Speed and Accuracy of Saccadic Eye Movements: Characteristics of Impulse Variability in the Oculomotor System

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Dynamic characteristics observed in the trajectories of saccadic eye movements reveal systematic variability of the force pulses used to move the eyes. This variability causes saccades to exhibit a linear speed–accuracy trade-off: As the average distance and duration of saccades toward specified target points increase, the standard deviations of saccadic-movement endpoints increase linearly with the saccades' average velocity. The linear trade-off, and other observed stochastic properties of saccades, may be attributed to noise in neuromotor processes and may be described in terms of an impulse-variability model originally designed for characterizing limb movements. According to the model, both eye and limb movements are controlled through stochastic force and time parameters that govern movement kinematics. Such an account may promote a unified conceptual framework for understanding a wide range of motor behavior.

Since the beginning of the present century, when it first became possible to monitor the position of the eyes precisely, researchers have been interested in the production of saccadic eye movements (Dodge & Cline, 1901). Saccades are rapid, steplike, voluntary movements of the eye that people produce as they scan a visual scene. They occur very frequently (up to 173,000 times per day; Robinson, 1981a) and play an important role in constructing perceptual representations of people's environments (Rayner, 1978). They may also reflect movements of visual attention (Remington, 1980). Thus, it is not surprising that saccades have been studied extensively.

One popular approach to studying the mechanisms that underlie saccades has been to measure the dynamic features of saccade trajectories, including movement duration, amplitude, and peak velocity. This approach has yielded numerous insights into the nature of oculomotor control, because the eye-movement system has properties that permit saccade trajectories to directly reflect underlying neurological signals (Robinson, 1981b). In this article, we investigate a number of previously unexplored features of saccade trajectories, including variability in the time of peak saccadic velocities and in the magnitude of peak acceleration.

Along with an interest in the mechanisms that underlie saccades, there has also been an interest in motor control mechanisms more generally. Several models have been proposed to account for details of aimed limb movements based on principles of stochastic variability in neuromotor force pulses (e.g., Meyer, Smith, & Wright, 1982; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979). The evaluation of these models has been hampered, in part, by the relative complexity of limb movements and the difficulty of obtaining accurate recordings of limb movement trajectories. For example, limb movements are often multidimensional, and biomechanical properties of the limbs can obscure details of the underlying force pulses. Saccadic eye movements do not have these complexities. Thus, saccades may provide an ideal opportunity to evaluate some of the assumptions upon which these models are based.

Variability in Saccadic Eye Movements

Our approach to studying saccades complements and extends the research of several earlier investigators. Paralleling previous accounts of limb movement production (Abrams, Kornblum, Meyer, & Wright, 1983; Meyer et al., 1982; Meyer, Abrams, Kornblum, Wright, & Smith, 1988; Meyer, Smith, Kornblum, Abrams, & Wright, 1990; Schmidt et al., 1979; Zelaznik, Shapiro, & McColsky, 1981), we focus explicitly on the variability, or "noise," in the motor commands (and resultant forces) used to move the eye. The variability of saccades is interesting because a number of prior studies have shown that it occurs ubiquitously, and it may mediate a variety of saccadic and perceptual phenomena. For example, the spatial endpoints of saccades tend to become more variable with fatigue (Bahill, Brockenbrough, & Troost, 1981; Bahill & Stark, 1975a). Saccades can sometimes be quite accurate (Kapoula & Robinson, 1986), but they usually undershoot their goal slightly and sometimes overshoot it

(Becker, 1972). The corrections made after an undershoot or overshoot may have a relatively long or short latency (Becker, 1972), and they may be completed fairly quickly (*dynamic overshoot* and *undershoot*; Bahill, Clark, & Stark, 1975) or take several hundred milliseconds (*glissadic overshoot* and *undershoot*; Weber & Daroff, 1972). Although saccades usually exhibit a highly stereotyped relationship between distance and duration (Robinson, 1964), they are slower than normal when made in darkness (Becker & Fuchs, 1969; Henriksson, Pyykko, Schalen, & Wennmo, 1980), when present in certain pathologies (Baloh, Konrad, Sills, & Honrubia, 1975; Fricker, 1971; Zee, Optican, Cook, Robinson, & Engel, 1976), when directed toward nonvisual targets (Zambarbieri, Schmid, Magenes, & Prablanc, 1982), and when influenced by some drugs (Hikosaka & Wurtz, 1985; Rothenberg & Selkoe, 1981). Also, repeated saccades between two fixed targets may travel different distances depending on what other visual stimuli are present (Findlay, 1982) and on what other saccades are being executed (Kapoula, 1985; Kapoula & Robinson, 1986).

These well-documented phenomena have potentially important implications for understanding both visual perception and the mechanisms that underlie movement of the eyes. Coren (1986) has shown that saccades play an important role in the perception (and misperception) of visual geometric illusions. According to his analysis, any factor that influences the eye movements used to scan a figure should also influence perception of that figure. A natural extension of this viewpoint is that variability in saccadic eye movements may produce variability in perception. Furthermore, such effects need not be limited to visual geometric illusions; they may also operate when complex visual scenes are viewed. Because eye-movement variability can contribute to a variety of perceptual phenomena, a detailed understanding of it should constitute an important part of any theory of visual perception.

In what follows, we first describe a simple model that was initially proposed to describe the control and variability of limb movements. This model might also conceivably apply to saccadic eye movements, and thus could provide insight into the production of saccades. We next discuss a number of similarities between eye and limb movements. Such similarities suggest that the model may indeed be appropriate for both types of movement. Then we outline several assumptions that the model makes about dynamic features of movements, and we report the results of an experiment on saccades designed to evaluate these assumptions. The results show that the model accurately characterizes numerous properties of saccadic eye movements.

Impulse-Variability Models of Movement Control

We treat the problem of saccade control from a perspective similar to one adopted previously in studies of aimed limb movements (Abrams et al., 1983; Meyer et al., 1982, 1988, 1990; Schmidt et al., 1979; Zelaznik et al., 1981). From this perspective, movement of any body part is viewed as resulting from a pulse of force applied for a certain time by opposing groups of agonist and antagonist muscles. The magnitude and duration of the force pulses are assumed to vary systematically as a function of the desired movement amplitude and speed

(e.g., movements that have short durations and traverse long distances would require brief large forces). Furthermore, assuming that the motor system is "noisy," repeated attempts to produce identical movements are assumed to have variability in the amplitude and duration of the associated force pulses. By making assumptions about the quantitative shapes of the force pulses and about the nature of the noise involved in their production, impulse-variability models can account for important features of aimed limb movements such as the form of speed–accuracy trade-offs and the shape of typical movement trajectories (Meyer et al., 1982, 1988; Schmidt et al., 1979; Zelaznik et al., 1981).

For present purposes, the important point is that the principles of physics, movement dynamics, and stochastic operation embodied in impulse-variability models may reflect properties of mechanisms that underlie saccadic eye movements as well as limb movements. However, the applicability of these models to the oculomotor system remains an open empirical question, given that no one has yet pursued this possible relation explicitly. One of our goals, therefore, is to evaluate a specific example of this theoretical class, the symmetric impulse-variability model (Meyer et al., 1982), for the characterization of saccades.

Symmetric Impulse-Variability Model

The symmetric impulse-variability model includes a number of assumptions about the shapes of force pulses used to produce movements and about the stochastic variation of force pulses across different movements. These assumptions may be tested with respect to saccades by examining dynamic aspects of movement trajectories and certain relationships between movement distance, duration, and spatial accuracy. In particular, the model assumes that rapid movements, including saccades, have the following properties (see Meyer et al., 1982, for further details).

Force–time functions. Producing a particular desired movement involves selecting a particular force–time function, which specifies the net amount of force applied to a body part (e.g., eye or limb) as a function of time. Because the force–time function is a representation of the net forces acting on a body part, it provides a complete and unambiguous description of the dynamics for a movement. In general, the net force applied to some body part will equal the force produced in the muscles minus other ancillary forces acting on the body part, including the viscosity and elasticity of the muscles themselves. The present model assumes that the motor system takes these other forces into account and selects a force–time function that, when applied to the muscles, would ideally yield the desired net force–time function for the intended movement.

Force and time parameters. The net force–time function for producing a movement is assumed to come from a family of similar force–time functions, all with the same general shape. The selection of this function is based on the values of a *force parameter* and a *time parameter*. These parameters, in combination with the prototype of the family, are sufficient for defining a complete force–time function associated with

an intended movement. The motor system supposedly attempts to select values of the force and time parameters that would produce a movement with the desired amplitude and duration.

Force-time rescalability. Changes in the values of the force and time parameters are assumed to rescale the force-time function over the force and time domains. For example, an increase of the force parameter would theoretically increase the speed of a movement, allowing it to traverse a greater distance, without changing the movement's duration.

Shape of force-time functions. According to the model, the net force operating on a moving body part is positive during the first half of a movement and negative during the second half. Furthermore, the force-time function for the second half of a movement is assumed to be a mirror image of the first half.

This assumption arises from a consideration of movement dynamics, along with some principles of physics. To begin moving a stationary object from one point to another, a positive acceleration force must first be applied to it. To stop a moving object, a negative deceleration force must be applied. These requirements are essentially Newton's first law of motion. Furthermore, to exactly overcome the acceleration force, the area under the deceleration portion of the force-time function must equal the area under the acceleration portion.

There is no physical necessity for the acceleration and deceleration to be exact mirror images of each other. Theoretically, the deceleration could be accomplished by a greater (or lesser) force exerted for a shorter (or longer) period of time, relative to the acceleration. Nevertheless, since a given set of muscles may play the role of the agonist in one movement and the antagonist in another, providing either an acceleration or deceleration force, respectively, it seems reasonable to assume that the time course of acceleration and deceleration will, on the average, be approximately equal. Also, in most physical systems, net force does not rise instantaneously to a maximum. Thus, the net positive force must gradually increase from zero, and the net negative force must gradually decrease to zero.

Variability of parameter values. The subject's ability to select desired force and time parameters is limited by internal noise in the motor system. According to the model, the force and time parameters are random variables whose standard deviations increase proportionally with their means, as in Weber's law from sensory psychophysics. Since these parameters determine the amplitude and duration of the force-time function used to produce a movement, variability of these parameters from movement to movement produces variability in the force-time functions, and hence variability in the movements' distance and duration.

This assumption is based in part on results reported by Schmidt et al. (1979; cf. Carlton & Newell, 1988; Newell, 1980). Variability may be introduced during an attempt to select a specific value for a parameter or during an attempt to implement the selected parameter in a movement. The model makes assumptions about the *net* variability in the specification and implementation of a parameter from a combination of these and other sources.

Figure 1 shows an example of the theoretical force-time functions assumed by the model (cf. Meyer et al., 1982). The thick solid curve represents a prototypical force-time function. Actual force-time functions under the model are rescaled versions of the prototype. The thin solid curve shows one function rescaled from the prototype in the time domain, and the dashed curves show other functions rescaled in the force domain. For each function, the force is positive during the first half of the movement, and the second half of the movement is a mirror image of the first half.

Taken together, the first three assumptions outlined above state that the production of a particular movement involves the selection, by the motor system, of a force parameter and a time parameter. These parameters determine the particular net force-time function that will be used for a given movement. Identical movements can only result from a combination of identical force parameters and time parameters. The fourth assumption constrains the shape of the net force-time function, simplifying the model sufficiently to let it make quantitative predictions about movements. The fifth assumption introduces the concept of neuromotor noise in movement production. It is this noise in the selection or implementation of the force and time parameters that, according to the model, causes variability in movements. Even when subjects attempt to produce nominally identical movements, the noise will prevent them from doing so.

Current Status of the Model

The assumptions outlined earlier, along with some other ancillary ones, allow the symmetric impulse-variability model to make a precise prediction about the relationship between
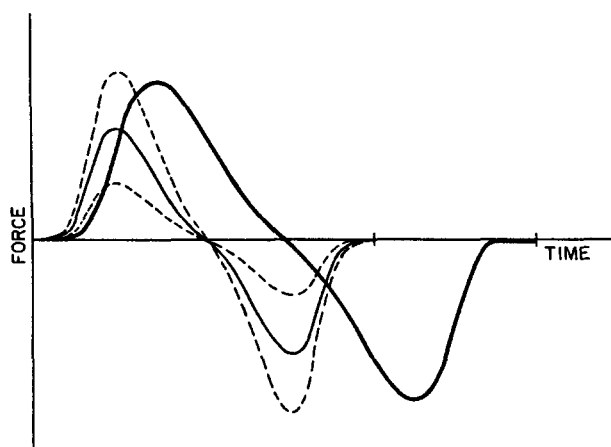

Figure 1. Force-time functions assumed by the symmetric-impulse variability model. (The thick solid curve represents a prototypical force-time function. The thin solid curve shows a function rescaled from the prototype along the time dimension. The dashed curves show functions rescaled up and down along the force dimension. From "Models for the Speed and Accuracy of Aimed Movements" by D. E. Meyer, J. E. K. Smith, and C. E. Wright, 1982, *Psychological Review, 89,* 449–482. Copyright 1982 by the American Psychological Association. Adapted by permission of the publisher.)

a limb movement's velocity and its spatial precision (the *speed–accuracy trade-off*; Meyer et al., 1982; Schmidt et al., 1979). For a set of movements, all of which are intended to travel the same distance (D) and have the same duration (T), the standard deviation of the movements' endpoints in space (S_D) should be a linear function of the movements' average velocity (V), if the model is valid; that is,

$$S_D = K_1 + K_2 V, \tag{1}$$

where $V = D/T$, and K_1 and K_2 are nonnegative constants. This prediction has been verified in a number of experiments on limb movements, including arm flexions and extensions (viz., stylus tapping; Schmidt et al., 1979; Zelaznik et al., 1981; Zelaznik, Mone, McCabe, & Thaman, 1988) and wrist rotations (Meyer et al., 1988; Wright & Meyer, 1983). It appears to hold whenever movements must have a brief precisely controlled duration while traveling a set distance on the average.

Although the symmetric impulse-variability model correctly predicts the form of the speed–accuracy trade-off for limb movements with strong temporal and spatial constraints, there are still reasons to question some of its assumptions. When it was introduced, quantitative measurements of movement force–time functions were unavailable, and many of the model's assumptions remained untested. Subsequently, a number of investigators have attempted to obtain data regarding these assumptions, with mixed success. In a study of wrist rotations, for example, Wright (1983) found evidence consistent with the assumption of linear (proportional) relations between the standard deviations and means of the force and time parameters. His results complemented previous ones of Schmidt et al. (1979), which also supported this assumption. However, Newell (1980) has suggested that the variability of the time parameter does not always increase monotonically with its mean value; under some circumstances, especially those involving low velocity movements, time-parameter variability may *decrease* as movement duration increases. Similarly, Carlton and Newell (1988; see also Newell & Carlton, 1988) have suggested that the standard deviation of the force parameter may not be a strictly proportional function of its mean value; instead, other factors could influence the apparent force-parameter variability as well. It likewise remains open to debate whether typical force–time functions really exhibit mirror-image symmetry in their acceleration and deceleration phases. Rather than such symmetry taking place, the deceleration phase may have a lower absolute magnitude but consume more time than the acceleration phase does (e.g., see Zelaznik, Schmidt, & Gielen, 1986).

Therefore, one of our goals in this article is to further examine the viability of the symmetric impulse-variability model and its assumptions. Saccadic eye movements provide an ideal opportunity for achieving this goal. As mentioned above, the oculomotor system has a number of features that allow saccades to reflect the underlying control signals directly. There are a number of reasons to believe that the model might apply to saccades. Although, on the surface, saccades differ in some respects from limb movements, they are also similar in other basic respects. Second, some available

data already suggest that saccades may satisfy the model's assumptions at least qualitatively.

Comparison of Limb Movements and Saccadic Eye Movements

Because of several apparent qualitative similarities between saccade trajectories and limb-movement trajectories, we believe that the symmetric impulse-variability model may describe saccades reasonably well. For example, Figure 2 shows actual force-time functions from a representative saccadic eye movement and a representative wrist-rotation movement (Abrams, Meyer, & Kornblum, in press). As can be seen, the general shapes of the two functions are very similar. Furthermore, both are similar to the theoretical functions predicted by the model (Figure 1).

Qualitative Similarities

These qualitative similarities between saccade and limb-movement trajectories have been known for some time. The velocity during such movements is typically a sinusoid-shaped function of time, with its peak close to the middle of the movement (for eye movements, see Baloh, Konrad, Sills, & Honrubia, 1975; Fricker, 1971; Hyde, 1959; for limb movements, see Brooks, 1979; Carlton, 1980; Langolf, Chaffin, & Foulke, 1976; Meyer et al., 1982; Schmidt et al., 1979). Acceleration profiles usually rise to a maximum and then return to zero about halfway through a movement, followed by an almost mirror-image deceleration phase (for eye movements, see Fricker, 1971; Thomas, 1969; for limb movements, see Brooks, 1979; Carlton, 1980; Meyer et al., 1982; Schmidt et al., 1979). Near the end of a movement, corrections are sometimes evident as the limb or eye "homes in" on the target (for eye movements, see Bahill et al., 1975; Becker, 1972; Westheimer, 1954; for limb movements, see Carlton, 1981; Langolf et al., 1976; Meyer et al., 1988). The occurrence of
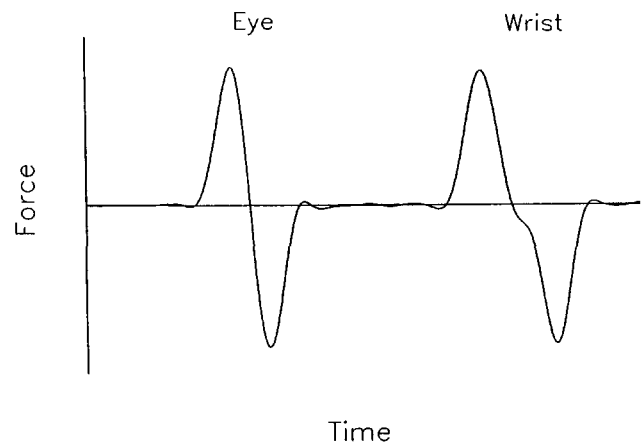

Figure 2. Typical force–time functions from a representative saccadic eye movement and a representative wrist-rotation movement. (The functions have been rescaled in force and time to demonstrate the marked similarities of their shapes [cf. Figure 1].)

corrective submovements is especially prevalent during the performance of "spatially constrained" movement tasks in which subjects must reach a well-defined target region as quickly as possible (Crossman & Goodeve, 1983; Jagacinski, Repperger, Moran, Ward, & Glass, 1980; Meyer et al., 1988).

There are also similarities between the neuromotor signals that control saccades and rapid limb movements. Both movement systems exhibit a pattern of activity characterized as a *pulse* followed by a *step*. At the beginning of a movement, there is increased activity (pulse) in the agonist muscles and a simultaneous inhibition of antagonist activity that rapidly accelerates the eye or the limb toward the desired new position (for eye movements, see Fuchs & Luschei, 1970; Miller, 1958; Robinson, 1970; Tamler, Marg, Jampolsky, & Nawratzki, 1959; Thomas, 1969; for limb movements, see Hallett, Shahani, & Young, 1975; Polit & Bizzi, 1979). The agonist activity subsides near the middle of the movement and is followed by a change in the steady-state activity (step) of opposing muscle groups, which serves to hold the new final position (for eye movements, see Fuchs & Luschei, 1970; Miller, 1958; Reinhart & Zuber, 1971; Tamler et al., 1959; for limb movements, see Polit & Bizzi, 1979). Thus, it appears that some common principles may underlie organization and control in both the eye and limb movement systems. This is exactly what we would expect if each system is characterized by the symmetric impulse-variability model.

Differences Between Saccades and Limb Movements

Nevertheless, some distinct differences exist between saccades and rapid limb movements that might limit the applicability of the symmetric impulse-variability model to saccades. Following the pulse of activity in the agonist muscles, limb movements are actively decelerated by activity in the antagonist muscles (Hallett et al., 1975; Polit & Bizzi, 1979). Antagonist muscle activity can also provide a braking force during saccades (Sindermann, Geiselmann, & Fischler, 1978). However, such activity may often be minimal or absent. The viscous nature of the ocular muscles is believed to be sufficient for passively stopping the eye without antagonist activity (Robinson, 1964).

Another potential difference between saccades and limb movements involves the proposed force and time parameters associated with the symmetric impulse-variability model. The model assumes that both of these parameters are adjusted by the subject to rescale the force–time functions for a desired movement. As Wallace (1981) has shown, people can vary the duration of EMG pulses to produce longer or shorter limb movements, and they can also vary the amplitude of the EMG bursts. Similarly, saccades smaller than 15° of visual angle may be controlled by varying both the magnitude and duration of the force pulse (Reinhart & Zuber, 1971; Robinson, 1981a; Thomas, 1969), as the model assumes. On the other hand, saccades over distances greater than about 15° may be controlled by modulating only the durations of the force pulses, not their amplitudes. At or beyond this amplitude, the muscles typically provide their maximum possible force regardless of distance traveled, and only the duration of muscle activity is adjusted (Bahill & Stark, 1975b; Sindermann et al.,

1978). These differences between eye and limb movements raise the possibility that different principles sometimes underlie their production. At the very least, longer saccades are perhaps controlled differently than shorter saccades.

Application of the Model to Saccades

As outlined already, the symmetric impulse-variability model makes a number of assumptions about dynamic features of movements. Given these assumptions, the model predicts a linear speed–accuracy trade-off. Some of the model's assumptions are supported by existing data on saccades, whereas others remain to be tested.

In what follows, we review previous results from the eye-movement literature that relate specifically to the model's assumptions about force–time functions. Next we consider how this literature bears on the speed–accuracy trade-off predicted by the model. Then we report the results of a new experiment designed to evaluate the model further with respect to saccades.

Evaluation of Assumptions

Variability of force pulses. Under the symmetric impulse-variability model, the variability (standard deviation) of the assumed force and time parameters for a movement should increase linearly with their means. No one has tested this assumption yet for saccades. However it may be possible to do so directly.

Given the relative simplicity of ocular mechanics, movement of the eyeball faithfully reflects underlying neuromotor activity (Childress & Jones, 1967; Robinson, 1981b). In particular, because only one set of muscles actively applies force to the eye during the "pulse" phase of a saccade, the velocity of the eye will continue to increase as long as this force is applied. The moment at which the peak velocity occurs during a saccade provides a measure of when the force pulse ends. Any increase (or decrease) in the time parameter of the pulse would be expected to increase (or decrease) the time of peak velocity relative to the beginning of the saccade. Hence, variability in the time parameter should be revealed by variability in the moment of peak velocity. Similarly, the magnitude of the force pulse reflects the magnitude of the force parameter. One measure of the pulse magnitude is provided by the peak acceleration (i.e., the maximum force attained) during the movement. Increases (or decreases) in the force parameter would result in increases (or decreases) in the maximum acceleration, so variability in the maximum acceleration manifests the force parameter's variability (cf. Carlton & Newell, 1988; Newell & Carlton, 1988).[1]

Some results in the literature suggest that increases in the force and time parameters associated with eye movements do

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[1] Technically, the maximum force could increase as a result of an increase in *either* the force parameter or the time parameter. However, the mean and standard deviation of the peak acceleration should closely approximate the mean and standard deviation of the force parameter as long as computations are performed on ensembles of movements that all have approximately equal durations.

lead to increased saccade variability. Several researchers have shown that the magnitude of peak velocity tends to become more variable as saccade amplitude increases (Boghen, Troost, Daroff, Dellosso, & Birkett, 1974; Henriksson et al., 1980; Hyde, 1959). Because the mean peak velocity also increases with amplitude, this result implies that the variability increases with the mean.

What remains to be determined, however, is the quantitative form of the increase in saccade variability. Past studies in the literature have not reported mathematical functions that relate the standard deviations of saccadic-trajectory parameters to their corresponding means, so they provide no firm basis to test the assumptions of the symmetric impulse-variability model per se. Furthermore, previously observed changes in the magnitude of peak saccade velocity could reflect changes in either the force or time parameter of the model. No data currently exist regarding the temporal variability in the moments of peak velocity for saccades.

Form of the force-time function. The symmetric impulse-variability model may also be relevant to the precise shapes of saccadic force-time functions. It assumes mirror-image symmetry for the acceleration and deceleration phases of a movement. This assumption has several implications. First, if the model is valid for saccadic eye movements, then the peak velocity (which marks the transition from acceleration to deceleration) of saccades should occur at their temporal midpoint. Second, because the model assumes that the net forces acting on a moving body part are equal and opposite in the acceleration and deceleration phases, the peak velocity of saccades should also coincide with their spatial midpoint. Third, since the acceleration and deceleration phases are assumed to be equal in magnitude but opposite in sign, the peak acceleration of saccades should have equal magnitude and opposite sign compared to their peak deceleration. Fourth, the interval of time between the beginning of a saccade and the occurrence of peak acceleration should equal the time between the peak deceleration and the end of the saccade.

Results for testing these implications with respect to saccades have not been reported previously. In particular, precise measurements of the temporal location and magnitude of the peak positive and negative acceleration in saccades remain to be determined. Much attention has focused instead on the form of the saccadic velocity profiles, partly because prior attempts to model the saccadic system have often failed to predict the shapes of velocity profiles accurately (Childress & Jones, 1967; Thomas, 1969).

Past research on the velocity profiles of saccades has shown that saccades do not always have acceleration and deceleration phases of equal duration. Rather, the peak velocity sometimes occurs before half of the saccade duration has transpired, and the peak velocity occurs earlier (relative to the total duration) for farther movements (Baloh, Sills, Kumley, & Honrubia, 1975; Hyde, 1959; Van Opstal & Van Gisbergen, 1987). For long-distance saccades (i.e., ones ranging from 30° to 90° of visual angle), increases in the overall saccade duration as a function of movement amplitude are almost entirely a result of increases in the duration of the deceleration phase. This result violates the symmetric impulse-variability model, which assumes that peak velocities should occur at the temporal and spatial midpoints of a movement. A possible reason for the violation is that the movement force parameter may become "saturated" (i.e., reach a maximum possible value) in the production of long-distance saccades, changing their dynamic characteristics relative to what the model would predict for saccades of lesser amplitude (e.g., ones less than 15°).

Given this scenario, the symmetric impulse-variability model could still hold under many circumstances. Indeed, the velocity profiles of small saccades (6° and 10°) studied by Baloh, Sills, Kumley, and Honrubia (1975) had reasonably symmetric acceleration and deceleration phases, as did the small saccade trajectories studied by Thomas (1969) and by Van Opstal and Van Gisbergen (1987). Thus, as suggested earlier, the assumptions of the model may apply at least for saccades whose amplitude is smaller than about 15°. Because such saccades constitute a large fraction of those made in real-world situations (Bahill, Adler, & Stark, 1975), there is still an important domain to which the model may apply.

Force and time parameter rescalability. The model also assumes that the particular force-time function used to produce a given movement arises from the rescaling of a prototypical function in force and time. As a result, the force-time functions observed for saccades over different distances should be rescaled versions of one another. Expanding or contracting the functions appropriately in force or time should superimpose them. Qualitative empirical support for this assumption has come already from studies of saccades in which force-time functions or velocity profiles for a range of movement amplitudes all had the same general shape (Baloh, Sills, Kumley, & Honrubia, 1975; Hyde, 1959; Thomas, 1969). It remains to be determined whether the assumption is valid quantitatively as well.

Modulation of force and time parameters. According to the symmetric impulse-variability model, the magnitude and the duration of a force pulse can be modulated at least somewhat separately. It is not necessary that the force and time parameters be independent of each other. The correlation between them must simply be less than 1.0

Similar assumptions have been made by previous researchers in understanding the mechanisms underlying saccades. For example, Reinhart and Zuber (1971) produced eye movements in anesthetized cats by electrically stimulating nerves projecting to the ocular muscles. To generate eye movements of different amplitudes that had trajectories like those of natural saccades, they adjusted both the duration and magnitude of the stimulation. Thomas (1969) likewise adjusted both the magnitude and duration of simulated force pulses for his model to produce force-time functions that matched naturally occurring ones. Thus, the hypothesis that the saccadic system adjusts a few key parameters (viz., force and time parameters) to produce saccades of different sizes, a central tenet of the symmetric impulse-variability model, has substantial precedent in the eye-movement literature.

There is also some precedent for studying variability in the parameters of force pulses used to move the eye. Thomas (1969) suggested that trial-to-trial variation in the duration of the force pulse (with the magnitude remaining fixed) might explain saccadic phenomena such as dynamic overshoot (a

rapid movement of the eye, immediately after a saccade, that takes it a short distance back toward the starting location). Easter (1973) suggested that glissadic overshoot (a slow, drifting movement appended to the end of a saccade) might stem from a mismatch between a pulse of force that accelerates the eye and a step change that holds the eye in the new postsaccade position. Subsequently, Bahill, Hsu, and Stark (1978) showed that the mismatch between the pulse and step is probably caused by an error in the duration of the pulse, not in its magnitude. So certain dynamic features of saccades may reflect variations in one parameter of the force pulses, or inappropriate matches between two of these parameters, consistent with the symmetric impulse-variability model.

Prediction of Linear Speed–Accuracy Trade-off

If saccadic eye movements satisfy the assumptions above, then we would expect such movements to exhibit the linear speed–accuracy trade-off (Equation 1) predicted by the symmetric impulse-variability model. According to the model, a trade-off would arise as the oculomotor system attempts to adjust the force and time parameters of saccades to achieve some desired movement distance and duration. Because these parameters are presumably noisy, increases in movement speed should be accompanied by increases in the variability of the force pulses, and hence increases in the variability of the movement endpoints (S_D) in space.

Some data already support this prediction qualitatively for saccades. Patla, Frank, Allard, and Thomas (1985) have shown that both S_D and average velocity of saccadic eye movements increase as movement distance increases, obeying the general type of relationship expressed in Equation 1. To our knowledge, however, no previous research has directly tested this specific prediction regarding the quantitative form of the speed–accuracy trade-off for saccades.

Overview of Present Experiment

The purpose of this study was to examine directly the nature of variability in the saccadic oculomotor system. Our aims were twofold: (a) to assess the validity of the various assumptions of the symmetric impulse-variability model, and (b) to learn more about saccades. The approach taken here builds on previous research regarding variability in saccadic eye movements, but has a somewhat different perspective. Past research on the variability of force pulses for saccades has arisen mainly from a desire to explain anomalous (but not rare) features of saccade trajectories (e.g., Bahill, Clark, & Stark, 1975). In contrast, we proceeded as if there is *always* noise present in the motor system. From this perspective, insight into the mechanisms that must move the eye despite such noise can be obtained by studying "normal" saccade behavior.

To study saccadic eye movements and to test the applicability of the symmetric impulse-variability model for them, we had subjects produce horizontal saccades having several different amplitudes. Horizontal saccades were selected for investigation because they have been examined most frequently in the past and are easy to monitor precisely.[2] Horizontal saccades also have the virtue of being controlled by a relatively simple set of muscles, unlike those involved in oblique saccades (Robinson, 1981b).

We limited our observations to saccades no greater than 10° in extent. There were two reasons for this. First, small saccades constitute the vast majority of all naturally occurring saccades (86% are less than 15°; Bahill, Adler, & Stark, 1975). Second, saccades on the order of 15° or more in extent require the maximum amount of force that the ocular muscles can provide. For larger saccades, only the duration of the force pulse (the time parameter of the present model) would presumably be adjusted (Bahill & Stark, 1975b; Sindermann et al., 1978). Thus, the processes involved in selecting force and time parameters may differ for larger saccadic eye movements and we would not expect them to accord with the symmetric impulse-variability model.

Method

Subjects

Six University of Michigan undergraduates drawn from a voluntary subject pool each participated in six 50-min sessions on separate days. None had any known visual–motor deficits. Each subject was paid a base rate of $3.75 per session, plus bonuses based on good performance.

Apparatus and Procedure

A Digital Equipment Corporation (DEC) PDP-11/60 computer controlled the presentation of stimuli and acquisition of data. Subjects were seated in a dimly illuminated sound-attenuation booth. They viewed a CRT (DEC VR17, P4 phosphor) from a distance of 43 cm. Their heads were held steady by a dental impression plate. The position of the right eye was monitored with a scleral reflectance device (Gulf & Western, Model 200).

At the beginning of each trial, the subject saw a display that included a fixation point (plus sign) in the primary position of gaze and a saccade target (dot) in the periphery. Vertical lines extending above and below the dot helped the subject locate the target. The subject had 2 s in which to examine the display, fixate on the fixation point, and prepare a saccade to the target.[3] Then the plus sign changed to a dot and the vertical lines disappeared. One second later, subjects heard a countdown sequence of three 400 Hz warning tones, each separated by 400 ms. The last warning tone was followed 400 ms later by a 1000 Hz response tone.

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[2] The apparatus that we used cannot accurately measure vertical movements.

[3] We chose to provide the subjects with advance information about the location of the saccade target, in contrast to Henson (1979) and others who have used randomly located targets. Henson (1979) found that saccade endpoints were more variable when targets appeared randomly, compared to a condition in which the subjects knew the target locations beforehand. Presumably, the additional variability with random target locations results from uncertainty regarding precisely what saccade will be required on a particular trial. We did not want such uncertainty to introduce additional variability into our saccades.

During the countdown sequence, subjects remained fixated on the central fixation point; departures greater than 1° from fixation invoked a calibration routine (described below), after which the trial was repeated from the beginning. Upon hearing the response signal, subjects moved their eyes as accurately as possible from the fixation point to the saccade target. We emphasized that they did not need to minimize either the latency or the duration of the movement; they were simply required to make a saccade to the target as accurately as possible. When the eye had moved 1° in either direction from the fixation point, the two dots on the display disappeared.[4]

After the trial, subjects received feedback regarding their response; the dots at the fixation and target locations reappeared, and an arrow was displayed, indicating where the computer determined that the saccade had ended. Subjects were also shown a score indicating the number of points earned on that trial. The point score was an inverse function of the deviation between the target location and the saccade endpoint. If the saccade did not begin within 400 ms after the response signal, or if the saccade ended more than 1° from the target, an error message was displayed, and the trial was repeated at the end of the trial block. Subjects were not penalized for such errors.

Eye-Movement Recording and Analysis

The analog output from the eye-movement monitor was digitized at a rate of 1 kHz and stored on magnetic disk for subsequent analysis. Calibration was accomplished by sampling from the eye-movement monitor while a subject fixated at each of 11 points spaced evenly across the CRT. The calibration was performed at the beginning of each session and verified before each trial. If fixation deviated by more than 1° from the expected value, then the calibration procedure was automatically invoked.

The eye-movement trajectories were digitally filtered and differentiated, using a low-pass filter with an 80 Hz cutoff (Kaiser & Reed, 1977). The resulting velocity profiles were analyzed to identify and measure the saccades. A saccade was defined to start at the first moment in time after the response tone such that (a) the velocity of the eye exceeded 10°/s (regardless of sign), and then (b) remained above that value while subsequently reaching 35°/s or more for at least 10 ms. Similarly, a saccade was defined to end at the first moment in time after the start of a saccade such that the velocity of the eye fell below 10°/s. The 35°/s criterion was selected because it is well below the velocities of the saccades that we studied, yet well above the noise level of our eye movement monitor. Saccades were defined to start and end when the velocity crossed 10°/s because this value is just above the noise level of the system. The resolution of the system was approximately .05° when properly calibrated.[5] We were able to reliably detect saccades larger than about .7°. Measurements of movement acceleration were obtained by differentiating the velocity profiles.

Design

Ten different saccade target locations were used: 3°, 4.5°, 6°, 7.5°, and 9° to the right and left of fixation. In each block of trials, subjects made one saccade to each of the 10 targets in a random order. On the first day, subjects completed five blocks of trials. These served as practice, and results from them are not reported. On subsequent days, subjects completed 9–11 blocks of trials per day. A total of 2,370 saccades were obtained. After each block, subjects took a brief break, and their performance was discussed with them.

Table 1
Overall Features of Saccade Trajectories

Target distance (deg)	Mean saccade distance (deg)	Mean saccade duration (ms)	S_D (deg)	Average velocity (deg/s)
3.0	3.0	32.3	.654	92.9
4.5	4.5	37.0	.724	121.9
6.0	5.7	40.6	.799	141.1
7.5	7.1	44.5	.859	159.3
9.0	8.5	48.4	.883	174.8

Note. S_D is the standard deviation of the saccade endpoints in space.

Results

Form of the Speed–Accuracy Trade-off

The data concerning the form of the speed–accuracy trade-off involve several overall features of the observed saccades, including the mean of the saccade distances and durations, and the standard deviation of the saccade endpoints (S_D). These data are shown in Table 1. Since no major differences were observed for nasal versus temporal saccades, the data have been collapsed over saccades to the left and right.

The observed saccade distances and durations increased systematically with increases in target distance, $F(4,20) > 500$; $p < .0001$, for both distance and duration. The relationship between saccade duration and amplitude is plotted in the top panel of Figure 3. As the figure shows, saccade duration increased linearly with saccade amplitude (slope = 2.94 ms/degree, intercept = 23.6 ms, $r = .99$). This result is consistent with previous reports by other investigators (e.g., Baloh, Sills, Kumley, & Honrubia, 1975).

A speed–accuracy trade-off occurred between the standard deviation of the saccade endpoints (S_D) in space and the average saccade velocity (amplitude/duration). These data appear in the rightmost two columns of Table 1, and the relationship is plotted in the bottom panel of Figure 3. S_D increased monotonically with average velocity, $F(4, 20) = 7.2, p < .001$. A linear trend accounted for nearly 99% of the variance in S_D ($r = .994$). Thus, as has also been found previously for limb movements (Schmidt et al., 1979; Wright & Meyer, 1983), saccades exhibit the form of speed–accuracy trade-off predicted by the symmetric impulse-variability model.

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[4] We extinguished the target when the eye began to move because pilot experimentation revealed that this reduced the frequency of secondary, corrective eye movements. Target removal rendered the eye-movement records reasonably clean and provided a better opportunity for assessing the dynamic characteristics of the primary saccades themselves.

[5] We could reliably distinguish between eye positions that differed by .05°. However, movement of the eye-movement monitor on the subject's head, or movement of the subject relative to the display, introduces constant errors in the measurement of *absolute* position that could be as large as 1°. (When fixation deviated by more than 1°, we recalibrated the eye movement monitor.) For this reason, all analyses were performed on the recorded saccade *distances*.
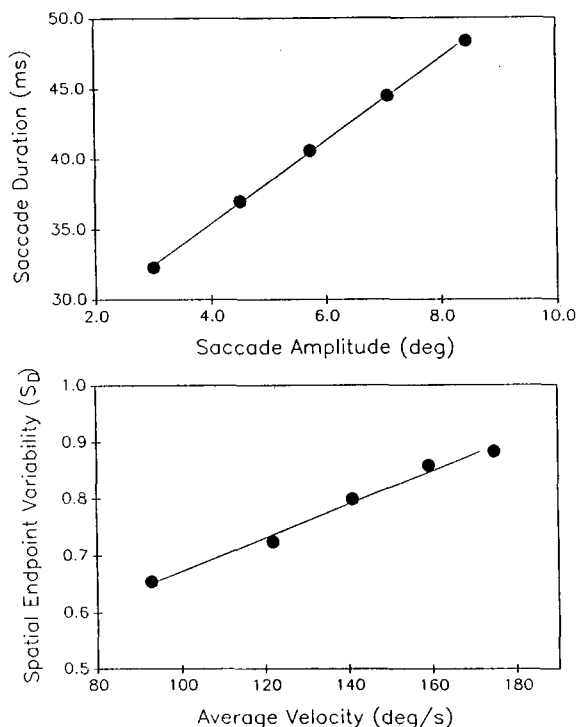
Figure 3. Top panel: Mean saccade duration as a function of observed saccade amplitude. (The line is the best-fitting regression function.) Bottom panel: Standard deviation of saccade spatial endpoints as a function of the average saccade velocity. (The line is the best-fitting regression function.)

Variability of Force Pulses

As discussed earlier, the magnitude of the force parameter in the model is manifested by the peak acceleration during a saccade, and the magnitude of the time parameter is manifested by the time at which peak velocity occurs. Variability in these measures reflects variability in the parameters themselves.

Table 2 shows the means and standard deviations of the magnitude of peak acceleration and time of peak velocity. Each measure in the table increased significantly with saccade amplitude, $F(4, 20) > 12.0, p < .0001$.

The top panel of Figure 4 shows the standard deviation of the peak acceleration versus the mean peak acceleration, and the bottom panel shows the standard deviation of the time to peak velocity versus the mean time to peak velocity. These standard deviations increased almost linearly with the corresponding means (for peak acceleration, $r = .962$; for time to peak velocity, $r = .963$). This suggests that the variability of the force and time parameters is indeed at least approximately proportional to their mean values, consistent with the symmetric impulse-variability model.

Form of the Force–Time Functions

Several other features of the saccade trajectories bear on the shape of the force–time functions assumed by the model.

Table 3 shows the mean *relative* times at which the peak velocity, peak positive acceleration, and peak negative acceleration occurred. The relative times were obtained by dividing the time at which a particular event occurred in a saccade (e.g., peak velocity) by the total saccade duration.

First note the values of the overall means in Table 3. The moment of peak velocity occurred, on the average, after 48.9% of the saccade duration had elapsed. This was not significantly different from the 50% value predicted by the symmetric impulse-variability model, $t(4) = 1.56, p > .10$. The maximum positive acceleration occurred 24.8% of the time into the saccade [not significantly different from the predicted 25%; $t(4) = .05$], while the maximum negative acceleration occurred with 21.5% of the saccade duration remaining (100%–78.5%). As the model assumes, the deceleration of the movements closely approximated a mirror image of the acceleration. However, the relative time of maximum deceleration was slightly, but significantly later than the predicted 75%, $t(4) = 4.1, p < .05$.

Table 4 includes some additional data that bear on assumptions about the form of the force–time functions. In the second column is the mean relative position of the eye at the moment of peak velocity for each movement amplitude. The relative position was obtained by dividing the distance traveled up until the time of peak velocity by the total saccade distance. Under the present model, one-half of the total saccade distance should be traversed up to the time of peak velocity. As seen in the table, the overall mean of .495 was not significantly different from the model's prediction, $t(4) = -.78, ns$. Nevertheless, the relative position at peak velocity did vary slightly, but significantly, with movement amplitude, $F(4, 20) = 9.8, p < .0005$. Except for the smallest target distance, the peak velocity occurred at relatively shorter extents as the amplitude of movement increased.

The rightmost column in Table 4 shows the absolute value of the ratio between the mean maximum negative acceleration and the mean maximum positive acceleration for each movement amplitude. We call this value the *acceleration ratio*. According to the model, these ratios should all be close to 1.0. As seen in the table, this is usually what happened. The only exception occurred for the most distant (9°) target, where the acceleration ratio was a bit less than one, $t(5) = 3.48, p < .05$.

Table 2
Variability of Force and Time Parameters

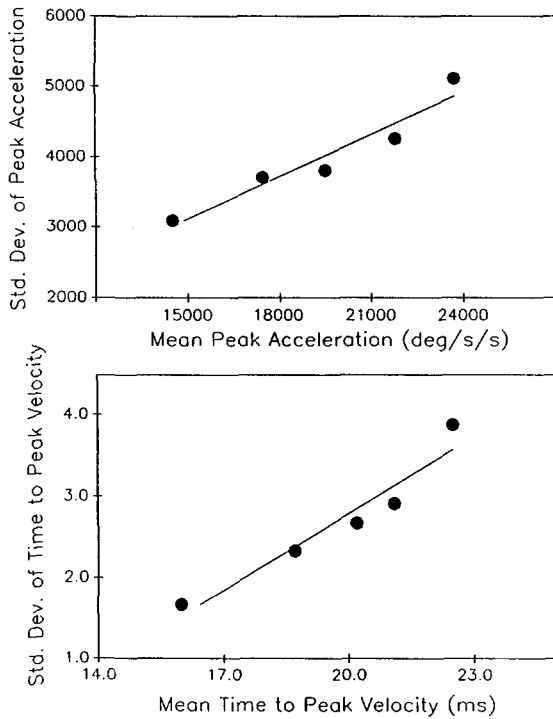| Target distance (deg)	Amplitude of peak acceleration		Time to peak velocity	
	M (deg/s/s)	SD (deg/s/s)	M (ms)	SD (ms)
3.0	14496	3088	16.0	1.67
4.5	17452	3704	18.7	2.33
6.0	19506	3805	20.2	2.67
7.5	21796	4263	21.1	2.91
9.0	23733	5115	22.5	3.87

Note. SD = standard deviation.

Figure 4. Top panel: Standard deviation of peak acceleration as a function of the mean peak acceleration for saccades. (The line is the best-fitting regression function.) Bottom panel: Standard deviation of the time to peak velocity as a function of the mean time to peak velocity (measured from the onset of the saccade). (The line is the best-fitting regression function.)

Force and Time Parameter Rescalability

The data in Table 3 also bear on the assumptions of force-parameter and time-parameter rescalability made by the symmetric impulse-variability model. If the force–time functions for movements of different sizes are rescaled versions of one another, then the relative timing of various critical events should be similar for saccades of different amplitudes. Our results generally support this prediction. The relative times of occurrence for the peak velocity, the peak acceleration, and the peak deceleration were quite similar across the different movement amplitudes.

Table 3

Relative Times of Occurrence for Selected Dynamic Features in Saccades

Target distance (deg)	Relative time of peak velocity	Relative time of peak acceleration	Relative time of peak deceleration
3.0	.496	.252	.807
4.5	.505	.250	.796
6.0	.499	.252	.788
7.5	.476	.253	.771
9.0	.466	.235	.760
M	.489	.248	.785

Note. The relative times of occurrence were obtained by dividing the time of the observed event, measured from the beginning of the saccade, by the total saccade duration.

Nevertheless, there were small but reliable differences between saccades of different amplitudes. The moment of peak velocity tended to occur slightly earlier in longer saccades, $F(4, 20) = 12.97$, $p < .0001$. The relative time of peak acceleration differed across movements of different amplitudes, being earliest for the largest amplitude, $F(4, 20) = 3.99$, $p < .05$. The relative time of peak deceleration also occurred earlier in longer saccades, $F(4, 20) = 3.05$, $p < .05$.

Figure 5 shows manifestations of the mean force–time functions for each target distance. These were obtained by plotting the mean acceleration and times of occurrence associated with five successive events in the saccades, namely movement onset, peak positive acceleration, peak velocity, peak negative acceleration (i.e., peak deceleration), and the movement end. The obtained acceleration plots match the shape assumed by the symmetric impulse-variability model quite well (cf. Figure 1). As indicated by Figure 5, the acceleration plots for large saccades appear to be rescaled in both force and time from those for smaller saccades. Further evidence of this rescaling is presented in Figure 6, which shows actual acceleration plots from representative saccades to each of the targets studied.

Figure 7 shows a representation of the acceleration plots from Figure 5 rescaled in both force and time. In the figure, the mean acceleration normalized with respect to the maximum positive acceleration is plotted versus the relative time of occurrence for the peak positive acceleration, peak velocity, and peak negative acceleration. If the symmetric impulse-variability model were correct, then these rescaled acceleration plots for different amplitudes should all fall at least roughly on top of one another. The data do not fit the model perfectly: Peak velocity occurred shortly before the temporal midpoint of the saccade rather than at the midpoint; the peak deceleration was slightly smaller in magnitude than the peak acceleration, rather than being exactly equal; and the deceleration phase was slightly skewed toward the end of the saccade. Nevertheless, despite these slight differences between saccades of different amplitudes, the similarities across different amplitudes at least roughly support the notion that saccadic force–time functions are derived from a common prototype, as expected under the symmetric impulse-variability model (Meyer et al., 1982).

If the force–time functions for saccades are all rescaled from a common prototype, then additional aspects of the trajectories beyond those reported above should exhibit certain similarities. And such evidence actually emerged from our study. In particular, the top panel of Figure 8 shows *phase planes* of the saccades for each movement amplitude. The phase planes are plots of mean movement velocity versus the distance traveled up to the moments of movement onset, peak acceleration, peak velocity, peak deceleration, and movement end. As expected from the symmetric impulse-variability model, the phase planes are all very similar, except that larger saccades traveled faster and farther than smaller ones. These data further support the notion that saccades of different amplitudes are derived from a common prototypical force–time function.

The bottom panel of Figure 8 shows the phase planes from the top panel rescaled in both velocity and position. For each

Table 4

Additional Measurements of Saccadic Trajectories

Target distance (deg)	Relative position at peak velocity	Acceleration ratio
3.0	.488	.98
4.5	.515	.99
6.0	.507	1.0
7.5	.483	.95
9.0	.480	.89
M	.495	.962

Note. The relative position at peak velocity was obtained by dividing the distance traversed from the beginning of the saccade until peak velocity by the total saccade amplitude. The acceleration ratio is the absolute value of the ratio of the peak deceleration to the peak acceleration.

target distance, velocity has been normalized with respect to peak velocity, and position has been normalized with respect to mean saccade amplitude. As assumed by the symmetric impulse-variability model, the phase planes for saccades of different amplitudes appear to be rescaled versions of one another, further suggesting that saccades of different amplitudes arise from a prototypical force–time function.

More detailed descriptions of some kinematic features of the eye-movement trajectories are included in the appendix.

Discussion

The present results reveal many important features of the mechanisms that produce saccadic eye movements. We have shown that the standard deviations of certain dynamic features (e.g., time to peak velocity and magnitude of peak acceleration) in saccade trajectories increase in an approximately proportional manner with their means, indicating the presence of neuromotor noise in the oculomotor system. Comparison of acceleration plots, phase planes, and other details of the eye movements across different movement distances suggests that small and moderate saccades may result from rescaling a prototypical force–time function in force and time. Most important, the processes associated with parameter selection, force–time rescaling, and noise in the
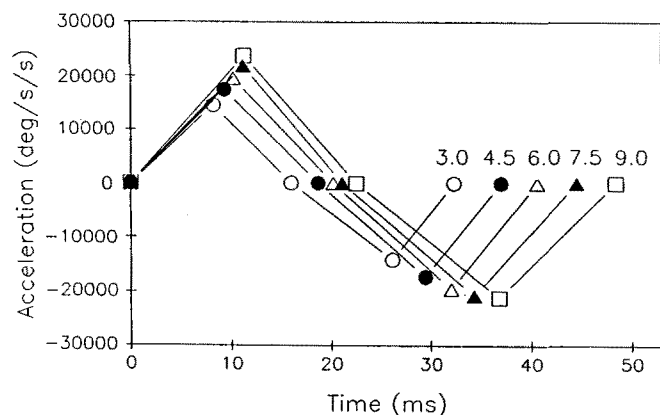

Figure 5. Mean acceleration-time functions for saccades of different amplitudes measured at five moments in time.

motor system lead directly to a linear trade-off between the average speed of a saccadic eye movement and its spatial accuracy.

These findings are consistent with assumptions and predictions made by the symmetric impulse-variability model initially proposed to account for limb-movement production (Meyer et al., 1982; Schmidt et al., 1979). When the model was originally formulated, precise quantitative data for testing some of its assumptions were not available. However, the experiment reported here provides some strong support for those assumptions, and also helps extend the model to the domain of eye movements. A single theoretical framework may therefore eventually describe the processes underlying a variety of different but related motor behaviors.

Implications for Saccadic Eye-Movement Mechanisms

Assuming that the symmetric impulse-variability model applies at least in part to the oculomotor system, a number of tentative conclusions may be drawn regarding the mechanisms that underlie saccades. Perhaps most important is the notion that saccades are produced by separately adjusting the values of a few key parameters. Several earlier researchers have shown that such adjustments are necessary for the overall shape of simulated saccade trajectories to match those of observed saccades (Reinhart & Zuber, 1971; Thomas, 1969). Our results extend these earlier findings by explicitly elucidating the mechanisms involved in the adjustment of the parameters. Furthermore, we have shown that the present model's assumptions can accurately describe stochastic details of saccade trajectories such as the distribution of spatial endpoints, the variability of peak acceleration, and the variability in time of peak velocity.

Another important aspect of our results concerns the role of neuromotor noise in the selection of force and time parameters for saccades. Our experiment suggests that variability in saccades results from variability in the parameters selected. Previous researchers have made similar suggestions to explain anomalous eye-movement behavior (Bahill et al., 1978; Easter, 1973; Thomas, 1969). However, these workers were not concerned with the exact quantitative nature of the variability. We have shown that a formal account of noise in the motor system may be useful for explaining not only anomalous eye-movement behavior, but also the production of "normal" saccades directed to a range of target locations.

At the same time, we did find several small departures between features of subjects' eye movements and predictions of the symmetric impulse-variability model. Perhaps most notably, systematic changes in the shape of the force–time functions appeared as saccade amplitude increased; for example, the peak velocity tended to occur slightly earlier (in relative time and position) with larger saccades. Similar observations have been reported by other investigators for saccades somewhat larger than the ones studied here (Baloh, Sills, Kumley, & Honrubia, 1975; Hyde, 1959; Van Opstal & Van Gisbergen, 1987). Although the observed changes were quite small, they were systematic, and they suggest that the present model may not entirely capture all details of saccade production. In particular, we suspect that saccades larger than
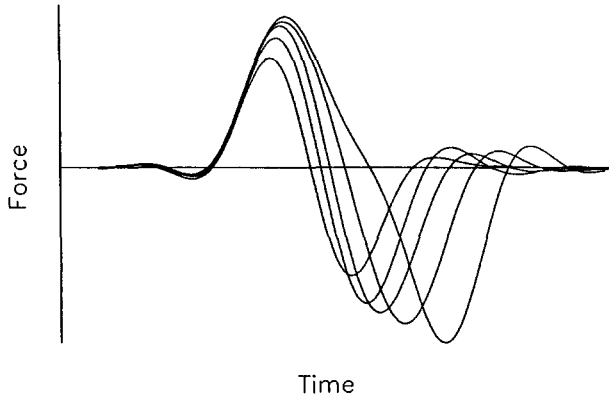
Figure 6. Force–time functions from five representative saccades (one to each of the five target distances studied).

about 10° may involve significant contributions from factors not currently addressed by the model.

Some potentially significant conclusions are also possible on the basis of slight asymmetries that we found in the velocity profiles of some saccades. These asymmetries may be related to the saturation of muscle activity that occurs with increasing saccade amplitude. As we remarked earlier, for saccades greater than about 15°, it is believed that the oculomotor system can only modulate the duration of the force pulse (the time parameter in the present model), because the eye muscles all provide their maximum force beyond that distance (Bahill & Stark, 1975b; Sindermann et al., 1978). Our findings are interesting because they suggest that, with sensitive measures, such asymmetries may begin to appear at even shorter distances (10° or less). Thus, some muscle fibers may actually reach their maximum force sooner than was previously believed.

Of course, a number of other important questions regarding saccades still remain unanswered. In particular, we have not addressed the precise nature of the biomechanical or neurophysiological mechanisms that underlie the actual production of saccadic force–time functions. A variety of different detailed mechanisms would be consistent with the principles of
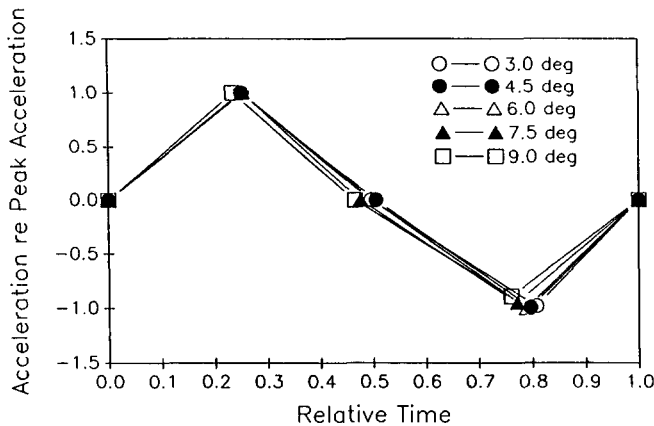
impulse variability and neuromotor noise for saccades (e.g., see Bahill & Stark, 1979). We hope our findings will inform future investigations into these and other aspects of saccade production.

Relevance to Perceptual Processes

Finally, our results may also be relevant to a better understanding of perceptual processes. For example, consider the question of how people accurately localize objects in space even after producing eye movements. Precisely what happens when eye position is monitored during visual perception has been the subject of considerable controversy. According to one hypothesis, information about where the eyes are pointing arises in the periphery, with some mechanism providing a signal that indicates the current eye position (*inflow*). According to an alternative hypothesis, information about where the eyes are pointing is obtained not from the periphery, but from monitoring the efferent commands used to move the eyes (*outflow*). The present results provide a potential means for distinguishing between these two hypotheses.

If the outflow hypothesis is correct, then variability in the error between the perceived and actual position of the eyes might be expected to increase systematically with the size of a saccade, in much the same way that we have demonstrated increases in neuromotor noise with saccade amplitude. This could happen because the noise would introduce variability in eye position that is not taken into account by the perceptual system, assuming the noise affects the system at a point peripheral to where the outflow is monitored. Alternatively,

Figure 7. Acceleration-time functions from Figure 5 rescaled in force and time.
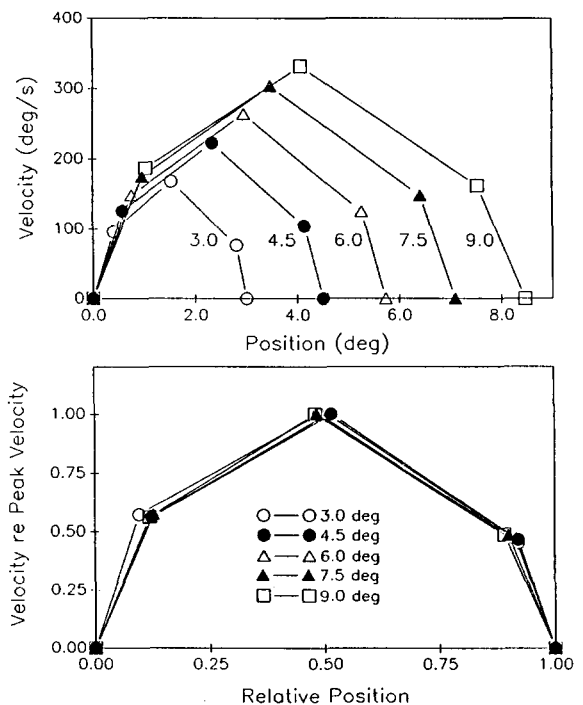

Figure 8. Top panel: Mean phase planes of saccades directed at each of the five target amplitudes. Bottom panel: Phase planes from the top panel rescaled in velocity and position.

if the inflow hypothesis is correct, then the error in perceived eye position would not necessarily be related to the neuromotor noise associated with a preceding eye movement. Perhaps inferences concerning these and other possibilities can be obtained through further studies of the noise that arises when people move their eyes.

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Appendix

This appendix contains a more detailed description of some of the kinematic features of the eye-movement trajectories that were collected in the experiment. Tables A1 and A2 present means and standard deviations of various saccade features separately for two groups of saccades: (a) the 25% fastest (i.e., shortest duration) saccades to each target amplitude, and (b) the 25% slowest saccades to each

target amplitude. Tables A3 and A4 present data about the shapes of rescaled acceleration–time functions for the two groups of saccades. Note that the statistics in this article were computed from the entire distribution of saccades at each target amplitude. The information presented here might be useful in comparing details of our distributions of saccades with data collected by others.

Table A1
Overall Features of Saccades Having Short and Long Durations

Target distance (deg)	Mean saccade distance (deg)		Mean saccade duration (ms)		S_D (deg)		Average velocity (deg/s)	
	Short	Long	Short	Long	Short	Long	Short	Long
3.0	2.7	3.3	29.6	35.4	.58	.59	91.2	93.2
4.5	4.1	4.8	33.9	39.9	.72	.85	120.9	120.3
6.0	5.5	6.0	37.8	43.9	.72	.80	145.5	136.7
7.5	6.9	7.4	41.6	48.0	.82	.86	165.9	154.2
9.0	8.2	8.8	44.8	52.2	1.0	.80	183.0	168.6

Note. Short = saccades whose durations were in the lowest quartile of the distribution for each target distance; Long = saccades whose durations were in the highest quartile of the distribution for each target distance; S_D = the standard deviation of the saccade endpoints in space.

Table A2
Variability of Force and Time Parameters

Target distance (deg)	Amplitude of peak acceleration				Time to peak velocity			
	M (deg/s/s)		SD (deg/s/s)		M (ms)		SD (ms)	
	Short	Long	Short	Long	Short	Long	Short	Long
3.0	14588	13927	4051	3181	14.8	17.6	1.30	1.93
4.5	18042	16304	4951	4289	17.3	19.7	2.26	2.46
6.0	20233	18433	5518	4700	19.7	20.8	3.43	3.41
7.5	22743	20134	6248	4862	20.1	22.2	3.29	3.84
9.0	24778	22373	6942	6034	21.7	23.3	4.27	4.42

Note. SD = standard deviation.

Table A3
Relative Times of Occurrence for Selected Dynamic Features in Saccades

Target distance (deg)	Relative time of peak velocity		Relative time of peak acceleration		Relative time of peak deceleration	
	Short	Long	Short	Long	Short	Long
3.0	.50	.50	.25	.26	.83	.79
4.5	.51	.49	.24	.25	.81	.78
6.0	.52	.47	.26	.23	.80	.79
7.5	.48	.47	.25	.24	.77	.76
9.0	.49	.45	.23	.24	.78	.75
Mean	.50	.48	.25	.24	.80	.77

Note. The relative times of occurrence were obtained by dividing the time of the observed event, measured from the beginning of the saccade, by the total saccade duration.

Table A4
Additional Measurements of Saccadic Trajectories

Target distance (deg)	Relative position at peak velocity		Acceleration ratio	
	Short	Long	Short	Long
3.0	.51	.50	1.02	.97
4.5	.52	.51	1.04	.98
6.0	.53	.48	1.14	.94
7.5	.50	.48	1.02	.97
9.0	.50	.47	.97	.90
Mean	.51	.49	1.04	.95

Note. The relative position at peak velocity was obtained by dividing the distance traversed from the beginning of the saccade until peak velocity by the total saccade amplitude. The acceleration ratio is the absolute value of the ratio of the peak deceleration to the peak acceleration.