System performance in the acceleration domain will also be studied since the impulse response is a more familiar analysis technique to some researchers. When the velocity responses are differentiated all DC components are removed so that only the transient characteristics of the pursuit system will be revealed. These transient responses can then also be studied for linear and nonlinear trends as a function of input pulse magnitude.

The results of the step/impulse response experiments can be used to evaluate the results of the more complex white-noise analysis to be described below. The average "impulse" responses obtained for the pursuit system should resemble the linear component of the latter analysis method since the tracking system has been shown to be indistinguishable from a linear system for a given input. In this way, the validity of the pseudo-random input technique with associated data reduction will be examined.

3.2.2 Double Velocity Step (Double Acceleration Pulse) Response

The theory behind a double step/pulse analysis is analogous to that of the single step/pulse analysis, with the added possibility of examining some nonlinear interactions within the pursuit system. In the case of double velocity step experiments the data will be analyzed in terms of acceleration only, in order to bypass the effects of DC components in the transient responses.

Again responses elicited by repeated presentations of the same acceleration pulse combination will be averaged. The resulting response waveform could be thought of as a probabilistic representation of system transient characteristics. The ordinate values represent the probability of eye acceleration at some abscissa value corresponding to time after the first pulse.

Basically, the double pulse response gives an estimate of the effect of past input pulses on the response to the present pulse. If the system is linear, the double pulse response should be equivalent to the superpostion of two single pulse responses separated in time by the interpulse interval. Any departure of the double pulse response from the predicted superposition response is a measure of system second-order nonlinearities. This property of the double pulse response provides a method of investigating the programming of pursuit responses. Depending upon the interpulse interval, the response to the second pulse can be affected in several different ways, e.g. inhibition or facilitation. Furthermore, if the second acceleration pulse is delivered within the latency period following the first pulse, the system may respond only to its most recent input suppressing the response to the first pulse. If two pulses are of opposite polarity and both are delivered within the response latency period of the first pulse, the only effect of the first pulse may be to increase the latency of the response to the most recent pulse. The latter type of interaction could be used to tease out the temporal processes involved in programming a pursuit response. The data will be closely examined for such time interactions and the results will again be compared to the results of the pseudo-random input analysis technique. The single and double pulse experiments will thus constitute a sensitive test of the validity of the more complex analysis techniques used for the first time on the human smooth pursuit oculomotor system.

3.2.3 Stimulus/Eye Velocity Match

In Chapter II, the problem of input to the smooth system was discussed. The possibility of a velocity driven control system was considered. In this scheme the oculomotor system tries to match eye velocity with target velocity in order to minimize retinal image slip. If the retinal slip is exactly cancelled by the eye movement, the velocity input to the control system will have been eliminated. If, however, eye velocity never exactly matches target velocity but achieves values in the neighborhood of target velocity, the retinal slip would be a constantly varying input signal thereby providing feedback to the oculomotor system. This type of control system is characterized by a very high gain feedback pathway; thus small retinal slip velocities would be magnified in order to achieve a feedback signal sensitive to plant performance.

The data from the single pulse experiments provide an excellent opportunity to investigate quantitatively the degree to which eye velocity matches stimulus velocity. A nonlinear least-squares curve fitting analysis will be applied to the eye position signal elicited by a step change in velocity. One of the parameters of the resulting best fit curve is the slope of a linear portion of the curve fit to the ramp part of the eye response. Given accurate calibration of eye movement signals, the slope of the linear portion of the curve can be defined as the steady-state eye velocity. The slope values from a number of responses can be compared to stimulus velocity and one of several statistical tests will give an indication of how well eye velocity matches stimulus velocity.

Other parameters of the nonlinear curve fitting analysis will be useful in evaluating system performance. One parameter is equivalent to the response latency. Since binocular eye movement recordings are obtained in all pulse experiments, the coordination of the two eyes during smooth pursuit can be studied. The results will be compared to the binocular coordination data for the saccadic system (Williams and Fender, 1977). The latency values obtained will be compared to previous published values (Robinson, 1965). The stimuli used in the present experiment contain very little position information, whereas previous experiments using spot stimuli have primarily stimulated a position sensing mechanism. The comparison of response latencies elicited by the two types of stimuli may produce some interesting speculation about position and velocity sensitivity of the oculomotor system.

Another parameter of the curve fitted to the eye movement data is the integration time, or the time it takes the eye to accelerate from the rest of its final velocity. This parameter is adjusted by the analysis program to achieve the best fit to the data. Statistical tests will also be applied to the resulting acceleration time of the pursuit response. The values obtained in this analysis can also be compared to the published results using position stimuli (Rashbass, 1961; Robinson, 1965).

This type of curve fitting analysis could be considered an analysis of the micro-structure of smooth pursuit eye movements since individual responses are considered in contrast to previous stages of the work where responses are averaged to generate a probabilistic response function. A sensitive quantification of the fine-structure of pursuit eye movements will be a valuable set of data to those attempting to simulate models of the pursuit system. Also the statistics of the micro-structure data will provide a quantitative evaluation of the variability of system responses. If it is found that the eye velocity, response latency, and acceleration times vary widely for the type of stimuli used, then some source for the variability must be postulated. Does the pursuit system possess some kind of stochastic component which controls the parameters of the response? Or could the variability be the result of the velocity-type stimuli used in this particular experiment? Perhaps the velocity sensing mechanism which provides input to the pursuit system is susceptible to cognitive variables, such as attentiveness or fatigue. Answers to these questions will provide important contributions to the final analysis of pursuit eye movements.

3.2.4 Isolation of First and Second-order Nonlinear Properties

The analysis up until now has centered around the problem of determining linear and nonlinear properties of the pursuit response. Classical engineering techniques, single and double-pulse input response analysis, have been proposed to tease out these system properties. The single pulse responses are produced mainly by linear system properties but also in part by nonlinear properties. The two-pulse responses when compared to results of single pulse experiments can be used to determine some second-order nonlinear system properties. However, to get a complete picture of the second-order properties of the system, all possible combinations of the double pulse presentation would have to be included in the stimulus ensemble. This would require an enormous effort in data collection.

It is for this reason that the technique of system identification using a random input signal has been proposed to analyze the smooth pursuit system. The stimulus motion theoretically contains all possible input waveforms to which the system can respond. In practice the input signal has been constructed so that it contains information only in the input domain of the pursuit system. In a single experiment, then, the responses to all combinations of single, double, triple, etc. pulses can be obtained. By cross-correlating the output eye movement signal with the random input signal, data reduction techniques produce a quantitative description of the first, second, third, etc.-order properties of the pursuit system. The details of the analysis technique will be described in Chapter V. For the present, consider the analysis technique a mere tool which can be applied to the system under investigation.

Some care must be exercised in the application of the white-noise technique. The method is not suitable under some conditions, but with some thought about the sytem to be studied, the results of "turning the crank" can be very useful to the scientist. First, some of the basic system characteristics should be known. This is usually accomplished through more conventional methods of analysis, such as sine wave and single/double pulse experiments. The response of the system to such inputs provides the basis upon which to design the white-noise experiment. The random input signal should be constructed so that it is within the dynamical range of system. If the black box is bombarded with a random signal to which it has not been programmed to respond, results of the analysis will be meaningless. In the pursuit system case, the input signal should not exceed the position or velocity capabilities of the oculomotor system. Also, the frequency bandwidth of the noise should fall within the known input domain for human eye tracking.

Second, we wish to know how the pursuit system responds to target velocity. Therefore, the motion of the target should be a random function in velocity, rather than position. The first and second-order responses to the velocity stimulus can then be compared to results of position input experiments. It is likely that one of the stimuli will elicit more meaningful experimental results than the other.

A mathematical description of a biological system serves little purpose unless the theory can be related to the activity of a physically realizable system. Furthermore, that relationship should contribute some insight into the unknown physiological structure or function of the system. Thus the third and perhaps most important consideration in applying the random input system identification technique is what the results might tell us that is yet unknown about the system. For just a quantification of the linear and second-order nonlinear properties of the smooth following system is not of great interest. What is of interest is the physical description of the sources of those linear and nonlinear properties. Thus, what part of the pursuit oculomotor system is linear, and where are the nonlinearities generated? We have learned that the composite tracking system is indistinguishable from a linear system for a given input. But when the statistics of the input are altered, the system somehow processes the information through a different channel possessing different parameters. For the eye movement tracking system, the different channel is responsible for reducing the time delay of the eye response to input motion when that motion contains less information (or equivalently, is more "predictable"). If the present analysis can answer such questions, then the re-examination of pursuit dynamics is a worthwhile endeavor.

One way of relating a mathematical description of a system to its real physical components, is to propose a model of system function. The model is then tested by comparing experimental responses predicted by the model. The present research concentrates on characterizing the response of the pusuit system alone. This has been accomplished by first restricting the attributes of the input to the oculomotor system to velocity and acceleration, minimizing position information. The saccadic system should not be stimulated by any information present in the motion of the stimulus. Thus, the second step, removing saccades from the eye movement recordings before further data processing, should not affect measures of gain, phase, or transient characteristics of the pursuit response. Note that we are not imposing the possibly false assumption of complete independence of saccadic and pursuit central mechanisms. Instead, the experiments have been designed so that saccadic responses contribute minimally to the pursuit response. The well-known abrupt changes in smooth eye velocity which accompany saccades are therefore not correlated with stimulus information and will have negligible effect on computed first and second-order response functions. These considerations allow a model of the pursuit system alone to be proposed and tested using input/output correlation techniques.

A model for control of smooth tracking eye movements employing a summed feedback signal consisting of retinal slip velocity and corollary discharge (Yasui, 1973) has been described (Sec. 2.2.1). The resultant signal, perceived velocity, then travels to an oculomotor information processing center to produce the efferent command for smooth tracking eye movements. This model was tested using various means of eliminating the retinal velocity pathway and found to be valid. The data, however, were based upon eye movements elicited by a moving spot stimulus, possessing considerable position information. The model presently proposed avoids such difficulties by assuming only velocity input to the pursuit system.

Consider the following hypothesis for control of smooth tracking eye movements. Motion of a high frequency, spatially periodic image on the retina stimulates two possibly distinct information processing systems. One, concentrated in the foveal receptor system, signals spatial structure and is primarily interested in position information. The other, possibly equally distributed throughout the retinal area, signals temporal events, including motion. Conceivably, the pursuit response to motion of the retinal image is generated only when both systems are activated. In the case of a single spot stimulus, both position and motion elicit strong afferent neural activity in central visual areas. The eye movement response then is a combination of saccades (responding to position) and smooth pursuit (responding to velocity). However, if the retinal image is a high spatial frequency repetitive pattern, only the presence of spatial structure may be signaled by the pattern system, position information being suppressed by the periodity of the image. The temporal frequency system, on the other hand, is maximally stimulated by the motion of the repetitive pattern. The eye movement response now consists only of a smooth following eye movement uninterrupted by saccades. The eye movement responses presented in a later chapter clearly depict this saccade-free eye response.

In light of the above hypothesis, the question of sources of the linear and nonlinear eye tracking properties takes on some interesting aspects. Let us consider the isolated pursuit system and its response to the spatially repetitive stimulus. The velocity signal must be generated from the temporal frequency of the movement of the dots across a retinal receptive field, since there is no position information available for a differentiator to process. Spatial pattern information must also contribute to the velocity calculation because of the high frequency structure of the retinal image. Velocity is then calculated as:

$$\text{VELOCITY} = \frac{\text{TEMPORAL FREQ.} \quad (\text{Hz})}{\text{SPATIAL FREQ.} \quad (\text{CYC/DEG})} = \text{DEG/SEC}$$

Since the stimuli are presented at 100% contrast, the linearity induced by working with threshold contrast values cannot be assumed. Therefore, the sensitivity of the oculomotor system to velocity could be a nonlinear function of either temporal or spatial frequency. One measure of oculomotor velocity sensitivity is the response of the smooth tracking system to a step velocity input, (i. e. impulse of acceleration). If the spatial frequency of the target is kept constant while the temporal frequency is varied, the eye velocity response to two-step changes of velocity can give an indication of pursuit system linearity. Any departure of the two-step response from superposition response, is a measure of system nonlinearity. Another way to obtain these measures is by using a random velocity input and applying the Lee and Shetzen (1965) method of determining the "kernels" of the system. Both of these methods have been used in the present work.

Although the motion of the eye while tracking a step change in target velocity, is a measure of oculomotor velocity sensitivity, included in that measured quantity are the possible nonlinear contributions of the oculomotor mechanics. To make this point clear, consider Fig. 3. 1, the perceptual feedback model of pursuit control (Yasui, 1973). The extraocular muscles and associated orbital tissues have been included in the diagram to complete the transformation from efferent command to eye velocity. If it is assumed that

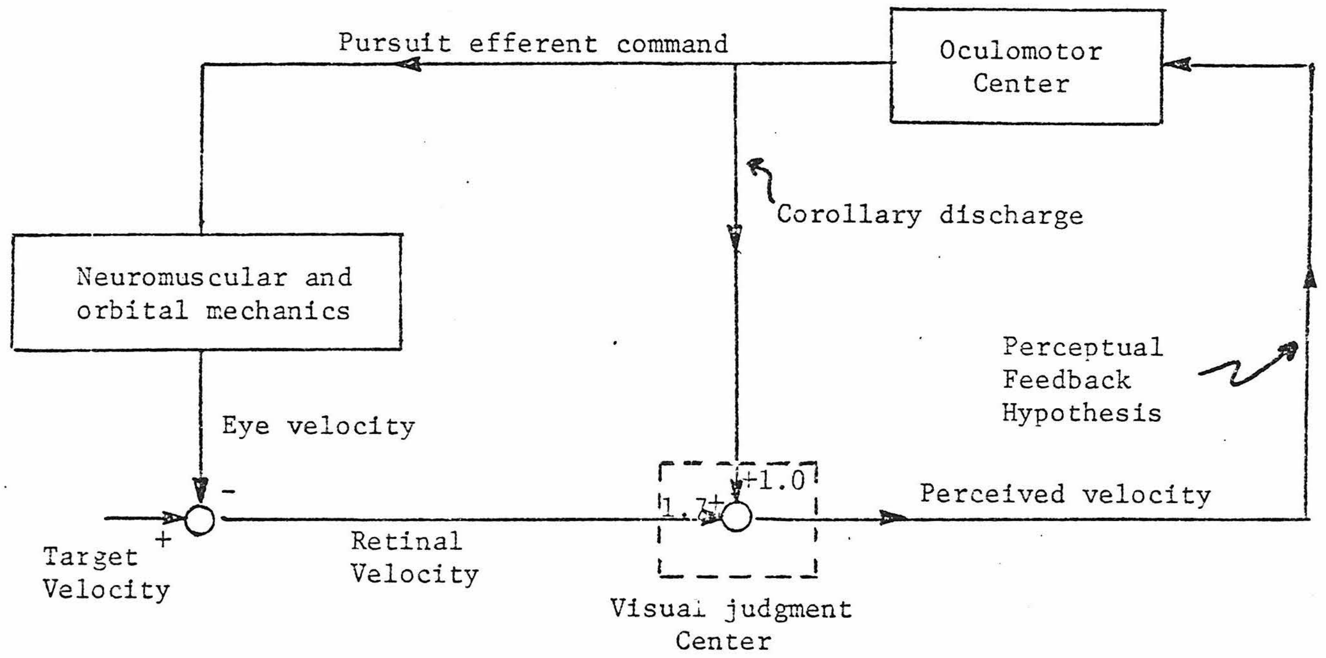


Fig. 3.1 Perceptual feedback hypothesis including effects of neuromuscular and orbital mechanics. (Redrawn from Yasui, 1973).

the summation of target and eye velocity is a linear process, then three possible sources of nonlinear response properties are left. The first source is the input stage to the oculomotor center, where retinal velocity and the corollary discharge of the efferent pursuit signal are combined to produce perceived target velocity. The second source is the oculomotor command center itself, where perceived velocity is transformed to a command sent the extraocular muscles, which in turn constitute the third source of nonlinearity.

The latter stage is the one component of the system about which detailed experimental studies have produced a model relating input efferent command signals to output eye rotation (Robinson, 1964, 1965). The transformation can be put into the form of a set of differential equations which produce responses in reasonable agreement to measured eye rotation and isometric muscle tension. The results of the modeling exercise showed that the pursuit system employs a rate of rise of muscle tension in excess of that required to maintain globe position against the passive resistance of the orbital mechanics. It was postulated that the reason for the excess muscle tension was to speed up the initial acceleration of the eye in order to reduce eye-target velocity lag. The excess muscle tension is produced by central patterning of the neural discharge rate into high frequency bursts applied to the extraocular muscles. The relevant observation is that larger target velocity changes are met with proportionally less excess increase in muscle tension. The result of this neuromuscular nonlinearity is that eye velocity changes occur over longer periods as the target acceleration pulse increases in size. In the present random input experiments this nonlinearity will be bypassed by imparting constant size pulses of acceleration to the target and randomizing only the sign of the pulses.

Some indirect evidence is available on the properties of the first stage in the model where summation of retinal and eye velocity produces the perceived velocity signal. When the stationary eye views a moving target, the velocity perceived is greater than when the subject is asked to track the target(Dichgans, Körner, and Voigt, 1969). Apparently the psychophysically measured perceived velocity is about 1.7 times greater when produced largely from afferent signals as compared to the perception generated by the corollary discharge command during active tracking. Thus, the afferent negative feedback signal does not exactly cancel with the efferent signal generated in the oculomotor center. As pointed out by Yasui (1973) this is an intelligent situation when the closed loop nature of this biological system is considered. If the efferent and afferent velocity signals were given even weights by the perceptual judgment system, effectively no feedback signal would be available to the pursuit system due to the positive and negative respective nature of the two signals. If the efferent signal were weighted more than the afferent, the eye would always lag behind the target never achieving the desired eye/target velocity match. Thus, when afferent signal is given more weight than the efferent command, some residual negative feedback is available to continually drive the oculomotor plant and maintain eye velocity equal to target velocity. So, although perceived velocity is not a simple summation of retinal and eye velocity, there is evidence that the relationship of the total to its parts is constant and does not change with input magnitude or waveform statistics.

The only remaining source of nonlinearity in this model is the oculomotor processor, responsible for transforming the perceived velocity signal into a neuromuscular efferent command to the extraocular muscles. It is this model component about which very little quantitative data have been produced. The above discussion has made the point that any response nonlinearities found in the course of the present random input experiments can be attributed to this stage of the pursuit model, since the others have been either bypassed or shown to be linear. Thus indeed, our experiments will center upon the velocity sensitivity of the pursuit oculomotor center.

A model has been proposed for the pursuit tracking system which relies on information from two types of processors, spatial and temporal, to generate a velocity signal. The present experiments have been designed to minimize the velocity information obtainable from the spatial processor by the periodicity of the target. Thus, the temporal processor must be the main source of the retinal velocity signal. It is informative to speculate what effect this situation will have on the movements recorded in response to a step velocity, spatial periodic stimulus as compared to conventional ramp responses. First, since the saccadic system has been minimally stimulated by position information, it might be expected that eye movement responses would consist of pure pursuit motion. Secondly, the latency of the response to a step of velocity might be different for a spatially periodic stimulus in contrast to a spot or line stimulus. The tracking system must rely solely on the temporal frequency information present in stimulus motion for a velocity calculation, whereas in the normal situation a change in target position is the cue to velocity sensation. Is the temporal pathway faster or slower than the combined spatial/temporal information flow? Since the temporal frequency system is relatively insensitive to high spatial frequency patterns, we might speculate that the velocity calculation will be slower for the periodic target. One to several cycles passing across the foveal region may be necessary to determine the correct target velocity. To this integration delay must be added the inherent neuromuscular delay measured by previous investigatiors. Furthermore, faster velocities may not produce the expected decrease in latency since sensitivity falls off as temporal frequency is increased. The high frequency pattern may be literally smeared over the retina preventing any calculation of velocity.

A third difference which might be expected is an increased integration time for the pursuit system, i.e. it may take longer for the eye to reach target velocity without the nonlinear augmentation of the saccadic response included in conventional tracking tasks. Without the added inhibition of the antagonist muscle produced during a saccade, the pursuit system may be more sluggish in its response.

In summary, the hypothesis that a foveal spatial processor and a homogeneously distributed temporal processor are responsible for the velocity calculation which takes place during the response of the pursuit system to motion is not unreasonable. Nonlinear components of the pursuit system may be isolated, the temporal processor may be preferentially stimulated thus suppressing saccades, and new experimental results may be cast in comparison to previously obtained data using the hypothesized model in conjunction with improved experimental and data processing techniques.

3.3 Conclusion

The problem outlined in this chapter has been generated as a result of shortcomings of previous work in the field of pursuit oculomotor dynamics. By experimenting on the isolated pursuit system a clearer picture of smooth following eye movement control will result. Both classical and relatively innovative nonlinear system analysis techniques have been proposed as part of the experiments. The results of the two techniques can be compared, side-by-side, on the same subject, using the same measuring equipment, as an attempt to evaluate the newer technique when used to study an adaptive control system such as the oculomotor plant. More important, however, is the fact that the results of the experiments will provide other vision researchers with new knowledge about the interaction between eye movements and perception. Such interaction can affect many areas of vision, and quantification of the properties of a perceptual/oculomotor system will aid researchers in their design of models of human visual behavior.

IV. VELOCITY STEP EXPERIMENTS

4. 1 Introduction

Two basic types of experiments, velocity step and random velocity input, are proposed to complement each other in the study of an adaptive control system such as pursuit eye movements. The velocity step experiments were designed to study the transient characteristics of oculomotor pursuit, an area which has received very little attention in the literature. The velocity response of the eye to a step change in target velocity reveals such pursuit characteristics as latency from stimulus onset, system transient characteristics, interaction between present and past responses, and steady state accuracy of the eye/target velocity match. The response of the pursuit system to a random velocity signal can be correlated with the input signal to reveal linear and second-order nonlinear characteristics of the system. The following sections describe the methods and data analysis procedures which were developed to study the velocity step response of the pursuit system. In Chapter V, the random input experiements will be treated.

4. 2 Methods

4. 2. 1 Stimuli

In general, tracking eye movements consist of a combination of saccades and smooth pursuit motion. Since the purpose of this work was to study characteristics of the pursuit system, a stimulus was desired whose motion would produce only smooth eye movements.

The pursuit component of the oculomotor tracking system is said to be only velocity sensitive. Therefore, the appropriate stimulus is one which gives velocity information only, no position information. Any saccadic eye movements included in the responses could therefore be attributed to involuntary, non-stimulus related events and could legitimately be removed from the eye movement recordings before further analysis.

A digital computer was programmed to generate the stimuli shown in Fig. 4. 1. The first type of pattern (Fig. 4. 1a) consisted of a horizontal string of uniformly spaced white dots presented in a completely dark background. The pattern could be moved at a uniform horizontal velocity without the endpoints of the string entering into the stimulus field. The subject's percept was that of an infinitely long string of dots moving through the field aperture. The dots were placed close enough together so that the inter-dot spaces subtended less than one minute of arc at the retina. The periodicity and high spatial frequency structure of the targets prevented absolute position information from entering into the experiment. As the target motion was initiated, the subject's task was to stabilize the image on his retina by matching eye velocity to target velocity. Saccades are completely useless in this task since any single dot is indistinguishable from all the others. The only position information available in the field of view is the relative position of fixation with respect to the edge of the aperture. That information was found not to affect the saccade-free smooth pursuit eye movements elicited by target motion.

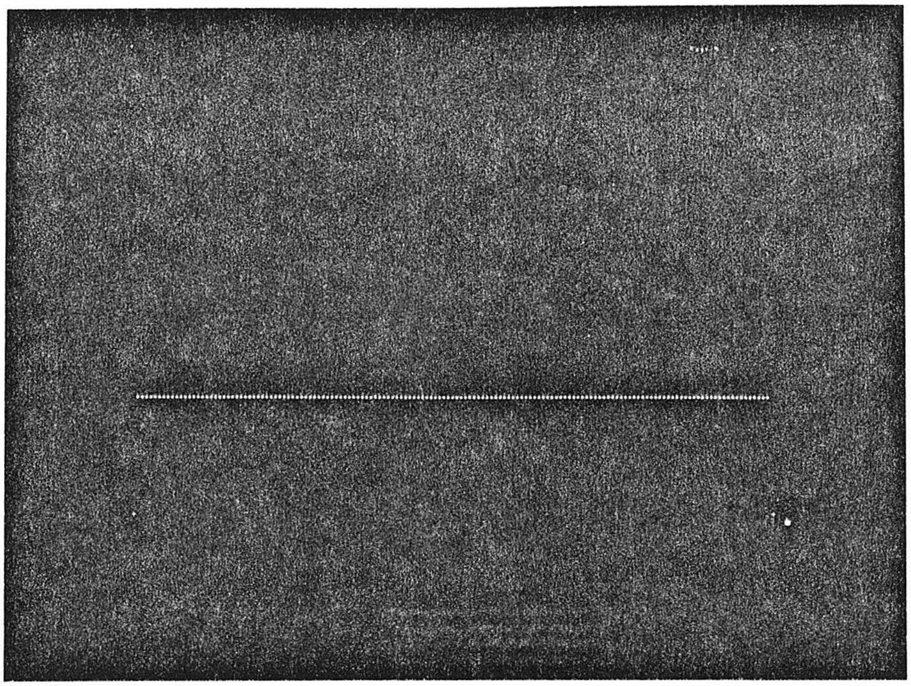


Fig. 4.1.a Stimulus pattern for horizontal velocity step experiment. Aperture = 6 deg.

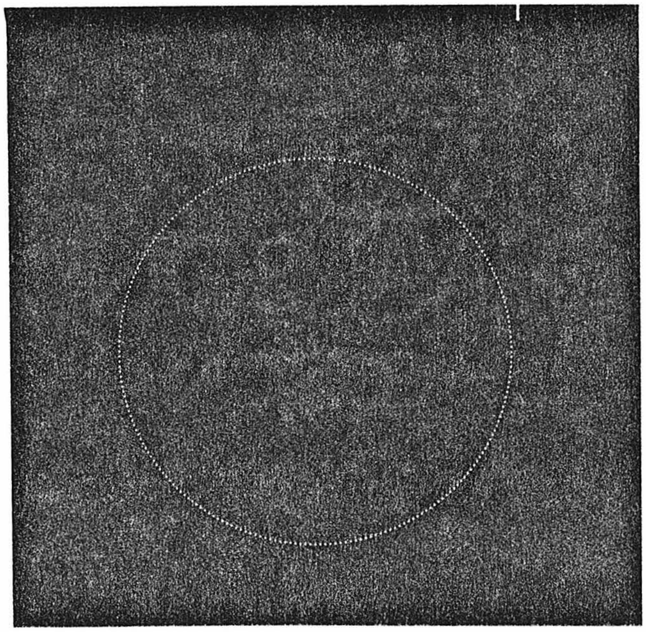


Fig. 4.1.b Stimulus pattern for rotational velocity experiments. d = 5 deg.

The second type of stimulus (Fig. 4. 1b) was designed to be used in the random velocity experiments. The high spatial frequency dot pattern was arranged in a circle so that velocity of target rotation could be modulated in a random fashion. The advantage of angular over linear velocity becomes clear when the nature of a random velocity signal is considered. When target velocity is modulated in a random fashion, target position becomes a random walk (see Chapter III). In a short period of time, the position of a random, linear velocity target will become large, exceeding the range of the apparatus. When target motion is rotary, position becomes a periodic quantity, returning to zero value from time to time, even for a monotonically increasing angular velocity signal. The dot spacing in the circular targets was also adjusted so that the distance between any two dots subtended less than one min arc at the retina. Position information was available in the circular stimulus in the form of distance of the fixation point from the center of the circle. However, since the subject's task was to track the angular motion of the target, variations in radial position were not correlated with the input signal.

4. 2. 2 Optical Projection System

A schematic diagram of the optical system used to present the targets is shown in Fig. 4. 2. The apparatus consists of two identical halves, one for the left eye and one for the right. Targets are mounted on slide transparencies and are presented in Maxwellian view; that is, an image of the source is brought to focus in the plane of the entrance

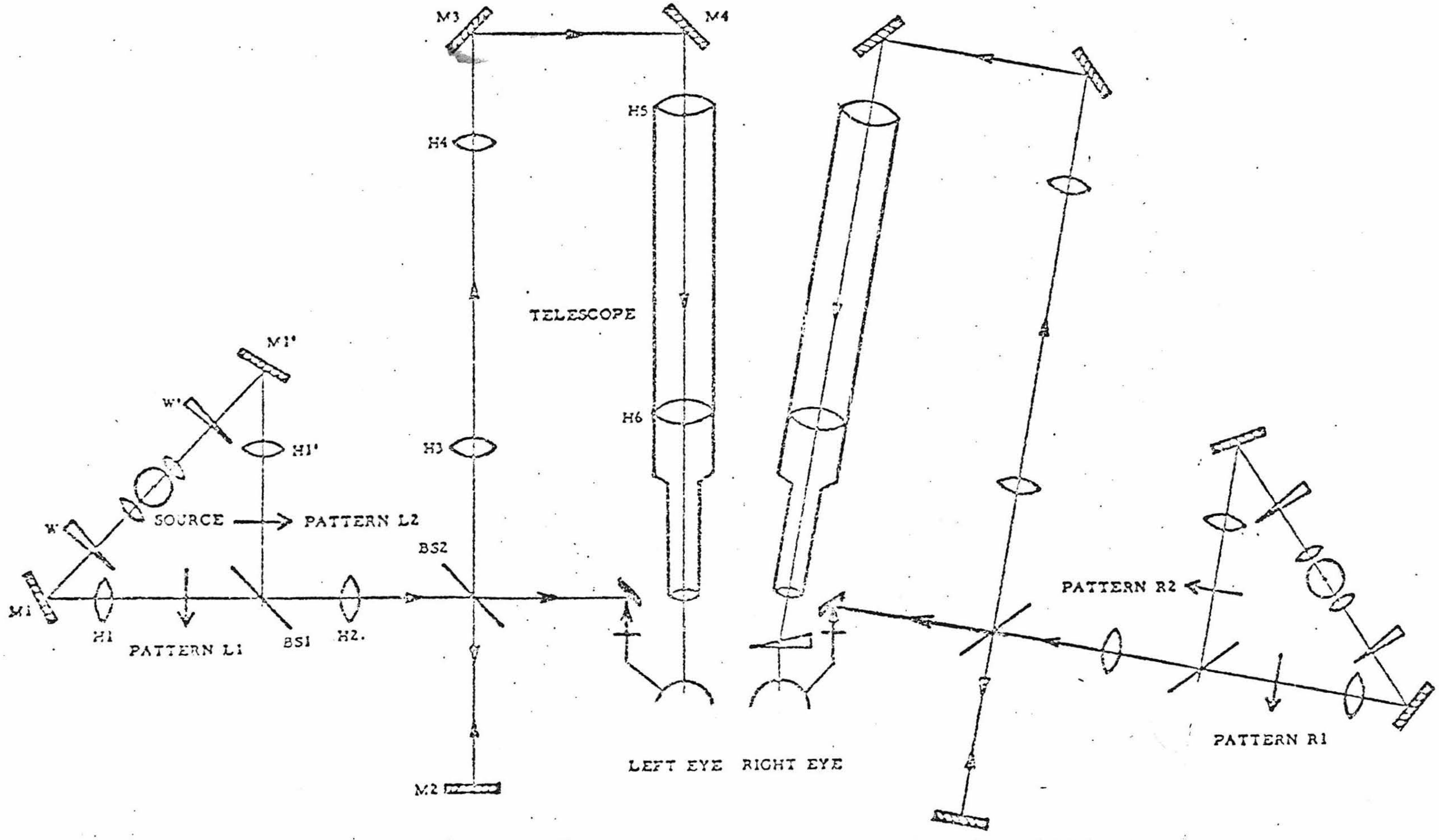


Fig. 4.2 Schematic of the optical system for presentation of normal and stabilized retinal images. (Redrawn from Lu, 1972)

pupil of the eye. The targets are viewed at optical infinity and the optics of contact lenses worn by each subject to record eye movements are ground to the individual's refractive prescription.

The retinal image stabilizing capabilities of this apparatus have been described elsewhere (e.g. Fender and Julesz, 1967). Briefly, a small mirror attached to the subject's contact lens acts as an optical lever in deflecting the target image through an angle twice that of the eye rotation. The telescopes through which the images are viewed are calibrated to xl/2 magnification, so that the retinal image of the target moves through an angle exactly equivalent to the angle of the eye rotation.

The subject's head is held stationary in the viewing position by a head rest and dental bit bar, both individually moulded for each subject.

4.2.3 Stimulus Motion

Control of the motion of the stimuli for all experiments was accomplished by a PDP 11/20 lab computer. For the horizontal velocity step experiments, stimulus slides were mounted on a stepping motor, carrier and rail apparatus in the target plane of the optical system. With computer control, the mechanism could impart a uniform velocity to the target over a range of about 7 degrees of visual angle. Each motor step corresponded to 1 min arc displacement at the retina. The rotation of the circular targets was accomplished by means of a specially adapted ball bearing apparatus driven by the same stepping motor system. In this case, 2560 steps of the motor were required to rotate the stimulus through 360 degrees. The maximum achievable velocities were 8.33 deg/sec linear motion and 80 deg/sec angular motion.

4.2.4 Eye Movements

Eye movements were measured using a variation of the contact lens technique. Scleral contact lenses were individually fitted to each subject by a local optometrist, Dr. Solon Braff. A mould was taken of each eye and a plexiglas lens was manufactured to the shape of the mould. Three curvatures were imparted to the inner surface of the lens as shown in Fig. 4.3. The outer curvature conforms to the shape of the scleral surface, the inner curvature was ground to provide minimum corneal clearance, and the intermediate curvature ensures that the pain sensitive limbal area is not disturbed. This triple curvature design allows for an extremely tightly-fitting yet comfortable lens, which can be worn without anesthetic. The outer surface of the lens was ground to a curvature corresponding to 20/20 Snellen acuity for optical infinity viewing.

To reduce slippage of the contact lens with respect to the eyeball, 23 cm negative water pressure was applied to the volume of fluid filling the space between the cornea and lens. This magnitude of pressure has been shown to be a safe level, while considerably reducing slippage (Fender, 1964). Pressure was applied through a small diameter medical quality teflon tube which is sufficiently flexible so as not to interfere with eye movements.

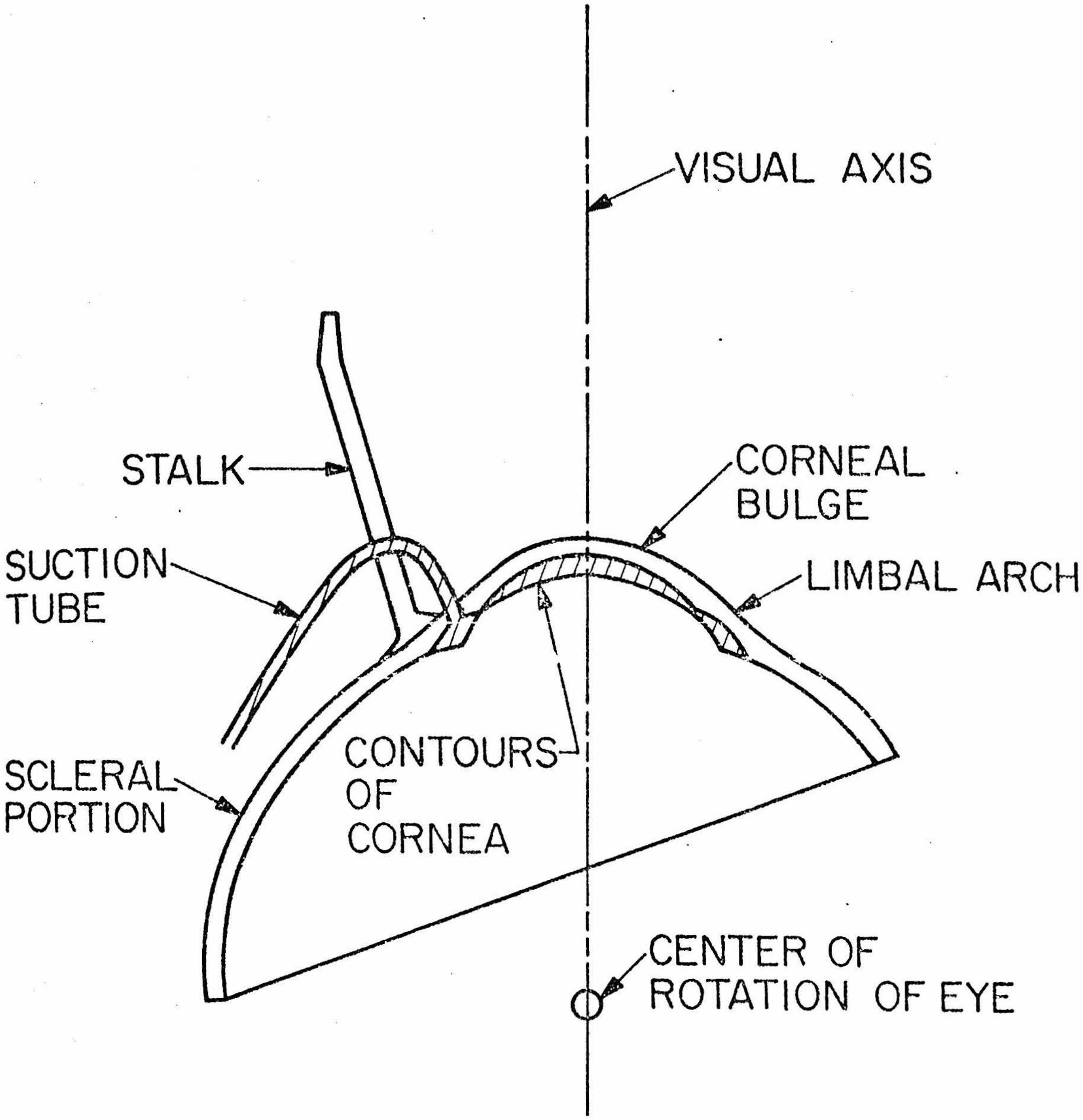


Fig. 4.3 Contact lens worn by the subject for the measurement of eye movements (Cross section). (Redrawn from St-Cyr, 1969)

An analogue signal proportional to the angular extent of horizontal and vertical eye motion was obtained in the following manner: A small, light rigid stalk is attached to the outer surface of the contact lens at a location chosen so as not to interfere with eye movements and to ensure minimal lens disturbance during blinks. At the tip of the 12 mm stalk a small pinlite is attached. The motion of the pinlite during eye rotation is monitored by a photomultiplier-knife edge system. As the eye moves, the shadow of the knife edge cast upon the sensitive surface of the photomultiplier tube moves in exact correspondence. This arrangement results in a voltage signal output by the photomultiplier which is linearly proportional to eye rotation within a ± 4 deg range. The photomultiplier output is buffered by a differential amplifer with a corner frequency of about 200 Hz. The precision of this system is limited by photomultiplier and ambient noise to about 1 min arc eye rotation.

The eye movement monitors are automatically calibrated during each experiment. The off-line calibration is achieved by positioning a mechanical eyeball in the recording position. A pinlite of the same type used on the contact lens is attached to the artificial eye ball at a location equidistant from the center of rotation of the globe as the lens pinlite. Known amounts of angular rotation can be imparted to the mechanical eye ball in order to set the magnitude of the automatic calibration steps. These steps are achieved by displacing a knife blade a fixed distance over the face of the photomultiplier tube, thereby occluding a fixed amount of light. The displacement of the blade is adjusted until the desired step in voltage corresponds to a known angular rotation. The gain of the system can thus be altered to achieve any desired voltage range while maintaining an accurate calibration of eye rotation with respect to voltage.

4.2.5 Data Acquisition System

A multiple channel digital data acquisition system was designed and built in this laboratory to serve several different experimental set ups. For this experiment four channels of data were sampled at 2 millisecond intervals, digitized, multiplexed and then stored on 9 channel digital magtape. Digitization was limited to 8 bit accuracy, corresponding to 2 min arc eye rotation on the eye movement channels. The activity of the data acquisition system was at all times under the control of the PDP11/20 computer.

4.2.6 Experiment Control

All experiments discussed in this thesis were under the supervision of a PDP 11/20 mini-computer. With the support of a specialized operating system program developed for this computer system, PAL 11 assembler programs were designed to control the experimental sequence. The monitor was designed to take care of all "housekeeping" duties, such as input/output operations between the various terminals and the computer, program control during interrupts, and system initializing. Thus, the user is left only with the chores of programming the desired sequence of events involved in each experiment.

Specifically, the 11/20 system was used to i) control the timing of the stepping motors used to move target slides; ii) initiate each experimental run with calibrations of eye and stimulus movements; iii) record subject responses and stimulus parameters; iv) control the data acquisition system to ensure correcting timing of eye movement responses to stimulus motion; and v) compute necessary on-line stimulus parameters, such as conversion of velocity changes to motor step interval changes.

4.3 Experimental Procedures

The following experimental procedure was used in all velocity step experiments. Since the subjects are allowed to wear their contact lenses for a maximum of 45 minutes each day, efficiency in running experiments was extremely important. Therefore, before inserting his contact lenses, each subject was asked to make all necessary adjustments of the optical apparatus so that the targets were imaged in Maxwellian view. This usually involved about 5-10 minutes of adjusting bite bar and headrest location and interocular separation of viewing telescopes. The subject then proceeded to insert his contact lenses and ensure that no air bubbles were present in the volume of fluid occupying the space between lens and cornea. This part of the procedure is very important for two reasons. First, a bubble within the eye-lens space usually results in double vision caused by the added refractive surfaces of the water-air and air-lens transitions. Secondly, any amount of air between the eye and lens will reduce the negative pressure used to improve adhesion of the lens to the scleral surface, the result being increased probability of lens slippage with respect to the eyeball.

Once the contact lenses were correctly inserted, the subject secured his head within the apparatus and the experiment began. The subject's visual field was completely dark ;with the exception of a string of closely spaced bright white dots subtending about 5 deg visual angle. Each eye viewed an identical field, and the subject perceived a single target when the two fields were fused. Each experimental run consisted of 30 to 40 trials. At the beginning of each run, the eye movement monitors were aligned so that only the linear range of the system would be used. The dc offset was adjusted to produce a zero voltage reading when the center of the visual field was fixated. The gain of the monitors was adjusted until a full field eye movement remained within the ± 2 volt range of the dignitizing system. Eye movements were monitored on a dual channel oscilloscope during the experiment to ensure proper on-line operation.

With eye movements correctly adjusted, the experimenter initiated the run by entering a character on the computer terminal. The program first started the data collection system and activated the calibration shutters in each eye movement channel. The calibration steps were used in later stages of data analysis to calibrate the reconstructed eye movement signals. At the beginning of each trial, the targets remained stationary for 1 second. The stepping motors were then activated and the targets began to move at a constant velocity set by the experimenter at the beginning of the run. The acceleration time of stimulus motion was instantaneous (equal to one motor step interval which corresponded to 7 to 10 msec, depending on desired target velocity). After 1.5 to 1.8 sec (again depending on stimulus velocity) of constant velocity motion, the target was halted for 1 second and then recentered, after the computer had stopped data collection and dumped the memory buffers onto a magtape record. Trials were separated by a 5 second rest period. During a single run of 30-40 trials, target velocity was held constant but the direction of motion was randomized from trial to trial. At the end of the run, the calibration shutters were again activated. About 120 trials could be obtained each day from a single subject.

The double step experiments followed a similar procedure, the only difference being that after a preset duration of motion at a fixed velocity, target velocity was either increased or decreased. The direction of the velocity change was randomized from trial to trial. The initial velocity, size of velocity change, and duration of the first velocity were set by the experimenter at the beginning of each run.

4.4 Single Step Data Analysis and Results

Analysis of single velocity step data fell into two categories, microstructure analysis and averaged response analysis. Each procedure was designed to reveal some basic characteristics of the eye movement response to the onset of motion of the periodic target.

4.4.1 Microstructure Analysis

The analysis of the microstructure of the eye movement response to the velocity step input began by submitting the raw eye movement signals to a curve fitting analysis. A computer program was written

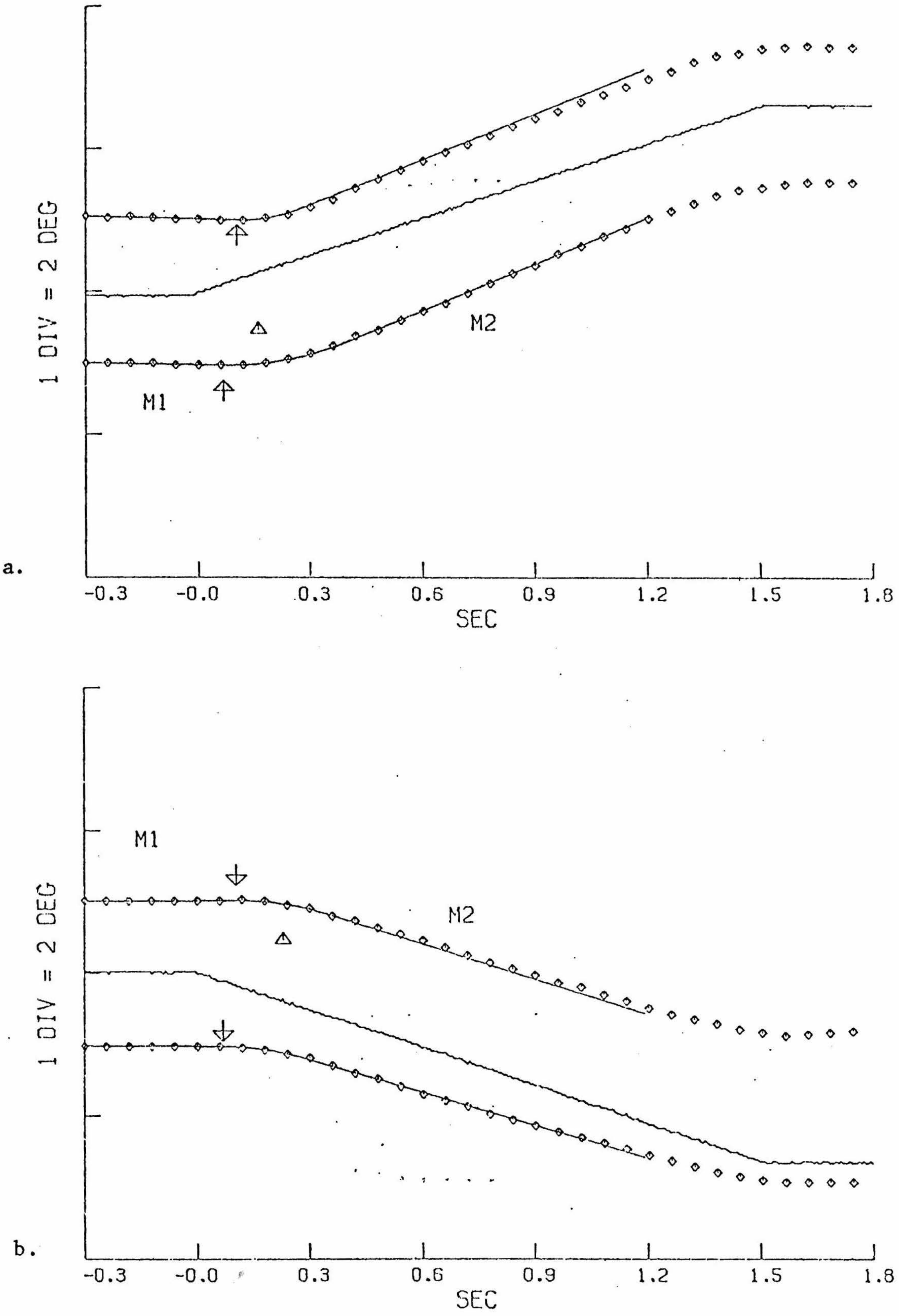


Fig. 4.4 Results of curve fitting routine on one pursuit response. Center trace-stimulus, ◇- eye position samples (Δt = 60 msec). Smooth curve generated by LSQENP program. ↑ - acceleration onset. a. rightward motion, b. leftward motion.

to utilize the method of least squares estimation of nonlinear parameters developed by Marquardt (1963). The first step in the method is to define a curve which, in general, describes the eye movement elicited in response to the velocity step stimulus. A typical binocular eye movement response with associated target motion is shown in Fig. 4.4 The shape of the position response could be described by a set of five parameters. Referring to Fig. 4.4., the slopes M1 and M2 represent eye velocity before and after, respectively, the acceleration phase of the eye movement. The third parameter is the time after stimulus onset when the eye begins to accelerate (marked by the arrow symbol in the figure). The eye position at that time is the fourth parameter. The fifth parameter is defined as the time period during which the eye is accelerating from velocity M1 to velocity M2, the integration time of the eye movement response.

The curve which is defined by these five parameters can be represented by the following set of equations:

$$Y = Y1 + M1\,(T - T1)\ ,\quad T \leq T1 \qquad (4\text{-}1)$$

$$Y = Y1 + M1\,(T - T1) + \tfrac{1}{2}\left[\frac{M2 - M1}{\Delta}\right](T - T1)^2\ ,$$

$$T1 < T \leq T1 + \Delta$$

$$Y = Y1 + \tfrac{1}{2}(M2 + M1)\,\Delta + M2\,(T - T1 - \Delta)\ ,$$

$$T > T1 + \Delta$$

where

M1 = eye velocity before stimulus onset

M2 = time of onset of eye acceleration

T1 = time of onset of eye acceleration

Y1 = eye position at time T1

Δ = acceleration time between velocity M1 and M2

Initial values of these five parameters are supplied to the curve fitting program. The routine for least squares estimation of nonlinear parameters (LSQENP) then proceeds to adjust the initial values until the best fit, in the least squares sense, of the curve to the data is obtained. The solid curves drawn through the data points in Fig. 4.4 were generated from the parameters returned by LSQENP by plugging the values into the equations (4 - 1).

Three important characteristics of the eye movement response to motion of the spatially periodic stimulus can be obtained from the micro-structure analysis. 1) The accuracy of the eye-to-stimulus velocity match can be determined by comparing the values of M2 obtained from the curve fitting procedure to the known stimulus velocity. 2) The latency of the onset of eye acceleration to the onset of stimulus acceleration is equivalent to the parameter T1. 3) The integration time, or the time it takes the eye to accelerate from the rest to the final velocity M2, is represented by the parameter Δ. The curve fitting procedure is sensitive to individual response variations and allows accurate estimation of the above parameters for each response. The values computed for a number of responses to the equivalent stimulus motion can be compared for small but possibly significant differences. Intersubject variations can also be estimated using this technique.

4.4.2 Microstructure Results and Discussion

The results of the microstructure analysis are tabulated for the three subjects in Table 4.1 a, b, and c, including means, their standard deviations and 95% confidence regions. Right eye and left eye responses were analyzed independently for rightward (positive velocity) and leftward (negative velocity) target motion.

Consider first the eye velocity data. Three types of comparisons were carried out: right eye/left eye velocity match, eye velocity/stimulus velocity match, and linearity with respect to input velocity. The 95% confidence regions indicate that for subject I:

i) The mean velocities of right and left eye differed significantly ($P < .05$) at four out of the six velocities used.

ii) In all cases, eye velocity differed significantly ($P < .05$) from stimulus velocity. For rightward motion, eye velocity was greater than stimulus velocity, while for leftward motion eye velocity was less than stimulus velocity.

iii) For both rightward and leftward motion, eye velocity varied nearly linearly (within 95% confidence limits) with target velocity.

The difference in velocity between the two eyes were not correlated to the direction of motion as would be expected if there existed a nasal-temporal asymmetry in the neuromuscular mechanism of the globe. Apparently, the binocular coordination is not as well developed for smooth pursuit as for the saccadic system (Williams

Table 4.1a

Results of microstructure analysis for Subject I
N = number of trials, m = mean, SDM = standard deviation
of the mean, L_1, L_2 = lower and upper 95% confidence regions

	Velocity				Latency				Delta			
	Left Eye		Right Eye		Left Eye		Right Eye		Left Eye		Right Eye	
V=90 $\frac{\text{Min arc}}{\text{sec}}$	←	→	←	→	←	→	←	→	←	→	←	→
n	9	15	9	15	9	15	9	15	9	15	9	15
m	-78.1	98.2	-78.5	92.2	109.0	93.0	96.0	89.0	344.0	293.0	441.0	261.0
SDM	1.4	1.5	1.6	1.2	28.4	7.8	10.5	6.6	44.6	23.6	25.2	17.3
L_1	-74.9	95.0	-74.8	89.6	43.2	76.1	71.4	75.0	241.5	242.2	382.7	224.3
L_2	-81.3	101.4	-82.2	94.8	174.2	109.5	119.8	103.4	447.1	343.4	498.9	295.5
V=111 $\frac{\text{Min arc}}{\text{sec}}$												
n	12	16	12	16	12	16	12	16	12	16	12	16
m	-103.0	133.0	-108.0	124.0	190.0	102.0	183.0	114.0	277.0	376.0	355.0	251.0
SDM	1.2	1.7	1.3	1.1	32.1	14.3	28.1	14.4	19.2	19.8	17.2	12.3
L_1	-100.3	129.7	-105.2	122.0	119.6	71.7	121.5	83.6	234.7	333.5	317.0	225.1
L_2	-105.5	136.9	-111.0	126.6	260.9	132.7	245.1	145.0	319.0	417.9	392.7	277.5
V=125 $\frac{\text{Min arc}}{\text{sec}}$												
N	13	10	13	10	13	10	13	10	13	10	13	10
m	-108.0	140.0	-114.0	145.0	113.0	174.0	95.0	189.0	218.0	325.0	299.0	241.0
SDM	0.6	4.2	1.0	0.8	8.8	53.8	7.6	57.7	17.8	23.0	14.2	22.6
L_1	-106.7	130.4	-111.6	143.2	93.5	52.6	78.6	58.4	179.2	273.4	268.6	189.5
L_2	-109.3	149.4	-115.6	146.8	131.9	296.0	111.8	319.4	256.8	377.4	330.4	291.7

Table 4.1b

Results of microstructure analysis for Subject II.
n = number of trials, m = mean, SDM = standard deviation of the mean, L_1 and L_2 = lower and upper 95% confidence limits.

	Velocity				Latency				Delta			
	Left Eye		Right Eye		Left Eye		Right Eye		Left Eye		Right Eye	
V=90 $\frac{\text{Min arc}}{\text{sec}}$	←	→	←	→	←	→	←	→	←	→	←	→
n	4	6	4	6	4	6	4	6	4	6	4	6
m	-106.0	100.0	-114.0	80.0	159.0	120.0	200.0	165.0	218.0	600.0	171.0	510.0
SDM	4.7	4.6	5.6	3.1	29.4	32.3	13.5	38.6	107.6	41.7	95.9	59.7
L_1	-91.1	88.0	-96.1	71.5	65.0	36.0	157.0	65.0	0.0	493.0	0.0	356.0
L_2	-121.1	111.6	-131.7	87.5	253.0	202.0	243.0	264.0	560.0	707.0	476.0	664.0
V=111 $\frac{\text{Min arc}}{\text{sec}}$												
N	6	10	6	10	6	10	6	10	6	10	6	10
m	-115.0	111.0	-124.0	100.0	196.0	154.0	208.0	167.0	239.0	553.0	237.0	555.0
SDM	3.0	4.3	1.3	4.3	18.9	36.8	13.2	26.3	34.5	37.6	18.3	41.3
L_1	-107.1	101.6	-120.9	90.8	147.0	71.0	174.0	107.0	151.0	468.0	190.0	462.0
L_2	-122.5	121.0	127.5	110.2	244.0	237.0	242.0	226.0	328.0	638.0	284.0	648.0
V=125 $\frac{\text{Min arc}}{\text{sec}}$												
n	14	6	14	6	14	6	14	6	14	6	14	6
m	-126.0	106.0	-146.0	108.0	153.0	173.0	194.0	148.0	363.0	507.0	325.0	557.0
SDM	3.6	3.1	3.8	4.3	16.1	54.7	14.5	34.7	36.9	56.3	27.6	82.0
L_1	-117.8	98.8	-137.7	96.9	118.0	32.0	162.0	59.0	284.0	363.0	265.0	346.0
L_2	-132.8	114.8	-154.1	119.1	188.0	314.0	225.0	237.0	443.0	652.0	385.0	768.0

Table 4.1c

Results of microstructure analysis for Subject III.
n = number of trials, m = mean, SDM = standard deviation of the mean, L_1 and L_2 = lower and upper 95% confidence limits.

	Velocity				Latency				Delta			
	Left Eye		Right Eye		Left Eye		Right Eye		Left Eye		Right Eye	
V=90 $\frac{\text{Min arc}}{\text{sec}}$	←	→	←	→	←	→	←	→	←	→	←	→
n	9	15	9	12	9	12	9	12	9	12	9	12
m	-77.0	102.0	-73.0	91.0	56.0	77.0	170.0	-17.0	456.0	494.0	458.0	490.0
SDM	5.1	3.7	1.5	3.2	64.9	28.8	60.5	28.4	58.5	47.2	71.9	98.2
L_1	-65.3	94.4	-69.6	83.8	-93.0	13.6	30.0	-79.0	321.0	390.0	292.0	274.0
L_2	-88.3	110.2	-76.4	97.9	206.0	140.4	309.0	46.0	591.0	598.0	624.0	705.0
V=111 $\frac{\text{Min arc}}{\text{sec}}$												
n	5	10	6	8	6	8	6	8	6	8	6	8
m	-89.0	117.0	-92.0	105.0	102.0	136.0	113.0	84.0	392.0	606.0	503.0	357.0
SDM	3.8	4.3	4.1	5.9	18.2	51.9	46.5	29.0	64.4	82.3	132.6	58.1
L_1	-78.9	107.5	-81.7	91.8	55.0	13.0	-7.0	15.0	226.0	411.0	162.0	220.0
L_2	-98.3	126.7	-102.8	119.0	148.0	258.0	233.0	152.0	557.0	800.0	844.0	494.0
V=125 $\frac{\text{Min arc}}{\text{sec}}$												
n	10	11	16	5	16	5	16	5	16	5	16	5
m	-103.5	143.0	-106.0	148.0	223.0	202.0	226.0	170.0	527.0	452.0	542.0	382.0
SDM	4.5	5.9	2.9	4.5	40.4	70.3	30.5	73.0	31.9	87.9	35.1	97.2
L_1	-93.5	130.0	-100.3	136.8	137.0	6.0	160.0	-33.0	459.0	208.0	467.0	112.0
L_2	-113.0	155.9	-112.7	160.0	309.0	397.0	290.0	372.0	595.0	771.0	616.0	651.0

and Fender, 1977), in terms of velocity of motion. The time course of saccadic eye movements is believed not to be under continuous feedback control, since visual sensitivity has been found to be suppressed during saccades (Volkman, 1962; Beeler, 1967). Smooth pursuit, on the other hand, seems to be very sensitive to retinal feedback and also to oculomotor feedback (in terms of a sense of eye velocity). The observed variation in binocular velocity coordination may be a demonstration of the noise level within the smooth pursuit system. This also may be taken as evidence that each eye performs its own retinal/eye velocity calculation. Perhaps the fusional mechanism is responsible for the degree of coordination observed, acting as a cross-channel between the right and left pursuit systems. Further support of the speculations put forth here will have to come from extensive binocular pursuit studies and from neurophysiology, for the main purpose at present is to study pursuit dynamics rather than binocular processes during pursuit.

The observed asymmetry between rightward and leftward motion, although statistically significant, may not be important to our study of pursuit dynamics, since this seems to be a subject-dependent effect. Further discussion of such an asymmetry in velocity dependent upon motion direction would have to be based on more extensive data than represented here. The observation relevant to the present study is that eye velocity does not exactly match target velocity. This result should be considered in terms of the summation of retinal and eye velocity which produces the perceived velocity signal. As discussed in Chapter III, the afferent negative feedback signal when given more weight than the efferent command by the oculomotor command center, makes available some resideual negative feedback to continually drive the oculomotor plant. Theoretically, the weighting factor should be of such magnitude as to ensure an accurate eye velocity to target velocity match. The data presented in Table 4.1 from three subjects showing similar eye to target velocity mismatches, are supportive of a theory of a velocity-controlled pursuit system, in which either the weighting factor or the retinal and eye velocity calculations exhibit a certain amount of error. Perhaps the asymmetry in leftward and rightward eye velocities is a manifestation of a subject-dependent preferred direction, such that the afferent weighting factor varies with velocity direction.

The degree to which eye velocity increases linearly with target velocity seems to be fairly sloppy. However, the experimental conditions were designed to study smooth pursuit transient characteristics. The magnitude of the eye movements was kept small (± 2.5 deg) so that steady-state velocity was assumed to be reached within 1 second. Thus, in this discussion of final eye velocity as compared to target velocity, the results should be viewed in relation to the small angular range used. An accurate eye velocity, target velocity match was therefore not reached within 2 seconds. Also, within experimental error eye velocity was linearly related to target velocity.

The response latency data generated from the microstructure analysis (Table 4.1) indicate that for the three velocity values used, response latency is independent of target velocity or direction ($P < .05$). The calculated 95% confidence regions are rather large (more than 100 msec in some instances). However, means and their standard deviations reveal two interesting aspects of the pursuit step response: i) The latency of onset of eye acceleration, on the average, occurs within 100-150 msec of target motion onset. ii) The onset of eye acceleration varies significantly between individual responses. The 100-150 msec value is inclusive of the latency value obtained by Robinson (1965) of 125 msec (± 20 S. D.). The standard deviations of the observed means obtained in the present experiments also are similar to Robinson's value of 20 msec. Therefore, although the variability in the data from a relatively small number of observations (10-15) prevents any firm conclusion about response dynamics or binocular coordination, the microstructure analysis of latency has shown that the velocity stimuli used produce an oculomotor response in about the same amount of time as conventional spot stimuli. Apparently the temporal aspects of the target determine the initiation of the smooth eye movement. Thus in the case of the single spot target, the motion of the spot rather than its position generates the pursuit response. Similarly, for the spatially periodic target, the absence of position information does not seem to alter the average response time. We can conclude from these data that the primary effect of position information in the motion of the target is to elicit a saccadic response.

The time it takes the eye to accelerate from rest to the final steady-state velocity can be considered the integration time of the neuromuscular components of the pursuit system. An "instantaneous" step change in velocity is transformed by the system into a smooth acceleration from the initial to the new velocity value. In effect the output of the pursuit system is a low-pass-filtered rendition of the input waveform. The parameter delta (Δ) of the curve fitting algorithm is the best fit value of the time period during which eye velocity changes from the value M1 to M2. The means, their standard deviations and 95% confidence limits of the delta values output by the curve fitting program for the three velocities used are listed in Table 4. 1. The means for Subject I nearly all fall around 300 msec with a standard deviation of about 20 msec. For Subject II and III, the delta values are larger and show more variability. In some cases there appear to be significant ($P < .05$) differences between right and left eye means and rightward and leftward movements, but the directions of the differences are not systematic.

The 300 msec (S. D. ≈ 20) is about twice as large as the value of 130 msec observed by Robinson (1965). It is likely that the difference is due to the stimulus used in the two studies. The previous work was based upon responses elicited by movement of a spot. Therefore, saccades were an integral part of the response and the rapid change in velocity known to occur during saccades must have contributed to reducing the acceleration time. In the present study, saccades were excluded from the obtained responses so that the pursuit system alone was responsible for the acceleration of the eye to final velocity. Another factor which could have contributed to the increased acceleration time observed in the present experiments, is the spatio-temporal content of the periodic dot stimulus. As discussed in Chapter III, the target velocity computation must be based only on the temporal frequency content of the motion, since the spatial periodicity of the target prevents a position-derivative type computation. The conflicting integration time results could be explained in that the system takes more time in this case to determine the relation between target and eye velocity.

A brief comment is in order now about intersubject differences in the results listed in Table 4. 1 a, b, c. The results for the other two subjects support the same basic conclusions discussed in the preceding paragraphs. The velocity data again show a preferred direction of movement in which eye velocity, on the average, exceeds target velocity. Also the velocities of the two eyes differ significantly ($P<.05$) in several cases as observed for the first subject. Within experimental error, eye velocity for Subjects II and III again vary nearly linearly with target velocity.

The latency data for the second and third subject exhibit means slightly larger and with more variability than for the other subject. Subjects II and III consistantly showed a higher occurrence of saccades in their step responses than did the other subjects. The activity of the saccadic system in this subject's performance could not have affected the results since only responses showing no saccades were submitted for analysis. However, his data became the exception in all the data analysis procedures included in this study, as will be seen shortly. The statement could be made that, in this case, the saccadic system seemed to dominate the pursuit system in the velocity step task even without a foveal position error stimulus. The variance in the data of Subject II compared to the other two subjects should be considered normal intersubject oculomotor variability, although the possibility of a pursuit dysfunction has not been tested.

An interesting asymmetry is observed in the acceleration time means for Subject II. Responses to leftward motion seem to require less time to complete the acceleration phase than those to rightward motion. In several cases, the asymmetry is significant at the $P<.05$ level. Furthermore, the integration times for rightward motion are consistantly greater than the 300 msec value cited for Subject I. Note that Subject II's preferred direction from the velocity analysis is to the left, the direction which also shows faster acceleration times Since this subject's data are different also in several other respects from that of the other two subjects, any speculation about causes would be likely to confuse the issues of pursuit system dynamics to be discussed later. The differences are only mentioned here to add to the documentation of oculomotor intersubject variability.

The detailed analysis of the structure of individual pursuit responses has yielded several interesting results. First, within the two seconds following onset of target motion in a velocity step experiment, eye velocity does not exactly match stimulus velocity in a steady-state manner. Second, the equivalent response latency values obtained for spot stimuli and for a spatially periodic pattern indicate that position information is not necessary for the initiation of a smooth following eye movement. Third, the integration time of the pursuit system seems to be dependent upon stimulus characteristics, including, possibly, the availability of absolute target position information and the temporal frequency content of the stimulus motion. The analysis has also shown that individual responses may vary in their time course and waveform, even when saccades are not present. Apparently, in order to obtain a true representation of pursuit reponse characteristics, a statistical analysis should be employed, which is relatively insensitive to small, individual response variations, while preserving the integrity of the general response waveform. An analysis technique involving the averaging of a number of responses to the same stimulus has been developed and is described next.

4.4.3 Average Response Analysis

Eye movement responses to conventional position ramp stimuli show a high degree of variability in response waveform (Robinson, 1965). This non-stationarity of the oculomotor response seemed to be due to the contribution of the saccadic system. The smooth pursuit eye movement could be interrupted by one or several saccades at varying times after onset of target motion. Eye velocity tended to overshoot target velocity by varying amounts, depending upon the time of occurrence and amplitude of the saccades. Also related to the occurence of saccades was the variability found in the abrupt eye velocity changes which usually accompanied the saccadic response. In the present research, the smooth pursuit system has been isolated from the saccadic system by stimulating with target velocity rather than position and by removing spurious non-stimulus related saccades from the eye movement recordings. Now, the stationarity of the pursuit system can be analyzed by averaging the eye movements elicited by repeated presentations of the same stimulus motion. The averaging of eye velocity and acceleration responses proceeded through the following data processing steps.

First, saccades were removed from the eye position data by a FORTRAN coded computer program. The position signal was first differentiated and a velocity threshold was set. The velocity signal was then searched for occurrences of saccades by detecting when eye velocity exceeded the preset threshold value. Once the saccade was detected, the time (Tmax) at which the eye reached maximum velocity during the saccade was determined. The point backward in time from Tmax where threshold was exceeded and the point forward in time equidistant from Tmax were then determined and related back to the position signal. The magnitude of the position difference between these two points was taken as an estimate of saccadic amplitude and subtracted from the entire position record following the saccade thereby producing the cumulative smooth pursuit position signal. To complete the procedure, the two points, just determined to enclose the saccade in time, were joined by a quadratic curve to account for the possible abrupt change in eye velocity which sometimes accompanies the saccade. This last step was deemed necessary in order to avoid concentrating the acceleration from pre-saccadic to post-saccadic velocity into one sampling period (4 msec) thereby introducing large artifacts into subsequent velocity and acceleration calculations.

The result of the first processing stage was a signal corresponding to the pure pursuit component of the eye position response. Since the analysis was to be performed on eye velocity and acceleration, the smooth position signal had to be differentiated, once for velocity, again for acceleration. However, the differentiation process acts as a high pass filter, removing all dc components from the signal and preferentially reducing the low frequency content. The high frequency noise problem is even more bothersome when the derivative is digitally computed, since quantization noise has been added to the high frequency content of the original signal. In order to suppress some of the high frequency noise in the differentiated signal, a low pass filtering stage was added before the derivative was taken.

Time domain filtering was chosen over frequency domain analysis to reduce the computation time which would be involved in Fourier transforming the time signal. A few attempts at reducing high frequency noise in the velocity signal indicated that a relatively low cutoff frequency (near 10 Hz) would be required to substantially improve the signal to noise ratio. Although 10 Hz is well above the frequency content of pursuit eye movements, conventional time domain filtering techniques introduce substantial phase shifts in the filtered signal when such low cutoff frequencies are used. The problem arises from the extent of the time window. Events far removed from the data point being considered may affect the waveform centered around the present datum, depending on the type of integration window. Since the shape of the velocity and acceleration responses was of prime importance, an attempt was made to find a filtering window which would minimize the time shift effect.

One method of digital filtering is to fit a curve to the data immediately surrounding the datum being considered. The number of points included in the fit determines the power of the low pass filtering effect, while the time relationship of the signal is mimimally perturbed. For the present purposes a least squares polynomial fit of second order was found to be sufficient. Consideration of the computing time which would be required to fit a quadratic curve to each data point of the signal forced a search for a more efficient method of performing the least squares fit. It was found that to each least squares fitted quadratic curve of say m points, there corresponds a parabolic time window which, when convolved with the input signal, has the equivalent filtering effect. For a second order polynomial least squares fit of m points, the coefficient, Ci, of the corresponding time window are determined by the equation:

$$Ci = \frac{1}{m} \left(1 + 5/4 \left[\frac{m^2 - 1 - 12i^2}{m^2 - 4} \right]\right), \; i = 1, 2, \ldots, m \quad (4\text{-}2)$$

Once the saccade-free, low pass filtered eye position signal was obtained, the velocity and acceleration signals were computed by consecutive applications of a differentiation routine. Care must be exercised when computing the derivatives of a signal since small noise artifacts in the original data can be greatly magnified in the computed signal and time shifts can be introduced by certain differentiation algorithms. To avoid these difficulties a differentiation method was developed which took a form similar to the low pass filter routine. Consider the Hamming filter window defined by the equation

$$G(\tau) = 0.54 + 0.46\cos\left(\frac{2\pi\tau}{T}\right), \quad \frac{-T}{2} \leq \tau \leq \frac{T}{2} \qquad (4\text{-}3a)$$

$$= 0 \qquad , \text{ elsewhere.}$$

Let $x(t)$ = eye position signal,

$x'(t) = \frac{d}{dt}x(t)$ = eye velocity signal,

and $G'(\tau) = \frac{d}{d\tau}G(\tau)$.

Then $G'(\tau) = -0.46\sin\left(\frac{2\pi\tau}{T}\right), \quad \frac{-T}{2} \leq \tau \leq \frac{T}{2}$

$$= 0 \quad \text{elsewhere.} \qquad (4\text{-}3b)$$

We wish to produce the low-pass filtered first derivative of the eye position signal, y (t).

Thus

$$y(t) = \int_{-\infty}^{\infty} G(\tau)x'(t-\tau)d\tau \quad . \qquad (4\text{-}3c)$$

By the chain rule of integration, Equation 4-3c can be written

$$y(t) = G(\tau)x(t-\tau)\Big|_{-\infty}^{\infty} - \int_{-\infty}^{\infty} G'(\tau)x(t-\tau)d\tau \quad . \qquad (4\text{-}3d)$$

However, since $G(\pm\infty) = 0$, we have

$$= \int_{-\infty}^{\infty} - G'(\tau)x(t-\tau)d\tau \quad . \qquad (4\text{-}3e)$$

Thus, by convolving the time window defined by Equation 4-3b with the eye position signal, we obtain the low-pass filtered first derivative of eye position. Of course, in the computer routines the dependent variable τ was replaced by a discrete index whose range, $-m/2 \leq i \leq m/2$, corresponded to the size of the low pass time window. The second derivative, or eye acceleration, was computed by the application of the differentiation routine to the previously computed first derivative.

The last step in this data analysis procedure was to accumulate eye velocity and acceleration responses elicited by repeated presentations of the equivalent target motion. The mean and standard deviation of the mean were computed by summing the responses and the squares of the responses as they were computed. Thus, the mean velocity response $\overline{v(t)}$ is:

$$\overline{v(t)} = \frac{1}{n} \sum_{1}^{n} v(t) \qquad (4\text{-}4)$$

where $v(t) = \frac{d}{dt} x(t)$

n = number of responses
$x(t)$ = position response

and the standard deviation of the mean is:

$$s(t) = \left[\frac{\sum_{i=1}^{n} v_i^2(t) - \left[\sum_{i=1}^{n} v_i(t) \right]^2 / n}{n(n-1)} \right]^{1/2} \qquad (4\text{-}5)$$

The mean and standard deviation for the acceleration response were computed from the velocity averages using the differention process described above.

4.4.4 Averaged Response Results and Discussion

The response of a system to a step change in the input is a basic characteristic of the system. For a constant-parameter linear system, the step response completely characterizes the system. For a nonlinear system the step response contains contributions from linear and higher order nonlinear system properties and therefore can be used as a test of the relative strengths of the linear and nonlinear components of the response. For example, the relationship between input and output amplitude gives an indication of the power transformation performed by the system on the input (e. g. response amplitude = stimulus amplitude to the nth power, where n is not necessarily an integer). Furthermore, response latency, rise time and damping characteristics are measures of first-order transient system properties which are easily obtained from a step response analysis.

Consider the case of the pursuit oculomotor system. In the introductory paragraphs of this dissertation, we postulated two possible input domains for pursuit, position and velocity. The oculomotor system responds to a step change in position not with a smooth eye movement, but with a saccade. In other words, the pursuit system does not respond to a step position input. It does, however, respond to a step change in veloctiy, as shown by Robinson (1965) and Rashbass (1961). In both of these studies, however, the input signal contained both position and velocity information and consequently, the response contained both position components (saccades) and velocity components (smooth pursuit). (Rashbass' step-ramp stimulus was a special case in which the position response was suppressed, leaving a pure pursuit response.) Thus, until now, it was not known how the oculomotor system would respond to a pure velocity step input.

In Fig. 4.5 the oculomotor response to a pure step change in velocity is shown for two subjects. The most notable property of the eye movement is the absence of saccades. It appears that a pure velocity input stimulates only the pursuit system. This statement must be qualified by considering the entire data set obtained in this study, for some small percentage of the responses contained saccades. In fact, data from one of the three subjects included nearly equal numbers of pure pursuit responses and composite responses containing saccades. A more accurate statement of the situation would be that the velocity stimulus used in these experiments stimulated primarily the pursuit system, the saccadic system responding occasionally to the remaining position cues in the visual field such as the aperture edges.

Given that the spatially periodic stimulus elicits primarily a pursuit response, we can proceed to use the stimulus to study the pursuit system as an independent entity, uncompromised by activity of the saccadic system. The fact that some of the step responses did contain saccades does not hamper the study if it is assumed that the saccadic contributions were not stimulus-related. The validity of this assumption is supported by the preponderance of saccade-free responses (for two of the subjects) and by the observation that, when saccades were present, their times of occurrence and directions

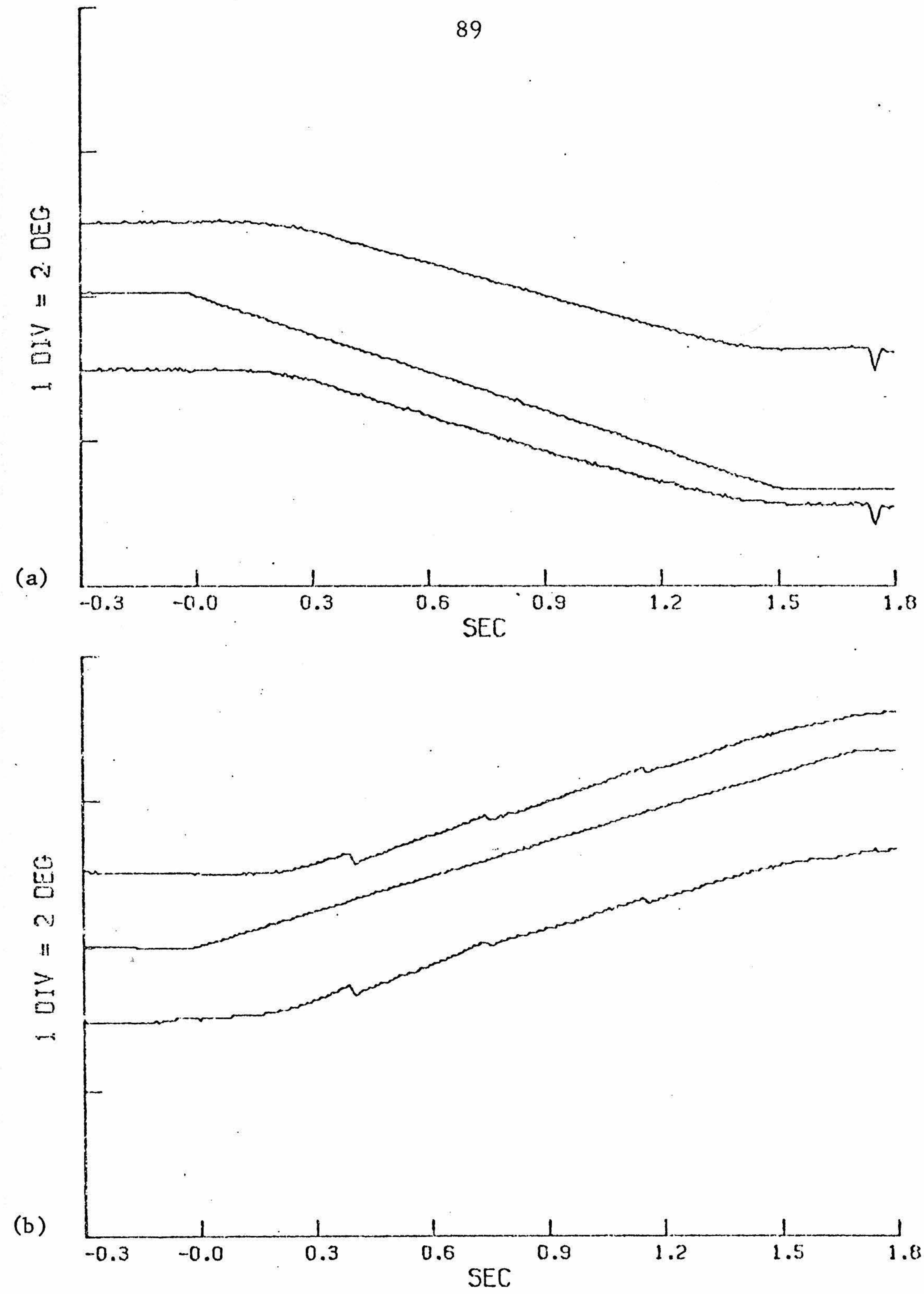


Fig. 4.5 Binocular eye position response to ramp position motion of spatially periodic target. (a) Subject I, leftward motion 125 min arc/sec. (b) Subject III, rightward, 111 $\frac{\text{min arc}}{\text{sec}}$.

showed no systematic relation to the pursuit component. Thus the only effect of removing the saccades from eye movement recordings was to improve the signal-to-noise ratio of the analysis which followed.

Perhaps the next most important property of the pursit step response is its repeatability, since further analysis of a system which changes its reponse characteristic over time would be quite frustrating. The study of the stationarity of the pursuit system was performed in the velocity domain, in order to take advantage of the clarity of an intuitively pleasing stimulus-response domain. The eye velocity responses, obtained by digitally differentiating the position signals, to randomly intermixed presentations of equivalent target motions were averaged to generate the mean velocity response. The standard deviation of the mean response was also computed to provide a quantitative evaluation of system stationarity.

In Fig. 4.6, an averaged eye velocity response, and plus and minus one standard deviation of the mean response, to the velocity step stimulus are plotted. As described in the last chapter each trial lasted about 4 seconds. The subject was given one second to fixate the approximate center of the field before the target motion was initiated. Thus in the figure, time zero corresponds to motion onset. The target moved at constant velocity for about 2 seconds, depending on velocity (motion had to be truncated when the edge of the slide just began to appear in the field). Notice that one standard deviation of the mean is only about 5% of the peak velocity of the response. Furthermore, during the acceleration phase of the response, the standard deviation shrinks to nearly 2% of the peak response. Fig. 4.6 was computed

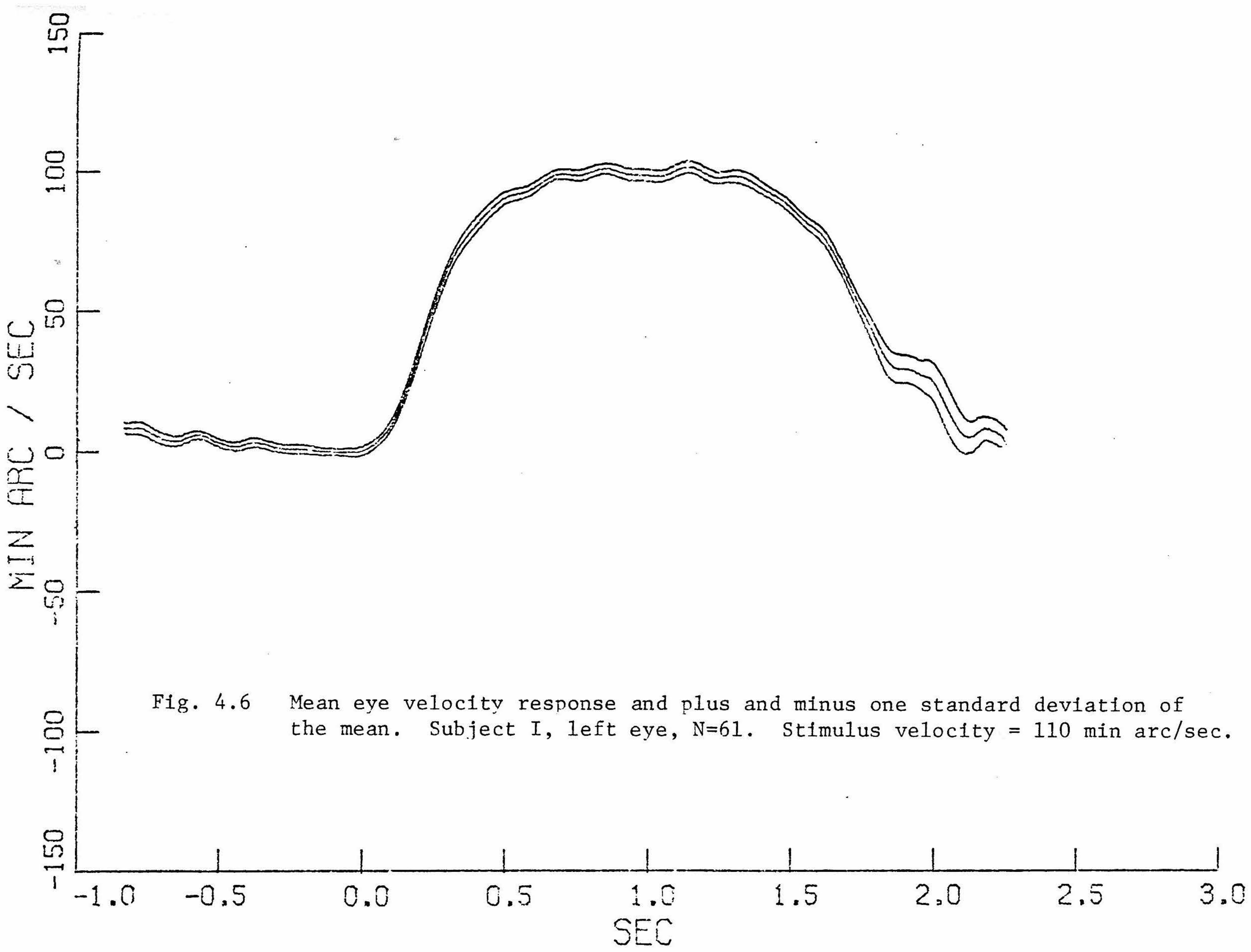


Fig. 4.6 Mean eye velocity response and plus and minus one standard deviation of the mean. Subject I, left eye, N=61. Stimulus velocity = 110 min arc/sec.

from 36 responses taken over several experimental sessions. Not only do these data indicate a high degree of pursuit system stationarity (time average), but they also provide evidence of the ergodicity (ensemble average) of the system.

The standard deviations of the mean responses show less response variability than indicated by the microstructure analysis for several reasons. One, the larger sample size has the effect of shrinking the standard deviation of the mean. Two, the averaging process is not as sensitive to response variations as the curve fitting procedure, since the latter technique was designed to accurately estimate response parameters on an individual basis. In any case, the repeatability of the smooth pursuit response is certainly better than shown in previous spot target studies in which a saccadic component, elicited by retinal position error, usually interrupted the smooth component of the eye movement at some variable time after onset of stimulus motion.

Now that we have evidence of the stationarity of the purusit system and have shown that velocity is the primary input to the system, with confidence we can begin to analyse the mean velocity-step responses for waveform characteristic, stimulus dependencies, and inter-subject variability as indicators of general pursuit system properties.

The acceleration phase of the step response is perhaps the most revealing in terms of pursuit transient characteristics. Mean responses to the three velocities used in this experiment are plotted in Fig. 4.7 a, b, c for Subject I and 4.7 d, e, f for Subject II. When the acceleration phases of the responses are closely compared, two features become obvious. First, the onset of acceleration for the 88.8 min arc/sec

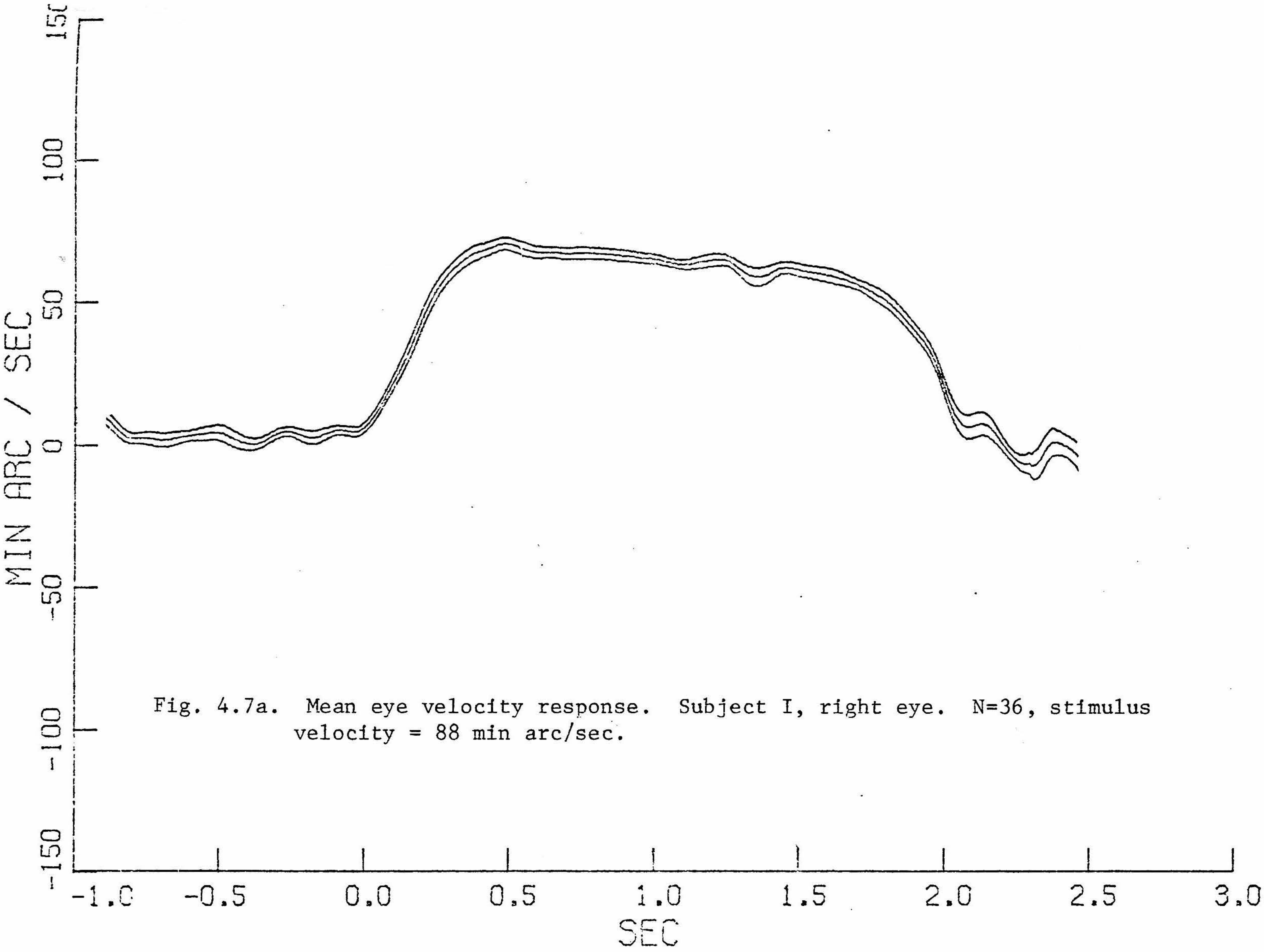


Fig. 4.7a. Mean eye velocity response. Subject I, right eye. N=36, stimulus velocity = 88 min arc/sec.

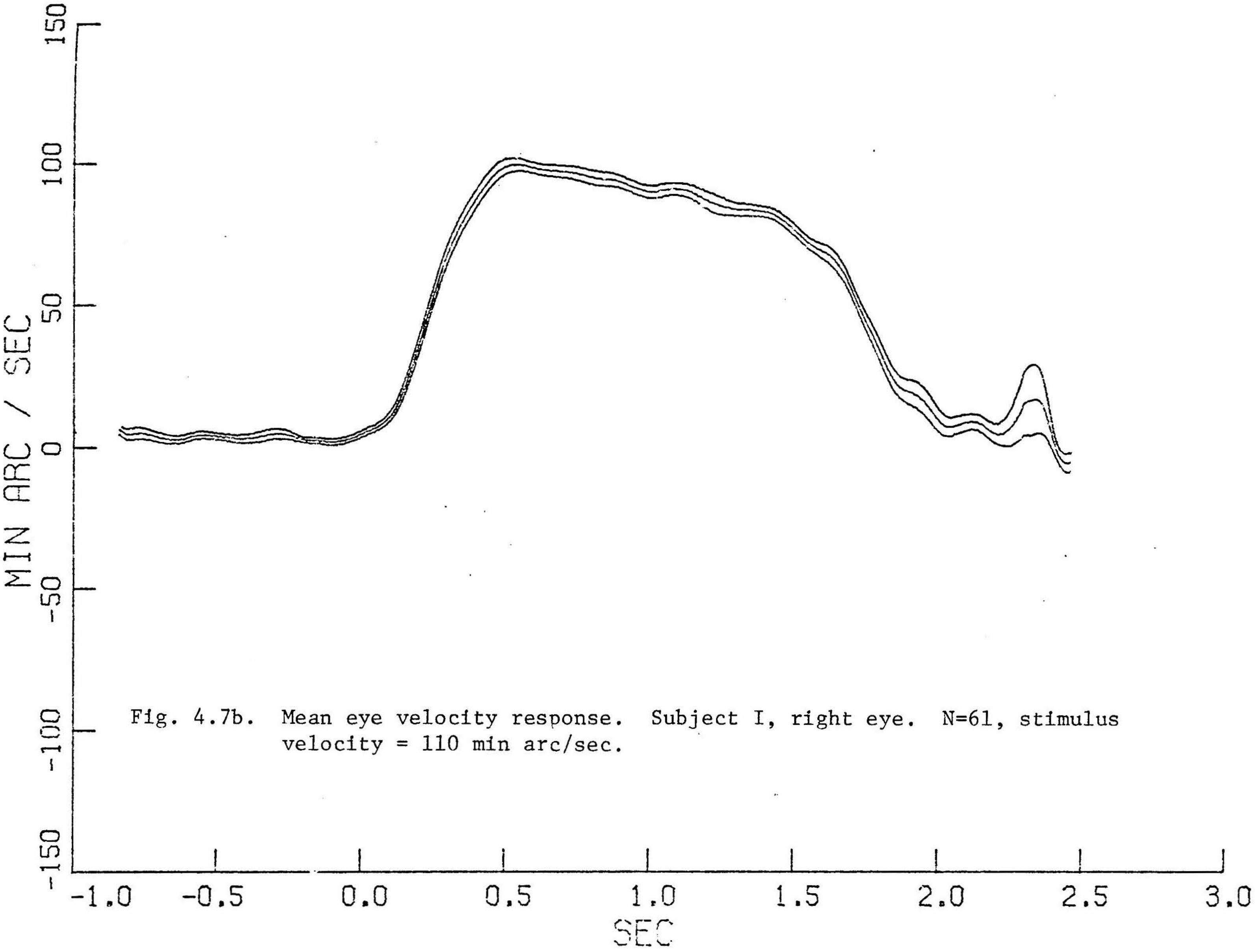


Fig. 4.7b. Mean eye velocity response. Subject I, right eye. N=61, stimulus velocity = 110 min arc/sec.

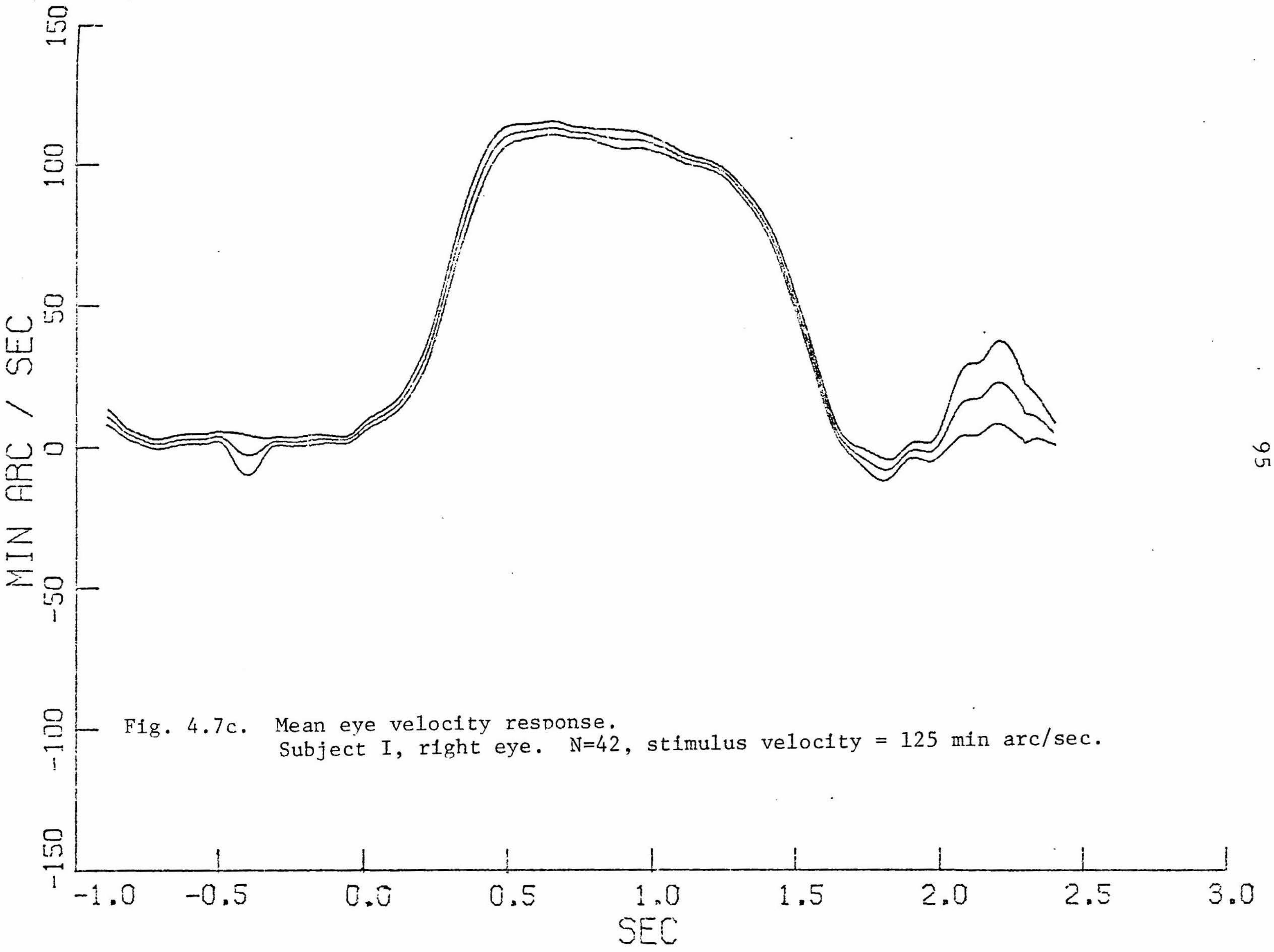


Fig. 4.7c. Mean eye velocity response.
Subject I, right eye. N=42, stimulus velocity = 125 min arc/sec.

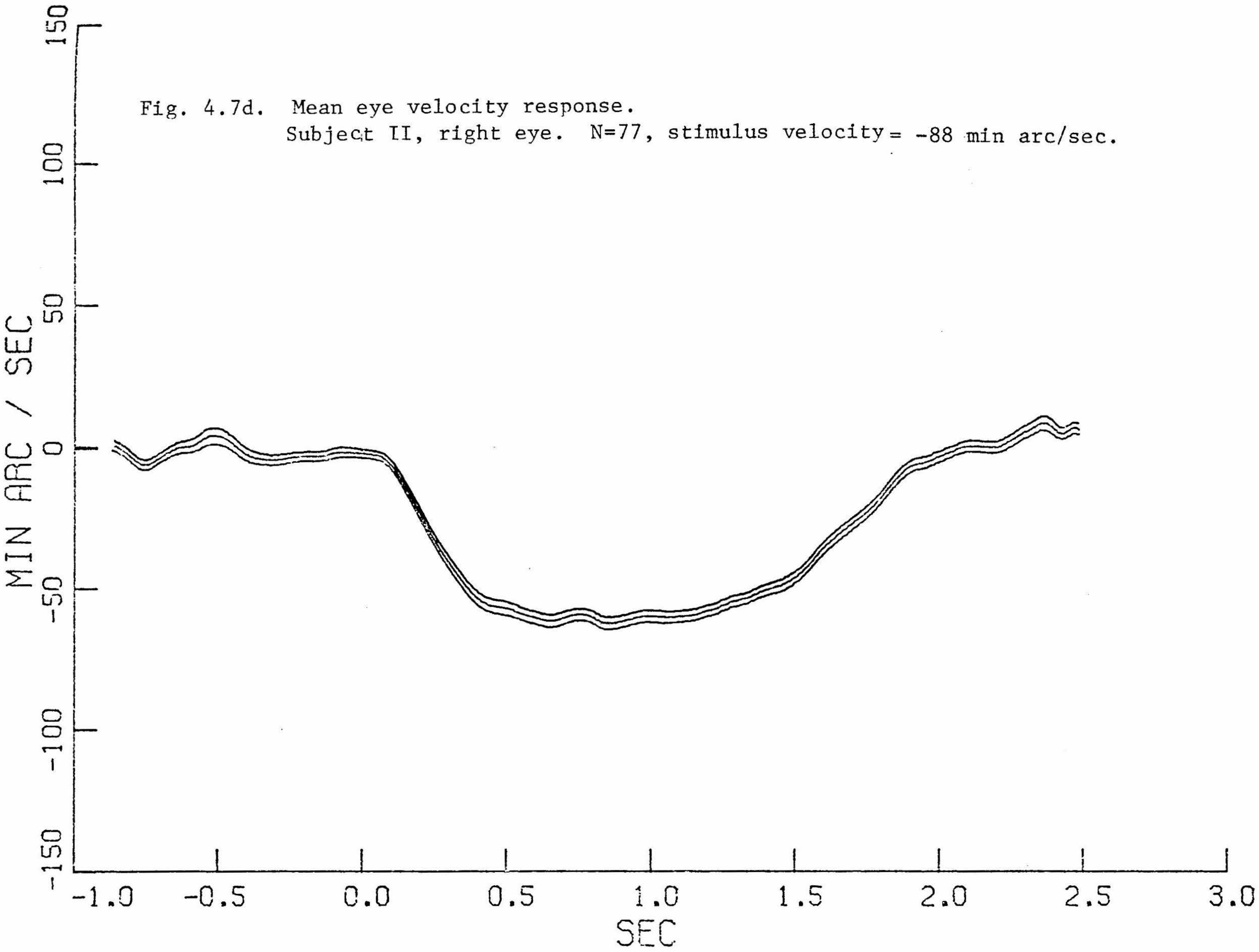


Fig. 4.7d. Mean eye velocity response.
Subject II, right eye. N=77, stimulus velocity = -88 min arc/sec.

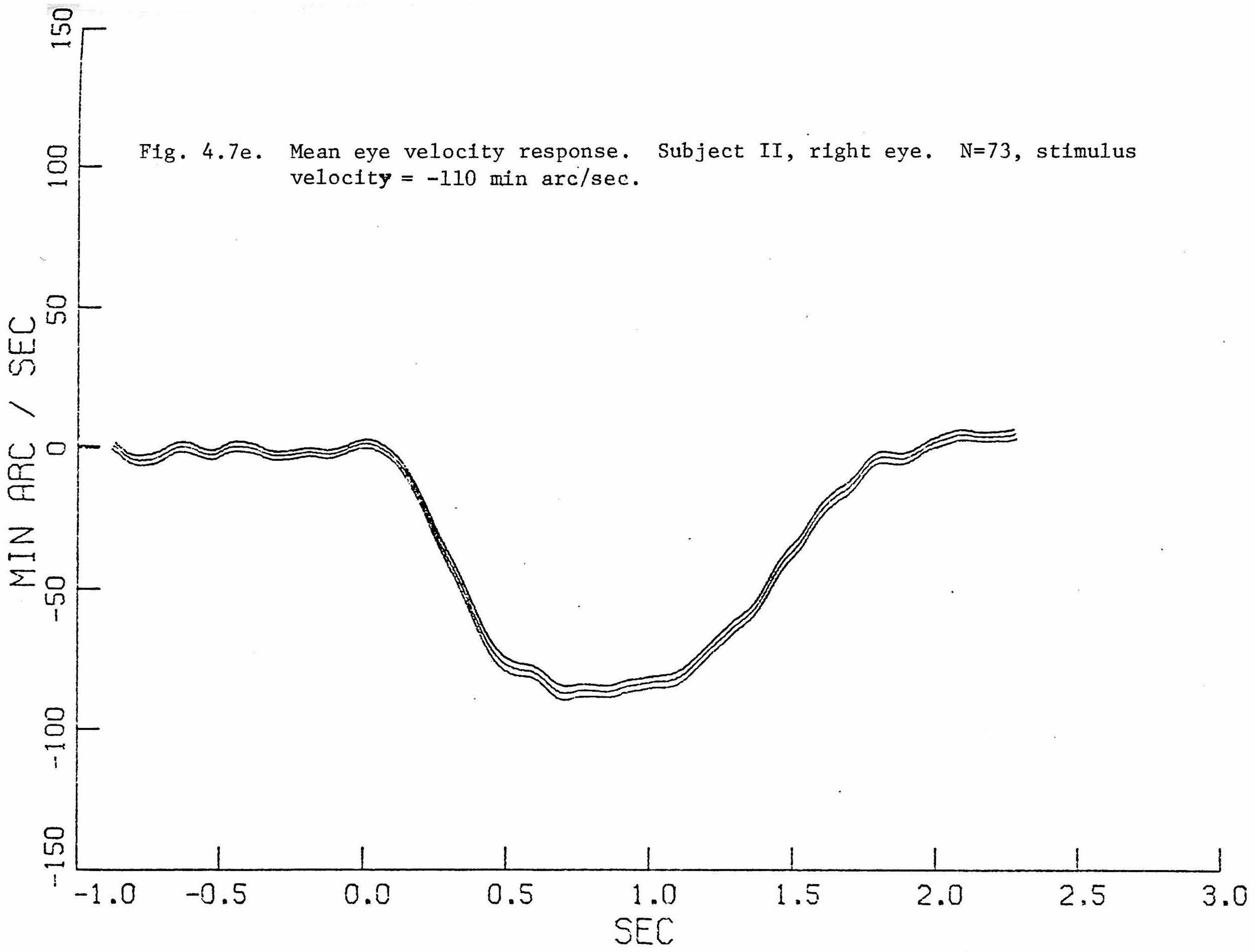


Fig. 4.7e. Mean eye velocity response. Subject II, right eye. N=73, stimulus velocity = -110 min arc/sec.

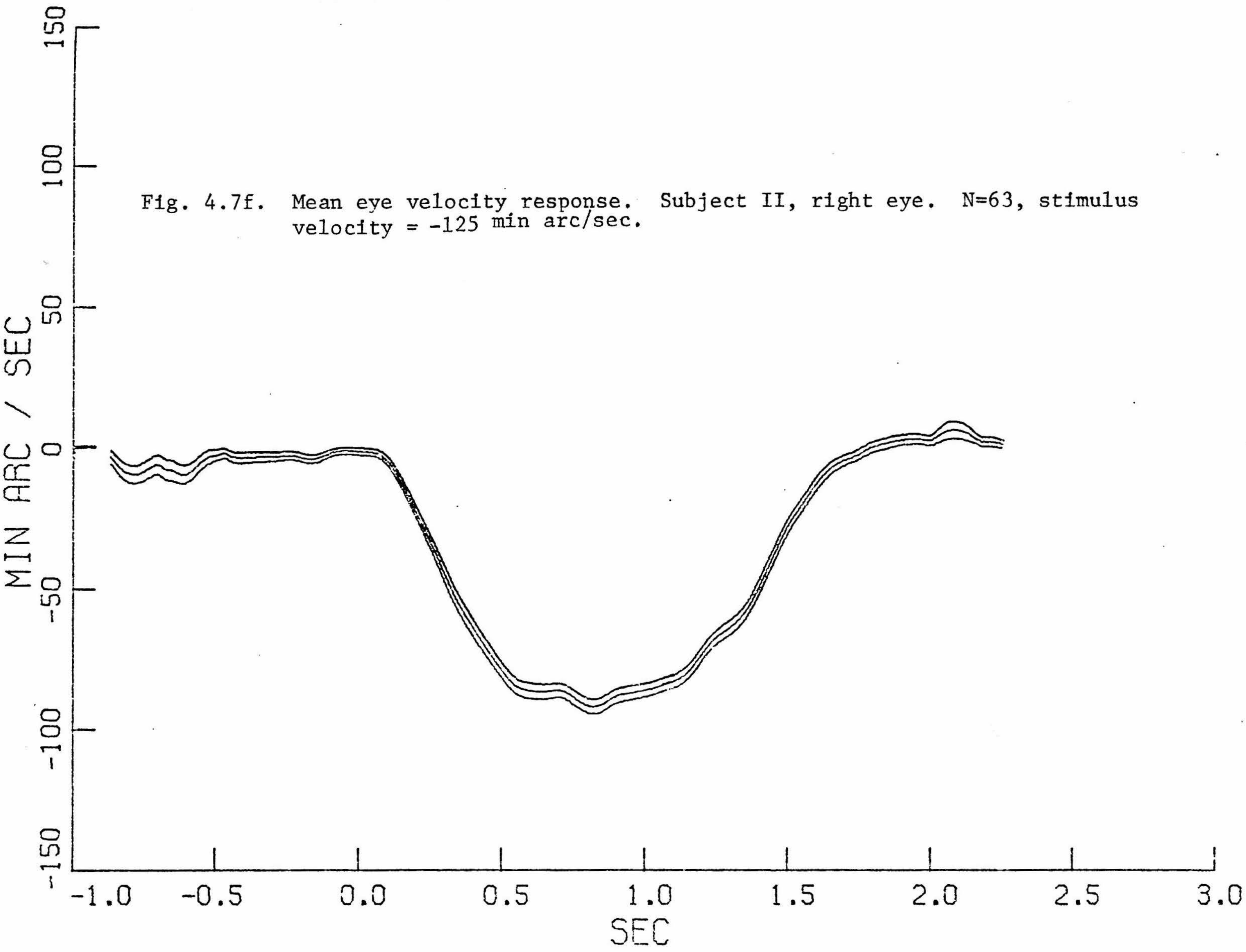


Fig. 4.7f. Mean eye velocity response. Subject II, right eye. N=63, stimulus velocity = -125 min arc/sec.

response (Fig. 4.7a) occurs nearly 100 msec earlier than for either the 110 min arc/sec or 125 min arc/sec responses (Fig. 4.7b, c). This latency difference is consistent among the responses to the three velocities for both eyes and for rightward and leftward movements. Two of the three subjects are similar in this respect.

The second acceleration phase feature that becomes obvious upon careful comparisons of the responses to the three input velocities is that the slope of the velocity change is very nearly the same in each case. Thus the final eye velocity value is determined in part by the duration of the acceleration phase of the response. This effect is better illustrated in a plot of the derivative of the velocity step response, the acceleration pulse response. Fig. 4.8 a, b, c (d, e, f) were generated by differentiating the mean velocity responses of Fig. 4.7. The peak acceleration values in Fig. 4.8 a, b, and c are about 100, 150, and 175 min arc/sec/sec. The peak values in Fig. 4.8 d, e, and f for Subject II are -100, -105, and -110. Although the amplitude of the pulse increases with input velocity, the relationship is certainly not linear. A close comparison of the acceleration pulses of Fig. 4.8 reveals that the change in amplitude is accompanied by changes in pulse shape and duration. The leading edge of the pulse remains relatively unchanged in shape for the three velocities, while the trailing edge moves forward in time and increases in slope of descent to zero acceleration. The overall effect of the changes in amplitude and shape is to increase the duration of the response pulse without substantially increasing its amplitude. Thus, the area under the acceleration pulse, i.e., the final eye velocity value, closely matches

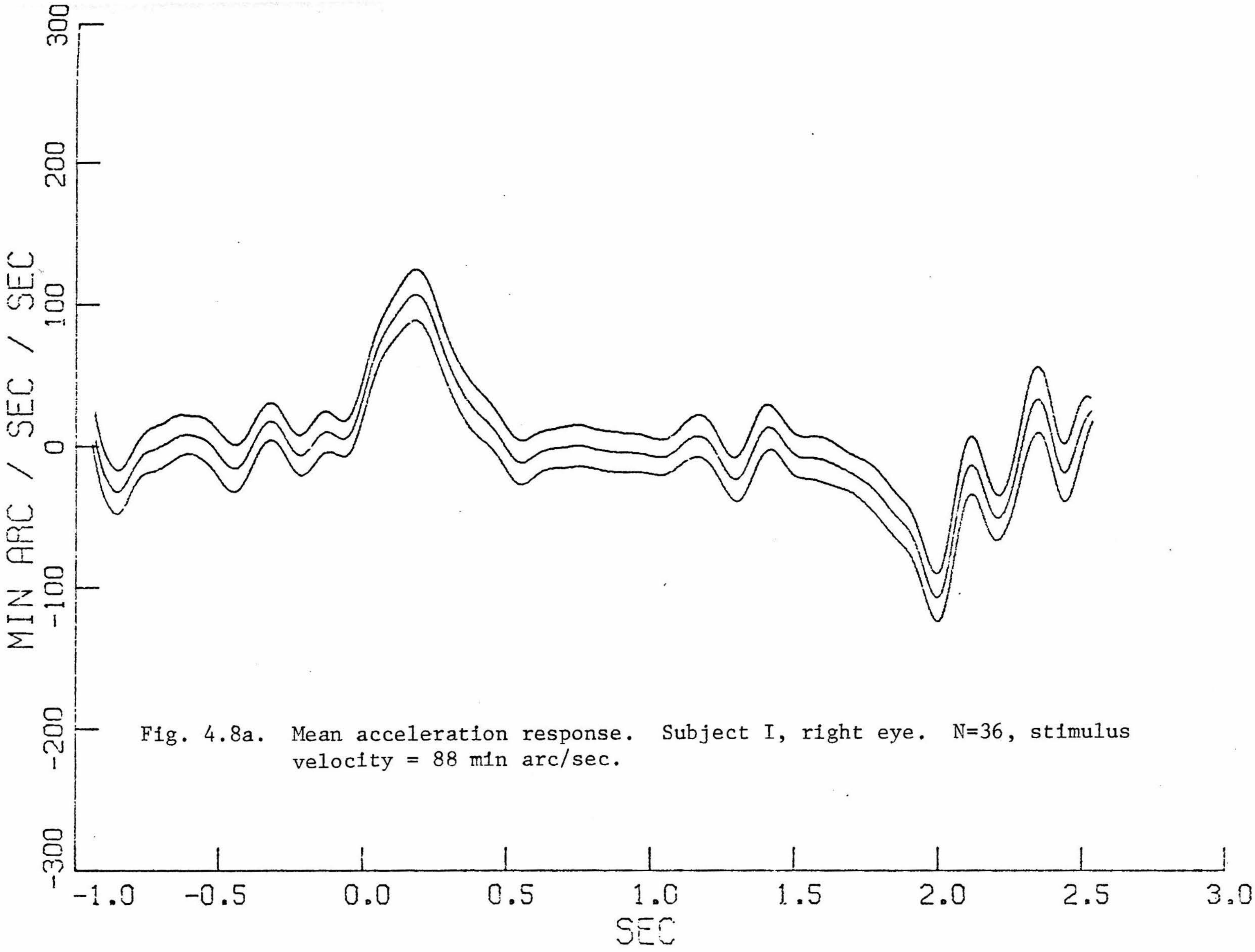
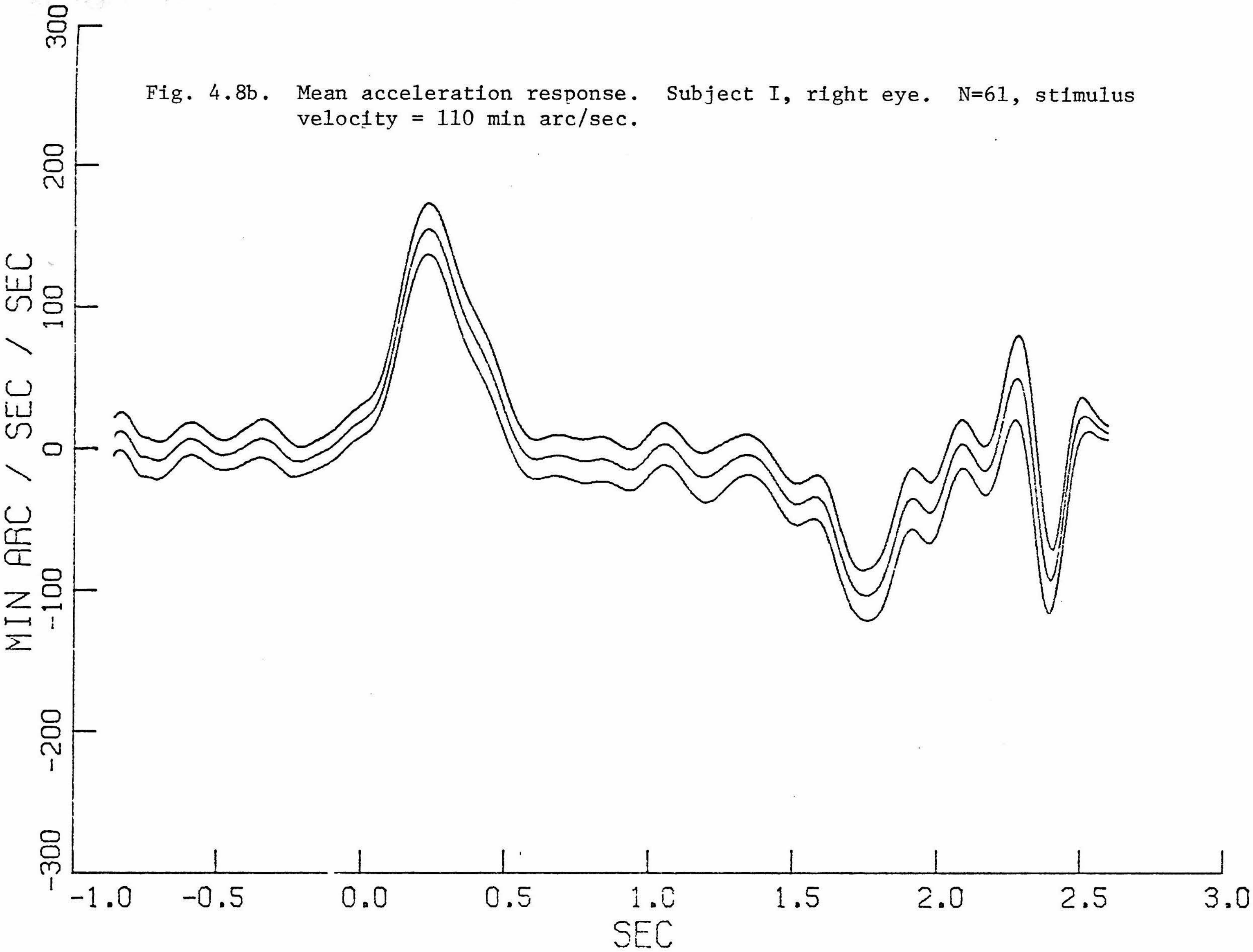


Fig. 4.8a. Mean acceleration response. Subject I, right eye. N=36, stimulus velocity = 88 min arc/sec.

Fig. 4.8b. Mean acceleration response. Subject I, right eye. N=61, stimulus velocity = 110 min arc/sec.



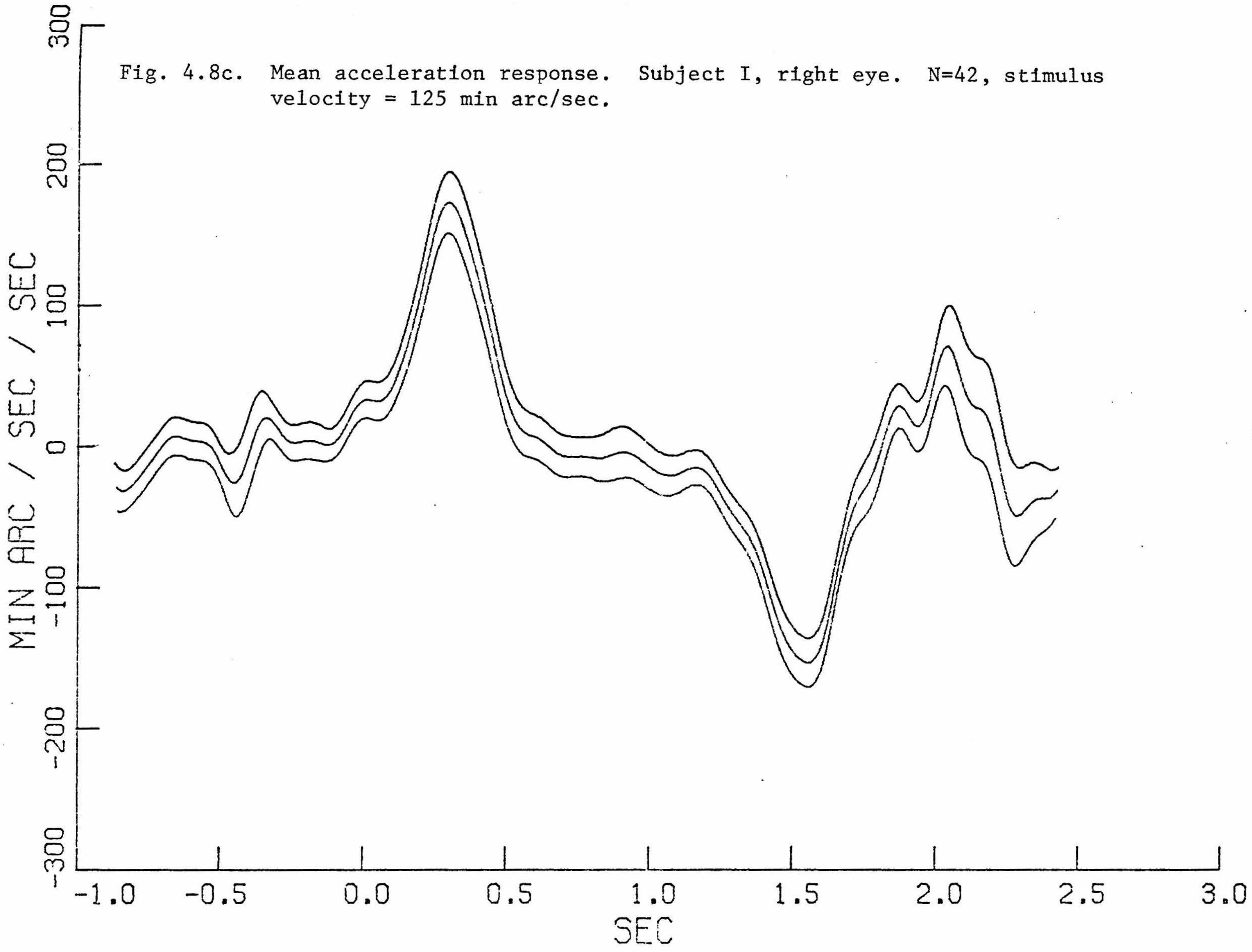


Fig. 4.8c. Mean acceleration response. Subject I, right eye. N=42, stimulus velocity = 125 min arc/sec.

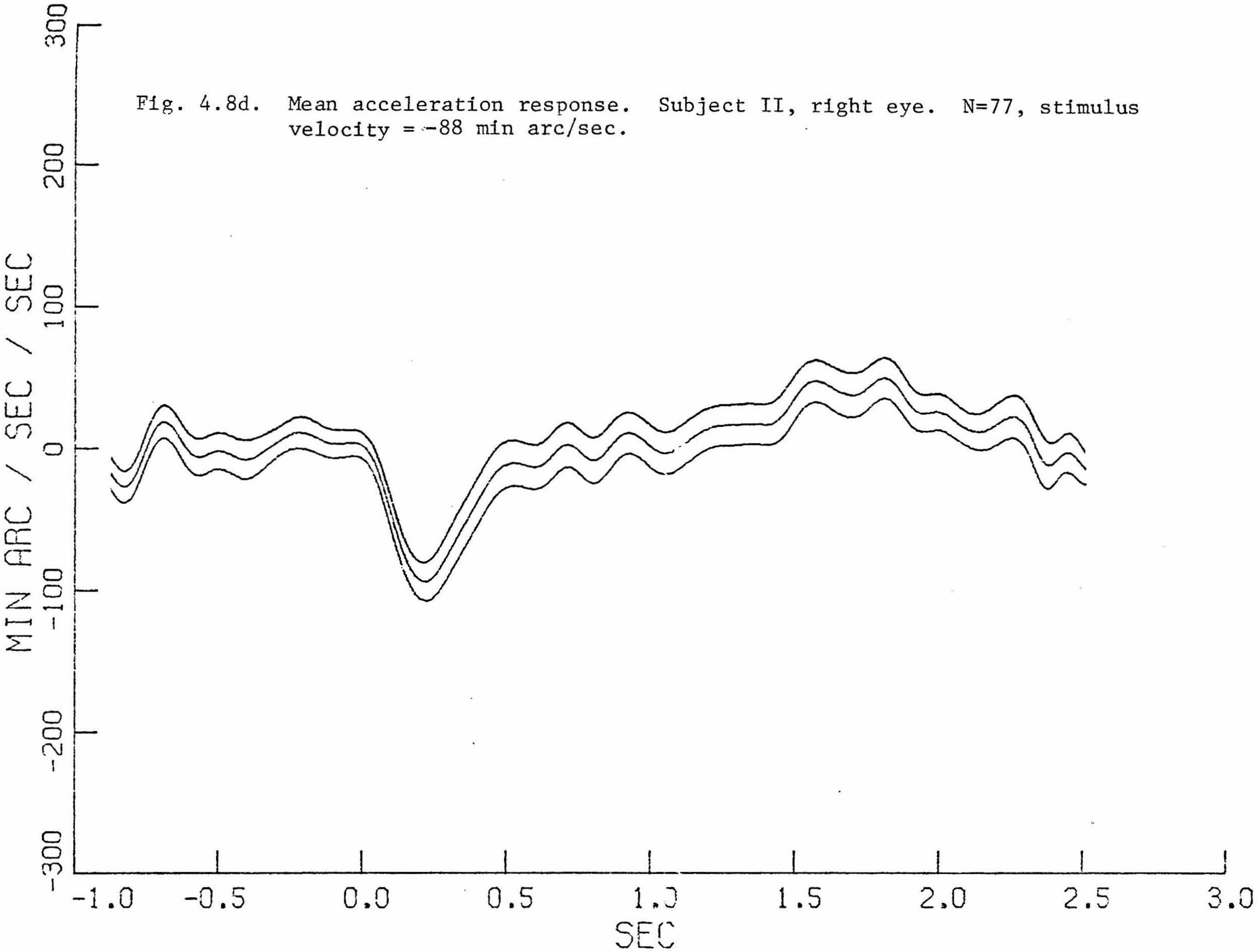


Fig. 4.8d. Mean acceleration response. Subject II, right eye. N=77, stimulus velocity = -88 min arc/sec.

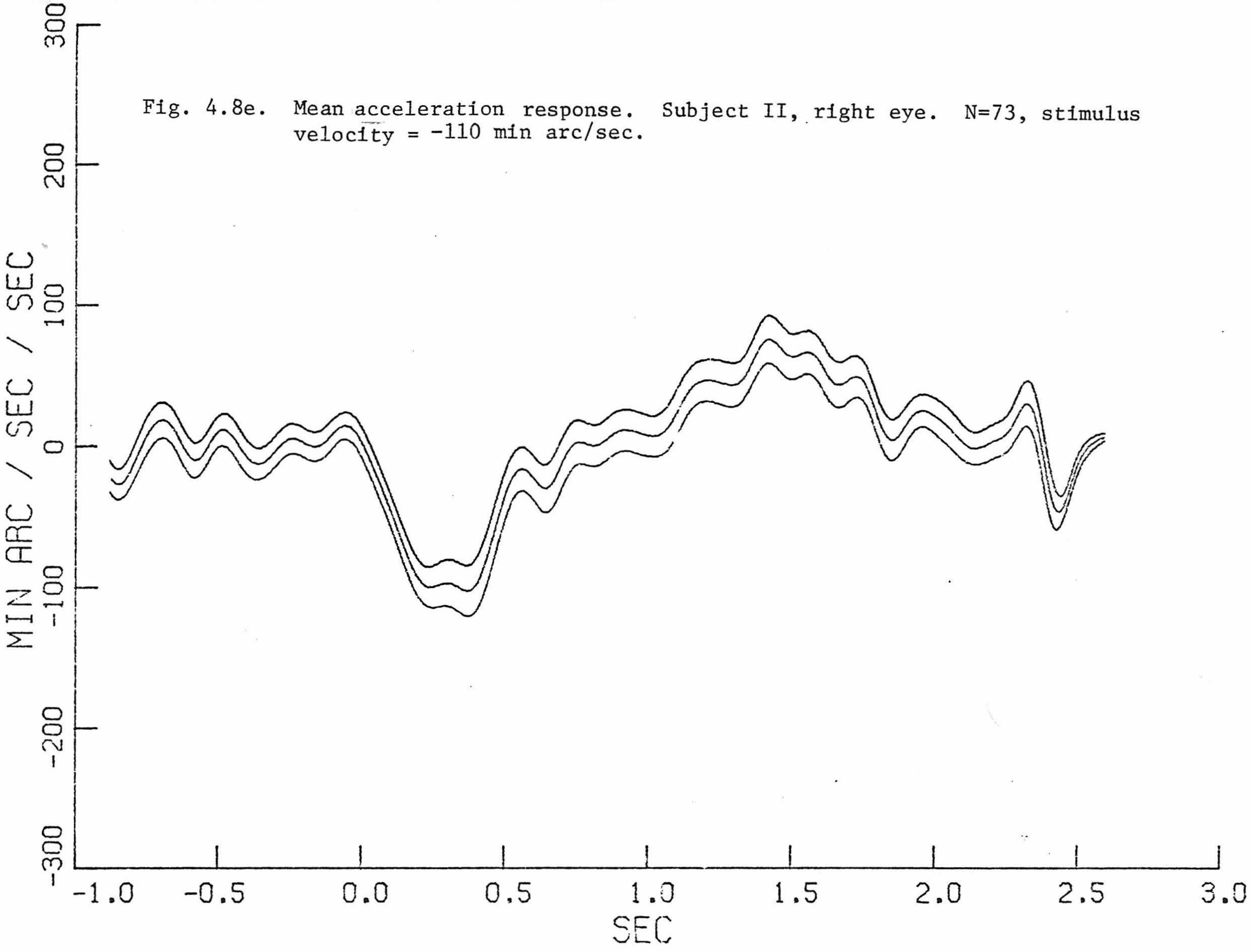


Fig. 4.8e. Mean acceleration response. Subject II, right eye. N=73, stimulus velocity = -110 min arc/sec.

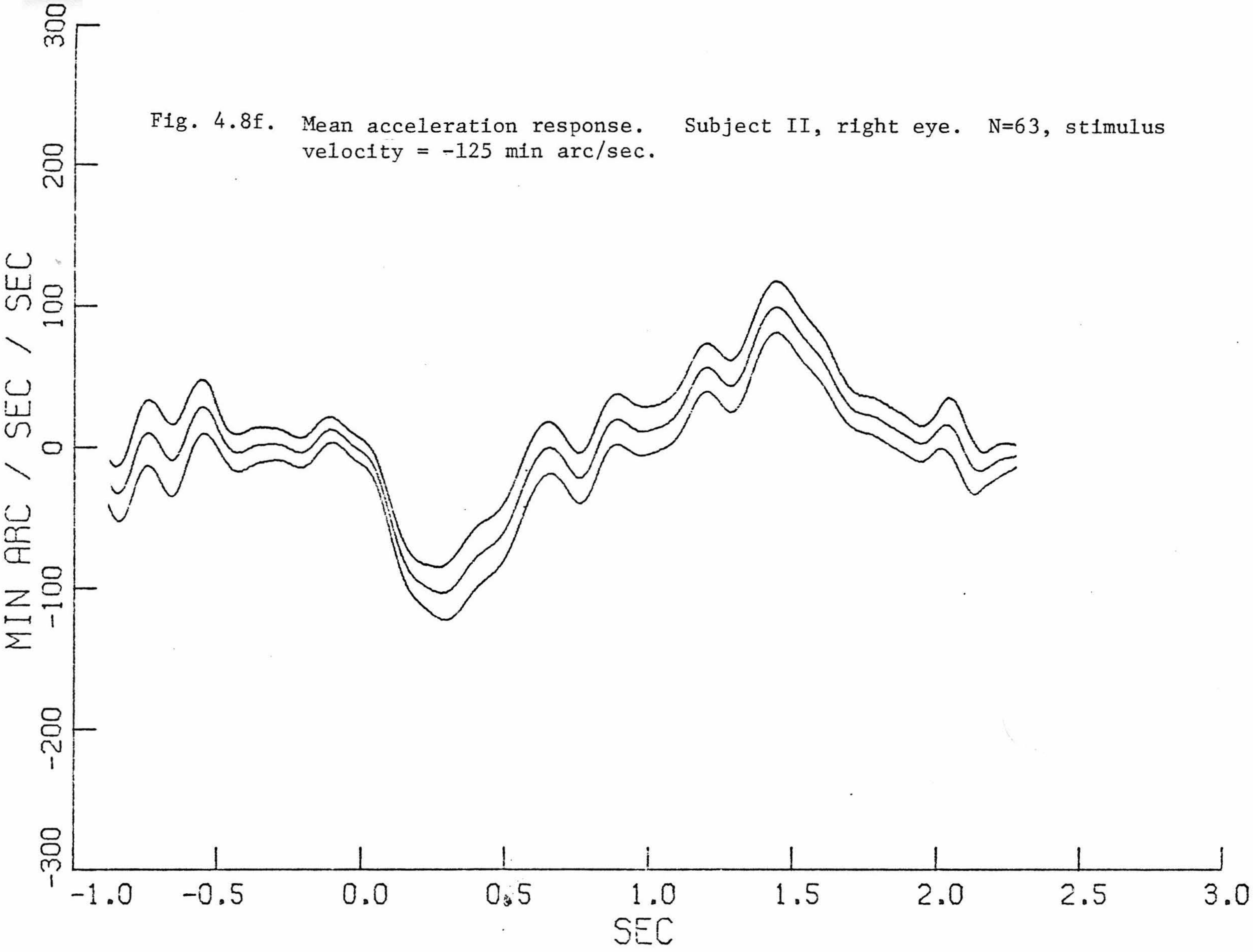


Fig. 4.8f. Mean acceleration response. Subject II, right eye. N=63, stimulus velocity = -125 min arc/sec.

the area under the stimulus acceleration pulse. If we had analyzed only the relationship between stimulus and eye velocity, the pursuit response would have appeared linear. However, by analyzing the transient properties of the velocity response, we have been able to show that the pursuit system processes input acceleration information in a nonlinear fashion.

Consider the above two features of the velocity step response in terms of the stimulus to which the oculomotor system is being asked to respond. In these experiments target spatial frequency was held constant at about 15 cpd, corresponding to a dot spacing of 4 min arc. Thus a 120 min arc/sec motion of the target would generate a 30 Hz temporal modulation of the light imaged on a stationary retinal receptive field. A temporal frequency of 30 Hz is well into the high frequency attenuation portion of the temporal modulation transfer function of the human visual system. The 90 min arc/sec velocity corresponds to a 20 Hz temporal modulation, to which the visual system is relatively more sensitive. It is reasonable, therefore, that some subjects would find the task of determining the initial direction of target motion easier for the lower temporal frequency stimulus. A shorter response latency might be the result. For the low velocity motion, movement of fewer cycles of the pattern across a retinal receptive field would be needed for a velocity calculation due to the increased sensitivity of the detection system. The subject dependency of the latency effect could be explained by variation in individual temporal MTF's.

The above discussion was based upon the assumption of a stationary retina. However, unless the retinal image is stabilized by some external optical or electronic projection technique, the continual motion of the visual axes during fixation produces a moving retinal image. Power spectral analyses of fixation eye movements (St. Cyr, 1969) depict a monotonic decrease in power ($\approx$ 28 db/decade) from about .5 Hz to 3. Hz. Thus the temporal modulation of the retinal image produced by target motion is accompanied by that produced by eye movements. At onset of target motion, the visual system must detect the stimulus temporal frequency signal within the temporal noise of a jiggling retinal image. Consider how such a noise component would affect the smooth tracking task in these experiments. First, the noise is uncorrelated with the stimulus signal since normal physiological factors (motoneuron spike discharges, release of neurotransmitter at motoneuron end-plates) are responsible for spontaneous fixation eye movements. Second, the frequency content of the signal and noise differ by nearly a log unit. Furthermore, the concentration of power at low frequencies in the noise makes this component of the retinal information signal a relatively strong factor in the detection task. However, since the noise is uncorrelated with the stimulus and the temporal visual sensitivity is greater at 20 Hz (90 min arc/sec target velocity) than at 30 Hz (125 min arc/sec), then the signal-to-noise ratio is better for the 20 Hz than for the 30 Hz tracking task. Thus the speculation that pursuit response latency is influenced by stimulus temporal frequency content is reasonable, even for a non-stationary retina.

The relationship between velocity amplitude and acceleration pulse duration should also be discussed in terms of the experimental regime, since the durations obtained in these experiments are more than twice the value determined by Robinson 1965 . In part, the larger acceleration times observed in these responses are due to the time spread effect of the low pass filter previously described. From plots of the stimulus acceleration signal produced by the same data analysis procedures used for the eye acceleration plots, the filtering effect is estimated to be about 100 msec. The trade-off for such substantial time smearing came in the form of greatly improved signal to noise ratio in the averaged responses. Without the low pass filtering operation, the acceleration responses would have been nearly indistinguishable from noise for the small number of responses included in the averages. Furthermore, the symmetry of the time filtering allows comparison between peak response values to be relatively immune from the time smearing effect. In the following pulse duration discussion, 100 msec was subtracted from all duration values.

In Fig. 4.9 acceleration pulse duration, determined from the acceleration responses of the three subjects, has been plotted as a function of target velocity (temporal frequency). The mean values and their standard deviations depict pursuit integration time as a monotonically increasing function of target velocity. This basic characteristic of the pursuit system transient response was observed by Robinson (1964, 1965). As discussed in Section 3.2.4, he observed that larger target velocity changes were met with proportionally less excess increase in muscle tension, a neuromuscular property which

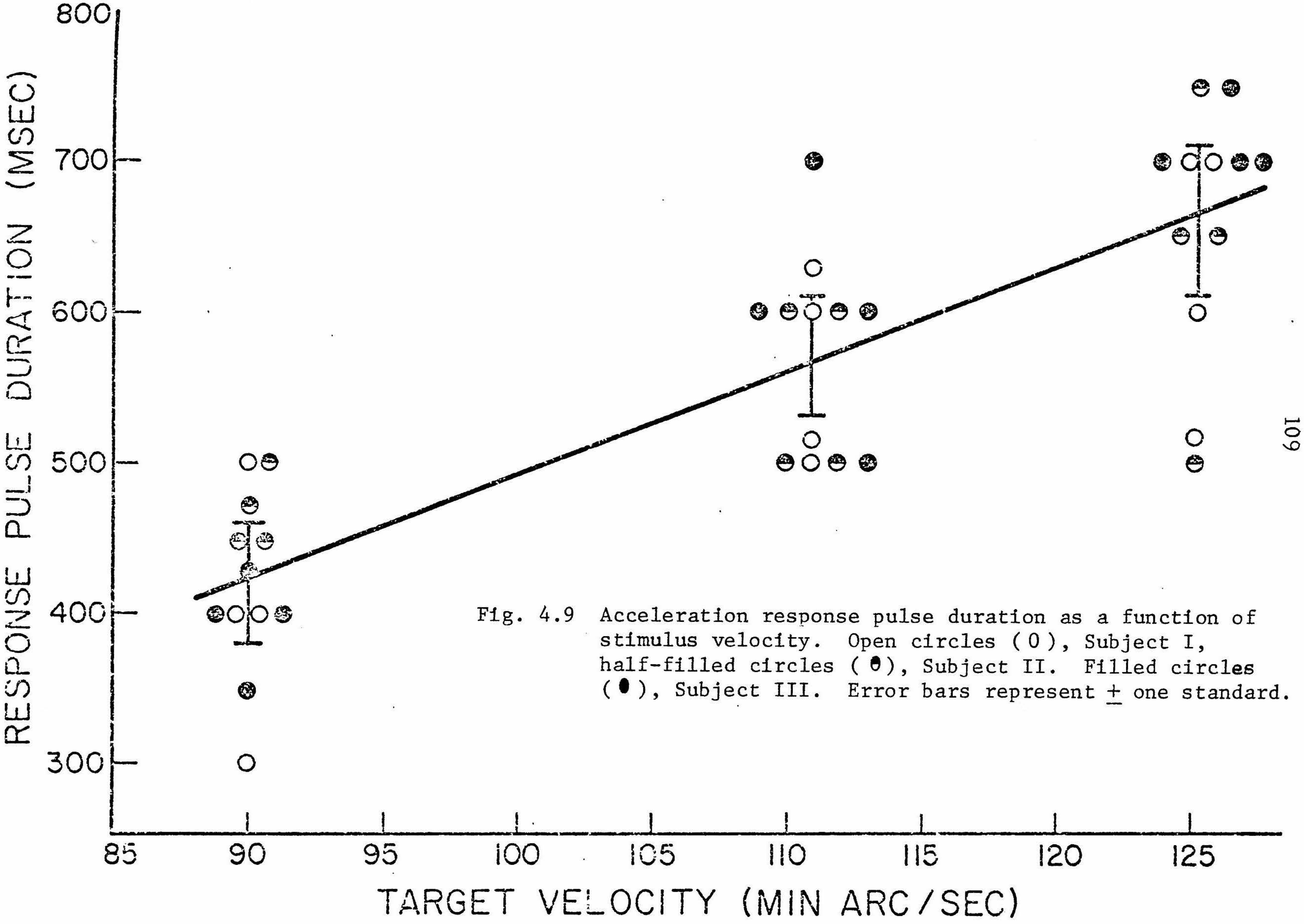


Fig. 4.9 Acceleration response pulse duration as a function of stimulus velocity. Open circles (0), Subject I, half-filled circles (◐), Subject II. Filled circles (●), Subject III. Error bars represent ± one standard.

extends the period of eye acceleration as the target acceleration pulse increases in size. However, as shown in the present results, a spatially periodic target increases the absolute eye acceleration pulse duration by about two fold. Furthermore, the velocities used in the Robinson study were about five times the value used here. As discussed in previous paragraphs, the use of a spatially periodic target adds a perceptual detection component to the oculomotor tracking task. The near threshold temporal frequency information which constitutes the stimulus for smooth pursuit must be sorted out from the noise level generated by spontaneous retinal image motion. It is possible that the increased integration time of the pursuit system in this type of tracking task and the variation of acceleration duration are due, at least in part, to the signal-to-noise and temporal frequency considerations which we have discussed. The loss of a position component in the stimulus, and intersubject variability may also have contributed to the variance of these results compared to previously reported data.

One may notice in the plots of mean velocity step responses that the offset of the response is in some cases slower than the onset. For a true step-on and step-off velocity input experiment, such an onset-offset asymmetry would be indicative of a nonlinear system. However, in the experiments reported here, offset of target motion was not equivalent to onset, since during the response the target motion carried eye position to the edge of the field aperture. Thus, there were two stimuli for eye velocity offset, cessation of target motion and encroachment of the aperture edges into the foveal fixation area. However, for the 88 min arc/sec stimulus, target

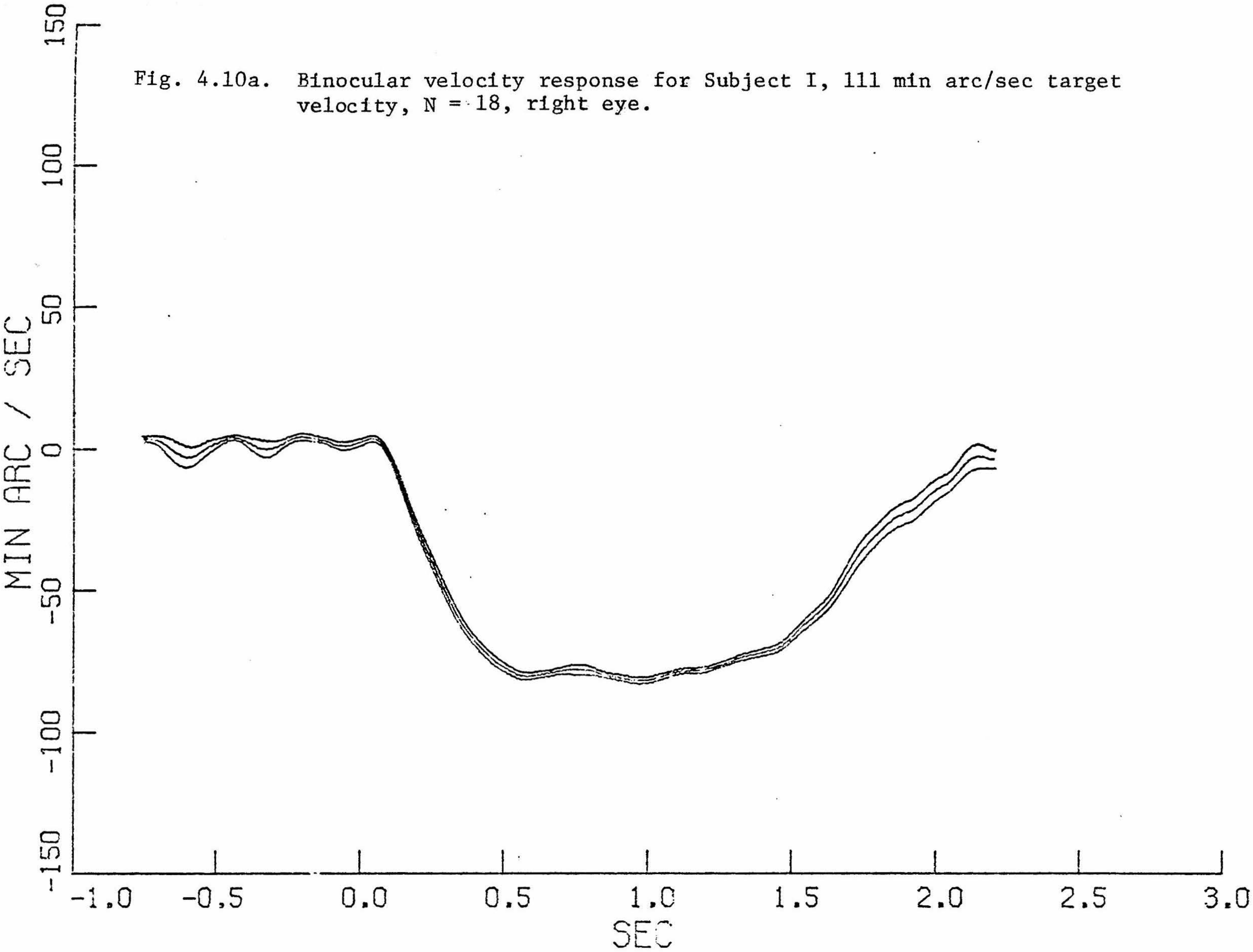


Fig. 4.10a. Binocular velocity response for Subject I, 111 min arc/sec target velocity, N = 18, right eye.

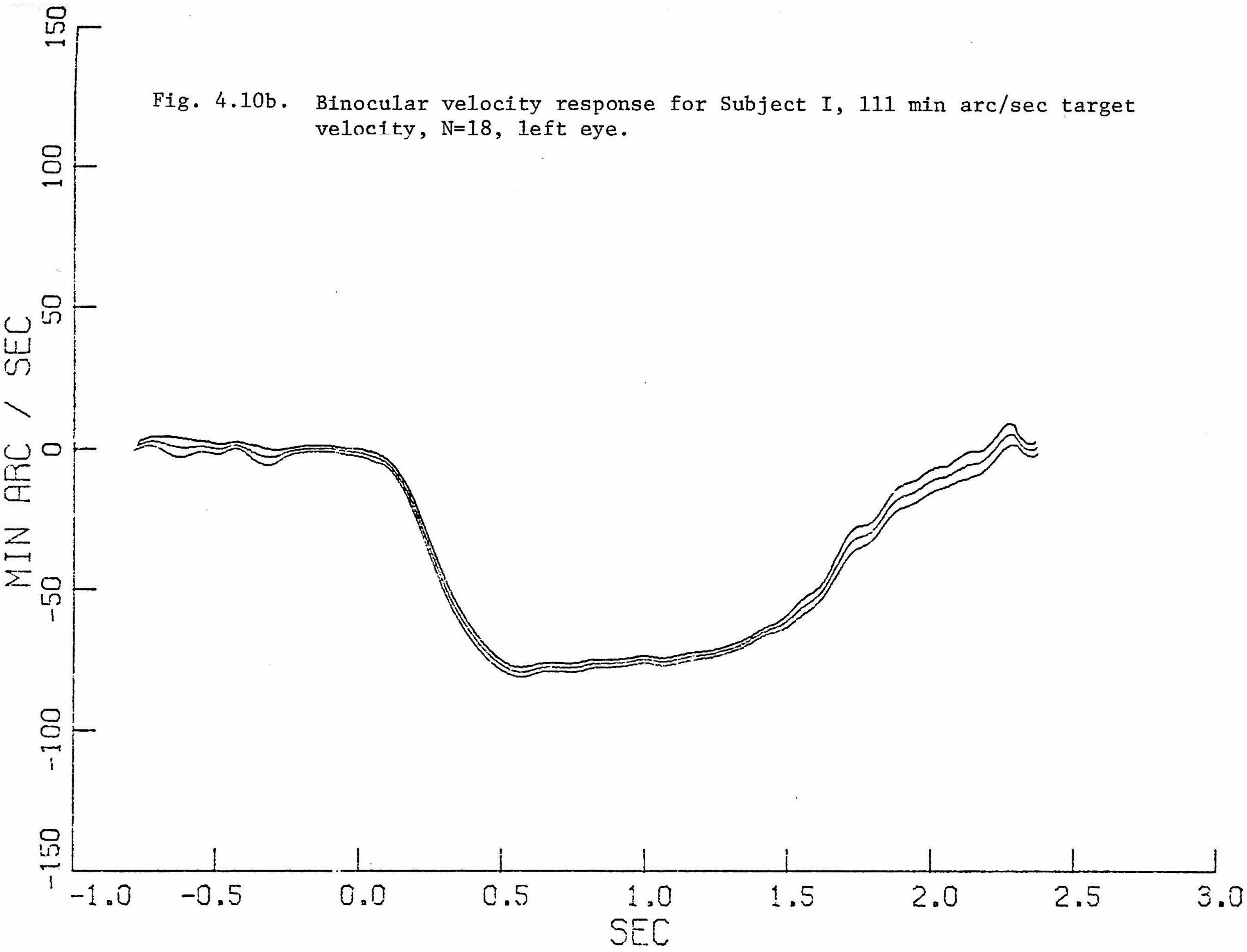
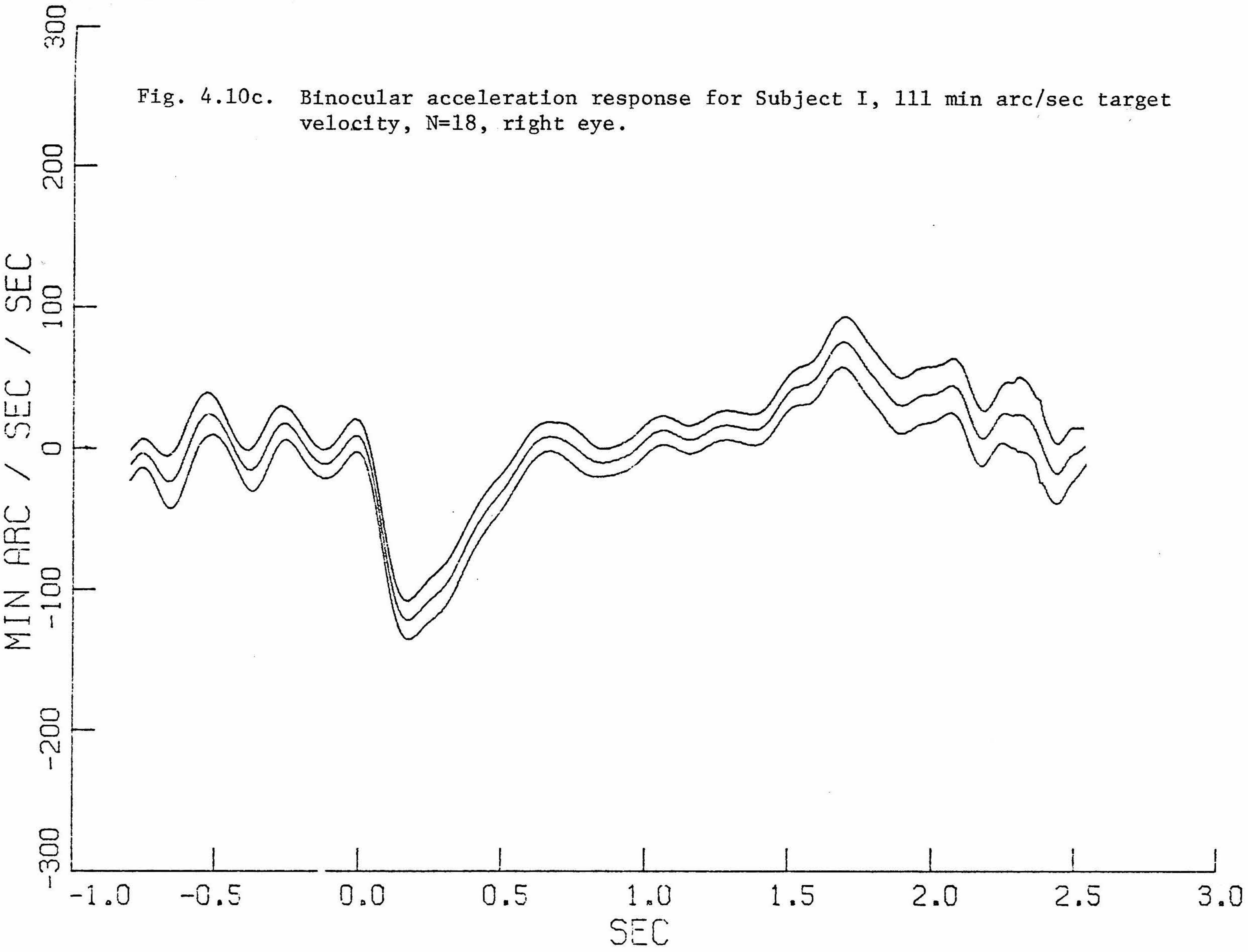


Fig. 4.10b. Binocular velocity response for Subject I, 111 min arc/sec target velocity, N=18, left eye.

Fig. 4.10c. Binocular acceleration response for Subject I, 111 min arc/sec target velocity, N=18, right eye.



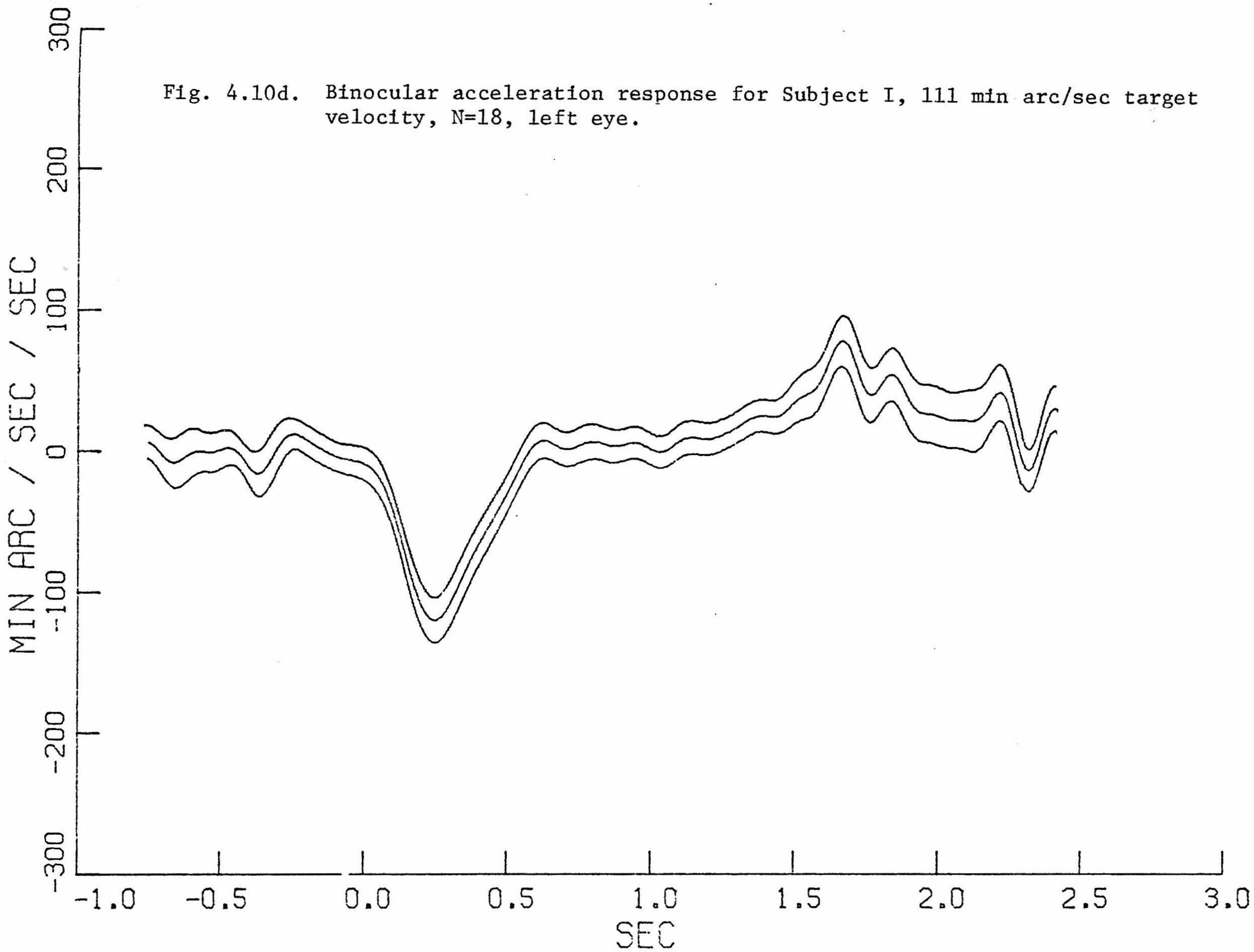


Fig. 4.10d. Binocular acceleration response for Subject I, 111 min arc/sec target velocity, N=18, left eye.

motion always ceased before the subject's gaze reached the edge of the field. The velocity responses for this stimulus also show non-equivalent onset and offset waveform (Fig. 4.7 and 4.8). In most cases the lower velocity responses show a more gradual fall off of the velocity step than the higher velocity responses, indicating that cessation of stimulus motion is a stronger stimulus for turning off smooth pursuit than is the position information constituting the aperture edge.

Although the averaged responses are at most an estimation of the actual pursuit response to a velocity step, we have been able to deduce some important system properties from this type of analysis. The comparison of more subtle characteristics, such as interocular differences, variability in latency of onset, and stimulus-eye velocity coordination were assessed by the micro-structure analysis previously discussed. However, individual mean responses for each eye were nevertheless computed and show (Fig. 4.10) that the two eyes on the average exhibit equivalent responses. Acceleration pulse amplitudes and durations are very similar in the two eyes. One interocular difference that shows up consistantly for Subject I can be observed in Fig. 4.10. Notice that the steady velocity of the leading eye (right eye for rightward motion, left eye for leftward motion) seems to gradually fall off during the velocity step while the other eye maintains a relatively constant velocity. Subject III also exhibited an interocular asymmetry. This subject's velocity responses were consistant in showing a longer latency for the leading eye. Furthermore, the position responses of the left eye of Subject III were not as smooth or as large as those of the right eye. This subject also showed a strong direction preference for rightward motion. These effects may be related to the nasal-temporal saccadic velocity difference noted by Robinson (1969). Again this binocular difference seems to be a subject dependent phenomenon, and no general conclusions can be drawn on that basis. However, the data from two of the three subjects show a surprising degree of binocular coordination in the average responses. The microstructure analysis of individual responses gave similar results.

In summary, three basic properties of the pursuit system, which have not been observed before, were revealed in the velocity step experiments and associated averaging analysis. i) A pure velocity input to the system elicits primarily a pure smooth pursuit eye movement, an observation supportive of the hypothesis of a velocity-sensitive pursuit system. ii) The system exhibits a fair degree of stationarity as it responds to a velocity step input. iii) A variation in amplitude of the velocity change input to the system is met with a corresponding change in amplitude, shape and duration of the acceleration pulse imparted to the globe. The latter observation cannot be fully explained by Robinson's (1965) finding of less excess increase in muscle tension for larger velocity changes, since the integration times reported here are nearly three times the values reported for a single spot target. In the present experiments, the integration time of the system includes both neuromuscular processes and integraion of the spatio-temporal properties of the visual percept generated by motion of the spatially periodic target.

4.5 Double Velocity Step Data Analysis and Results

The double step velocity experiments were undertaken with the idea that an estimation of some second order interactions in pursuit eye movements could be obtained upon comparison to single step data.

The experiments were therefore structured so that the data processing procedures developed for the single step experiments could be applied to the double step raw data. Any differences observed between the results of the two experiments could thus be attributed to real pursuit interactions, rather than data analysis methodology. It was determined by a few preliminary attempts that a micro-structure analysis of the individual double step responses would not be sufficiently productive to warrant the computing time that would be involved in fitting an eight-parameter curve to the eye movement. The preliminary attempts yielded fitted curves with large residuals and associated parameters with large standard errors. Only the averaged response analysis was performed on the double-step data, since probabilistic relations between past input and present pursuit response were of particular interest in this case.

4.5.1 Analysis

Following removal of saccades, the raw position signals were low pass filtered to suppress eye movement monitor noise and quantization noise. The next step was to compute the filtered first and second derivatives of the smoothed position signal so that velocity and acceleration responses to equivalent input motion could be averaged and associated standard deviations computed. The resulting mean double step velocity responses were then analyzed for their departure from the superposition response (sum of two single pulse responses separated in time by the interpulse interval). (In the following, the word "pulse" will refer to the acceleration pulse associated with each step change in stimulus or eye velocity since neither stimulus nor response waveforms can be considered a true impulse.) Evidence of this form of pursuit non-linearity might be manifested in any of the following response characteristics, i. Output pulse separation varies as a function of the time between input pulses. This type of interaction would suggest that the latency of the response to the second pulse is affected by the presence of the first pulse. The response to the first pulse may be still propagating through the system at the time of the second pulse, thus, inhibiting the second pulse response. If the input pulse separation is small, the latency to the second pulse may be reduced by some kind of neuromuscular facilitation indicating augmentation of the second response by residual antagonist inhibition from the first response. ii. Amplitude of the second response varies as a function of pulse separation. Similar types of interactions as described in (i) would affect the amplitude of the response to the second pulse, depending on the activity (inhibiting and facilitating) in the system remaining from the response to the first pulse. iii. Amplitude of the first pulse is a function of pulse separation. It is conceivable that for very small interpulse intervals (so that two pulses are delivered with the response latency time after the first pulse) the response to the first pulse could be partially or completely suppressed by the presence of the second pulse. The system may preferentially respond to its most recent input if the response to the previous pulse has not been completely programmed.

In order to contain the data space of the double step experiments within attainable bounds, the initial target velocity was kept constant for all trials. Thus the size of the initial acceleration pulse was constant. The independent variable of interest was interpulse interval. Four values of this variable, believed to span the response capabilities of the pursuit system, were used (500, 350, 250, 150 msec). The subject was prevented from anticipating either pulse by the random ordering of the direction of the initial target motion and by including a few negative acceleration pulses (velocity decreased after the interpulse interval rather than increasing). This data space allowed detailed analysis of the transient characteristics of the pursuit double velocity step response while keeping experiment length to manageable proportions. (The advantage of an input motion which stimulates the system with all possible pulse combinations now becomes clear.)

4.5.2 Double Step Response Results and Discussion

The double velocity step experiments were designed to test the temporal interactions within the pursuit system which result from velocity changes in the input target motion. Since we are primarily interested in the transient response characteristics of the system, the following discussion of results will again be structured in terms of acceleration. The analysis of pursuit transient properties with acceleration pulse stimuli allows the formulation of results and conclusions in engineering analysis terms. Evidence of nonlinearities is easily obtained from results of double pulse experiments, when the system responses are compared with the theoretical superposition response, generated by the linear addition of two single pulse responses separated in time by the interpulse interval.

A set of responses for one subject to a pair of positive pulses is plotted in Fig. 4.11. The stimulus acceleration signals for each response plot are also included in the Figure. The mean acceleration plots exhibit larger standard deviations than shown in the single pulse

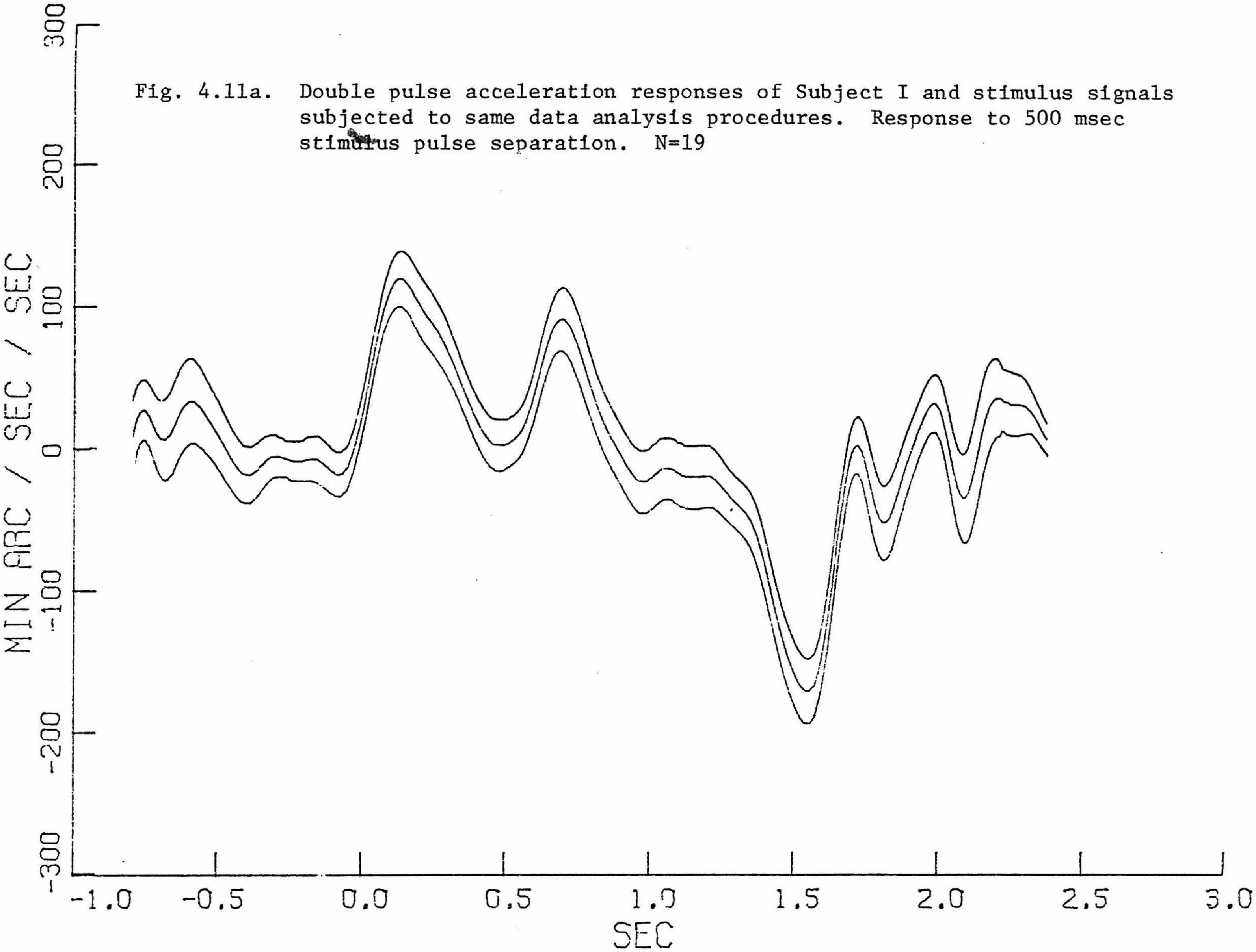


Fig. 4.11a. Double pulse acceleration responses of Subject I and stimulus signals subjected to same data analysis procedures. Response to 500 msec stimulus pulse separation. N=19

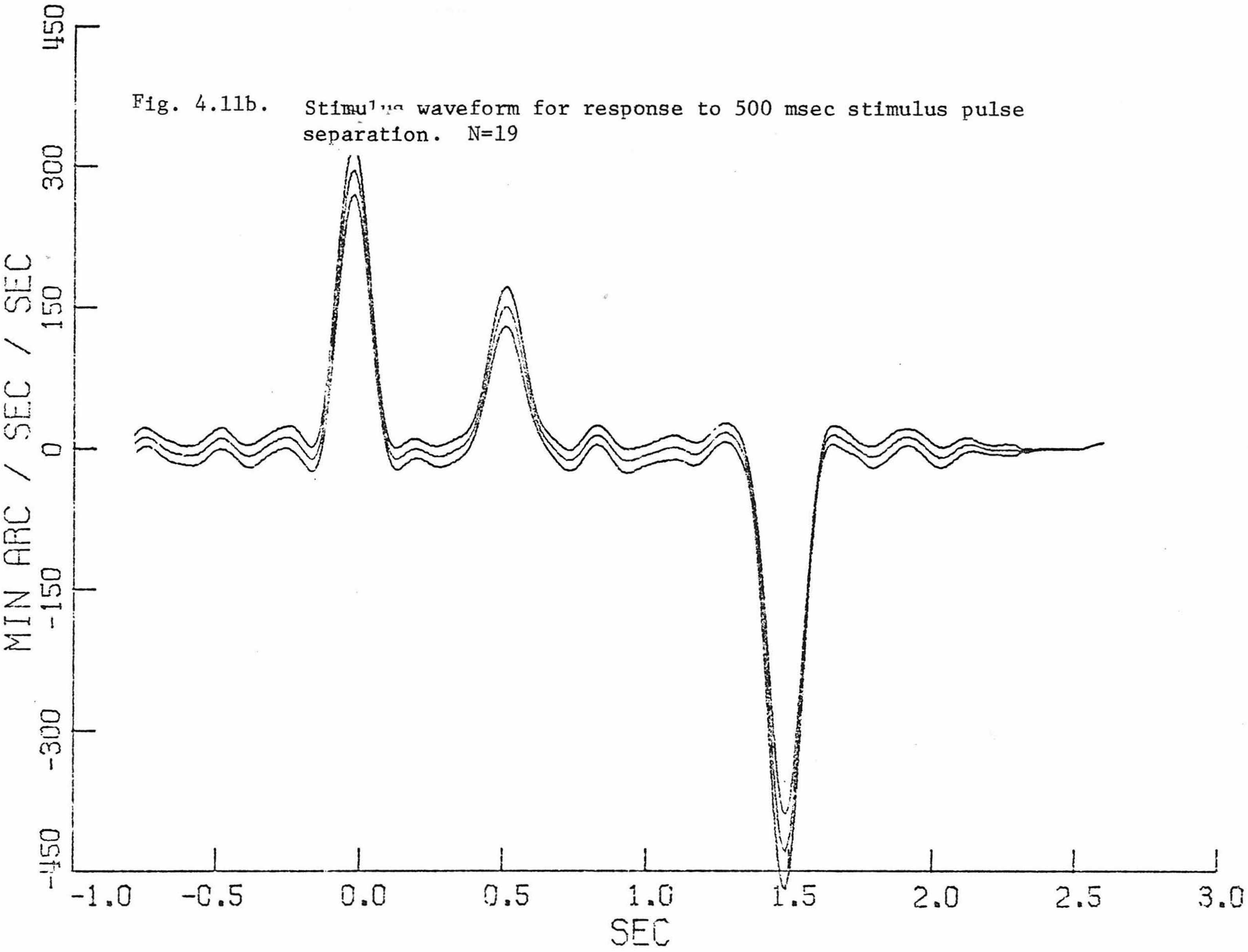


Fig. 4.11b. Stimulus waveform for response to 500 msec stimulus pulse separation. N=19

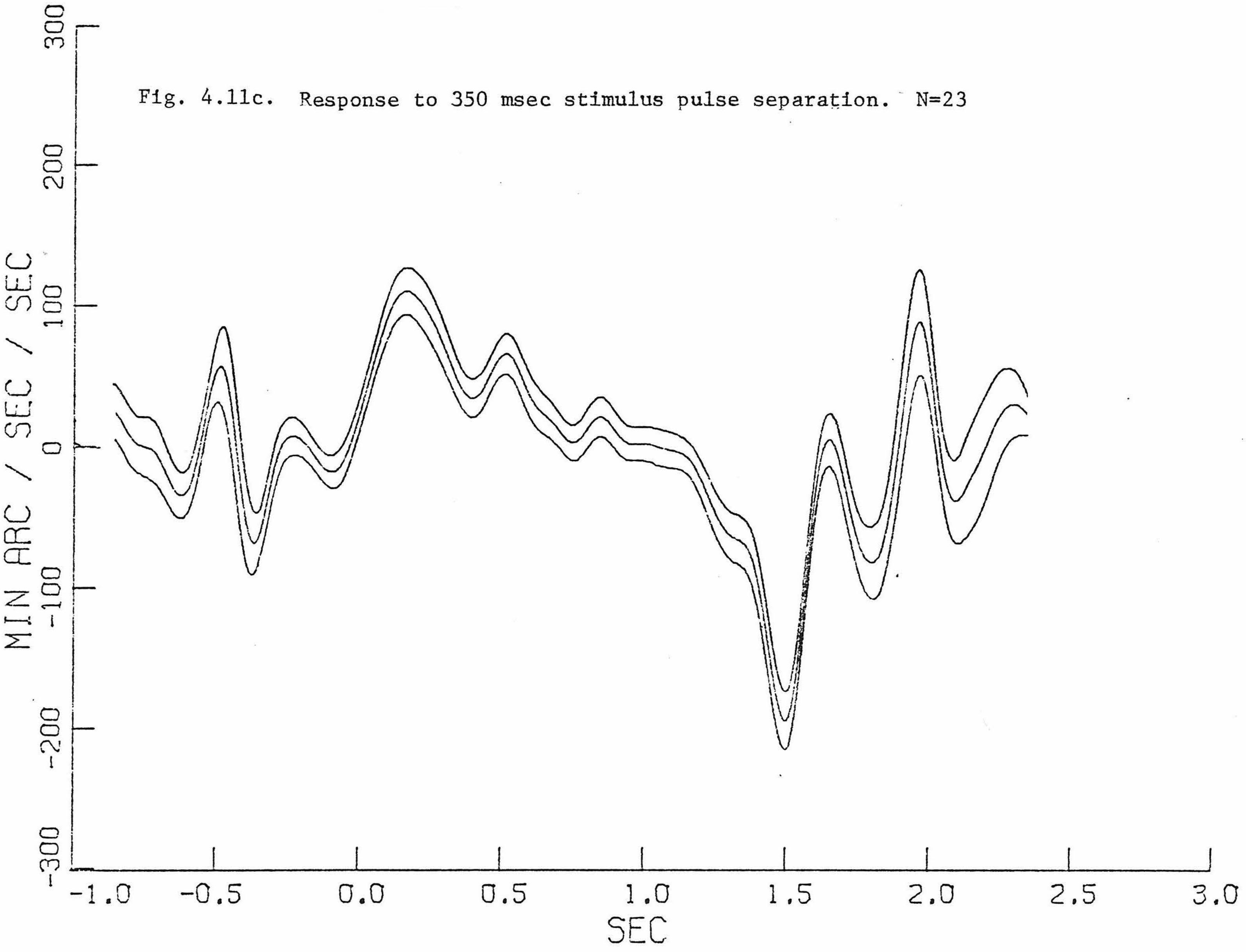


Fig. 4.11c. Response to 350 msec stimulus pulse separation. N=23

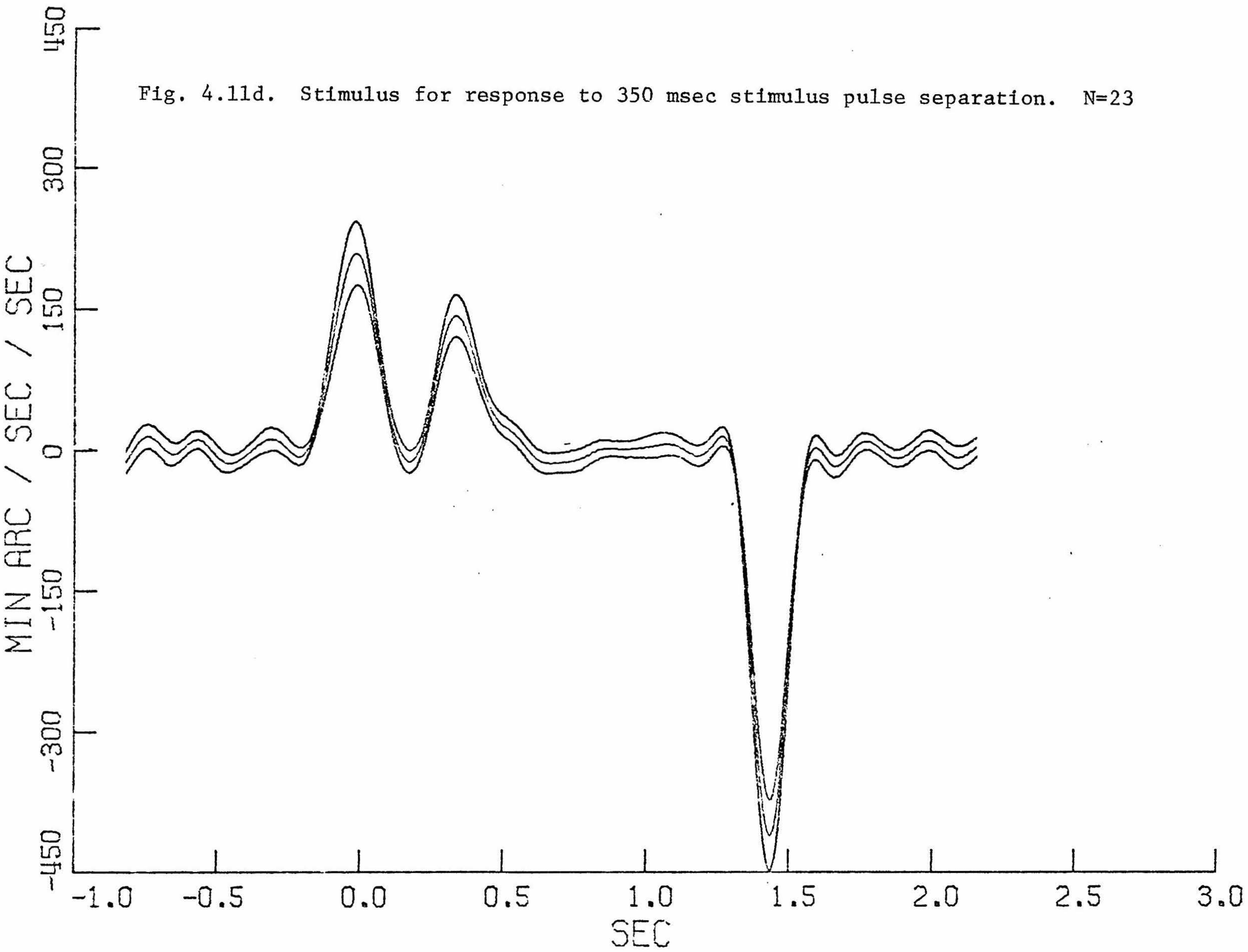


Fig. 4.11d. Stimulus for response to 350 msec stimulus pulse separation. N=23

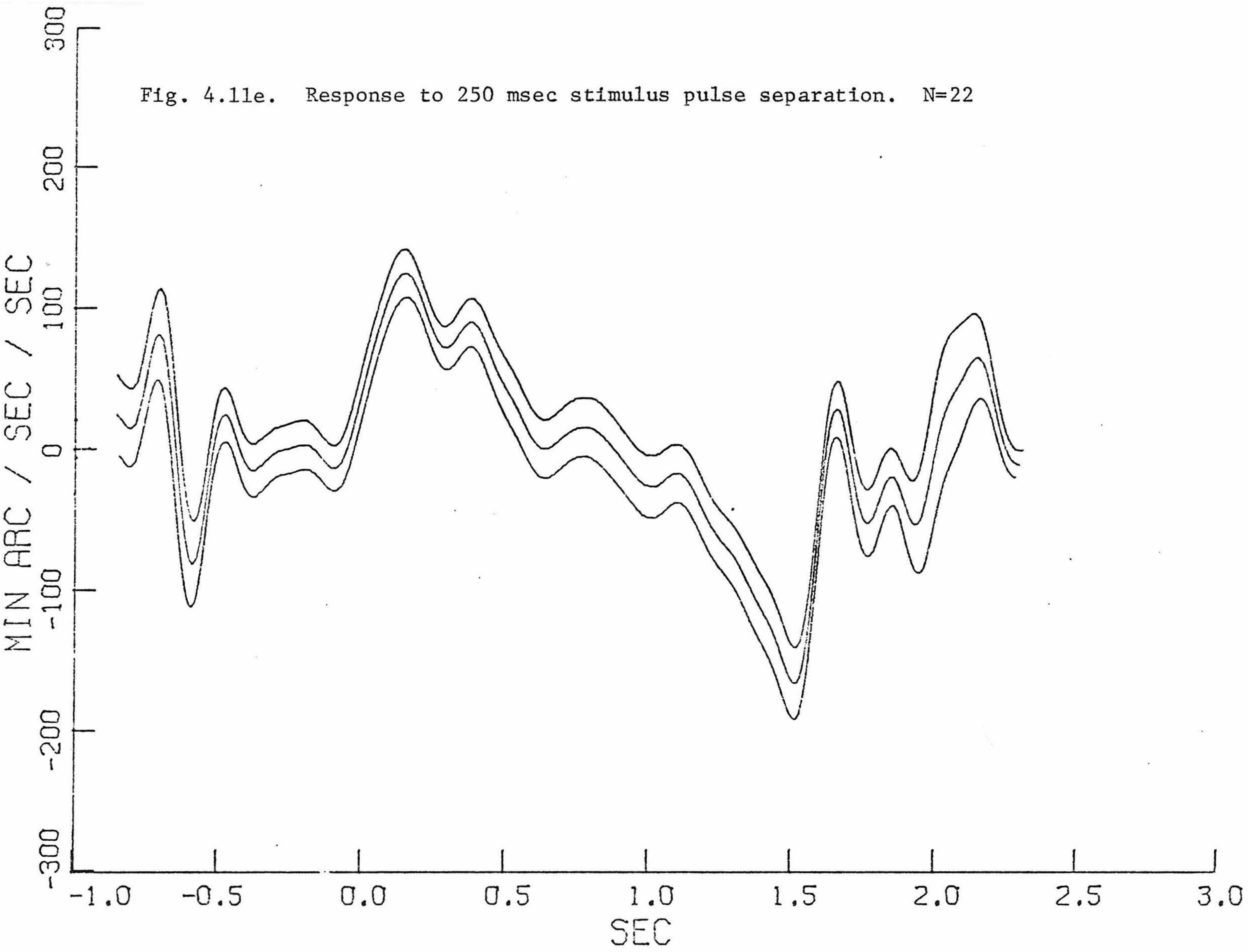


Fig. 4.11e. Response to 250 msec stimulus pulse separation. N=22

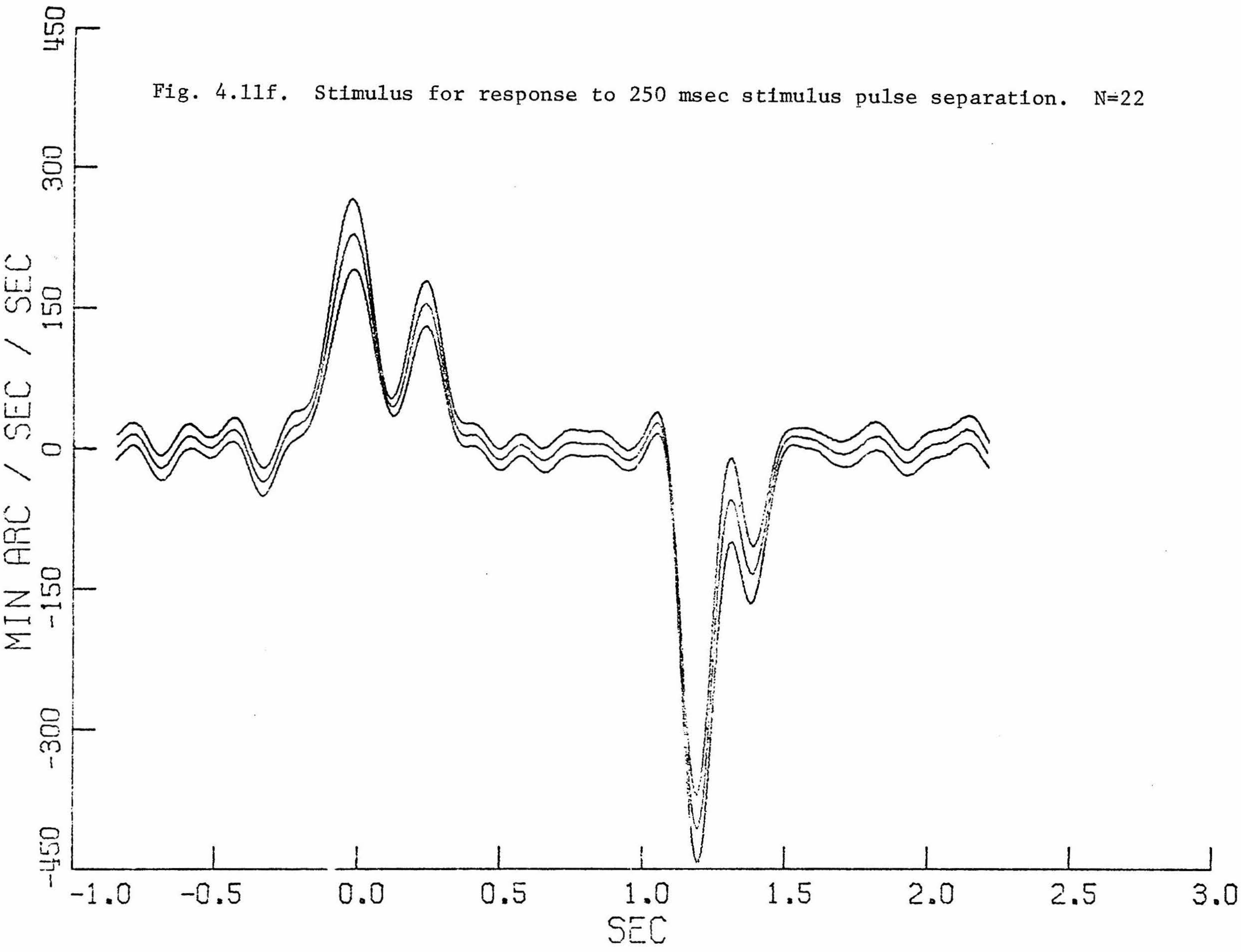


Fig. 4.11f. Stimulus for response to 250 msec stimulus pulse separation. N=22

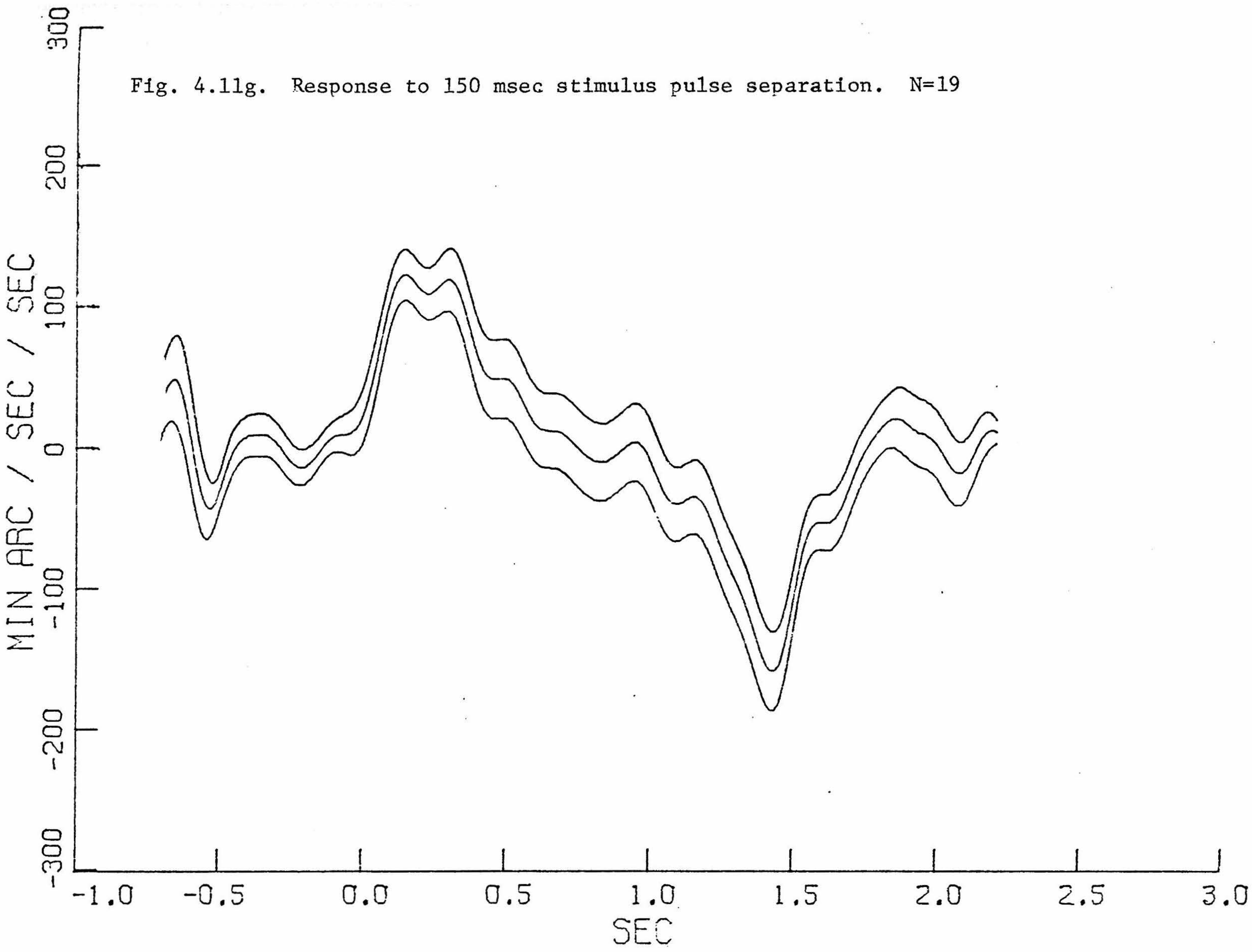


Fig. 4.11g. Response to 150 msec stimulus pulse separation. N=19

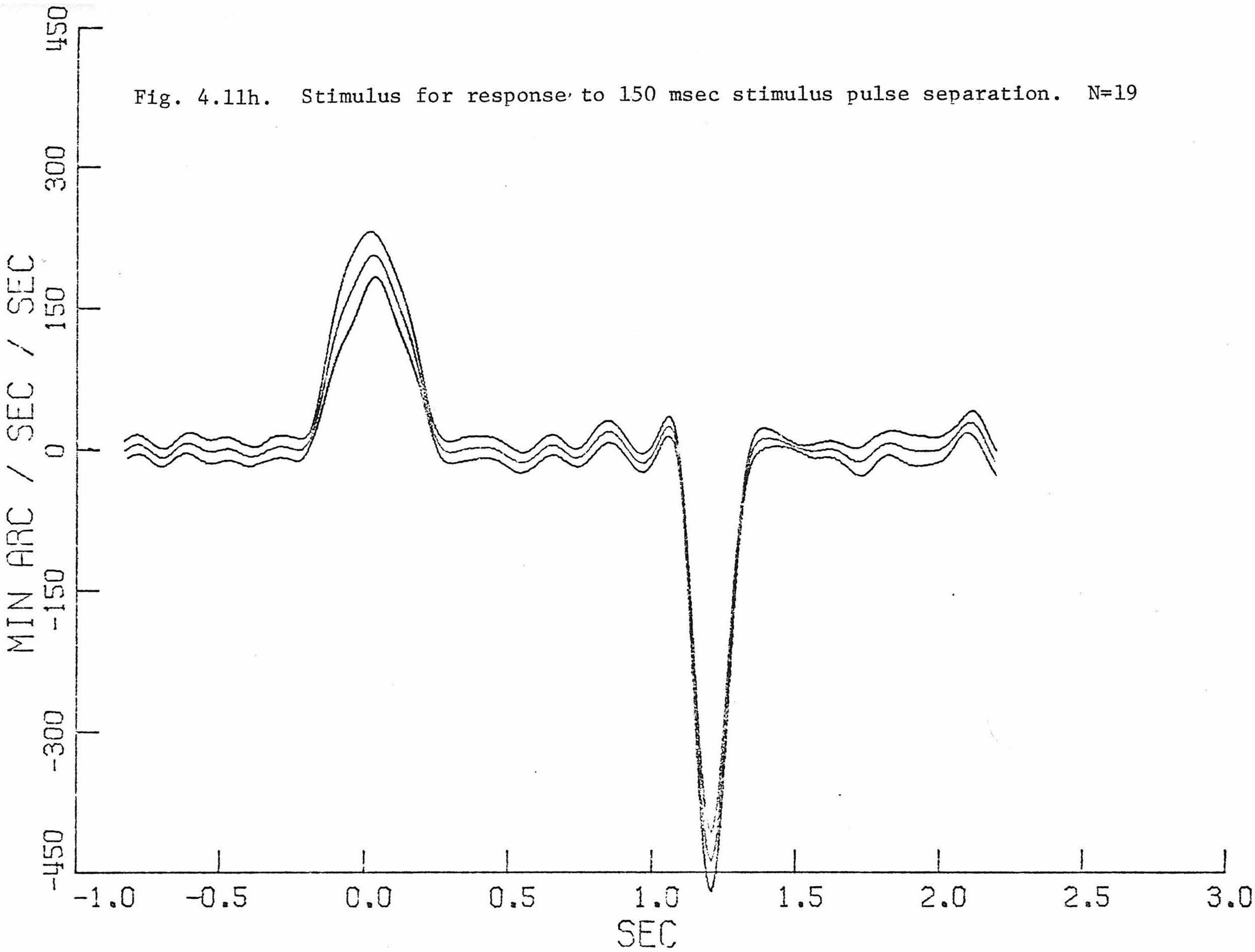


Fig. 4.11h. Stimulus for response to 150 msec stimulus pulse separation. N=19

velocity plots. However, since these response plots were generated from the mean double step velocity response by differentiation, the larger standard deviation of the mean represents the noise amplification within the digital differentiation process, rather than true system response variability.

The stimulus acceleration plots were generated by the same analysis procedures as carried out on the eye movement data. Thus, a comparison of stimulus and response averages reveals only true system transient interactions, since any effects the data analysis procedures may have had on the time course of the raw data (time-smearing) will be subtracted out in the comparison process. These precautions were made necessary by the degree of low pass filtering needed to reduce differentiation noise and increase the relative signal level of the acceleration responses.

The response averages plotted in Fig. 4.11 are representative of the results obtained from two of the three subjects. (Responses of Subject II will be discussed below.) At first glance, the series of responses to two pulses separated by 500, 350, 250, and 150 msec appear as one would expect a linear system to respond. We shall show that this statement is true if only the time relations between the responses to each member of the input pulse pairs are considered. However, the superposition principle is not supported by these data.

In Table 4.2, some temporal characteristics of the double pulse responses have been tabulated for the three subjects. Measurements from the two eyes and from rightward and leftward motions are included in the average values listed. The latencies of the first and second pulses and their time separations were measured from peak values of

Table 4.2

Double pulse response properties measured from peak values of acceleration plots for three subjects. All values in msec. m = mean value, SD = standard deviation of the observations. Data from right and left eye and from rightward and leftward movements were included in the calculation of statistics (i.e. n = 4 in all cases).

	Pulse Separation (msec)							
	500		350		250		150	
Subject	m	SD	m	SD	m	SD	m	SD
	Latency of First Pulse (msec)							
I	174.0	29.7	212.0	24.3	159.0	15.4	185.0	17.5
II	210	41.2	239.0	40.0	217.0	23.6	224.0	33.8
III	200	43.7	232.0	49.2	201.0	36.1	165.0	17.3
	Latency of Second Pulse (msec)							
I	176.0	12.1	212.0	56.8	166.0	16.8	170.0	32.8
II	269.0	82.6	376.0	18.1	272.0	49.5	304.0	63.9
III	191.0	45.2	194.0	14.3	212.0	33.0	182.0	40.3
	Pulse Separation (msec)							
I	515.0	43.3	332.0	45.8	257.0	31.1	162.0	13.9
II	556.0	42.7	471.0	43.7	299.0	60.4	226.0	33.5
III	478.0	71.2	315.0	69.4	262.0	67.0	168.0	20.6
	Amplitude Ratio 1st Pulse/2nd Pulse							
I	1.3	0.10	1.9	0.34	1.7	0.22	1.4	0.31
II	1.9	0.79	1.6	0.14	1.3	0.24	1.15	0.31
III	1.6	0.40	1.4	0.30	2.1	0.42	2.0	1.4

each pulse. For Subject I and III, the latencies of the first pulse are in the 150 to 200 msec range as determined from single pulse experiments. The response latencies for Subject II are larger, falling between 200 and 250 msec, as noted in single pulse data for this subject. Latency of the second pulse for Subject I and III are equivalent, within experimental error, to values measured for the first pulse. Subject II exhibited relatively longer latency values for the second pulse response. This effect is probably due to the tendency for this subject to make a saccade in response to the arrival of the second pulse, as observed in the raw data (Fig. 4.12).

Response pulse separation is apparently a linear function of input pulse separation for the values tested in these experiments. For Subject II, the larger response pulse separations reflect the longer latency to the second pulse observed above. In most cases, the response pulse interval is within 20 to 30 msec of the actual stimulus pulse interval, even for the 150 msec double pulse stimulus.

These time relationships between stimulus and response are indistinguishable from those that would be generated by a relatively noisy linear system with an approximate 150 msec response latency. There is no evidence of the types of non-linear interactions which were hypothesized above. The observation that latency to the second pulse is independent of input pulse separation down to 150 msec indicates that the first pulse has no effect on the programming of the response to the second pulse, even when the second input pulse is delivered before or during the system response to the first pulse. There is no evidence of a refractory period existing between 150 and 500 msec

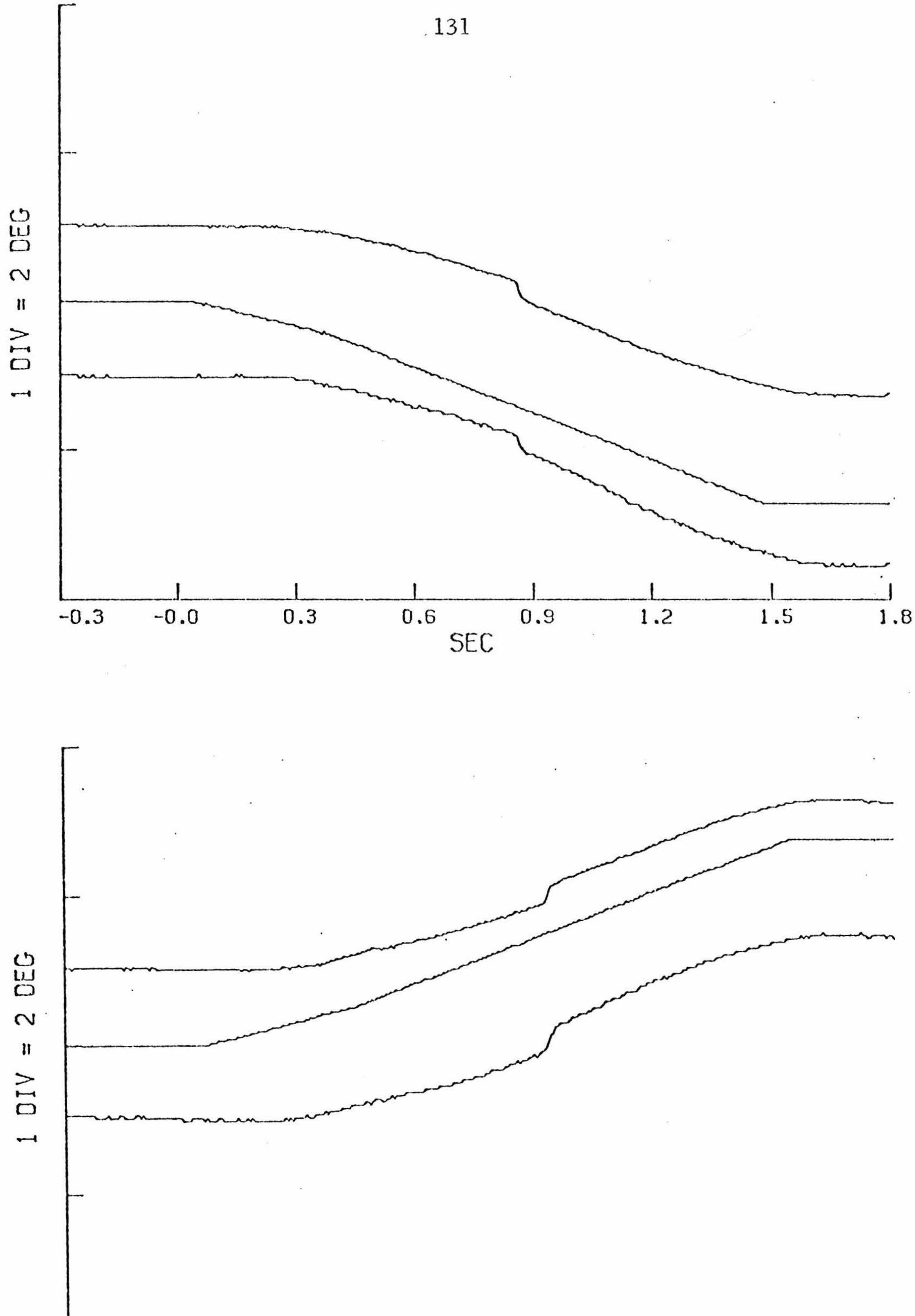


Fig. 4.12a Responses of Subject II to double pulse stimulus. Center trace stimulus. (Note occurrence of saccade 500 msec after velocity change.) Leftward and rightward motions.

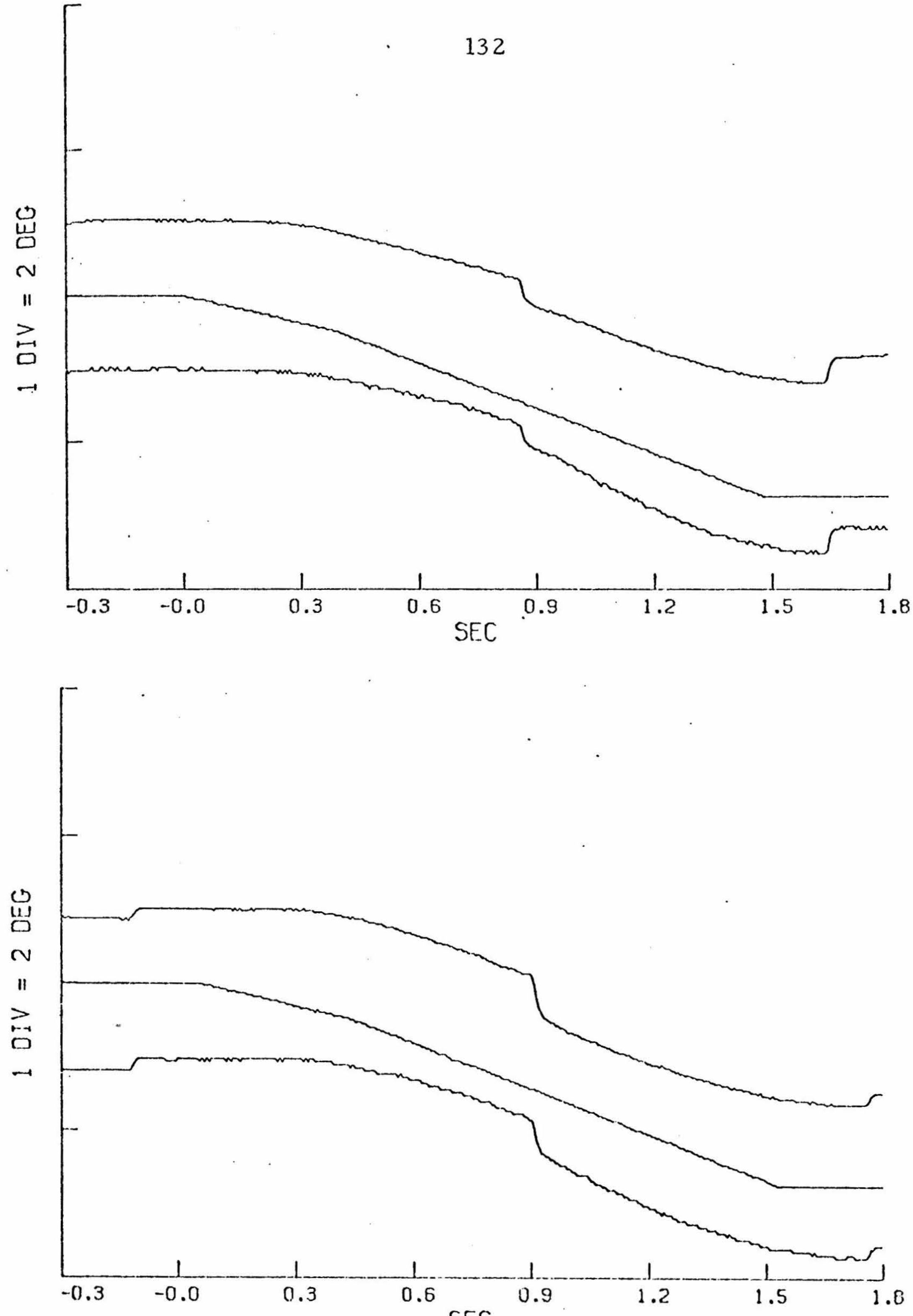


Fig. 4.12b Responses of Subject II to double pulse stimulus. Center trace stimulus. (Note occurrence of saccade 500 msec after velocity change. Two leftward motions.

following a response pulse. Below we shall suggest that the input sensitivity of the system is suppressed during a response, a phenomenon similar to the suppression of visual sensitivity observed during saccadic eye movements. Thus the inhibitory and facilatory effects postulated in the first few paragraphs of this section are not to be found in pursuit eye movement responses within the time limits represented in these double pulse experiments.

The plots of stimulus acceleration (Fig. 4.11) show that the first pulse was larger than the second (ratio of about 1.5 : 1.). The intent was that the two pulses be equivalent in amplitude. However, a round-off error in the assembler program which generated the velocity changes caused the amplitude reduction of the second pulse. This artifact does not affect the analysis of the double pulse amplitude effects as long as the 1.5 : 1. ratio is considered in the input-output comparisons. For Subject III, this artifact was corrected so that the two stimulus pulses were of equal magnitude.

The bottom row in Table 4.2 lists the amplitude ratios of first response pulse to second response pulse measured from the double pulse response averages. Although the values range from 1.1 to 2.0, the overall average for Subjects I and II is about 1.5. Also, there appears to be no systematic dependence of the ratio upon pulse separation. Thus, again, the types of nonlinear interactions postulated above are not present in these response data. Even when the second pulse is delivered before the system has responded to the first pulse, the input amplitude relations are retained in the output response waveform.

Although the time and amplitude relations discussed so far reveal no non-linear interactions between response pulses, the double pulse response as a whole is not the simple sum of two single pulse responses separated in time by the stimulus interpulse interval. The first indication of this effect is the preservation of the input pulse amplitude ratio with output. The responses predicted by simple addition of two single pulse responses do not preserve the input pulse amplitude ratio. In Fig. 4.13, the departure from the linear superposition principle is analyzed.

The 500 msec double pulse response for Subject I (Fig. 4.11) exhibits nearly complete independence between the two response pulses. The response to the first pulse is over before the response to the second pulse begins, as indicated by the return of acceleration to the zero level between pulses. Thus, we can consider each response as an independent system pulse response and use them to investigate the superposition relationship. In Fig. 4.13, these two pulse responses have been arranged with 350, 250, and 150 msec pulse separations. The dotted curve in each case represents the double pulse response that results from the graphic addition of the two individual responses. These computed curves should be compared to the actual pursuit responses of Fig. 4.11. Apparently, the 350 msec response is not very different from the superposition response. However, the 250 and 150 msec pursuit responses do not resemble the waveforms predicted from linear addition. In both cases, superposition predicts a larger acceleration response than actually observed during the period of overlap of the two pulses. Furthermore, the

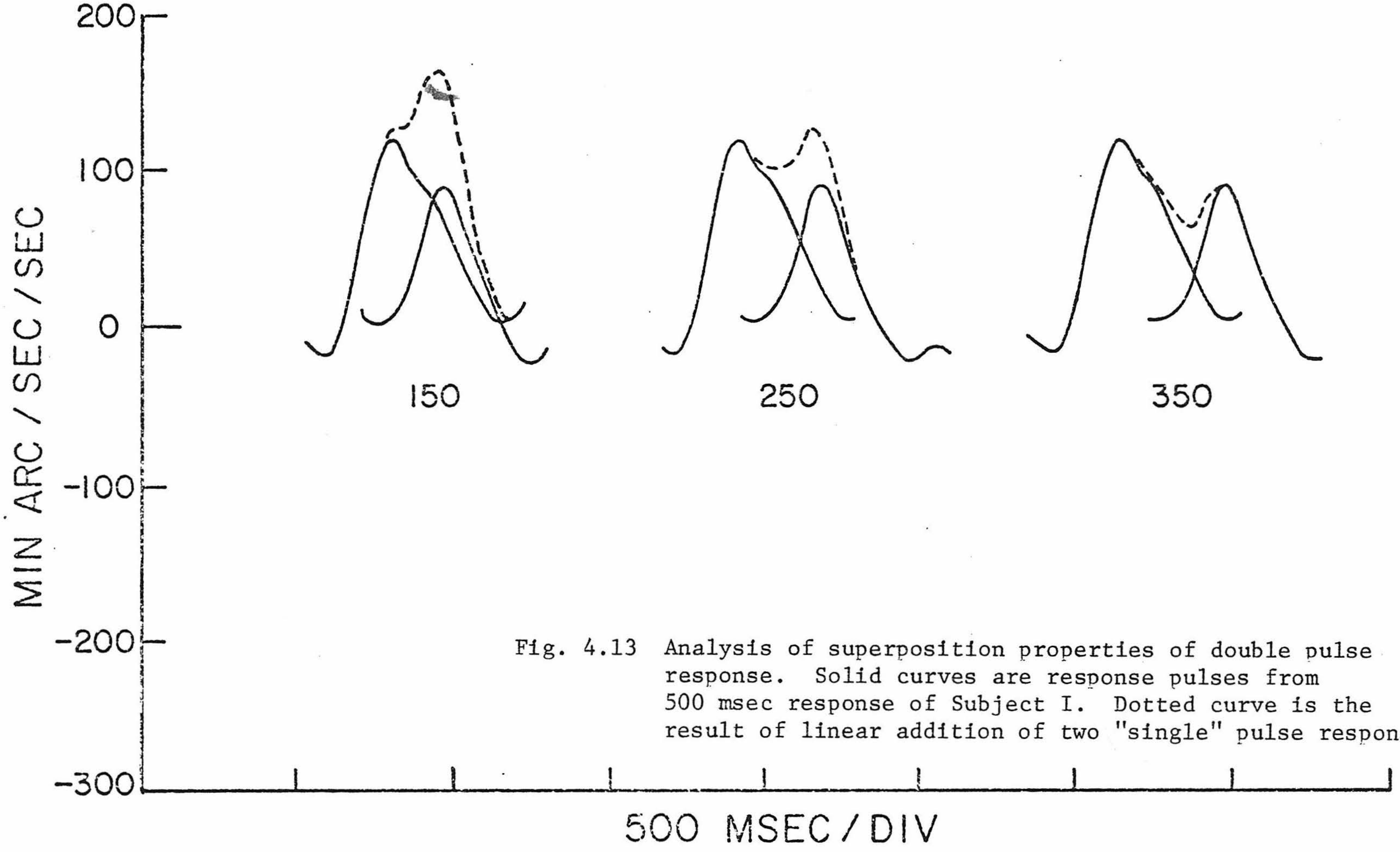


Fig. 4.13 Analysis of superposition properties of double pulse response. Solid curves are response pulses from 500 msec response of Subject I. Dotted curve is the result of linear addition of two "single" pulse responses.

system compensates for the lost double pulse amplitude by extending the duration of the second response pulse, as seen in Fig. 4.11. Thus, the area under the double pulse response is approximately equal to the area under the predicted superposition response. This must be the case if final eye velocity is to match final target velocity.

The difference between the actual and predicted responses at each instant in time is a measure of the second order non-linear properties of the system. If we performed the double pulse experiment for all possible pulse separations and then measured the difference between actual and superposition responses at all instants of time following the first pulse, we would have a complete representation of the second order non-linear properties of the pursuit system. It is this representation of which the second order Wiener kernel, computed from the system response to a Gaussian white-noise input, is an estimate. This property of the white-noise analysis technique will be discussed in the next chapter.

When compared to the superposition responses, the double pulse responses of Fig. 4.11 seem to exhibit a threshold effect in velocity sensitivity. That is, the system does not recognize the presence of the second pulse until eye acceleration has dropped below a certain value (75 min arc/sec^2 in Fig 4.11). The presence of the valley between the two response pulses which is not found in the predicted response (150 , 250 msec) is the manifestation of this hypothesized effect. A decrease in oculomotor velocity sensitivity during the acceleration response could explain such a phenomenon. The overall effect of the threshold of velocity sensitivity is to extend the duration of eye acceleration without increasing the absolute acceleration magnitude. The analogous system property was observed in the single pulse responses in which the duration of the response pulse increased with the amplitude of the input pulse.

Another type of nonlinearity is revealed upon comparison of single pulse responses (Fig. 4.8) and the leading edge of the 500, 350, and 250 msec double pulse responses (representing the accleration response to an 88 min arc/sec velocity step). This portion of the double pulse response is analogous in latency and waveshape to the acceleration response to a single 88 min arc/sec velocity step. If the pursuit system integrates two acceleration pulses separated by 150 msec or less, then the response to a single pulse of 148 min arc/sec (the sum of the two velocity steps represented in the double pulse experiment) should resemble the 150 msec double pulse response. However, when the 120 min arc/sec single pulse response (this was the largest velocity used in the experiments) is compared to the 150 msec double pulse response, some differences are observed. Although latency and duration of the two responses are similar, the amplitude of the single pulse response is larger and its rise time is slower than the double pulse response. Thus, it appears that the system does not integrate the two smaller pulses into one larger pulse but responds to each individual pulse of the pair. The response to the first pulse resembles an 88 min arc/sec single pulse response in its rise time characteristics. The total response then exhibits the nonlinear threshold effect discussed above.

The double pulse responses of Subject II are difficult to interpret in terms of the types of interactions observed in the data from the other two subjects. When the second pulse was delivered, the raw data from Subject II nearly always exhibited a saccadic response about 500 msec after onset of the pulse. In the plots of averaged acceleration responses (Fig.4.1.4) the effect of the saccade shows up as an extra bump in the acceleration response. The pursuit response to the second pulse is thus easily confused with the acceleration response which remains after the saccade is removed from the position data. Again, we observe that Subject II's saccadic system is capable of dominating the pursuit system in these velocity tasks. The residual position information available in the visual field of the apparatus is apparently enough to bring the saccadic system into action.

To conclude the discussion of the double pulse acceleration experiments, let us summarize the basic pursuit system properties which were determined from the observed results. Within the temporal range tested in these experiments (150 to 500 msec pulse separation), the system continuously samples its input channel. Thus, if there exists a refractory period, its value is less than 150 msec. The observation that input temporal relations remain unchanged in the system output indicates that temporal nonlinearities (e. g. inhibitory or facilitatory effects) do not enter into the pursuit response down to 150 msec separation of input events. Although the temporal properties of smooth pursuit are well-behaved, the double pulse response is not the simple sum of two equivalently spaced single pulse responses. Response pulses seem to add only when eye acceleration falls below

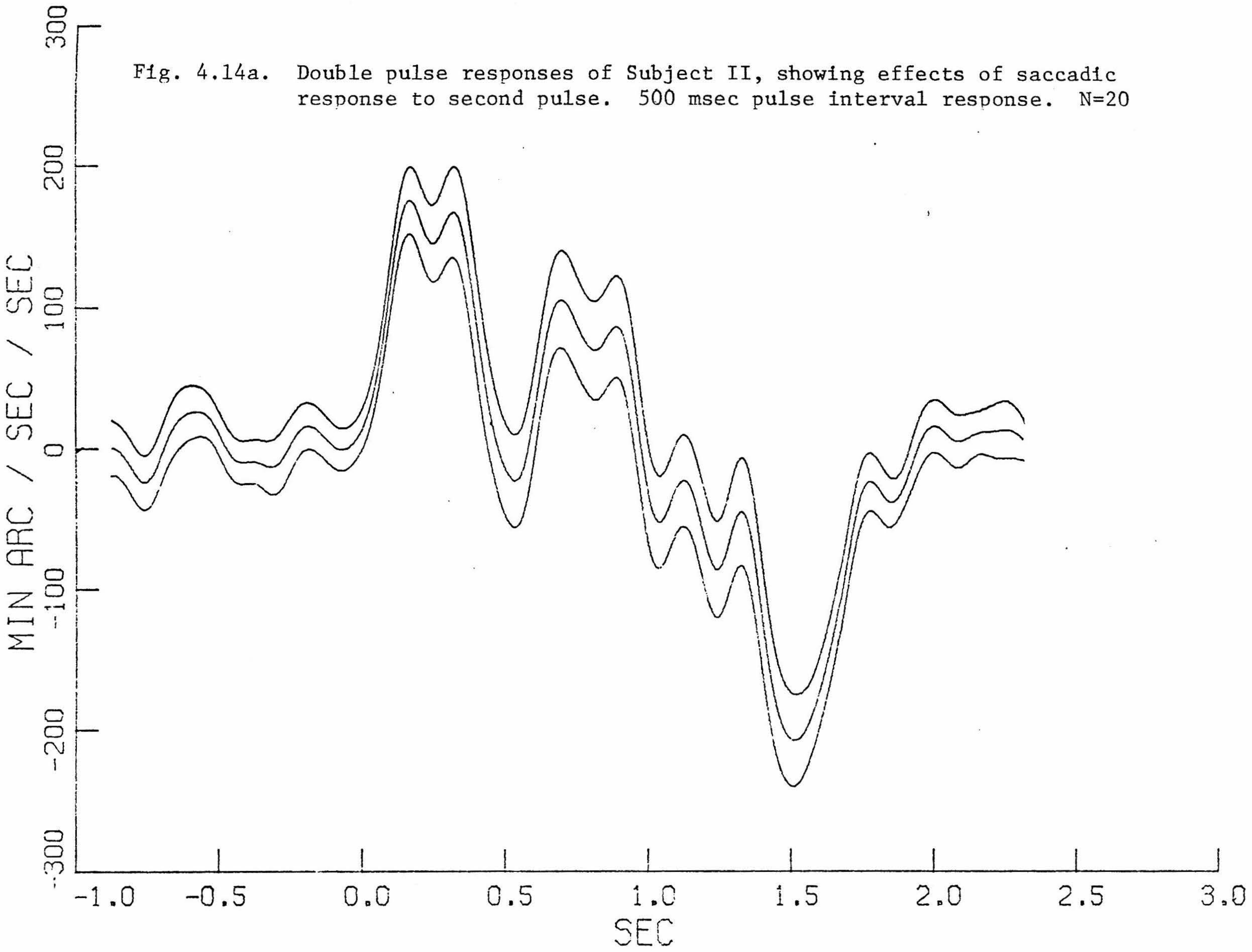


Fig. 4.14a. Double pulse responses of Subject II, showing effects of saccadic response to second pulse. 500 msec pulse interval response. N=20

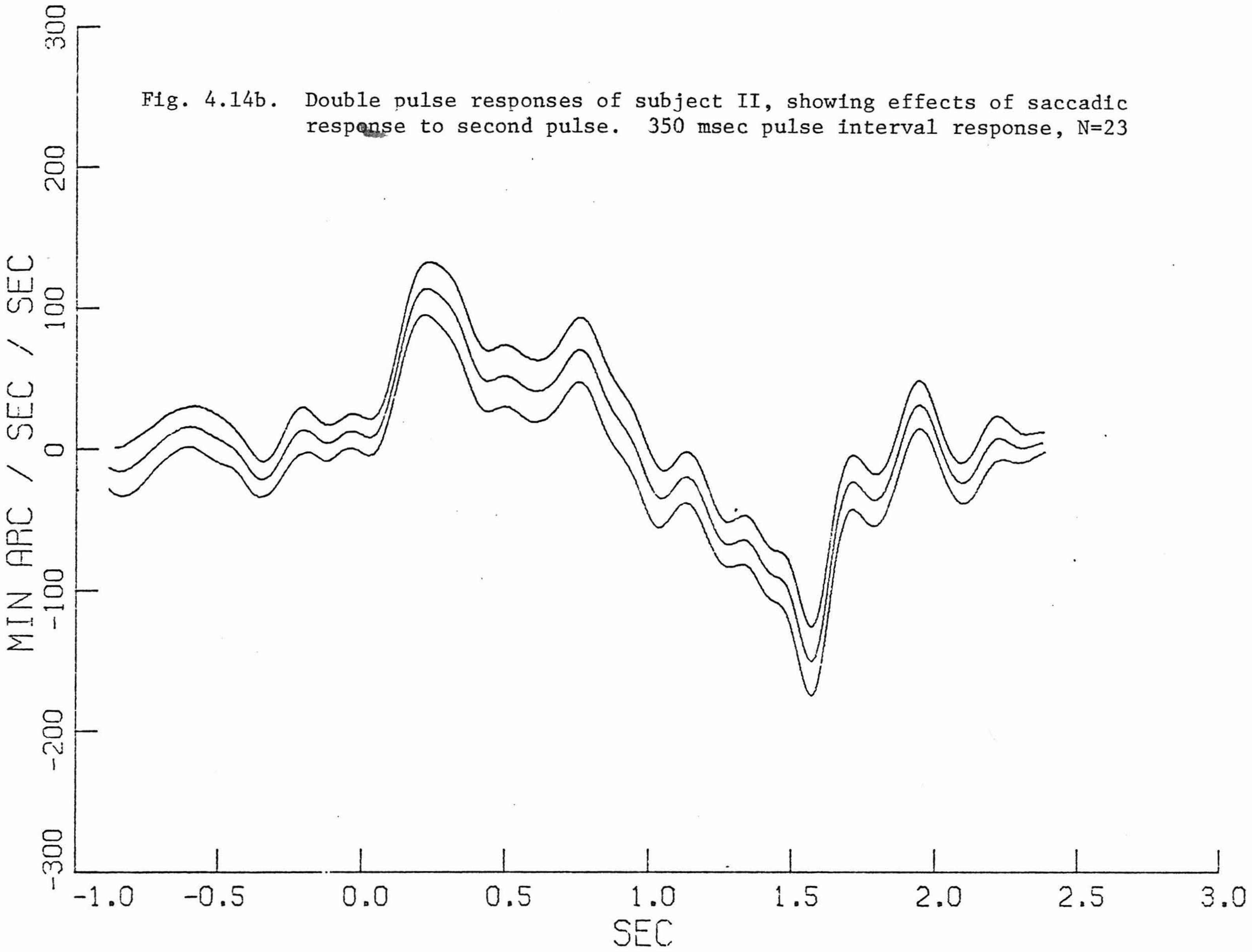


Fig. 4.14b. Double pulse responses of subject II, showing effects of saccadic response to second pulse. 350 msec pulse interval response, N=23

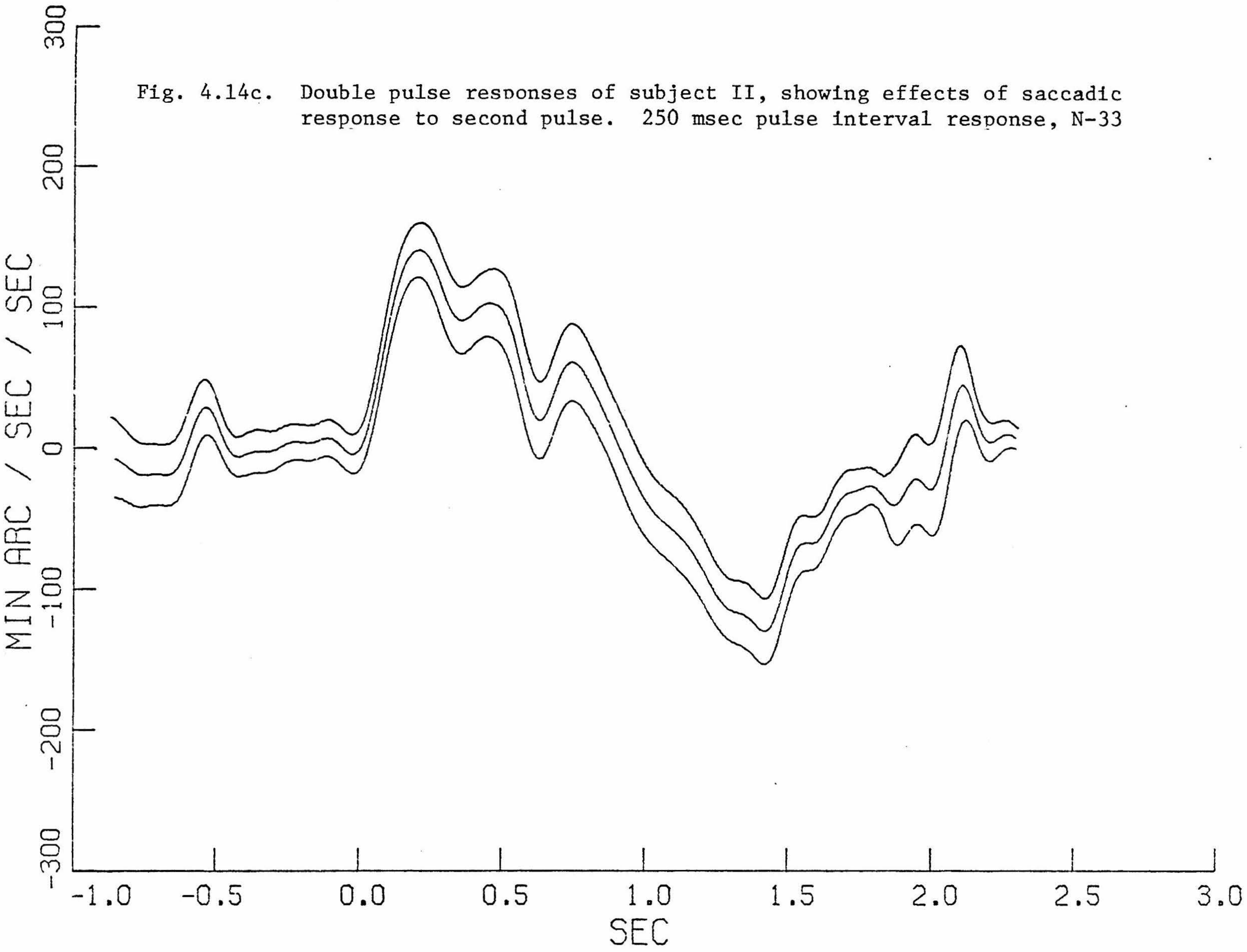


Fig. 4.14c. Double pulse responses of subject II, showing effects of saccadic response to second pulse. 250 msec pulse interval response, N-33

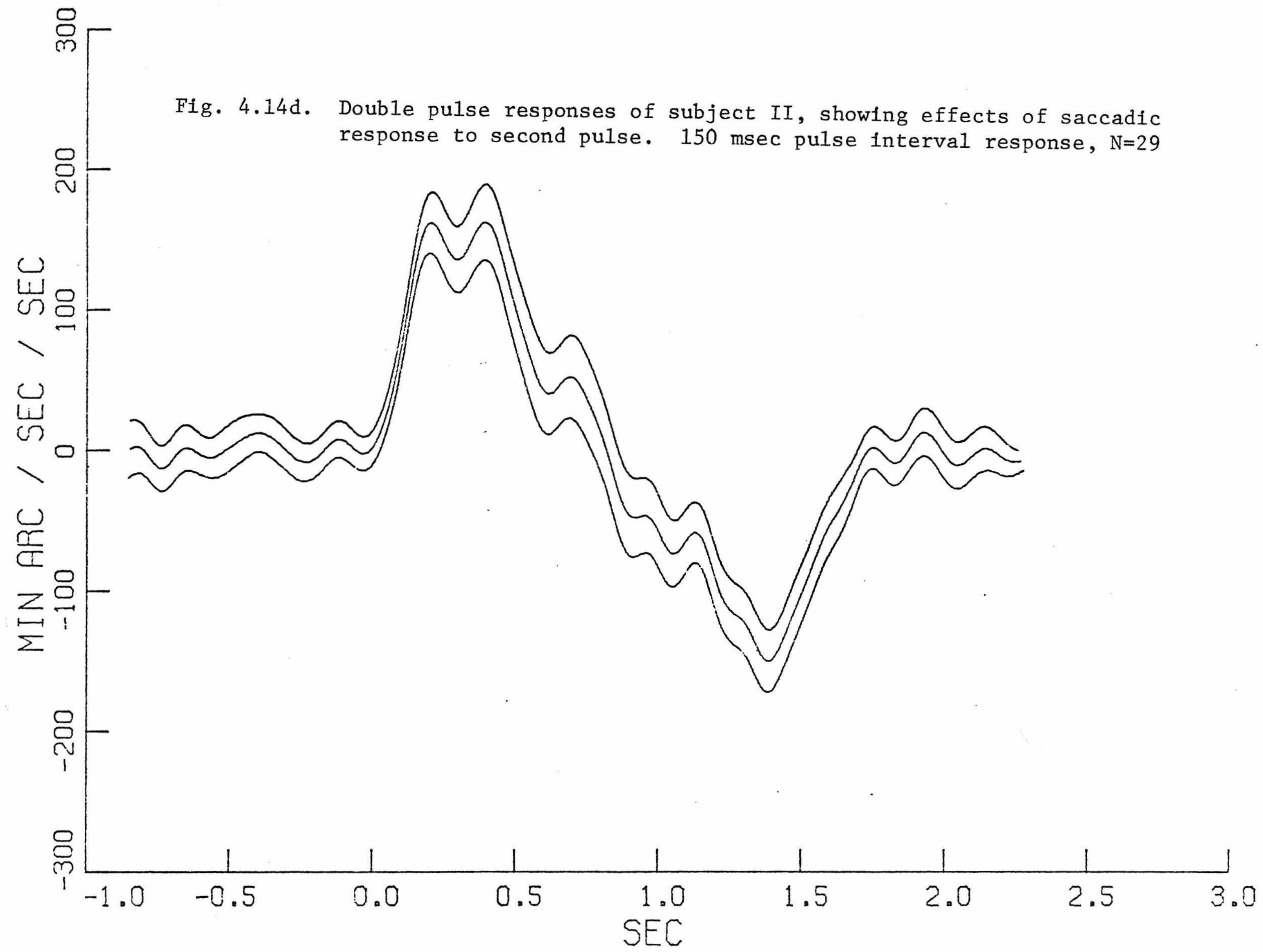


Fig. 4.14d. Double pulse responses of subject II, showing effects of saccadic response to second pulse. 150 msec pulse interval response, N=29

a threshold value. Apparently, pursuit system velocity sensitivity decreases during the response to an input velocity change. These nonlinear effects begin to appear in the output when input pulse intervals are less than 250 msec.

These results provide evidence of substantial nonlinear interactions occurring within the smooth pursuit tracking system when the input bandwidth exceeds 4 Hz. Only the pursuit response, uncontaminated by saccadic eye motions in most instances, was measure by stimulating with pure velocity information. Therefore, this work constitutes the first study which has provided quantitative evidence about the linear and nonlinear properties of the smooth component of the oculomotor tracking system. However, the results show that nonlinear interactions begin at 4Hz and are even stronger at 6 Hz. One might ask what happens below 150 msec pulse intervals. The techniques described so far are not sensitive enough to measure system interactions below 150 msec. The averaging and filtering procedures do not distinguish output events closer together in time than about 150 msec. It is this limitation which stimulated the search for an analysis technique which could explore the pursuit system down to its limits of sensitivity. The white noise method of nonlinear system identification, to be described in the next chapter, is capable of testing a system across its entire bandwidth. Previous attempts at applying this method to the oculomotor tracking system have not been entirely successful. The work constituting this dissertation represents a new approach to the problem, by matching input and system characteristics. The next section describes some preliminary experiments which will tie together the pulse experiments and the continuous random input experiments.

4.6 Velocity Step Response of Composite Horizontal-Vertical System

Up to this point, only horizontal eye motions have been considered. However, as discussed in Section 4.2.1, the stimulus developed for use in the random input experiments employs rotary motion to achieve a continuous random velocity input signal. In order to track such motion, the oculomotor system must call into play both the horizontal and vertical tracking systems. Not only are both types of eye movement involved, but the two must work in very close correspondence in order to follow the circular traverse of the target. The question then arises, is the oculomotor response of the combined horizontal-vertical system equivalent to the response of either of its components to an equivalent pure horizontal (vertical) motion?

To provide a complete answer to this question would take us out of the domain of this dissertation. The question is however critical to the applicability of the results to the oculomotor system in general and will therefore be given some consideration. The oculomotor system can be described as consisting of two independent channels, horizontal and vertical, with some small amount of mutual crosstalk. Although horizontal-vertical interactions in tracking tasks have not been abundantly treated in the literature, a study by Goodwin (1972) strongly supports the above statement. Therefore, in the analysis of the combined horizontal and vertical eye movements to be described below, it has been assumed that the mutual and symmetric nature of the crosstalk (Goodwin, 1972) is an integral part of the pursuit response to a circular target movement.

4.6.1 Circular Velocity Step Data Analysis

In order to quantify the variance between circular and pure horizontal pursuit responses, the single velocity step experiments were repeated using step changes in angular velocity of the circular target. Stimulus motion could be described in terms of tangential velocity,

$$v = r\dot{\theta} \tag{4-6}$$

where v = tangential velocity

r = radius of circular target

$\dot{\theta}$ = angular velocity

In order to relate the oculomotor response to the stimulus motion, horizontal and vertical eye position components were combined in the calculation of eye tangential velocity. Data analysis in terms of tangential velocity rather than angular velocity includes the effects of the drift of eye position from exact target radial position. If eye position drifts towards the center point, the angular velocity calculation overestimates true eye velocity. The raw data showed that eye position tended to drift toward the center during the circular tracking, eliciting a radial position-correcting saccade. Thus, tangential velocity was determined to be a more representative estimate of the pursuit velocity response.

Rather than computing the arctangent of the horizontal and vertical component and then differentiating to obtain $\dot{\theta}$, tangential velocity was computed from the horizontal and vertical velocity components as follows:

$$v = \frac{\bar{r} \times \bar{v}}{|r|} \quad = \quad \frac{x\dot{y} - y\dot{x}}{(x^2 + y^2)^{1/2}} \qquad (4\text{-}7)$$

where $\bar{r}$ = radial position vector

$\bar{v}$ = tangential velocity vector

$\bar{v} = \dot{x}\bar{i} + \dot{y}\bar{j}$; $\bar{i}$, $\bar{j}$ unit vectors

x, y = horizontal and vertical position components

$\dot{x}$, $\dot{y}$ = horizontal and vertical velocity components

This method of determining eye velocity removes the effects of variations in radial position, which can be considered noise in the circular tracking task.

From this point the analysis procedures were identical to those of the horizontal motion experiments. Step velocity responses to equivalent target motions were averaged and the standard deviation of the mean response was calculated. The waveforms of the mean circular velocity step responses were than compared to the results of the single component horizontal velocity step responses. Since data analysis for the two experiments was analogous, any differences observed in the results of the two experiments could be attributed to the difference between the tracking tasks.

4.6.2 Results and Discussion

In Fig. 4.15, horizontal and vertical position components have been combined to produce a plot of the eye position with respect to target position during the step velocity response. The four plots are representative of the majority of the position responses obtained in

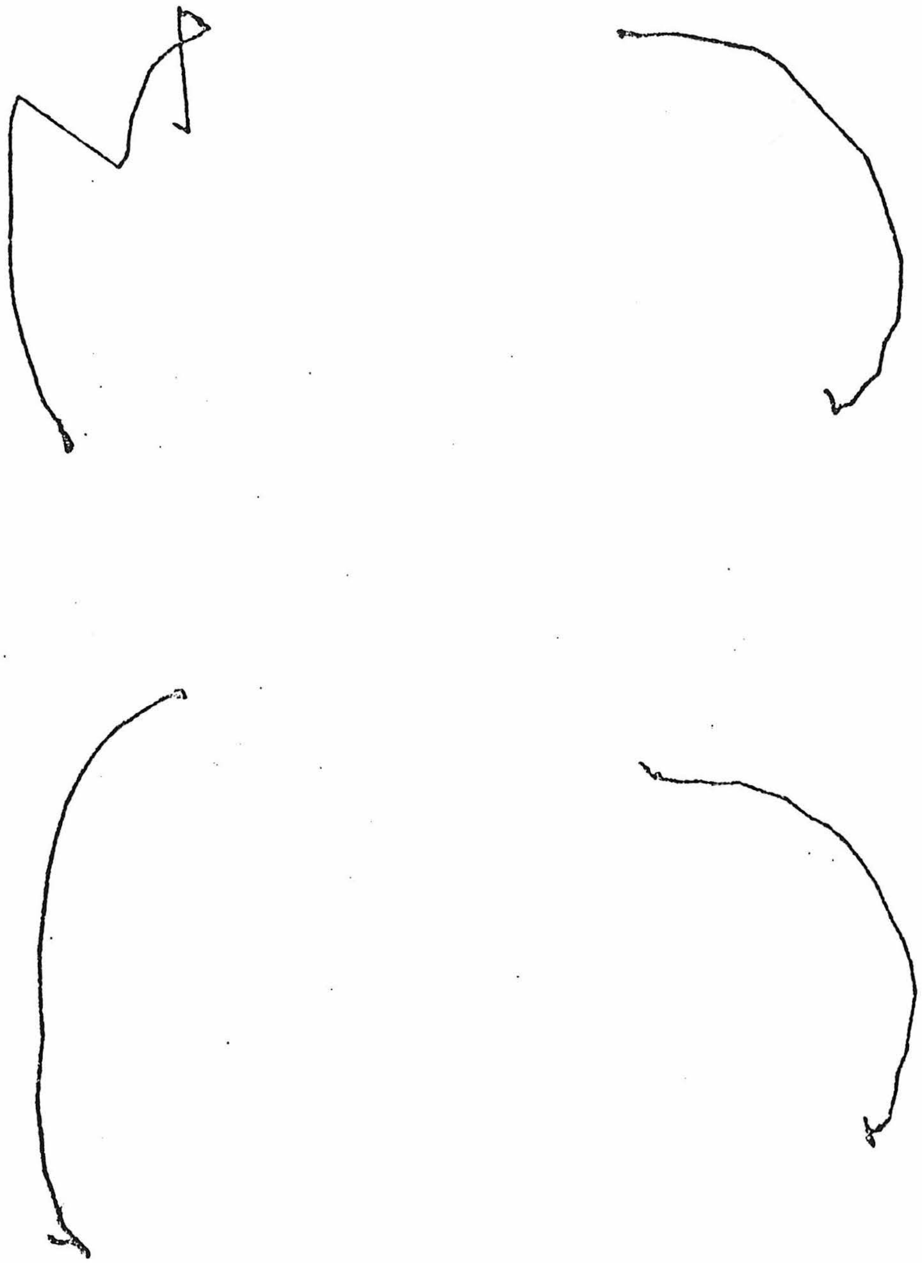


Fig. 4.15 Two-dimensional plot of eye position responses to circular step velocity stimulus. Eye movement begins at top in all traces. Note the occurrence of radial and tangential saccades in several responses.

these experiments. Saccades were usually either tangentially or radially directed. Radial saccades were almost always directed outward to correct for the centralward drift of eye position during the response. Tangential saccades were in the direction of target motion. In the many saccade-free trials, the centralward drift went uncorrected. These observations indicate that the circular tracking task involves more position information than did the single direction component task. The tracking system must worry not only about target velocity, but also about radial eye position. The presence of tangential saccades indicates that the perceptual system also worries about angular position along the ring of dots.

It appears that the position information involved in the circular tracking task is enough to bring the saccadic system into action more often than observed in the horizontal tracking tasks. However, several properties of the circular motion response favor the use of this stimulus in a random velocity tracking experiment. First, many of the trials contained no saccades. The system appears to be capable of saccade-free composite horizontal-vertical eye movements. Also radial saccades had little effect upon smooth eye velocity. Third, tangential saccades seemed to be generated by perceptual rather than retinal position errors. It was found that with training, subjects could suppress such tangential saccades. Thus both types of saccades can be removed from the data without seriously affecting the computed smooth pursuit signal.

Further support for the latter statement comes from the results of the averaged velocity response analysis (Fig. 4.16). A complete

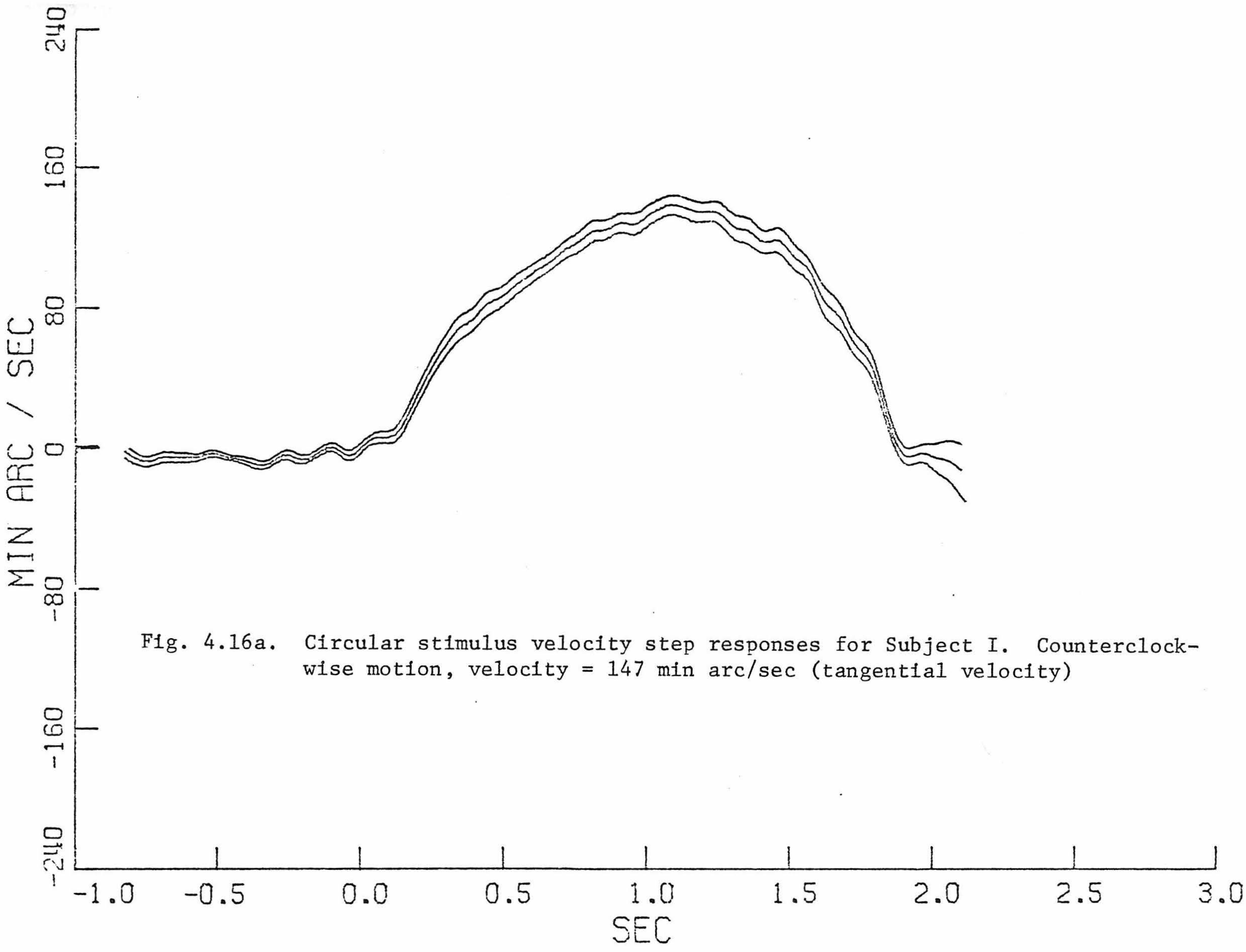


Fig. 4.16a. Circular stimulus velocity step responses for Subject I. Counterclockwise motion, velocity = 147 min arc/sec (tangential velocity)

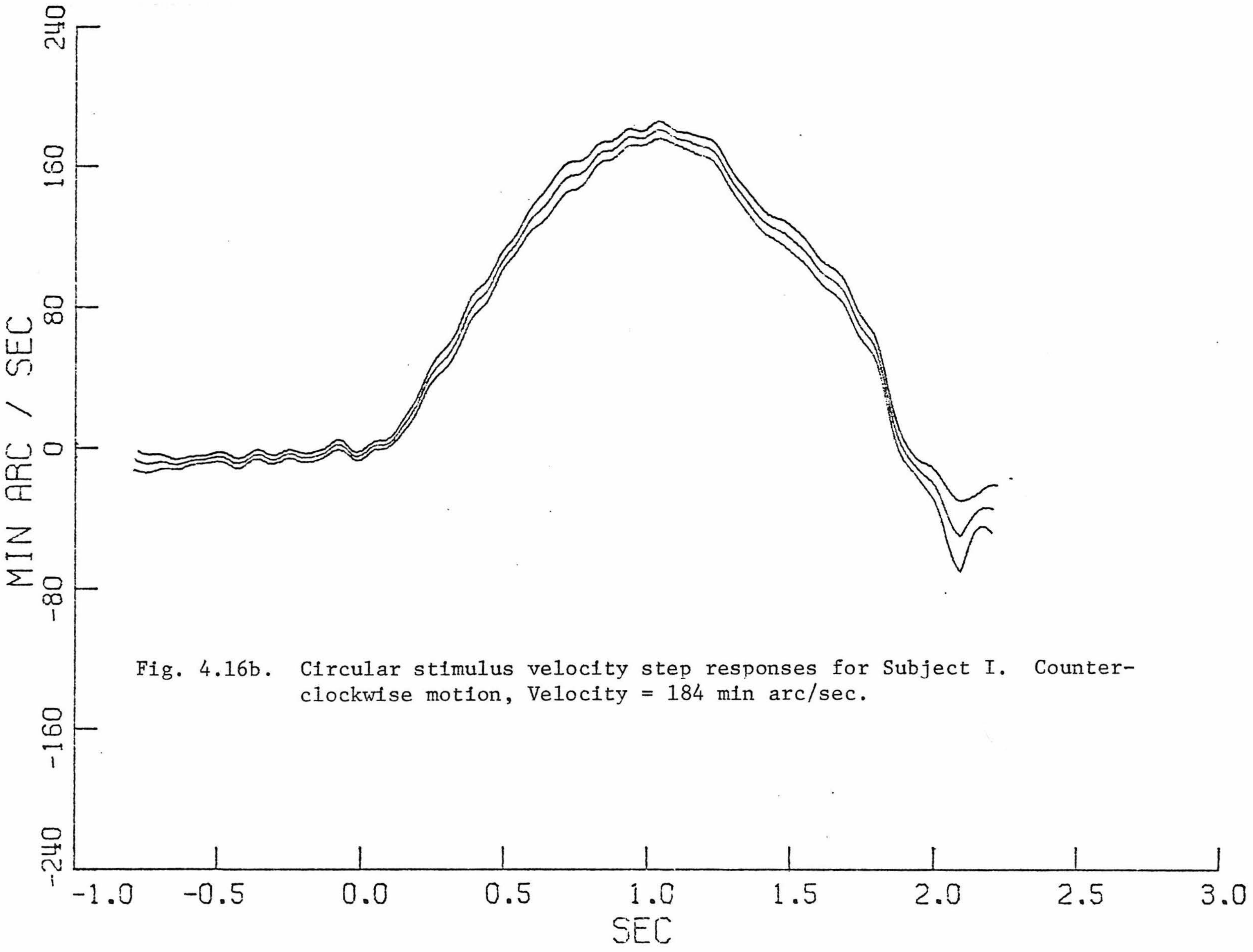


Fig. 4.16b. Circular stimulus velocity step responses for Subject I. Counterclockwise motion, Velocity = 184 min arc/sec.

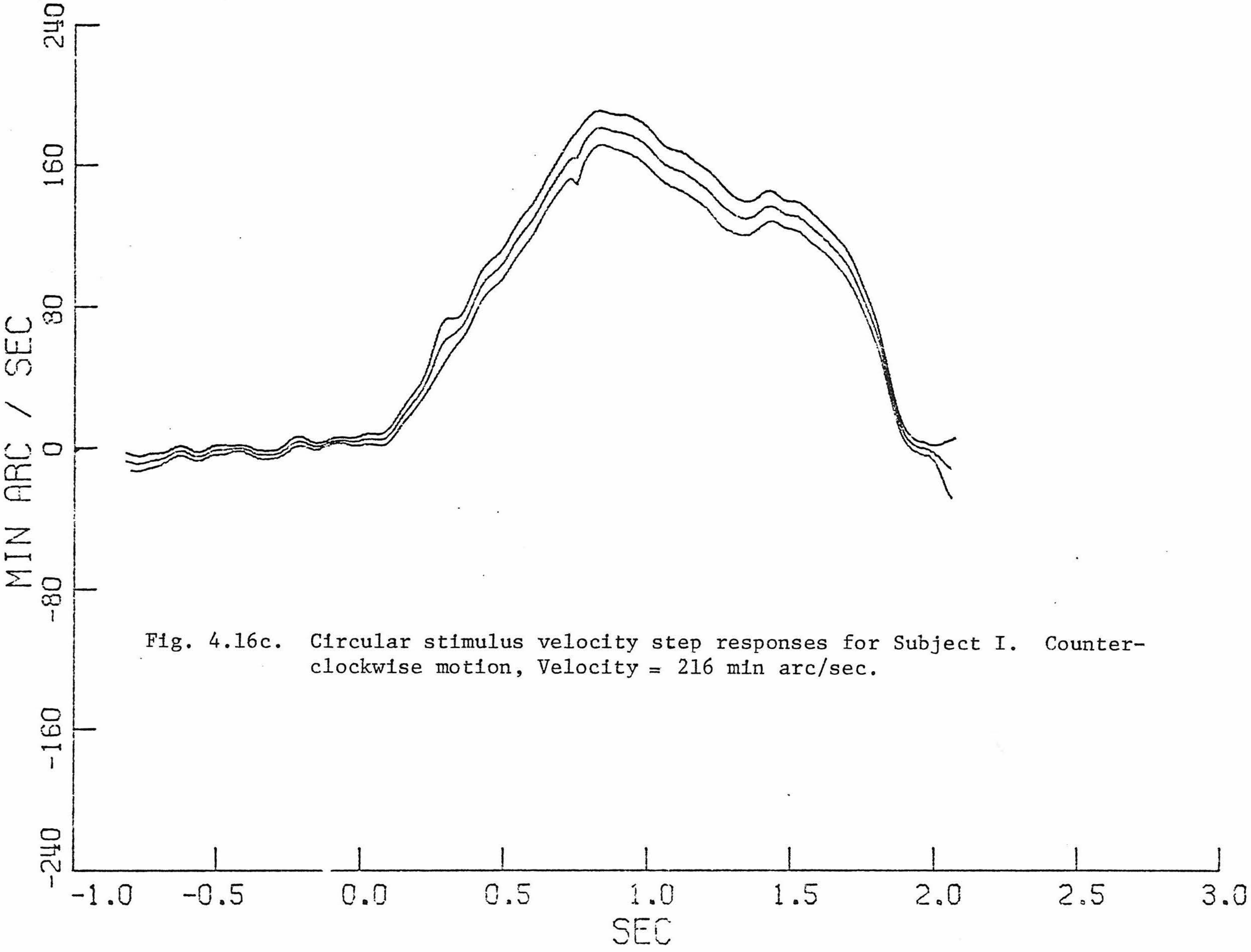


Fig. 4.16c. Circular stimulus velocity step responses for Subject I. Counterclockwise motion, Velocity = 216 min arc/sec.

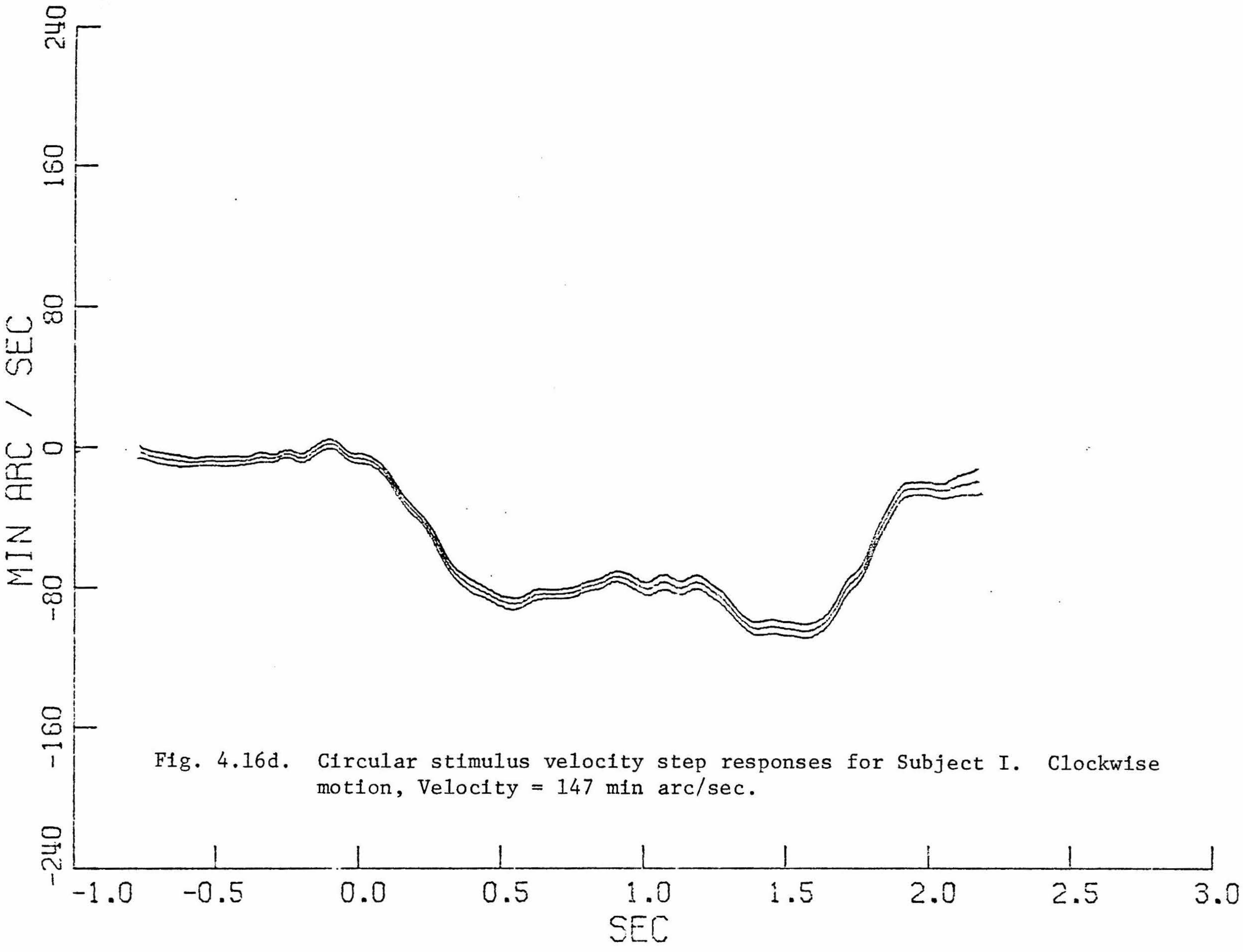


Fig. 4.16d. Circular stimulus velocity step responses for Subject I. Clockwise motion, Velocity = 147 min arc/sec.

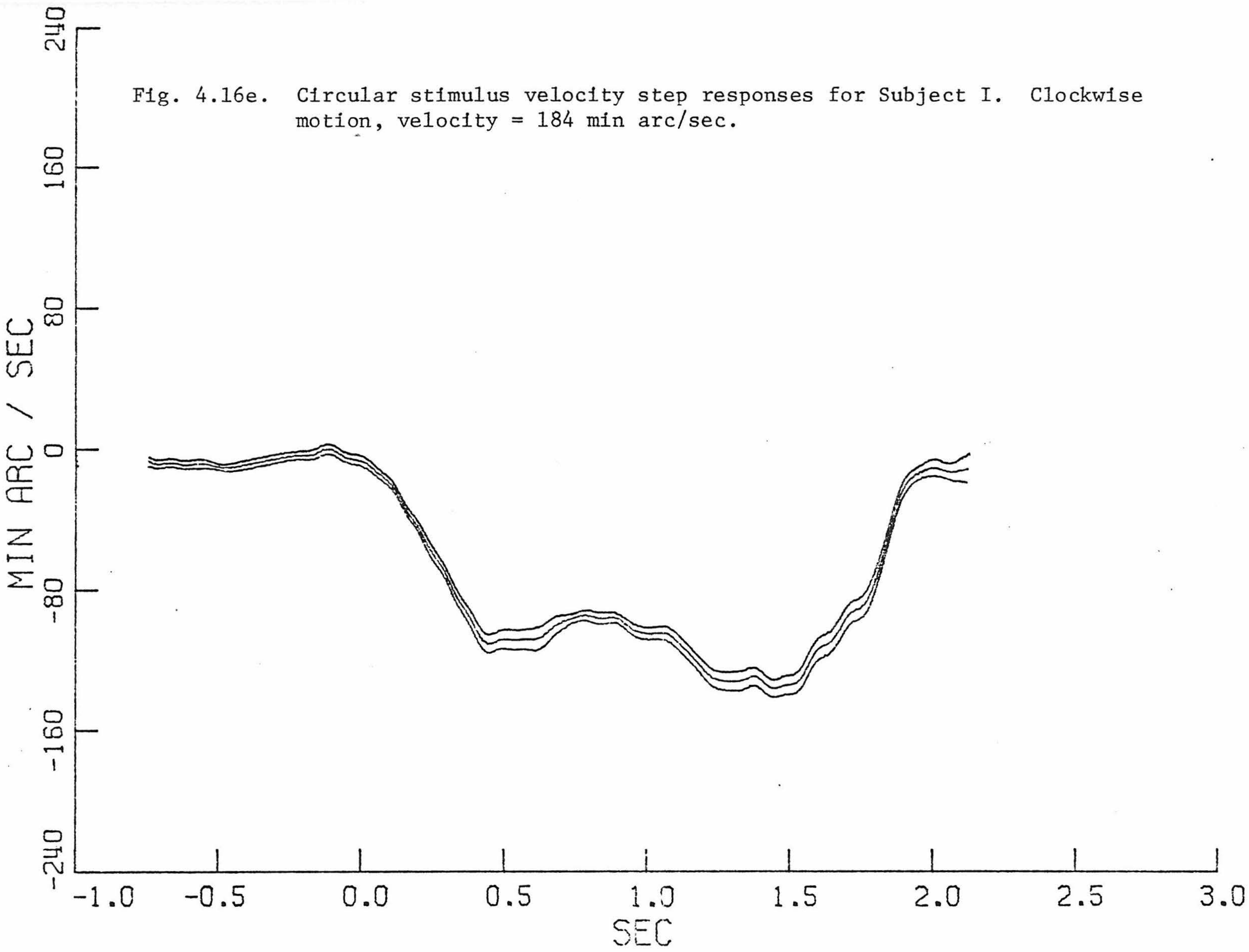


Fig. 4.16e. Circular stimulus velocity step responses for Subject I. Clockwise motion, velocity = 184 min arc/sec.

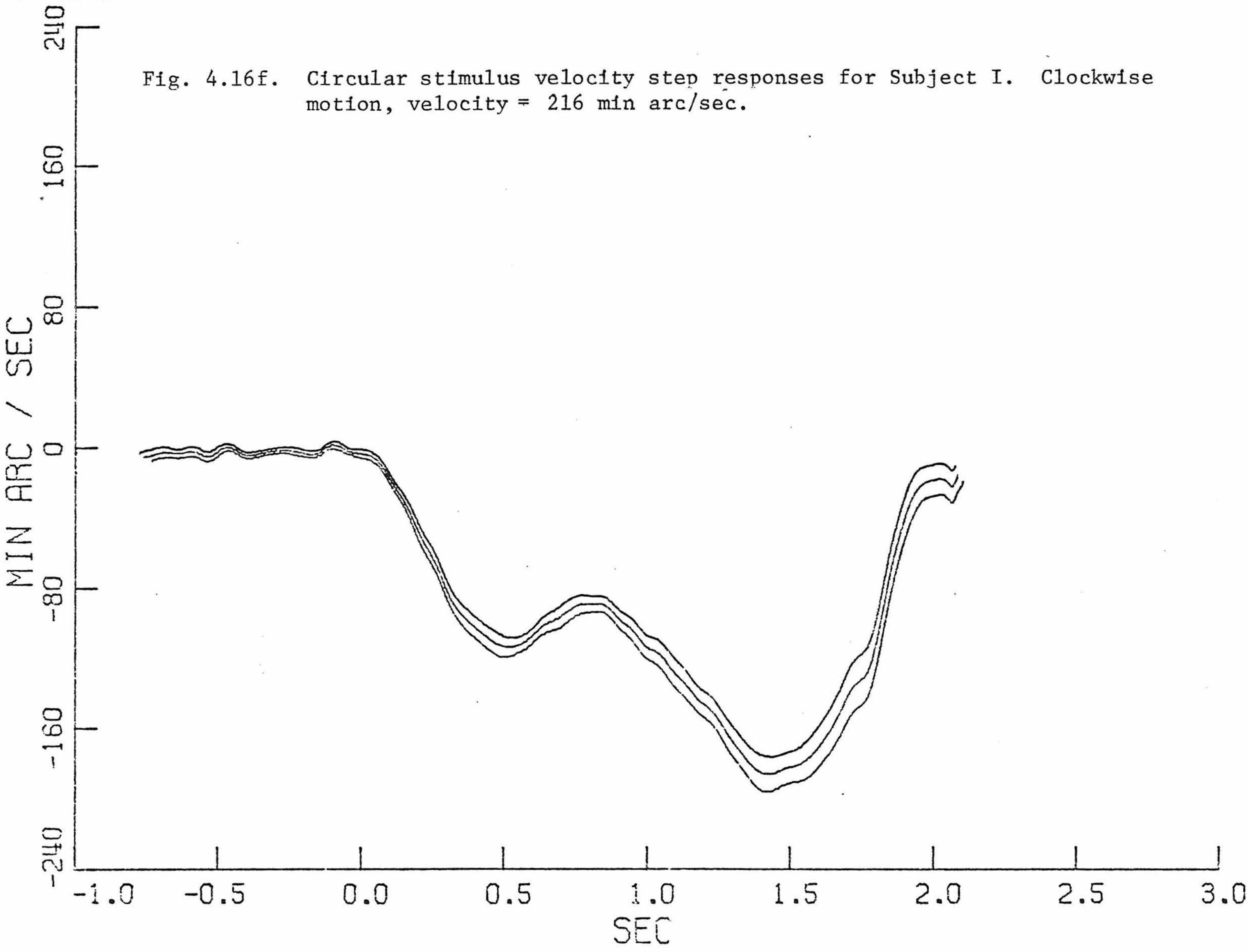


Fig. 4.16f. Circular stimulus velocity step responses for Subject I. Clockwise motion, velocity = 216 min arc/sec.

set of responses (three stimulus velocities, clockwise and counterclockwise motion) are shown for Subject I. As observed for horizontal responses, the standard deviation of the mean response is, in most cases, only a small percentage of the peak response magnitude. Thus, even the increased incidence of saccades in the circular position data has not contributed a response variability.

Let us examine the circular velocity step responses for the characteristics observed in the discussion of the horizontal step responses (Section 4.4.4).

The response latencies indicated by the plots in Fig. 4.16 are nearly equivalent to the values observed in the horizontal velocity response plots. However, when clockwise (negative) and counterclockwise responses are compared, a slight asymmetry appears. The clockwise responses for all three velocity values begin an estimated 50 msec before the counterclockwise responses. No such direction asymmetry was observed in the horizontal response data. The waveshapes of the initial acceleration phase of the two types of motions are nearly indistinguishable. However, final target velocity appears to be achieved in two steps. This effect is most visible in the clockwise (negative velocity) responses. The double step waveform of the circular responses is possibly generated by the independence of the horizontal and vertical systems. During the experiments, subjects were instructed to fixate the top of the circle before each trial. The responses could then be analyzed for repeatability without the effects of variation in angular position on the circular target. Thus, the eye movement began with a large horizontal component, the vertical component coming in when the target motion drew the eye position downward. The second step of the velocity response therefore represents the response of the vertical system. This effect is not as pronounced for counterclockwise movements. The latter velocity responses exhibit a sharp rise in velocity followed by a gradual increase to peak velocity. The response latency difference between positive and negative velocity observed above may be related to the waveshape asymmetry between the two directions of movement.

These variations in response characteristics depending upon direction of eye motion, appear to be nonlinearities generated by the combination of the horizontal and vertical tracking systems. The raw position data also exhibited such directional properties. Most subjects found a particular angular range on the circular target in which their smooth following eye movements broke down into sequences of saccades. Furthermore, the subject represented by the data of 4. 16, showed a direction preference. Clockwise tracking motions showed diminished horizontal-vertical coordination. Thus, the eye position did not correspond with target position for clockwise tracking, while counterclockwise motions showed reasonably good reproduction of the arc of the target circle.

It is difficult to speculate on sources of these directional nonlinearities. A likely possibility is that visual experience has produced a directional preference in composite horizontal-vertical tracking. This line of thought is supported by the observation that each subject exhibited different preferred directions and angular locations for best tracking performance.

Since the target motions in these experiments were rotational, onset and offset of the velocity step were equivalent. The velocity response data then provide an opportunity to inspect the symmetry of eye velocity increase and decrease. In the data of Fig. 4.16, the return to zero eye velocity seems to be sharper than the initial rise of eye velocity from rest. This effect is visible in each plot of the figure and was observed in data from other subjects. Such a velocity response nonlinearity could be generated from either neuromuscular or perceptual phenomena. In circular tracking of an angularly periodic stimulus, both types of effects probably contribute to the nonlinearity. Evidence for a neuromuscular onset-offset asymmetry would have to come from neurophysiology. Recordings of muscle tension and innervation during a velocity step task would indicate whether the reciprocal action of agonist and antagonist is equivalent for onset and offset. Perceptually, cessation of target motion may be more detectable than motion onset. Also, at offset, the system does not have to calculate a new velocity value but must only stop the eye from moving. The onset-offset acceleration time difference is an indication of the time it takes the tracking system to determine target velocity at onset. If it could be shown that neuromuscular activity is equivalent in the two cases, then the above hypothesis would be supported.

The relationship between input acceleration pulse amplitude and output pulse duration was again examined for the circular velocity case in the acceleration response plots of Fig. 4.17. Although the standard deviations are much larger for the acceleration data, compared to the velocity results, response waveshape is preserved.

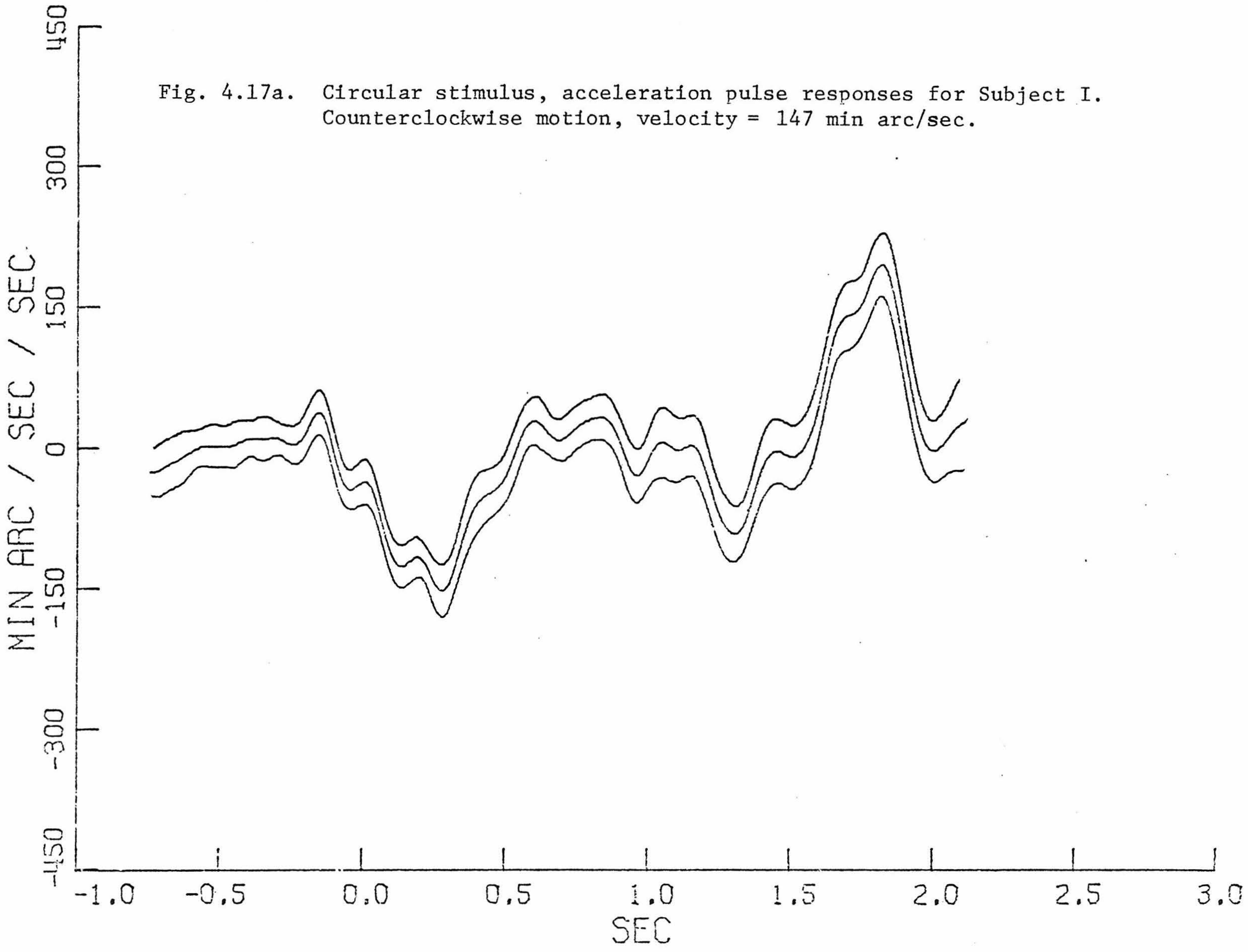


Fig. 4.17a. Circular stimulus, acceleration pulse responses for Subject I.
Counterclockwise motion, velocity = 147 min arc/sec.

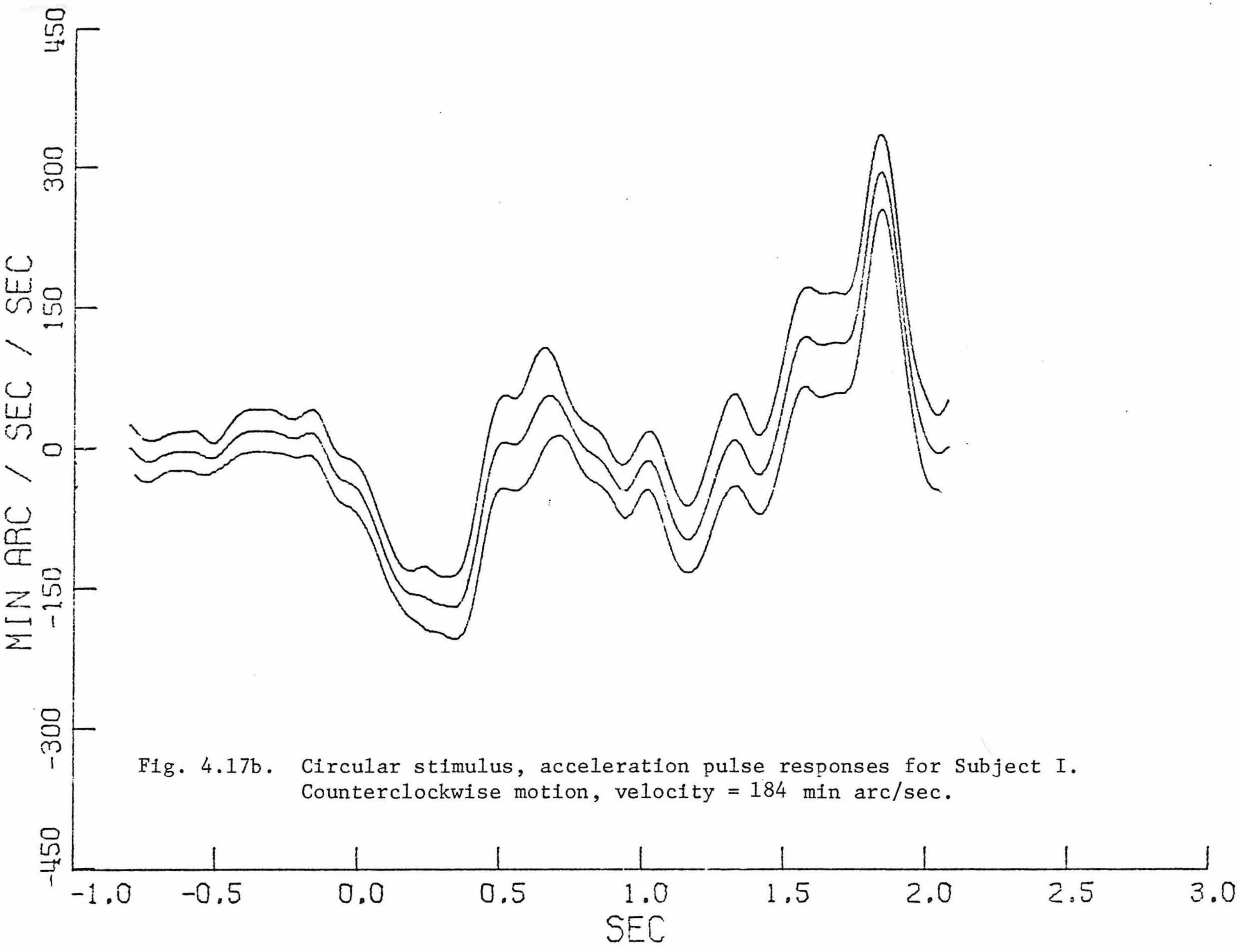


Fig. 4.17b. Circular stimulus, acceleration pulse responses for Subject I. Counterclockwise motion, velocity = 184 min arc/sec.

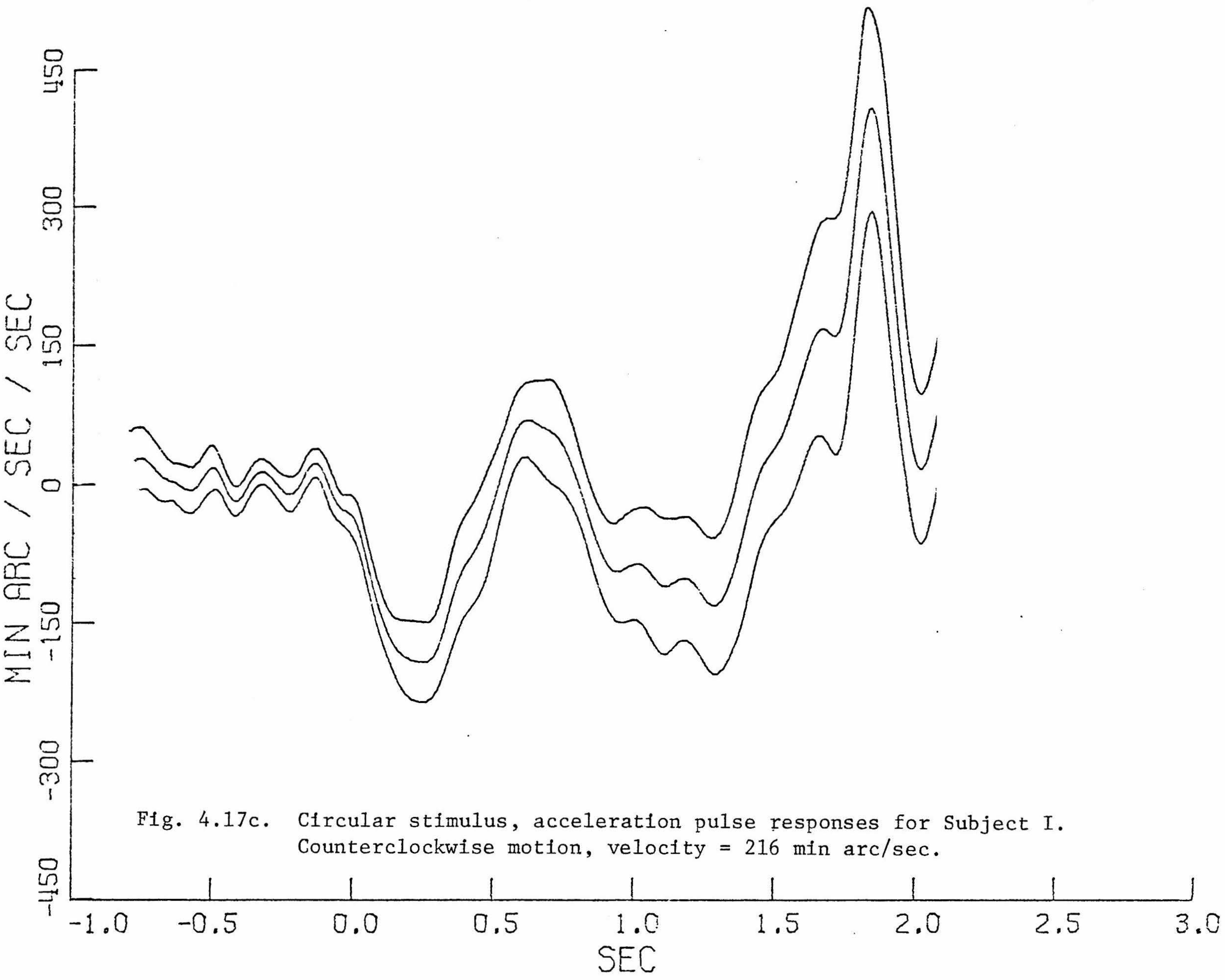


Fig. 4.17c. Circular stimulus, acceleration pulse responses for Subject I. Counterclockwise motion, velocity = 216 min arc/sec.

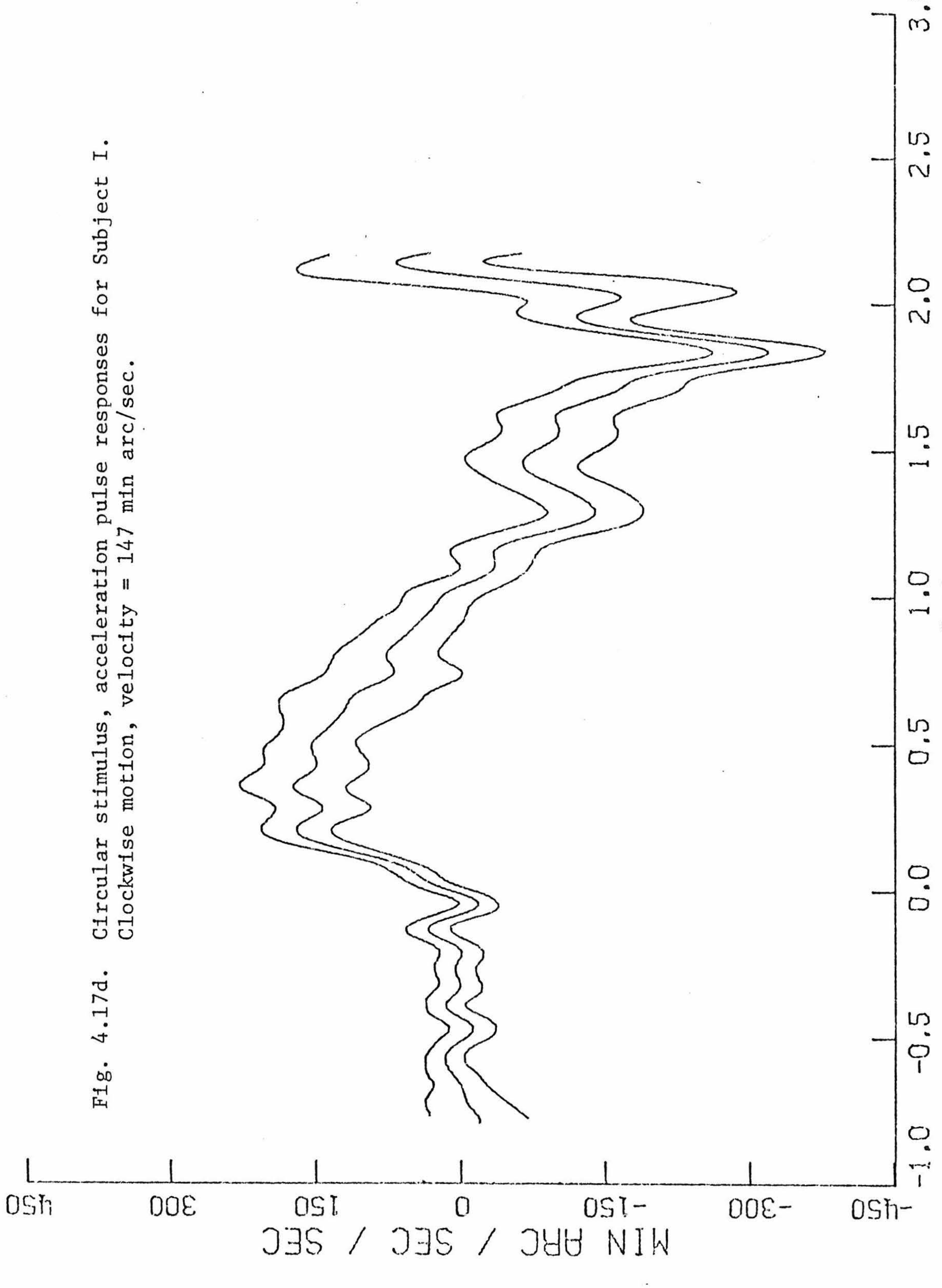


Fig. 4.17d. Circular stimulus, acceleration pulse responses for Subject I. Clockwise motion, velocity = 147 min arc/sec.

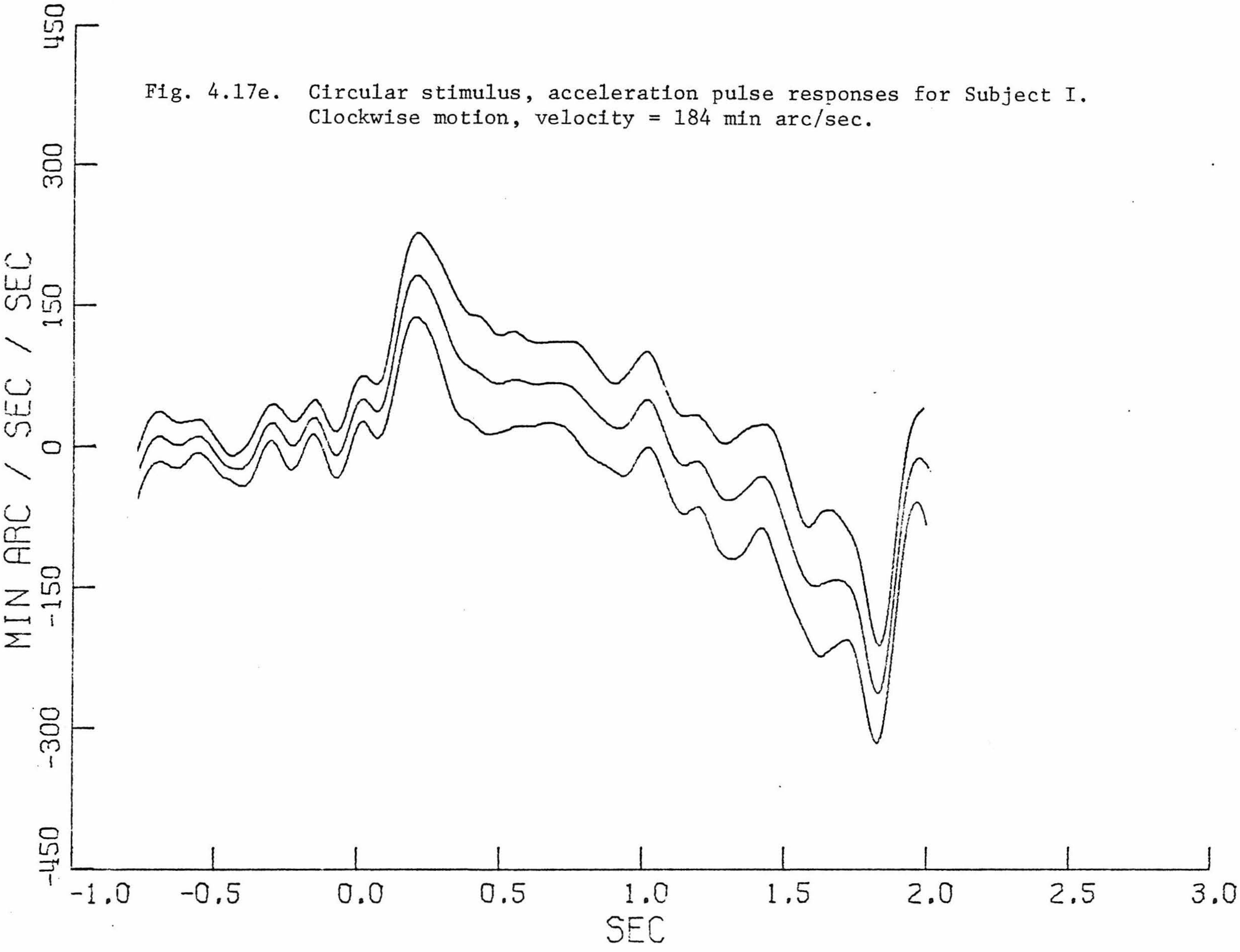


Fig. 4.17e. Circular stimulus, acceleration pulse responses for Subject I. Clockwise motion, velocity = 184 min arc/sec.

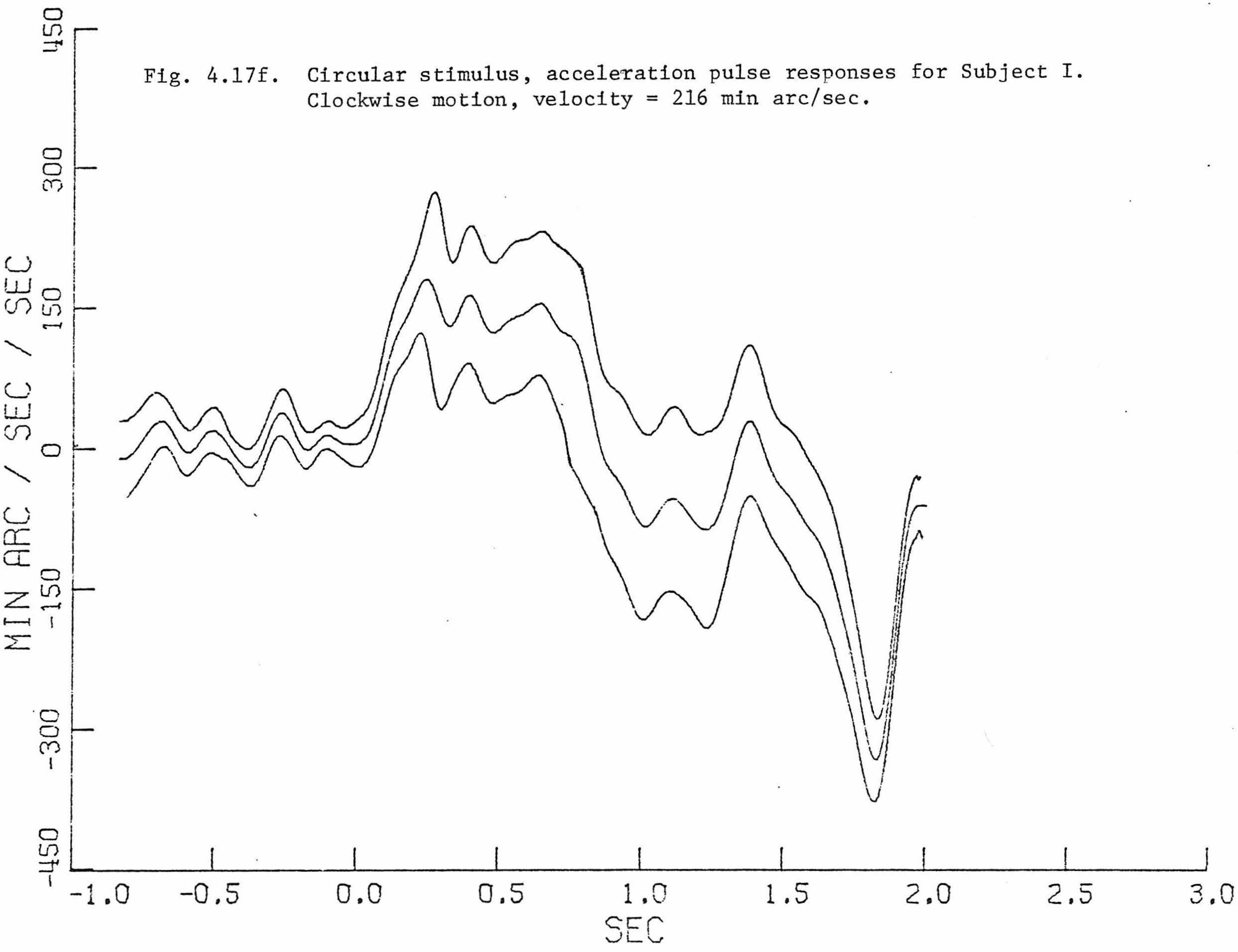


Fig. 4.17f. Circular stimulus, acceleration pulse responses for Subject I. Clockwise motion, velocity = 216 min arc/sec.

Careful comparison of the response onset pulses for the three stimulus velocities show an analogous input pulse amplitude, response pulse duration relationship as observed for horizontal acceleration pulse responses. The effect is easily demonstrated by comparing the leading and trailing edges of the three onset response pulses. The leading edges are nearly superimposable. But as stimulus velocity increases, the trailing edge changes shape and moves forward in time. For the 147 and 216 min arc/sec responses, fall-off of acceleration is rather sharp. The intermediate velocity response exhibits a gradual fall-off in acceleration. The clockwise responses do not show such a clear effect, but the trailing edge of the acceleration pulse still moves forward in time with increasing input velocity. The pulse duration relationship is also demonstrated in the second of the two acceleration pulses of the clockwise circular responses (arising from the double step waveform of the clockwise velocity responses). Furthermore, the increase in pulse duration of the second response pulse is achieved by a shift of pulse onset backward in time with increasing input amplitude while the time of acceleration offset remains relatively stable.

These characteristics of the circular velocity step, acceleration pulse responses indicate that the oculomotor system dynamics are independent of the directional components of the target motion. The latency of acceleration onset, the activity of the saccadic system, onset-offset symmetry, and the relationship between input pulse amplitude and output pulse duration are equivalent with respect to the velocity characteristics of the two types of tracking tasks, horizontal and circular. The data also show, however, that the horizontal and vertical tracking systems maintain relative independence in a task which requires close cooperation between the two components of an eye movement response. The latter characteristic shows up in the double step (double pulse) form of the circular velocity step (acceleration pulse) response. When the major component of target motion is horizontal, the horizontal system dominates the response. As the orthogonal direction component of the stimulus motion increases, the orthogonal system enters into the response. When the velocity of target motion is increased, the onset of activity of the orthogonal system shows a corresponding decrease in latency from stimulus onset, thus achieving the increase in pulse duration with increased angular acceleration pulse amplitude.

The intent in these experiments was to show that a circular tracking task is equivalent to a horizontal task. The results show that the two are not entirely equivalent, the dissimilarity arising from the independence of the horizontal and vertical oculomotor tracking systems. How will such orthogonal system independence affect the results of a general pursuit system analysis based upon a continuous random modulation of target angular velocity? It is likely that the most serious effect will be increased noise in the response data. The noise might take the form of response variability dependent upon the angular position, along the circle, which is being tracked at any given time. Such position information is lost when the position data are converted to tangential velocity. Thus, the additional noise will be uncorrelated with the input signal, and the result of the input-output cross-correlation process will be independent of the noise effect.

The observation that pursuit response transient characteristics were unchanged by the addition of a vertical component to the tracking tasks lends further support to the validity of the circular motion stimulus in analyzing the pursuit system. The latency and acceleration characteristics of a composite horizontal-vertical eye movement seems to be equivalent to those of a unidirectional movement. It might even be argued that the composite movement is a more general case of smooth pursuit tracking. In any case, it seems safe to proceed with the pseudo-random input experiments with the realization that the added angular position information included in the circular stimulus may increase the noise level in the eye movement data in the form of both saccadic responses and horizontal-vertical system independence. We can be confident, however, that the results of the nonlinear analysis will be a true representation of smooth pursuit transient-response characteristics.

V. PSEUDO - RANDOM INPUT EXPERIMENTS

THEORY - PROCEDURES - RESULTS

5.1 Nonlinear System Identification Theory -- Review

In Chapter III (3.2.4) the need for a quantitative description of pursuit linear and nonlinear properties was expressed. The experiments thus far described were intended to explore such system properties in limited situations, that is several velocities of target motion and the transition from one velocity of motion to another. In this section an analysis technique will be described which is capable of testing the system of interest over a much broader range of input conditions within a relatively short period of time. The basic technique and various modifications have been described in detail elsewhere (V. Marmarelis, 1976). It is the purpose here only to provide a general description of the supporting theory behind this nonlinear system identification technique so that when the experimental results are cast in the form of system kernels, the reader will be able to grasp their meaning in terms of oculomotor system characteristics. For more detailed studies of the technique and its applications, the references cited above are an excellent source.

When studying a system whose properties are unknown, it may be helpful to cast the problem in terms of a "black box," the output of which is measurable y(t) with respect to the input x(t). Fig. 5.1 is a block diagram of a system whose properties can be described by a functional F:

$$y(t) = F[\, x(t)] \qquad (5\text{-}1)$$

It is the characteristics of the functional F upon which the identification process is directed. The study of a physically realizable system enables us to express the input-output relation as a function of past time, since in a causal system the present state of the system cannot be affected by events in the future. "Identification" of the system is defined as a mathematical expression of the functional F, consisting of a set of parameters and a set of constants. Thus estimation of the parameters of F is the object of the identification process.

V. Volterra (1930) suggested expanding the functional F as a power series, when the system is a member of the class of systems satisfying three major criteria: i stationarity -- that is, the functional characteristics are time invariant, ii. finite memory -- the response of the system to a stimulus decays to zero in finite time, iii. differentiability -- derivatives of all orders are continuous. The Volterra series takes the form

$$y(t) = \sum_{n=0}^{\infty} \int_{-\infty}^{\infty} \cdots \int_{-\infty}^{\infty} k_n(\tau_1, \cdots, \tau_n) x(t-\tau_1) \cdots x(t-\tau_n) d\tau_1 \cdots d\tau_n \qquad (5.2)$$

where $x(t)$: function input to the system

$k_n(\tau_1, \cdots, \tau_n)$: kernels of the system relating to n th order derivative of F .

Note that the kernels are a function only of τi, a time-shift value, and are thus time independent (expressing the stationarity of the system). The deterministic property of the analysis is manifested in the fact that the kernels take on the value zero for negative argument values (i.e., forward shift in time).

Unfortunately, a mathematical method to estimate the Volterra kernels has not been found. Stimulated by the elegance of the Volterra theory, Wiener (1958) searched for an estimation method and proposed a new functional series, based upon the Volterra series, whose terms are orthogonal to each other for a Gaussian white noise input. The series takes the form

$$y(t) = \sum_{n=o}^{\infty} G_n[h_n(\tau_1,\cdots\tau_n);x(t'),t'\leq t] \tag{5-3}$$

where $x(t)$: Gaussian white noise

G_n: n-th order Wiener functional

h_n: Wiener kernels

The first three Wiener functionals are:

$$G_o(t) = h_o \tag{5-4}$$

$$G_1(t) = \int_o^{\infty} h_1(\tau_1)x(t-\tau_1)d\tau_1$$

$$G_2(t) = \int_o^{\infty}\int h_2(\tau_1,\tau_2)x(t-\tau_1)x(t-\tau_2)d\tau_1 d\tau_2 - P\int_o^{\infty} h_2(\tau,\tau)d\tau$$

where P = Gaussian white noise power level.

The Gaussian white noise (GWN) input and functional orthogonality constituted the real breakthrough in the method. A GWN function is characterized by a unit impulse autocorrelation function, flat power spectrum from zero to infinite frequency, and a Gaussain amplitude distribution. The response of a system to GWN, an input consisting of all possible stimulus functions, provides a complete description of system behavior. Furthermore, since a finite memory system correlates successive input samples, passage of GWN through the system can describe its behavior in terms of the correlation between successive output samples. This intuitively appealing property of the Weiner functionals together with their orothogonality provides the basis for estimating the Wiener kernels, as described by Lee and Schetzin (1965).

A simple illustration of the power of the cross-correlation method of kernel estimation is obtained by considering the case of a constant-parameter linear system. Thus in Fig. 5. 1, the functional F operates on the input x(t), a GWN signal, in a linear fashion to produce the output signal y(t). For a linear system, the system response to any input can be constructed from the superposition of the system impulse responses elicited by unit impulses delivered at time $t' = t - \tau$. Thus

$$y(t) = \int_{-\infty}^{\infty} h(\tau)x(t-\tau)\,d\tau \qquad (5\text{-}5)$$

where $h(\tau)$: system impulse response.

For a physical system

$h(\tau) = 0$, for $\tau < 0$ (causality)

and $h(\tau) \longrightarrow 0$ as $\tau \to \infty$ (finite memory)

Multiplying both sides of equation (5-5) by x(t+ υ) and taking the expected value,

$$R_{xy}(\nu) = \int\int_0^\infty h(\tau)x(t-\tau)x(t+\nu)d\tau \tag{5-6}$$

$$= \int\int_0^\infty h(\tau)x(t+\nu-\tau)x(t)d\tau$$

$$= \int_0^\infty h(\tau)R_{xx}(\nu-\tau)d\tau$$

However, if the input x(t) is GWN with zero mean, $\overline{x(t)} = 0$, then the autocorrelation of x(t) is a unit impulse, so

$$R_{xy}(\nu) = \int_0^\infty h(\tau)\delta(\nu-\tau)d\tau \tag{5-7}$$

and since the delta function has value only at $\upsilon - \tau = 0$

$$R_{xy}(\upsilon) = h(\upsilon) \tag{5-8}$$

Thus, the cross-correlation of the response of a linear system with a GWN input yields the impulse response of the system. Note that for a linear system, the first-order kernel is by definition the system impulse response. The estimation of the n th order Wiener kernel follows an analogous procedure for the case of a nonlinear system.

$$h_n(\tau_1, \ldots \tau_n) = E[\, y(t)x(t-\tau_1) \ldots x(t-\tau_n)]$$

The term kernel estimation is used due to the fact that only finite record lengths are available for real computation. An additional and more serious limitation of the Wiener method arises from the observation that GWN is a physically unrealizable signal, having power at infinite frequency. The solution in practical applications has been to use band-limited GWN, truncating the frequency spectrum of the input at a frequency beyond the response capabilities of the system. The estimation errors introduced into kernel computations by this method have been studied elsewhere (V. Marmarelis, 1976).

The practical limitations of the Wiener GWN method led some researchers to look for other random signals for which a functional series could be orthogonalized and which possess the necessary autocorrelation properties, namely: i. all odd order autocorrelation functions are zero, ii. all even order autocorrelation functions are zero at all off-diagonal points. Marmarelis (1976) has suggested a new random test signal combining the properties of non-redundancy of psuedo-random sequences with the randomness of GWN.

The constant-switching-pace symmetric random signal (CSRS) is defined by two characteristics: (1) the value of the signal switches randomly and independently at each time instant $t = t_o + n\Delta t$, (where Δt is the fundamental finite time interval of the signal), taking values defined by a symmetric probability density function, (2) the value of the signal remains constant between two successive switching times (Marmarelis, 1976). As Δt decreases, the bandwidth of the signal increases, and in the limit approaches that of ideal white noise. The CSRS family satisfies the autocorrelation properties listed above and therefore qualifies as a quasi-white signal for use in nonlinear system identification.

The CSRS kernel estimation procedure is analogous to the GWN case. Thus, the n th order kernel estimate is generated from the cross-correlation of the n th order response with n time-shifted versions of of the stimulus. The equation for the n th order CSRS kernel is similar to that of the Wiener kernel with the addition of a normalizing factor, determined by the time interval Δt and the moments of the signal. The computation of CSRS kernels requires fairly long records as is the case for GWN. The computing time can be reduced by using a ternary CSRS which assumes the values +1, 0, or -1. A variation of this method has been adopted in the present work in order to take advantage of the ease of stimulus generation in the laboratory and to avoid the problems involved in the Wiener method when the GWN signal is band limited, as discussed earlier.

The preceding paragraphs were intended to bring the reader into the domain of nonlinear system identification through quasi-white stimulation. For more detailed treatment of this topic, the references cited within the text provide excellent treatment of mathematical derivations and error estimation. The technique has been implemented on a PDP 11/45 computer and has been made available for this study. I have taken the standpoint of the system user, and the preceding theoretical discussion is indicative of my understanding of the method. My principal interest is in results, rather than rigorous deriviation, while a basic understanding of the technique is deemed a precursor to its use.

5.2 Stimulus Properties and Data Analysis

As described in the last chapter, the stimulus for the pseudo-random input experiments consisted of the rotary motion of the circular target (Fig. 4.1b). From the single pulse experiments using this stimulus, it was determined that angular position along the arc of the circle provided position information to the occulomotor system.

The result was an increased number of saccades which were radially directed in order to correct for drift of gaze position from the stimulus arc. The velocity and acceleration analyses of the last chapter showed that such position information did not alter the properties of the step and pulse responses of the pursuit system. It was concluded that motion of the circular target could be used as the stimulus for a non-linear analysis of the pursuit system using a pseudo-random input signal.

5.2.1 Statistical Generation of the Pseudo-random Stimulus

In the last chapter, the results of ramp position experiments were analyzed in terms of both velocity and acceleration. As interest turned towards the transient properties of the pursuit system, the acceleration analysis proved to be the more valuable method. The results of double acceleration-pulse experiments indicated that the response to two pulses of acceleration was not the simple sum of two single pulse responses spaced in time by the stimulus interpulse interval, as would be predicted from the time superposition principle for linear systems.

The success of the double pulse acceleration analysis was applied to the pseudo-random input experiments in terms of desired stimulus properties. Preliminary attempts with a random modulation of target velocity produced a stimulus which was very difficult for the subject to follow. Since velocity could take on either positive or negative values randomly, direction reversals were quite frequent. When velocity changes were spaced less than about 500 msec, the subject failed to produce eye movements which were well correlated with the stimulus. Since it was the high frequency of large velocity changes which reduced the repeatability of the oculomotor response, a stimulus motion was generated in terms of uniformly spaced acceleration pulses which could take on values -a, o, or + a, according to a uniform probability distribution. Thus during each stimulus interval velocity remained constant. At the end of each interval, velocity could either decrease, remain the same, or increase with the probabilities, 0.25, 0.5, 0.25, respectively. This decision regime increased the occurrence of sequences of "no pulse, pulse, no pulse." With this type of acceleration algorithm, interpulse intervals could be made smaller while decreasing the probability that two successive pulses of opposite polarity will cancel in the response. However, the occurrence of a short string of pulses is not ruled out. Thus, the stimulus is a compromise, allowing the analysis of responses to closely spaced pulses while providing a more easily trackable target motion.

The random acceleration of the target was controlled by the PDP 11/20 lab computer. Sequences of random numbers uniformly distributed between 0 and 255 were generated on another computer (PDP 11/45) using a FORTRAN library subroutine. The sequences output by the program did not repeat up to 2^{32} elements. Several different sequences (generated using different starting numbers) were stored on magtape and subsequently read by the 11/20 experiment control program. This program divided the 0 to 255 range into three ranges such that the probability of an element of the sequence falling into the first range =1/4, second range =1/2, third range =1/4. The program was structured so that an interrupt occurred at the end of a preset stimulus interpulse interval. This time interval was constant for any single two minute run, but could be set by the experimenter at the beginning of the run to 75, 100, 150, or 200 msec. When the interrupt occurred the program retrieved a random number from memory, determined into which range it fell, and changed the target velocity (interval between steps of the motor driven rotary apparatus) correspondingly, i.e. increase, no change, or decrease. The magnitude of the velocity change (acceleration pulse amplitude) was constant throughout a single two minute run, but also could be set by the experimenter before each run. The program then reset the computer's clock and maintained target velocity at the new level until the next interrupt occurred. Analogous to the relationship between a random velocity signal and a random walk position signal (Section 2.1.5), this algorithm produces a variation of a CSRS in acceleration and a random walk velocity signal. Due to the mechanical limitations of the stepping motor apparatus and the velocity tracking limitations of the oculomotor system, an upper velocity limit had to be set. When stimulus velocity reached this level, the system reset itself to zero velocity and then continued in the sequence of random numbers. Through trial and error, it was found that with the pulse interval values listed above, eighteen velocity levels (nine in one direction, nine in the other) and a velocity increment of 7 deg/sec angular velocity produced a pseudo-random motion which elicited strong acceleration responses from the pursuit system without frustrating the tracking abilities of the subject. In a 2 minute run, no more than three or four zero resettings occurred with this stimulus.

The 11/20 program also controlled data acquisition as described for previous experiments. Horizontal and vertical motions of one eye were recorded on magtape. The stimulus position signal was recorded from a potentiometer which was mechanically linked to the rotational apparatus. All experiments were viewed binocularly, a target rotation apparatus being located in the target plane of each side of the optical system.

5.2.2 Extraction of Acceleration Information from Position Data

The stimulus in these experiments was random in acceleration. Therefore, the acceleration information contained in the stimulus and response position data had to be extracted for input to the kernel estimation procedures so that the results could be discussed in terms of input and response acceleration. Angular eye position $\theta(t)$ along the circular target was computed from the horizontal $x(t)$ and vertical $y(t)$ components of the eye response using the arctangent method, i.e.

$$\theta(t) = \text{arctangent}\ (y(t)/x(t)) \tag{5-10a}$$

The radial position component $r(t)$ was also determined as

$$r(t) = (x^2(t) + y^2(t))^{1/2} \tag{5-10b}$$

Thus tangential velocity $v(t)$ is computed from the arctangent and radial data as

$$v(t) = r(t)\ \frac{d}{dt}\ \theta\ (t) \tag{5-10c}$$

and tangential acceleration as

$$a(t) = \frac{d}{dt}\ v(t) \tag{5-10d}$$

The arctangent method was determined to be more expedient for the continous data since only one position signal had to be differentiated to achieve tangential velocity.

The original intent was to apply the low pass filter routines previously developed to the stimulus and response angular position data. However, preliminary attempts proved this method unsatisfactory when power spectra were computed for the position velocity, and acceleration signals. The differentiated data exhibited a concentration of power at high frequencies (20-50Hz) indicating that differentiation noise had swamped the eye response components. Cross-correlations of stimulus and response revealed no components above the noise level. Further low pass filtering of the acceleration signals reduced the high frequency noise component but also distorted the eye acceleration response component.

Obviously, a radical method of determing the second derivative is needed when the original signal is not completely noise-free. In the response data the noise sources are both physiological (eye tremor) and electronic (photomultiplier noise, ambient noise picked up by amplifiers). Noise in the stimulus channel arises mainly from the quantization operation of the potentiometers and the A/D system and partly from amplification of the signals.

The solution to this problem arose from consideration of the nature of the stimulus signal. At each stimulus pulse instance, target velocity was randomly either increased, not changed, or decreased. The theoretical stimulus velocity signal thus would resemble a staircase-type signal, velocity remaining constant throughout the interpulse interval and changing to the new value in the next interval. Such a velocity staircase signal can be regenerated from the target position signal recorded from the digital potentiometers, if the time at which the velocity was changed is known. During each experiment a timing channel was recorded along with eye and stimulus position data. Each time the experimental control program generated an interrupt and changed the target velocity, a 5 msec pulse was sent to the timing channel. A computer program was developed which utilized the stimulus position and timing data as follows. The onset time of each timing channel pulse was first determined. A least mean squares straight line was then fit to the stimulus position data for the time interval between adjacent onset times. The staircase velocity signal was then generated from the velocity values determined from the slope of the fitted line and the corresponding channel onset times. Stimulus acceleration was evaluated as the difference between successive velocity levels. The end result was a sequence of acceleration pulses corresponding to the actual time of event and acceleration amplitude information which was input to the oculomotor for system.

The technique produced a relatively clean representation of stimulus acceleration (Fig. 5. 2). Response velocity is certainly not a staircase-type signal, since the pursuit system generates smooth changes in velocity as evidenced in the last chapter. However, for this stage of the analysis we are concerned with the magnitude and timing of the changes in velocity of the response as compared to the stimulus. Therefore, the response position data was processed using an algorithm similar to the stimulus data analysis.

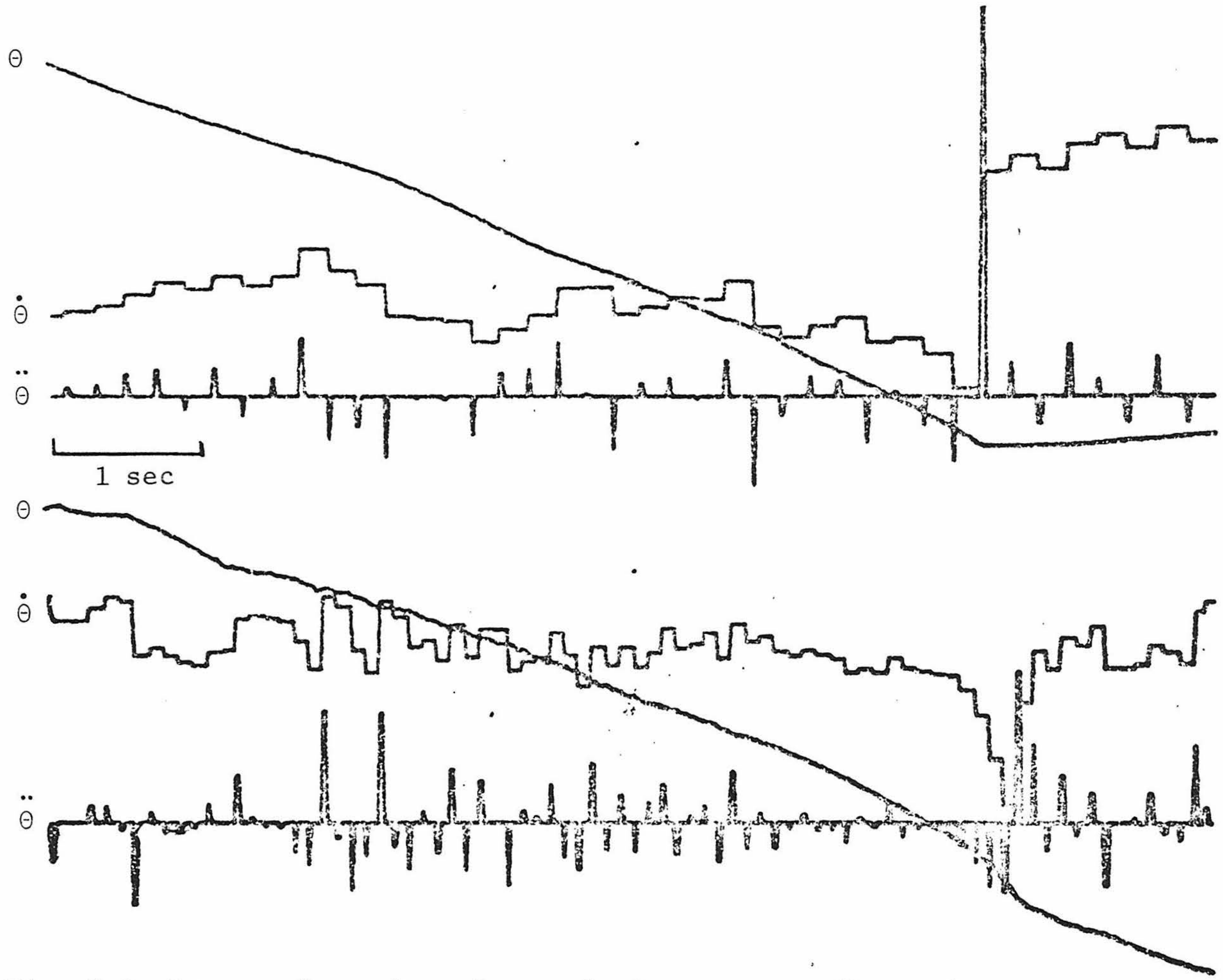


Fig. 5.2 Output of acceleration analysis program. Upper three traces: stimulus position (Θ), velocity ($\dot{\Theta}$), acceleration ($\ddot{\Theta}$). Lower three traces: response position (Θ), velocity ($\dot{\Theta}$), acceleration ($\ddot{\Theta}$).

The response angular position signal was first passed through the saccade and low-pass filtering (15 Hz) program in order to reduce the possibility of generating velocity and acceleration artifacts from saccadic movements and from quantization noise. The time of event (TOE) of each stimulus timing channel pulse and the midpoint of each interpulse interval were determined. The slope of the least mean squares line fit to the response data between the stimulus pulse and the midpoint of the next interval was used to generate a staircase angular velocity signal. Tangential staircase velocity and acceleration-pulse signals were computed by multiplying the angular velocity value by the average radial position component within the corresponding time interval. Including the TOE of the midpoint of the stimulus interpulse interval in the response analysis increased the resolution of the method twofold. However, for stimulus interpulse intervals 100 msec or less, the increased noise in the acceleration signal was too high a price to pay for increased time resolution of the analysis so the midpoint was not used for those data.

This method of extracting the acceleration information from an eye position signal may seem quite radical. However, the nature of the data, i. e. physiological and electronic noise superimposed upon slow eye velocity changes, makes a conventional differentiation analysis useless. The truncation of the data into time bins, 100 msec and larger, is not as harsh as filtering at extremely low frequencies in order to reduce differention noise. Adjacent velocity step calculations are completely independent whereas, in a filtering operation, each data point is highly correlated with all data points within the extent of the filter window. The results to be presented will show that the new data analysis techniques are valid and that, without directly measuring an acceleration signal, the procedures produce the best attainable representation of the acceleration information of stimulus eye position data.

5.2.3 Stimulus Autocorrelation Properties

In Section 5.1, the autocorrelation properties which characterize a quasi-white signal were described. For a physically realizable quasi-white signal, the autocorrelation function should attain its peak value at $\tau = 0$, i.e. zero time shift. If other peaks are present, their amplitude should be a small percentage of the main peak amplitude, and they should occur at small time shift values. The side lobes are generated by the departure of a signal from true white noise. The truncation of the frequency spectrum at a finite value by filtering causes some correlation of neighboring points of the signal.

In Fig. 5.3, the first-and second-order autocorrelation functions of some of the stimulus records used in the present study are plotted. All the first-order functions are similar in showing the largest peak centered at $\tau = 0$ and two negative side peaks at τ equal to the stimulus interpulse interval. Also, no other major peaks are present out to time shifts of 2 sec. Apart from the negative side lobes then the stimulus autocorrelation functions represent the acceleration input as a quasi-white signal. The side lobes can be explained by considering the nature of the computation of the acceleration signal. Each acceleration pulse is a function of the difference between the average velocity in the interval after the pulse TOE and the average velocity

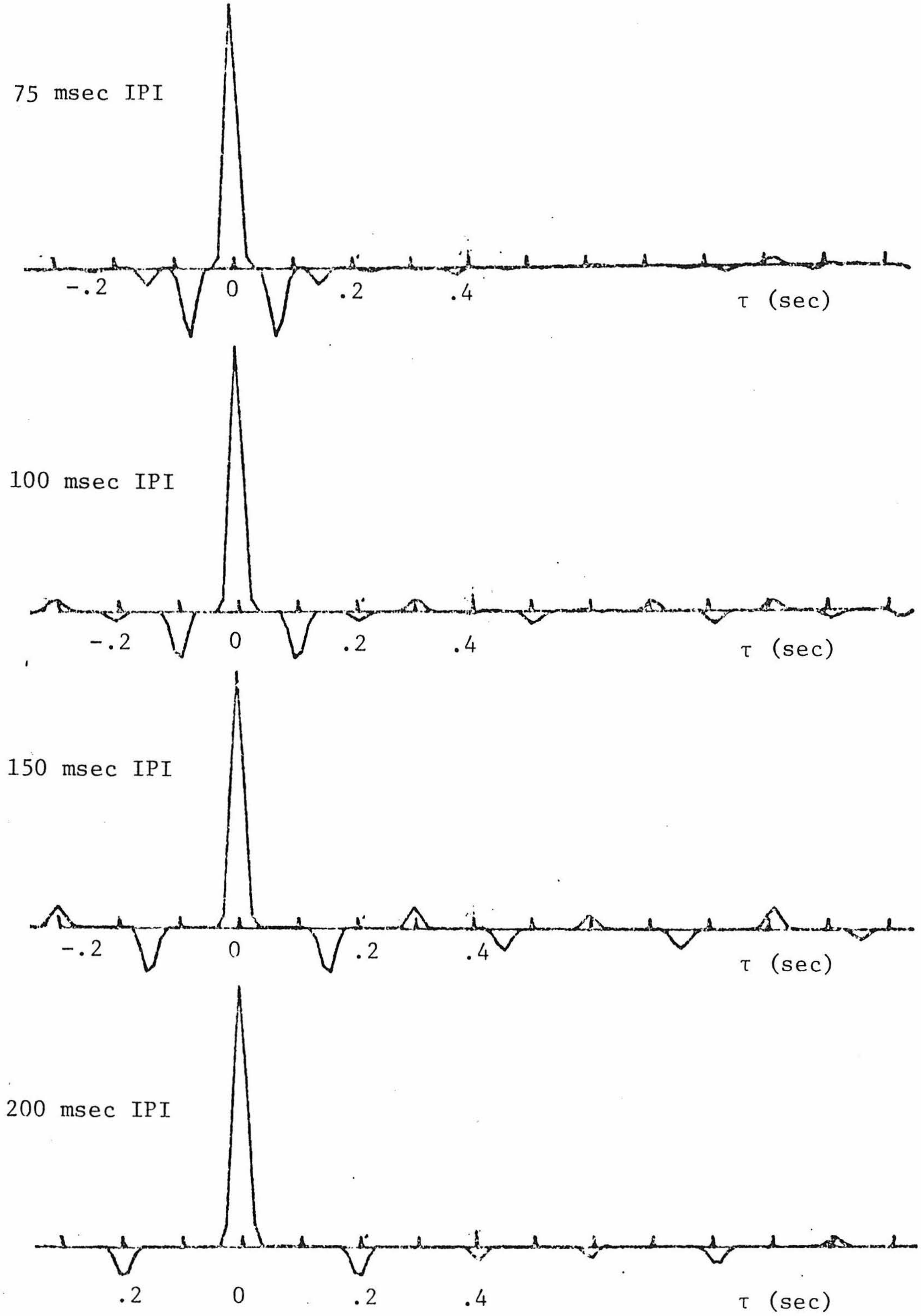


Fig. 5.3a Stimulus first-order autocorrelation functions for 75, 100, 150, and 200 msec interpulse intervals.

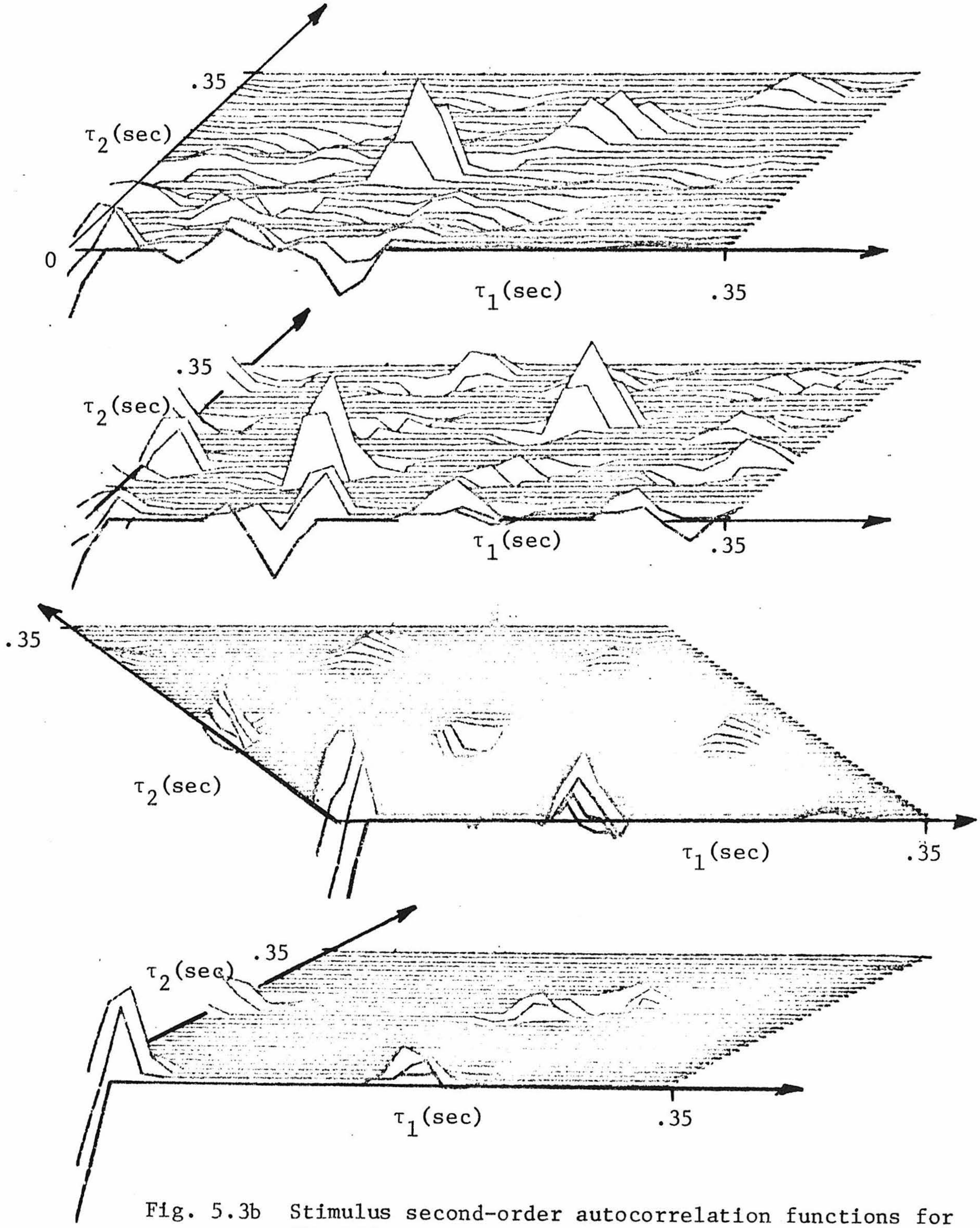


Fig. 5.3b Stimulus second-order autocorrelation functions for 75, 100, 150, and 200 msec interpulse intervals. (150 msec function viewed from different angle)

in the preceding interval. The differencing operation generates a negative correlation between neighboring pulses, and thus the side lobes of the first-order functions of Fig. 5. 2. At attempt was made to correct this artifact in the data analysis procedures by computing the magnitude of the acceleration pulses from the average velocity a half interpulse interval before and after the pulse TOE. However, the small number of points included in the estimates of velocity increased the noise level of the analysis above an acceptable level.

The second-order autocorrelation functions of Fig. 5. 3 are a representation of the interaction between pulse pairs in the stimulus signal. In all plots of second-order functions, the x- and y-axes, τ_1 and τ_2, represent time between stimulus pulses; and: the z-axis is the magnitude of the nonlinear interaction between the two pulses occurring τ_1 and τ_2 seconds before. The form of the second-order stimulus autocorrelation functions Rxx (τ_1, τ_2) indicates that the major interaction occurs when $\tau_1 = \tau_2$ = interpulse interval and when $\tau_1 - \tau_2$ = interpulse interval. The negative peak of the function on the main diagonal is a manifestation of the negative correlation between each pulse and the preceding pulse due to the velocity differencing operation discussed above. The positive off-diagonal peak at τ_1 = interpulse interval, $\tau_2 = 0$, shows that the negative correlation with the preceding pulse is not as strong as the correlation of the present pulse with itself. The fact that very little structure is present when τ_1 and τ_2 are greater than the interpulse interval supports the use of this stimulus signal as a quasi-white input for nonlinear system analysis.

5.3 Results of Nonlinear Analysis of Pursuit Acceleration

The random acceleration experiments required the total concentration of the subject on the task of tracking circular motion of the circle of dots. Experimental runs were limited to two minutes in length. The subject relaxed for a few minutes, then another run was initiated. In this regime, nine to ten experiments could be completed before the subject began to fatigue. The experiments were terminated at this point since correlation between the eye movements and the stimulus motion degenerated drastically if the subject was not sufficiently alert. In the preliminary stages of data analysis, the effects of subject fatigue could be seen as increased frequency of saccades and blinks and wander of gaze position from the arc of the stimulus circle. Data from such experiments were not included in the cross-correlation results to be presented.

Four experiments are included in the analysis. Stimulus acceleration pulse amplitude and maximum allowed velocity were held constant for all experiments. Four values of stimulus interpulse interval (IPI) were used: 75, 100, 150, and 200 msec. As discussed previously, response acceleration pulses were computed every IPI for the 75 and 100 msec data, and every IPI/2 for the 150 and 200 msec data.

The first-order kernels for one set of the four experiments are plotted in Fig. 5.4a-d. The computations were extended to negative time in order to assess the noise level in the cross-correlation calculation. Any correlation of the response with the stimulus before time zero must be attributed to noise by the causality principle. Consider the sampled nature of the data in Fig. 5.4. Response peaks uniformally occur at the sampling interval of the acceleration data analysis procedure, i.e. 75 or 100 msec. The half-width of the stimulus autocorrelation function (Fig. 5.3) is an estimate of the precision of the correlation method, and is a function of the sampling interval of the data and variations in the time of event of the stimulus pulses. The half-width for both stimulus and response functions is approximately 40 msec, while the peak response, in all four plots of first-order kernels, occurs no earlier than 150 msec. The reliable occurrence of peaks in the acceleration kernels between 150 and 300 msec is an effect which cannot be attributed to chance. We must conclude that the functions are a representation of the true response properties of the pursuit system.

The kernels for the four experiments are consistent in predicting a pursuit acceleration response which begins at 150 msec and is over 300 msec after the stimulus pulse was delivered. Although the amplitude characteristic of the plots is significantly above the noise level, the kernels exhibit some variation in the response amplitude envelope which they describe. The variation is not apparently related to the stimulus properties, but to the existence of noise in the timing and amplitude information generated by the acceleration extraction procedures.

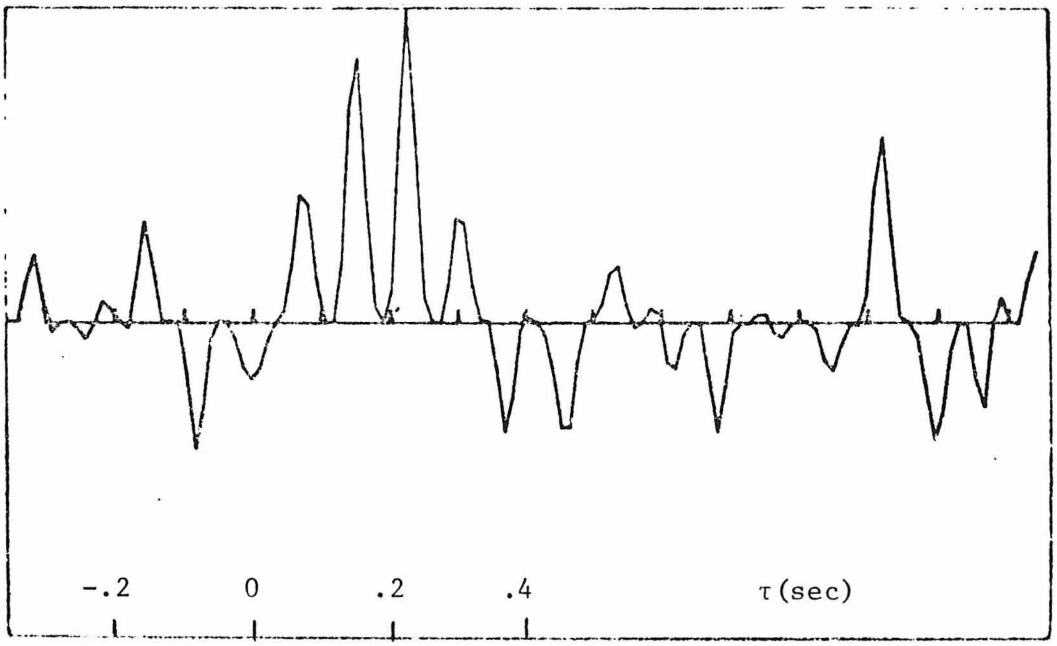


Fig. 5.4a First-order kernel for 75 msec IPI experiment.

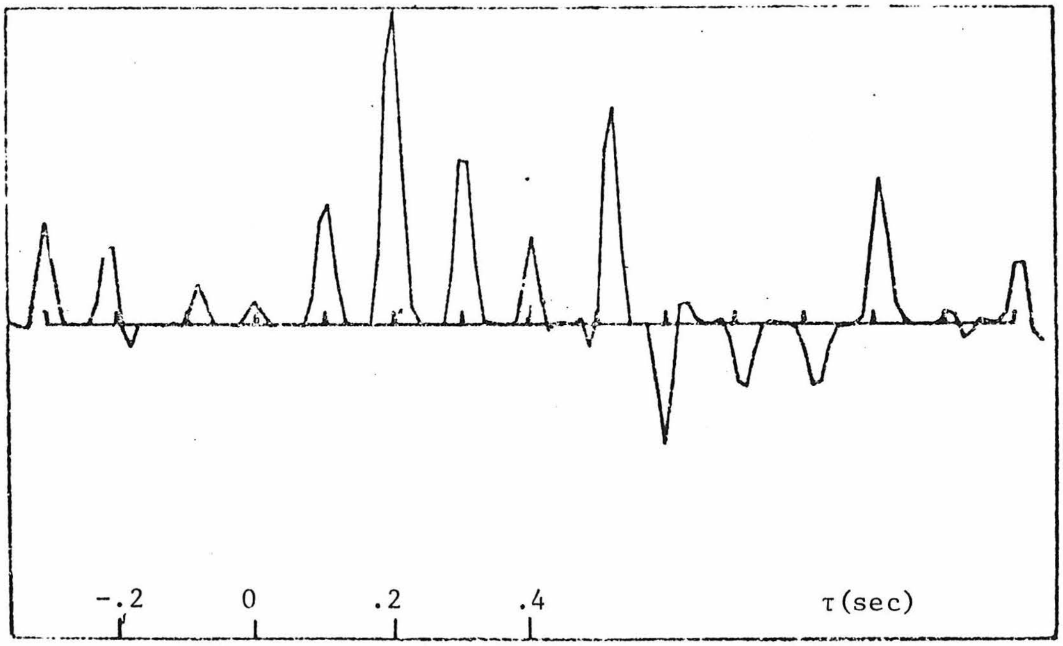


Fig. 5.4b First-order kernel for 100 msec IPI experiment.

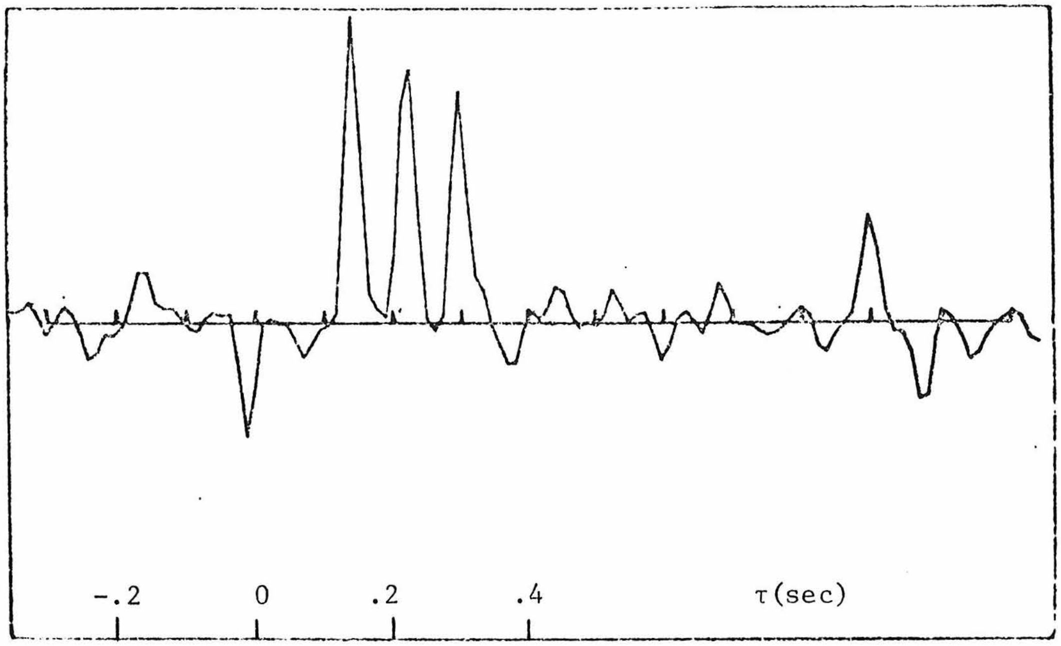


Fig. 5.4c First-order kernel for 150 msec IPI experiment.

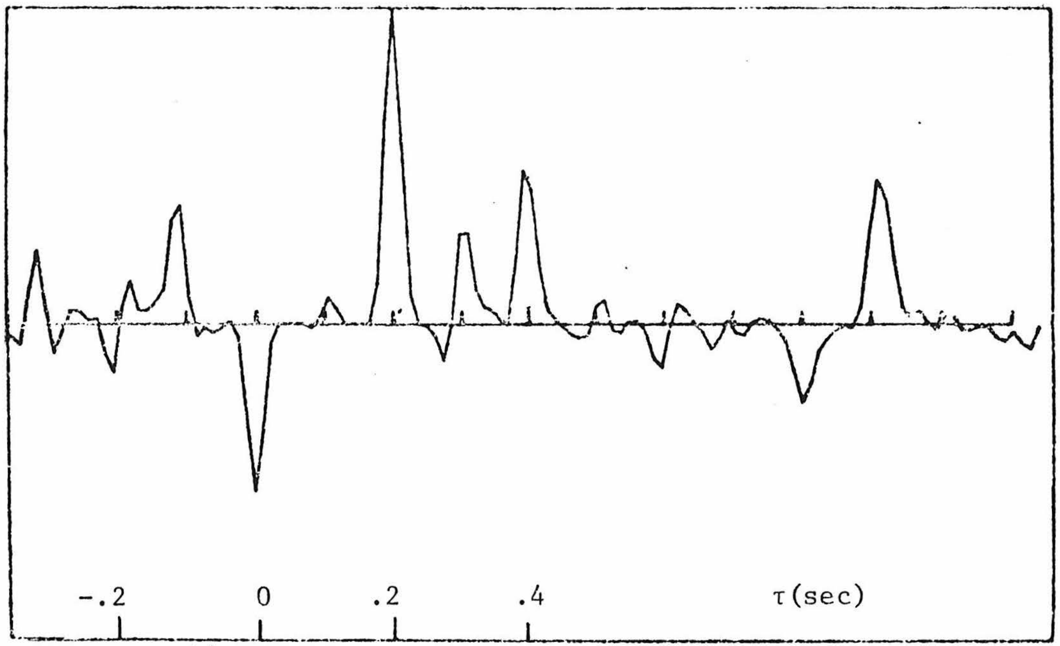
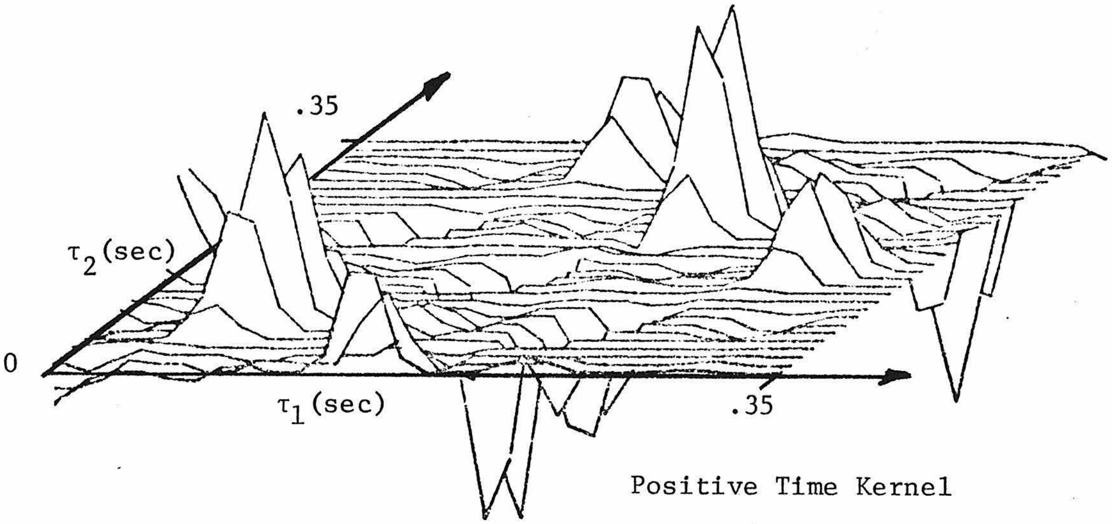


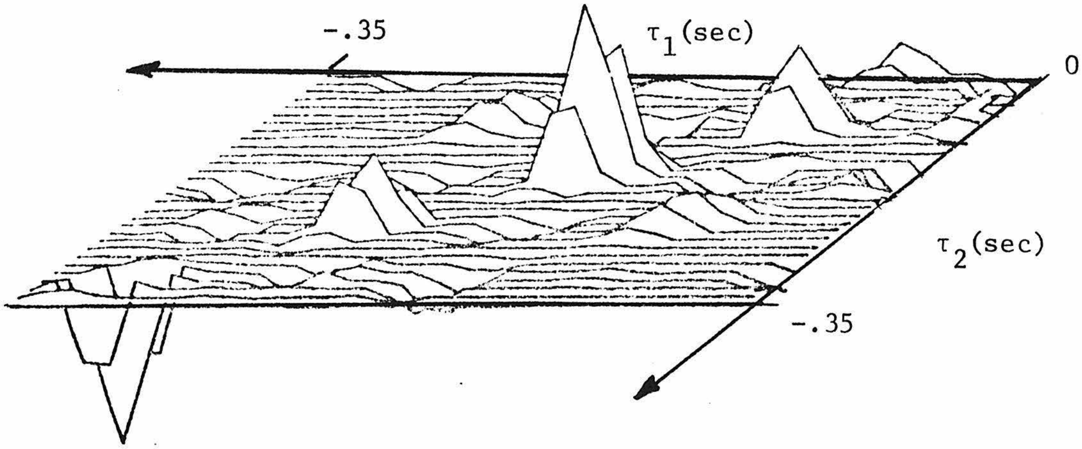
Fig. 5.4d First-order kernel for 200 msec IPI experiment.

If the four plots of Fig. 5.4 are considered independent samples of the true pursuit response characteristic, an amplitude envelope of the Wiener system kernel is obtained. The independence of the system time characteristics, indicated by the set of plots, from the frequency bandwidth of the stimulus (an inverse function of the interpulse interval) indicates that the first-order kernels are a reliable estimate of the linear component of the system function.

Relief plots of second-order kernels obtained from the data sets used to compute the kernels of Fig. 5.4 are plotted in Fig. 5.5a-d. All four kernels of Fig. 5.5 show structure concentrated about the main diagonal, $\tau_1 - \tau_2$ 40 msec, and a diagonal which corresponds to the UPI of the stimulus signal, i.e. $\tau_1 - \tau_2$ -IPI 50 msec. The 40 msec half-width of the diagonal structure corresponds to the precision of the analysis technique as defined by stimulus

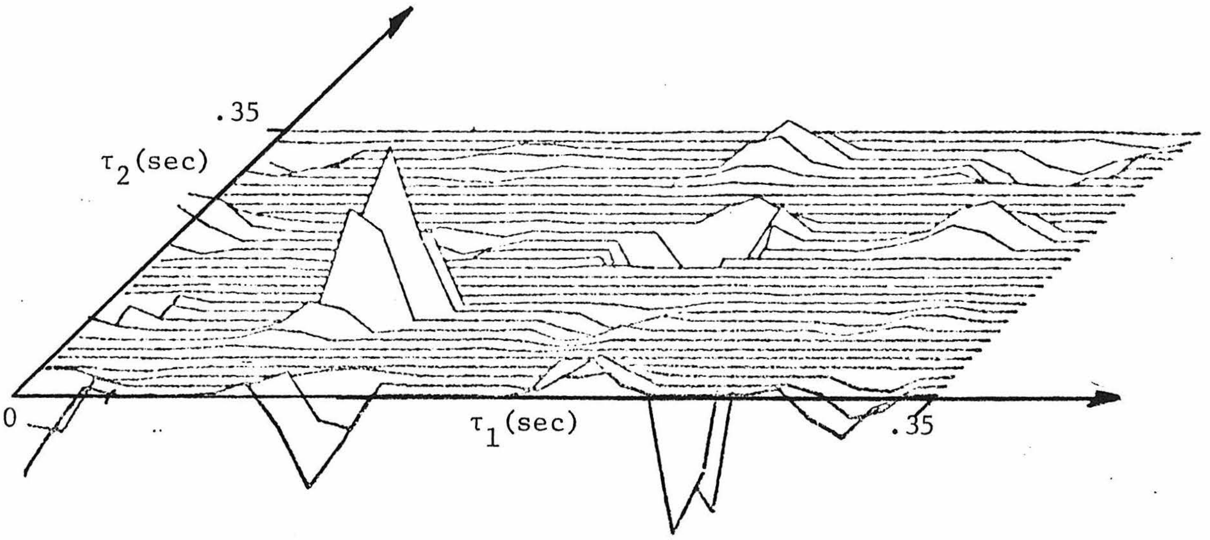


Positive Time Kernel

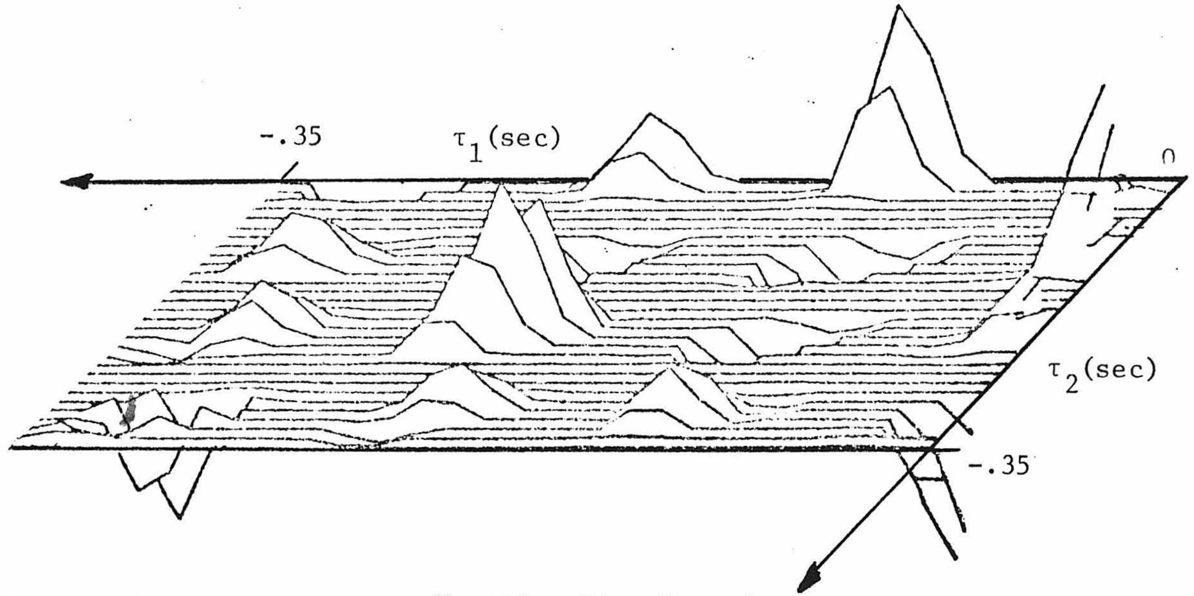


Negative Time Kernel

Fig. 5.5a Second-order kernel for 75 msec IPI experiment.
Upper plot: positive time kernel.
Lower plot: negative time kernel.

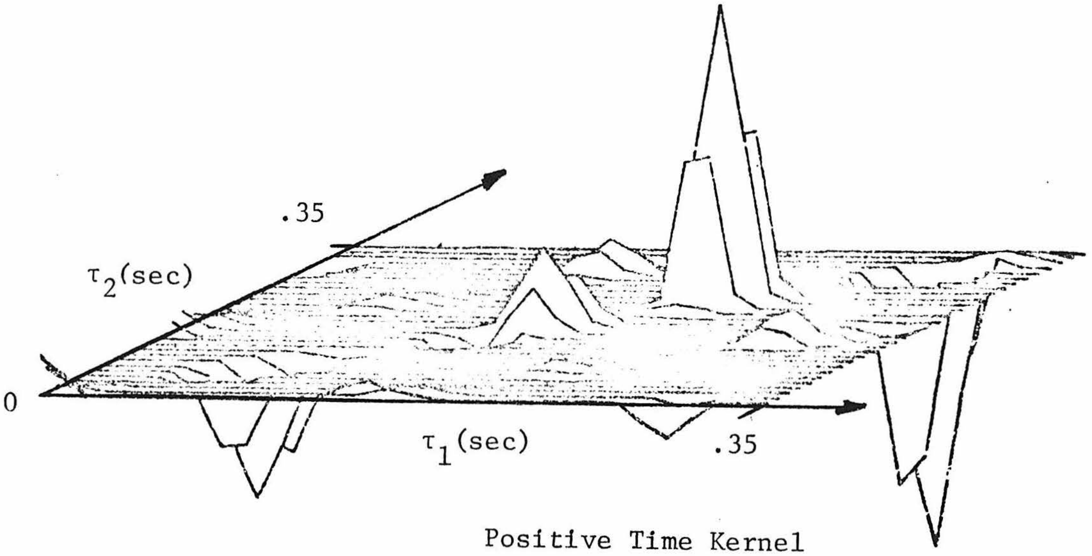


Positive Time Kernel

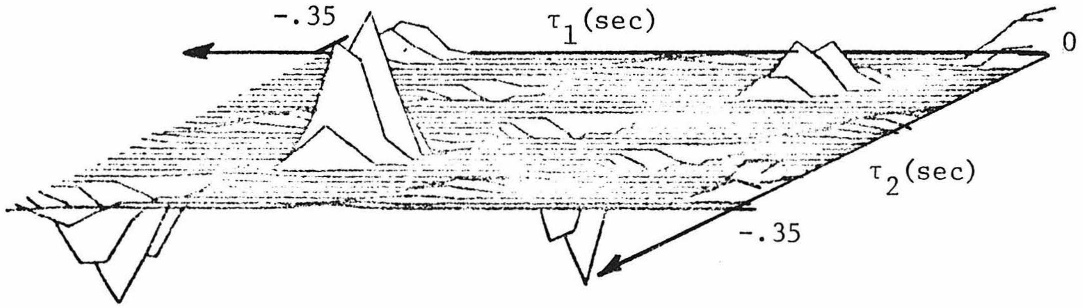


Negative Time Kernel

Fig. 5.5b Second-order kernel for 100 msec IPI experiment.
Upper plot: positive time kernel.
Lower plot: negative time kernel.

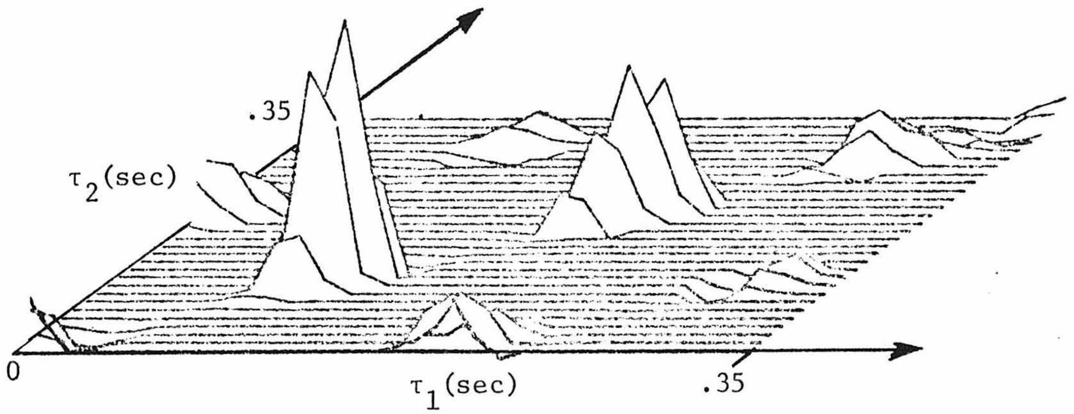


Positive Time Kernel



Negative Time Kernel

Fig. 5.5c Second-order kernel for 150 msec IPI experiment.
Upper plot: positive time kernel.
Lower plot: negative time kernel.



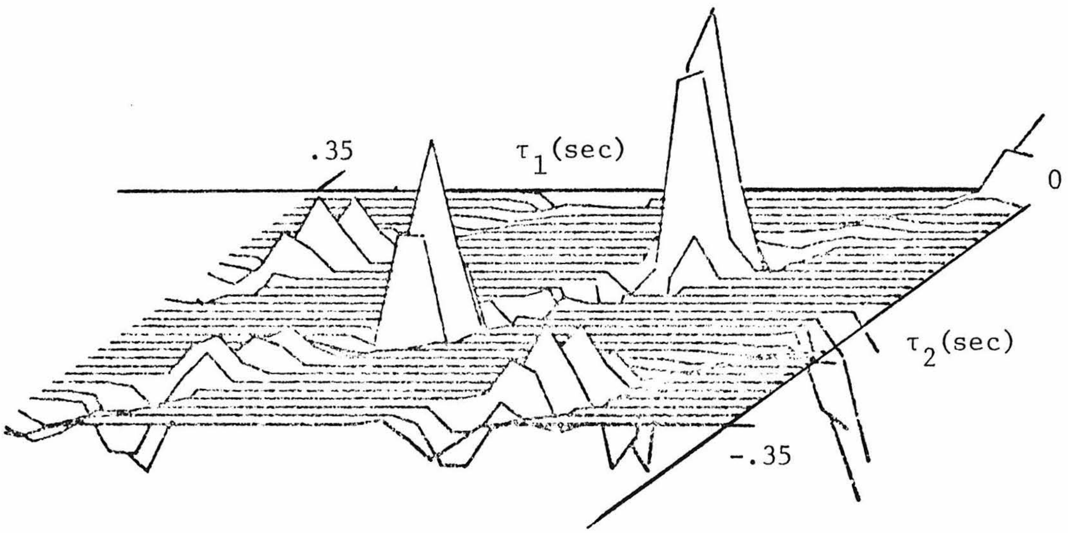


Fig. 5.5d Second-order kernel for 200 msec IPI experiment.
Upper plot: positive time kernel.
Lower plot: negative time kernel.

autocorrelation functions. Analogous to the first-order kernel structure, the second-order kernels contain significant information only at time intervals along the main diagonal axis which correspond to the sampling interval of the data analysis procedure. As a test of the significance of the diagonal form of the second-order kernels, kernel computations were extended to negative time. The pursuit response was cross-correlated with the stimulus shifted forward in time to evaluate the magnitude of the correlation between the two signals due to chance. The negative time kernels are displayed below each corresponding positive time kernel in Figs. 5. 5 (a-d). For the positive time kernels, $\tau_1, \tau_2 = 0$ occurs at the lower left corner of the relief plot. In the negative time plots, $\tau_1 = \tau_2 = 0$ occurs at the upper right corner of the plot. Second order kernels were generated only for data which gave relatively clean first-order kernels, i. e. those in which the response peaked at 150 to 300 msec. Examination of the negative regions of both first and second-order kernels reveals the occasional presence of large peaks, or substantial stimulus-response correlation before the stimulus had occurred. In the first-order kernels, the peaks which occur between 150 and 300 msec are very repeatable from one experiment to the next, independent of the stimulus IPI, while the peaks for $\tau < 0$ occur at non-repeatable times. For the second-order kernels this type of evaluation is not applicable since it is unlikely that the second-order response is independent of the stimulus characteristics. Thus the presence of peaks in negative time which are of comparable amplitude to positive time peaks, makes the interpretation of second-order functions of questionable value.

Fig. 5.5a indicates that the second-order kernel for the 75 msec IPI stimulus may be a reliable representation of the system second-order kernel for this stimulus IPI. The negative time plot shows only one relatively large peak at $\tau_1 = \tau_2 = -150$ msec. The main diagonal peaks in positive time are larger than the artifacts in negative time and were found to be repeatable in several experiments. The large peak in negative time in Fig. 5.5b overpowers any of the peaks in positive time for the 100 msec IPI kernel. For the 150 msec IPI kernel (Fig. 5.5c), the negative time plot again indicates that the positive time function may be a reliable second-order kernel. Also, note that the negative time kernel shows no structure in the secondary diagonals ($\tau_1 - \tau_2 = 150$ msec), whereas the positive time kernels show several peaks at $\tau_1 = 300$ msec, $\tau_2 = 150$ msec. Other 150 msec kernels exhibited some correlation in structure--more data are needed however before a mathematical model could be based upon these kernels. The 200 msec IPI kernel (Fig. 5.5d) is likely to be unreliable because of the strong main diagonal structure in negative time. Other kernels, first and second-order, obtained with this stimulus were also unreliable. The 200 msec stimulus pulse spacing may have allowed target velocity to remain near zero for extended periods. The resulting fixation eye movements would generate substantial response activity uncorrelated with the stimulus.

Unlike the first-order kernel structure, the second-order kernels are not independent of stimulus bandwidth. A comparison of the 75 msec and 150 msec response kernels, each computed at 75 msec sampling rate, indicates variations in both main and secondary ($\tau_1 - \tau_2$ = IPI) diagonal structure. The 100 msec and 200 msec functions should also be compared. In some instances corresponding peaks are inverted in these comparisons. Again, we cannot distinguish between the possibilities that such variations are a manifestation of unreliability or true stimulus dependence. Also, note that although the 150 and 200 msec response functions were computed from 75 and 100 msec sampled acceleration signals respectively, the secondary diagonal is always displaced from the main diagonal by the stimulus IPI. This effect is due to the fact that stimulus acceleration occurred only at the IPI (150 msec) while the response acceleration pulses were computed every 75 msec. In the second-order kernels, time from stimulus onset increases along the diagonal direction of the plot. Thus response information is available every half IPI. The x and y axes represent the time separation of the stimulus pulses, i. e. the IPI. Therefore information is available only at the stimulus pulse time of event.

5.4 Discussion

The hypothesis has been advanced that the first and second-order kernels produced in this study are a sampled estimation of the true pursuit system acceleration kernels. The sampled form of the functions is a direct result of the pulse nature of the stimulus and response signals. The system was tested with stimulus interpulse intervals which closely corresponded to the integration time of the system as determined from single pulse experiments. The latter two properties of the experimental analysis are responsible for the discrete nature of the kernels. If we had been able to elicit reliable responses with closely spaced pulses (5-10 msec) and if a clean continuous acceleration signal had been available for kernel calculations a more complete representation of the pursuit functional would have resulted. Apparently a complete nonlinear identification of the pursuit system is not achieved by these results. However, several of the kernels which have resulted from the analysis contain information significant above the level of chance and therefore can be interpreted in terms of some characteristics of the pursuit system.

We shall clarify the sampled nature of the second-order kernels and their guarded interpretation via the following argument. In the Wiener formulation of nonlinear system identification, the response y(t) is a function of the sum of the n th order functionals defined by equations (5-4). Assume for the moment that the pursuit response can be well represented by the first three terms of the function (5-3). The first term $G_o = h_o$ is merely the time average of the response y(t). In our case $h_o \simeq 0$ since the response has been computed in terms of the second derivative of a position signal, a process which removes all dc information. The system response at any time t can then be written,

$$y(t) = \int_0^\infty h_1(\tau_1)x(t-\tau_1)d\tau_1$$

$$+ \iint_0^\infty h_2(\tau_1,\tau_2)x(t-\tau_1)x(t-\tau_2)d\tau_1 d\tau_2 \qquad (5\text{-}11a)$$

If an impulse of acceleration was delivered at $t=0$, $x(t)=\delta(t)$, the response would be

$$y(t) = \int_0^\infty h_1(\tau_1)\delta(t-\tau_1)d\tau_1 + \iint_0^\infty h_2(\tau_1,\tau_2)\delta(t-\tau_1)\delta(t-\tau_2)d\tau_1 d\tau_2 \qquad (5\text{-}11b)$$

Since the delta function $\delta(t-\tau)$ is non-zero only when $\tau = t$,

$$y(t) = h_1(t) + h_2(t,t). \qquad (5\text{-}11c)$$

Similarly, the response to an impulse at $t=t_o$, $x(t) = \delta(t-t_o)$, is

$$y(t) = h_1(t-t_o) + h_2(t-t_o\ ,\ t-t_o) \qquad (5\text{-}11d)$$

Now, the response of the system to a pair of pulses, i.e. $x(t) = \delta(t) + \delta(t-t_o)$ is

$$\begin{aligned} y(t) &= \int_0^\infty h_1(\tau_1)[\delta(t-\tau_1) + \delta(t-t_o-\tau_1)]d\tau_1 \qquad (5\text{-}11e) \\ &+ \iint_0^\infty h_2(\tau_1,\tau_2)[\delta(t-\tau_1) + \delta(t-t_o-\tau_1)][\delta(t-\tau_2)+\delta(t-t_o-\tau_2)]d\tau_1 d\tau_2 \\ &= h_1(t)+h_1(t-t_o)+h_2(t,t)+h_2(t,t-t_o)+h_2(t-t_o,t) \\ &+ h_2(t-t_o,\ t-t_o) \end{aligned}$$

Now, if the response of the system to each impulse when delivered alone (equations 5-11c and 5-11d) is subtracted from the total response, then we have,

$$y'(t) = 2\,h_2(t,\ t-to) \qquad (5\text{-}11f)$$

since the second-order kernel $h_2(\tau_1, \tau_2)$ is symmetric about the main diagonal.

Thus, the second-order kernel can be interpreted as the deviation of the system double pulse response from the linear time superposition of the response to each pulse when delivered alone. Negative regions in the kernel mean that the double pulse response is less than predicted by linearity at the specific values of pulse separation and time from the first pulse. Positive regions indicate a nonlinearity in the positive direction relative to the linear prediction. In the experiments the stimulus actually consisted of a series of pulses with finite width which were separated by 75 to 200 msec. Thus in the above argument, the delta function is replaced by a pulse, and the integral can be replaced by a summation. The argument for this real case is analogous to equations (5-16) resulting in the interpretation of the second-order functions of Fig. 5. 5 as finite width samples of the actual system kernel at integral multiples of the stimulus pulse separation time.

As an example, consider the 75 msec IPI kernel of Fig. 5. 5a. If a diagonal cut is taken through the positive time kernel at $\tau_1 - \tau_2 = 150$ msec, a single-valued function of time from occurrence of the first pulse is obtained. The extension of this diagonal in negative time shows very little activity. At 75 msec after the occurrence of the second pulse, the negative peak indicates that the double pulse response is suppressed as compared to the predicted superposition response. At 150 msec after the second pulse (i. e. $\tau_1 = 300$, $\tau_2 = 150$) the peak has become positive indicating a greater response amplitude than predicted by linearity. This time course of the difference between actual and linear responses corresponds to the results of the double pulse experiment of Chapter IV. In the discussion of those data (Fig. 4. 13), the actual response amplitude was found to be smaller and the duration longer than the linear predicted response to two pulses. Similar occurrences of negative regions followed closely by positive regions can be found in several of the other kernels which are believed to be reliable.

These guarded interpretations of second-order kernel structure establish some agreement with the results of the more conventional analysis of the last chapter. It must be emphasized, however, that the second-order kernels are only marginally reliable. In the concluding chapter we shall discuss some suggestions for improving the nonlinear analysis methods for the study of the pursuit system. The space and time limitations of this dissertation do not allow a complete modeling study of the system with this technique. We have shown, however, that meaningful results can be obtained when the oculomotor system is stimulated with a signal matched to the system input sensitivity. This work represents a study of the feasibility of the random input system identification method as applied to the human oculomotor system.

The first-order component of the analysis met with somewhat greater success. First-order kernels exhibited repeatable activity at times which correspond to isolated single pulse acceleration responses. However, the first-order kernel cannot be directly compared to the single pulse response, since the latter contains nonlinear components. The single pulse response can be reconstructed from first and second-order information by summing the first-order kernel and the main diagonal of the second-order kernel (equation 5-16c). In the present case, this summation cannot be determined, since the second-order kernels are rather unreliable. Thus, the first-order kernels can only be qualitatively evaluated from known pursuit linear characteristics, as was discussed in Section 5. 3.

The experiments discussed in this chapter were originally directed towards presenting a quantitative identification of the linear and quadratic properties of the smooth pursuit system in terms of acceleration. However, when the problem of differentiation noise was encountered, a data reduction technique was developed which substantially reduced the information content of the system response signal so that a rough estimate of eye acceleration could be obtained from position data. The resulting characterization of the system became a rather sketchy estimation of the true pursuit acceleration properties.

This work has been successful, however, where previous attempts at a Wiener-type analysis of an oculomotor component have not. First, we have shown that the pursuit system will reliably respond to a random stimulus, when the statistics of the input are defined in terms of the system input domain, i. e. velocity. This is an important result for those who wish to carry on the study of pursuit eye movements, for the establishment of the relevant input domain is a first step in the analysis of any physical system. Second, the analysis has shown that reliable results can be obtained using the random input technique. Even with the extremly coarse data reduction methods employed, the kernels which resulted were three times more sensitive to time variations in the response than the averaged-single response analysis of Chapter Third, although we have not produced a mathematical model of the first and second-order pursuit characteristics as was proposed in Chapter III, some new insight into pursuit dynamics has been generated. The departure of the acceleration response from linearity for pulse stimuli has been described in detail by two different methods. Robinson (1965) described an analogous nonlinearity in the neuromuscular mechanism of pursuit eye movements (Section 3. 2. 4) when the amplitude of the acceleration input pulse was changed. In Chapter III several sources of oculomotor nonlinearities were discussed. This type of interaction was to be bypassed by using constant amplitude pulses in the random input signal. In practice this was not the case (Fig. 5.2), so that the neuromuscular nonlinear source cannot be distinguished from the oculomotor command center transformation (perceived velocity to neuromuscular efferent command).

In the next chapter, suggestions will be proposed that can improve the sensitivity of the random acceleration method. The lessons learned from the present experimental and data analysis procedures can be put to use in a more detailed study of pursuit interactions. In conclusion, the work reported in this chapter, although not entirely successful at producing meaningful second-order results, is an important contribution to the field of oculomotor research in terms of methodology and pursuit system first and second-order characteristics.

VI. CONCLUSIONS

In the introductory and background chapters of this dissertation, the close relationship between smooth pursuit and the visual perceptual system was documented. The relationship is based on the fact that a visual motion percept is a generation of smooth tracking eye movement. The inverse relationship, although it indeed exists, is not as strong, i. e. smooth tracking eye motion is a sufficient but not a necessary condition for the generation of a visual motion percept. The latter concept is embodied in the observation that a velocity percept can be assessed with or without a pursuit eye movement. Furthermore, the velocity percept in the two cases is different -- perceived velocity is greater with a stationary eye than when the velocity is tracked. In the experiments described in the previous two chapters, the transformation from target velocity to eye velocity was investigated. From the above discussion it is apparent that the dynamic properties of the pursuit system assessed from input-output relations consist of oculomotor and perceptual components. In the next few paragraphs let us take another look at the results of this study, considering at each stage how perceptual and oculomotor effects may have interacted to produce the observed results.

The observation that a pulse velocity signal which is input to the oculomotor system elicits a pure smooth pursuit eye movement is a simple yet elegant demonstration of the velocity processing capabilities of the system. Inclusion of position information in the input signal does not disturb the pursuit components and adds a saccadic response. Thus the pursuit system assesses retinal image velocity with or without the presence of position information. The calculation of retinal image velocity is then not a simple differentiation of the position signal, but is measured from the spatial and temporal properties of the target motion. Such a complex interaction requires the higher order information processing capabilities of the perceptual system. Therefore, in the very first stage of the pursuit system information pathway, a perceptual component has entered into the input-output transformation.

The perceptual feedback hypothesis for smooth pursuit eye movements (Fig. 3. 1) was adopted early in this dissertation as a working model for the generation of a smooth tracking eye movement. According to this model once retinal image velocity has been determined, a perceptual judgment center outputs a perceived velocity signal as a weighted sum of retinal image and eye velocity. The perceived velocity signal is then used by the oculomotor system to generate a new efferent command to drive the neuomuscular system. During a single or double pulse acceleration response, retinal image and eye velocity change as inverse functions of each other, continuously until final eye velocity is reached. The results of double pulse experiments indicate that the system does not continuously compare retinal image and eye velocity. As new information is input in the form of a second acceleration pulse, the pursuit system appears to continue processing the old information until eye acceleration begins to fall off and eye velocity approaches the old value of target velocity. At some point the new target velocity is assessed and the system begins a new acceleration in response to the new target velocity information. Apparently the perceptual velocity processor is suppressed during a pursuit acceleration and new input is not continuously processed. The nonlinear characteristic of the double pulse response determined in Chapter IV, may be a manifestation of this perceptual suppression effect.

Of course, the double pulse experiment does not distinguish between perceptual, neurophysiological, or neuromuscular nonlinear sources, since the input was processed by all three stages before the point at which output was sampled. It might be possible to bypass the perceptual processor by stimulating the system directly with a perceived velocity signal. Yasui (1973) performed an experiment in which the perceived motion of an afterimage target was the tracking stimulus. Perceptual motion was induced from a vestibular source. A similar experiment could be performed with a stabilized retinal image. If perceptual acceleration could be modulated in a pulse fashion (vestibular input), the pursuit response could be analyzed for nonlinear double pulse interactions in the manner of the experiments of Chapter IV. Sources for any observed nonlinearities could now be narrowed down to the perceptual velocity -- efferent command transformation or the efferent command -- eye motion transformation. The latter source may also be eliminated using Robinson's (1969) velocity -- tension data and compensating for that nonlinear source in the eye movement responses. If the nonlinearity disappears in the last step, then the true source must have been the perceptual suppression effect. Otherwise, we would have a description of the nonlinear properties of the perceptual velocity--oculomotor command transformation.

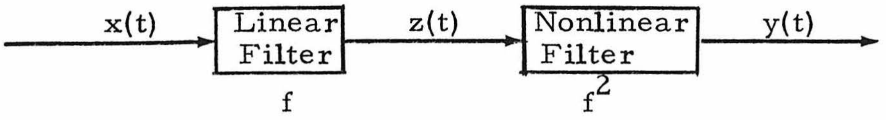
The line of thought expressed in the preceding argument could also be applied to a nonlinear system analysis using the random input cross-correlation method. This approach, with appropriate data handling procedures, would give a more complete representation of the nonlinear characteristics of the isolated oculomotor command center. The perceptual acceleration signal could be randomly modulated through some type of vestibular stimulation. The resulting system kernels could then be corrected for the neuromuscular velocity-tension nonlinearity, in order to isolate the nonlinear properties of the command center.

If the Wiener kernel approach could be improved to achieve a more complete and reliable estimation of the pursuit functional, the data obtained in the present experiments could be reanalyzed as follows. The acceleration response signal is first corrected for the neuromuscular nonlinearity by passing the data through a nonlinear filter which is the inverse of the transformation performed at the velocity-muscle tension level. The two remaining possible sources, perceptual and oculomotor command centers, are then evaluated for linear-nonlinear as opposed to nonlinear-linear order (assuming only one of the two is nonlinear) of system components as follows:

In general, the quadratic component of the system response is predicted by the second order kernel as follows,

$$y(t) = \int_{-\infty}^{\infty} h_2(\tau_1,\tau_2)x(t-\tau_1)x(t-\tau_2)d\tau_1 d\tau_2 \qquad (6\text{-}1a)$$

For the system structure



,

we have by **superposition**,

$$y(t) = z^2(t) = \int_{-\infty}^{\infty} f(\tau_1)x(t-\tau_1)d\tau_1 \int_{-\infty}^{\infty} f(\tau_2)x(t-\tau_2)d\tau_2 \qquad (6\text{-}1b)$$

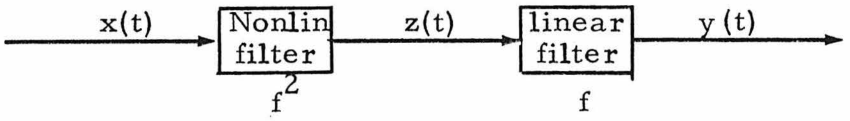
$$= \iint_{-\infty}^{\infty} f(\tau_1)f(\tau_2)x(t-\tau_1)x(t-\tau_2)d\tau_1 d\tau_2 \qquad (6\text{-}1c)$$

Comparing (6-1a) and (6-1c) we see that

$$h_2(\tau_1,\tau_2) = f(\tau_1)f(\tau_2). \qquad (6\text{-}1d)$$

In this case the second-order kernel is just the product of the linear filter with itself. The contour maps of such kernels possess symmetric structure evenly distributed throughout the range of τ_1 and τ_2.

Now for the system structure



we have $z(t) = x^2(t)$ and

$$y(t) = \int_{-\infty}^{\infty} f(\tau_1)x^2(t-\tau_1)d\tau_1 \quad . \qquad (6\text{-}2a)$$

Equation (6-2a) can be expanded as

$$y(t) = \int_{-\infty}^{\infty} f(\tau_1)x(t-\tau_1)x(t-\tau_2)\delta(\tau_1-\tau_2)d\tau_1 d\tau_2 \qquad (6\text{-}2b)$$

where the delta function is included to account for the added integration variable τ_2. Again, comparing equations (6-1a) and (6-2b), we see that

$$h_2(\tau_1,\tau_2) = f(\tau_1)\delta(\tau_1-\tau_2).$$

The contour map of this kernel would consist of structure only along the main diagonal, where $\tau_1 = \tau_2$.

Thus depending on the structural characteristics of the second-order kernel, the perceptual feedback model could be analyzed for the occurrence of a nonlinear followed by a linear filter as opposed to a linear followed by a nonlinear filter. Since the perceptual and oculomotor centers are the only two components which can affect the corrected response in a nonlinear fashion, we could predict which component contributes the nonlinearity in the pursuit response.

The above argument has assumed that the kernel estimation procedure has been improved over its present state as described in this dissertation. Based upon the shortcomings of the present work, the following suggestions for improvement are noted. First, the extraction of acceleration information from the data should be performed on a finely sampled signal, i. e. the 2 msec sampling interval of the raw data. The analogous acceleration pulse (velocity staircase) method can now be used with more closely spaced pulses since more data samples are available for velocity averaging. Also, adjacent acceleration pulses should be evaluated independently. This can be accomplished by computing average velocity before and after each pulse but extending the velocity average only far enough such that the next acceleration calcuation will be completely independent of the data used in the previous acceleration computations. This procedure will eliminate the negative side lobes (Fig. 5.1) in the stimulus and response autocorrelations. The amplitudes of the stimulus and response pulses are then deposited in corresponding tables. First and second-order kernels are then computed from these data tables in a fraction of the time necessary for a continously sampled signal. Various methods of displaying kernels, either as number tables or plots of the functions themselves, could be developed. Acceleration pulse tables from several equivalent runs could be normalized with respect to each other and concatenated so that kernels are computed from longer experiments, thereby improving their accuracy.

The kernels resulting from this improved analysis technique are likely to be free from the negative time artifacts which appeared in the results of the analysis included in this work. It will be possible then to draw strong conclusions regarding the linear and nonlinear composition of the perceptual feedback model for the pursuit system, a step which was made impractical in this dissertation by data analysis limitations. It is hoped that in the coming months, the facilities for this proposed analysis will be made available to author in order that better use can be made of the data which was so carefully collected.

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