

COMPUTER SIMULATION OF OVERSHOOT IN SACCADIC EYE MOVEMENTS

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The human horizontal eye movement system produces quick, precise, conjugate eye movements called saccades. These are important in normal vision. For example, reading tasks exclusively utilize saccadic eye movements. The majority of saccades have dynamic overshoot. The amplitude of this overshoot is independent of saccadic amplitude, and is such that it places the image of the stimulus within the retinal region of maximum acuity within a minimum of time.

A computer based model of the saccadic mechanisms was used to study the origin of this overshoot. It was discovered that dynamic overshoot cannot be attributed to biomechanical properties of the eye movement mechanism, but must instead be explained by variations in the controlling nervous activity. The form of this neural controller signal is very similar to that required for a time optimal response of an inertial system.

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|---------------|---------------|----------------------|
| Saccade | Overshoot | Neurological control |
| Glissade | Damping | Oculomotor neurons |
| Main sequence | Eye movements | Time optimal control |

1. Introduction

Saccadic eye movements have overshoot when the eye movements takes the eye beyond its final position, so that the eye must then return in the opposite direction. The term overshoot describes both the initial motion beyond the target and the subsequent return to the final position. The return phase of this overshoot yields the most information about the underlying neural mechanisms, and therefore the types of overshoot are named by the type of return phase that they exhibit. There are three types of saccadic overshoot: dynamic overshoot, glissadic overshoot, and static overshoot (fig. 1). The first type is produced by motoneuronal control signal reversals and is the primary topic of this paper. Investigation of dynamic overshoot allows inferences to be made about the firing patterns of neurons associated with saccadic eye movements and about the control strategies used by the Central Nervous System (CNS) to control movement.

2. Methods

Eye movements were measured by aiming a pair of photodiodes at the iris-scleral border, converting the resulting photocurrents into voltages and differentially amplifying the resultant voltages. The complete electronic system had a bandwidth extending from DC to 1000 Hz. Bandwidths smaller than 80 Hz prevented the measurement of most dynamic overshoots. These methods have been discussed extensively by Bahill et al. [2]. The target configuration seems to have no effect on the dynamic overshoot. Dozens of different stimulus conditions have been used, and all yield similar dynamic overshoot statistics [2].

We have used linear control system theory, as well as a non-linear model to investigate dynamic overshoot. Our model (fig. 2) incorporates a variant of the Clark-Cook-Stark model [2, 3, 6, 8] for the extraocular plant. It is a sixth order non-linear system. We simulated the model on a META 4 digital computer coupled to an IBM 2250 interactive graphics unit using SNAP, a variant of the CSMP language.

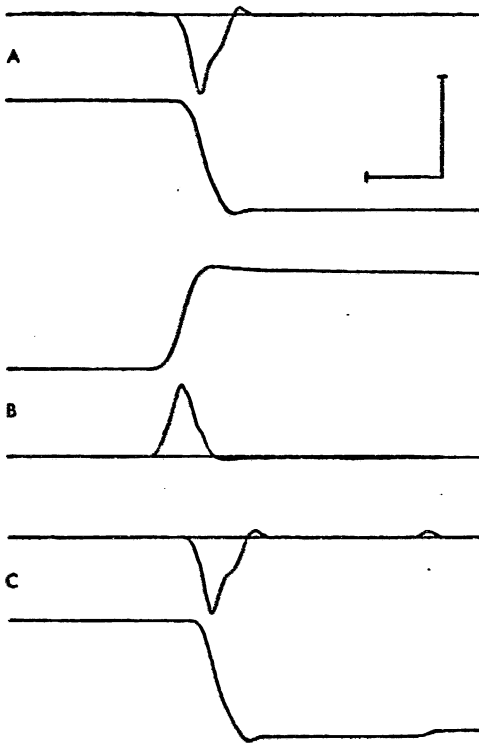


Fig. 1. Eye position and eye velocity as functions of time for three saccadic eye movements executed in a two minute time span that demonstrate dynamic overshoot (A), glissadic overshoot (B), and both dynamic and static overshoot (C). The calibrations represent 18.2 degrees, 750 degrees/sec, and 80 msec.

3. Results

3.1. Experimental results

The existence of dynamic overshoot is quite capricious. On one day most of a subject's saccades will have dynamic overshoot, while on another day very few will. Fig. 3 shows a sequence of ten degree saccades illustrating this variability. Some of these saccades have dynamic overshoot, and some do not. We have recorded both microsaccades (fig. 4) and 50 degree saccades [2] both with and without dynamic overshoot. Care was taken to insure that the recording devices were not saturated by the eye movements, for if any part of the recording system saturates, no overshoot will be seen. It may not be obvious that the device has saturated, however, because it may be a soft saturation, which will still permit the records to look

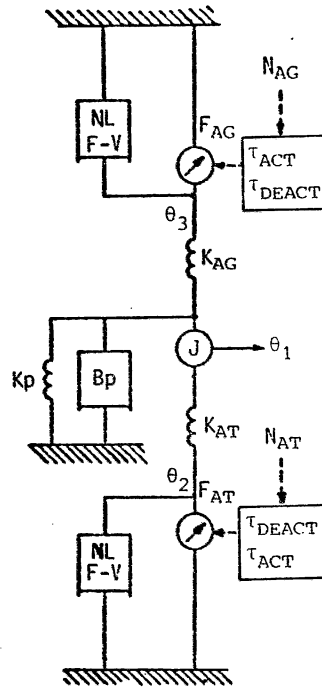


Fig. 2. Model of the extraocular plant. F_{AG} represents the active state tension of the agonist muscle. The nonlinear force velocity relationship (NL $F-V$) is governed by the Hill equation for the agonist and by Katz' active lengthening function for the antagonist. K_{AG} and K_{AT} represent the series elasticities of the two muscles, and K_P represents the parallel elasticities of the muscles as well as globe orbit elasticities. B_P represents the globe viscosity. N_{AG} and N_{AT} represent the motor-neuronal activities. J represents the inertia of the eyeball.

smooth and normal.

About 70% of horizontal saccadic eye movements have dynamic overshoot. Its average size is about 0.25 degrees for saccades 10 degrees and less in magnitude: the overshoot size increases with saccadic size [2]. Vertical saccades can also have dynamic overshoot (fig. 5), although it is less frequent. Purely vertical saccadic eye movements had dynamic overshoot for 36% of the upward and 15% of the downward movements.

The existence of dynamic overshoot is not limited to certain initial conditions or direction of travel, for saccades have been shown [2] with dynamic overshoot for temporal and nasally directed saccades both at primary position and with the eye abducted 35 degrees from primary position.

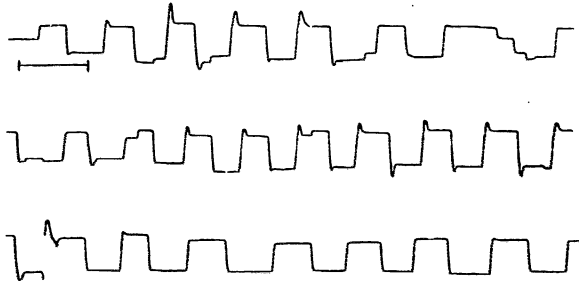


Fig. 3. A sequence of consecutive saccades illustrating the variable dynamic responses of saccadic eye movements. The calibration represents one second. The eye movements were in response to a sequence of predictable ten degree target jumps.

3.2. Theoretical results

When the response of a system has overshoot, a common assumption is that it is an underdamped system. The term underdamped is derived from the study of linear second-order systems with step inputs. These linear second-order systems are often analyzed in terms of this differential equation.

$$\frac{d^2\theta}{dt^2} + 2\zeta W_n \frac{d\theta}{dt} + W_n^2 \theta = \frac{F(t)}{J} \tag{1}$$

For rotation of a mechanical system

$$\zeta = \frac{B}{2\sqrt{KJ}}, \quad W_n = \sqrt{\frac{K}{J}} \tag{2a), (2b)}$$

θ is the angle of rotation, J is the inertia, B is the viscous co-efficient, K is the coefficient of elasticity, $F(t)$ is the applied force, zeta (ζ) is the damping ration, and W_n is the undamped natural frequency.

When zeta (ζ) is greater than one, the system is overdamped, and the roots lie on the real axis of the s plane. If zeta equals one, then the system is critically damped, and the roots are also on the real axis. If zeta is less than one, then the system is underdamped, and the roots are a complex conjugate pair in the s plane. By Murphy's law [10], the UNDERdamped system has OVERshoot, the OVERdamped system has UNDERshoot, and the critically damped system has no shoot. The step response for these three systems is shown in fig. 6.

Special criteria are often used to describe specific systems. One special case of an underdamped system

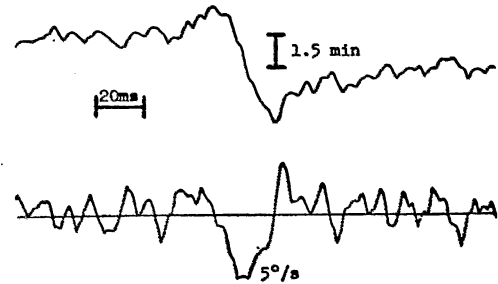


Fig. 4. A microsaccade with dynamic overshoot. The calibrations represented 1.5 min of arc and 20 msec. saccadic peak velocity is 5 degrees per second. The noise is of biological origin.



Fig. 5. Oblique saccadic eye movements with dynamic overshoot in both the horizontal and the vertical components. In the left column, from top to bottom, are shown: vertical eye position, vertical eye velocity, horizontal eye position, and horizontal eye velocity, all as functions of time. The right column shows (top) the eye position in space, or the $X-Y$ trajectory, and (bottom) the horizontal eye position record rotated 90 degrees and aligned with the $X-Y$ trajectory above it. The calibrations represent four degrees, 150 degrees/sec, and 100 msec. In the left column, rightward (temporal) and upward eye movements are represented by upward deflections.

that is often utilized in engineering systems has roots on lines at 45 degree inclinations to the real axis, and zeta equal to 0.7. This is the system with minimum settling time; meaning that it is the damping ratio, zeta, that allows the system to get to and stay within 5% of the final position in the least possible time. What is magical about 5%? Nothing. It is perfectly arbitrary. The saccadic eye movement system uses a dif-

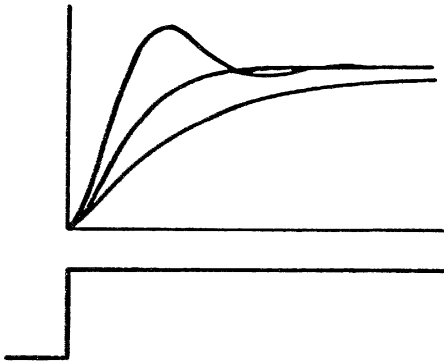


Fig. 6. Temporal response of a linear second order system excited by a step input for (from top to bottom) an underdamped ($\zeta = 0.4$), a critically damped ($\zeta = 1.0$), and an overdamped ($\zeta = 2.0$) system.

ferent optimality criterion. Dynamic overshoots of saccades usually have magnitudes of one fourth degree or less. The radius of the fixational fovea, that part of the retina with the best acuity, is also one fourth of a degree. Therefore, allowing overshoot of one fourth of a degree enables the saccadic system to get the fovea to and keep it on the target in the least possible time.

In the literature the terminology of linear second order systems has been applied to the saccadic system. Most saccades have dynamic overshoot. Some investigators saw this overshoot and said the system was underdamped [14, 15, 17]. Westheimer [15] and Zuber et al. [17] went on to estimate the damping ratio, zeta, to be about 0.7 for the particular saccades shown in their reports. However, the existence of overshoot implies an underdamped system only if the response overshoots when the system is driven by a step input. The input to the extraocular plant is not a step, but is a pulse step of motoneuronal activity.

Dynamic overshoot in the saccadic system cannot be explained as being the response of an underdamped, linear, second order plant for many reasons: first, our model shows that the experimental data of saccadic eye movements is fit best by a non-linear sixth order plant model (fig. 2); second, the magnitude of dynamic overshoot is not a constant percentage of the step size, third, the extraocular plant by itself is overdamped [8, 11] as can be seen in the simulated response of fig. 7; fourth, the input to the extraocular plant is not a step function; and fifth, there is tremendous variability in eye movement responses — all saccades do not

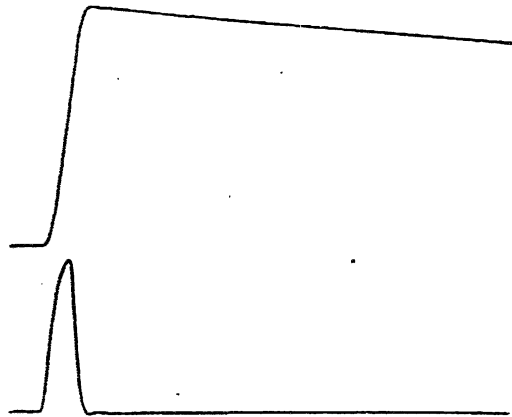


Fig. 7. Simulated eye position and velocity for a ten degree saccade with a glissade appended to the end. The glissade was created by mismatching the pulse and step components of the motoneuronal controller signal. Each record is 500 msec in duration.

have dynamic overshoot (fig. 3). The model is based on physiological data of human eye muscles [6]; and the viscosities and elasticities are assumed to be relatively invariant from saccade to saccade. Therefore, the damping ratio will not vary, so the variations in output response must be due to variations in the input signal, the motoneuronal control signal.

3.3. Model results

The controller signal is in the form of a pulse step (similar to figs. 9E and F), and represents the firing frequency of the agonist and antagonist oculomotor neurons [4, 8]. The pulse, or high-frequency burst of firing in the agonist motoneuron pool and pause in the antagonist pool, causes the rapid change in eye position; then, the step holds the eye in its new position.

To investigate the possibility that dynamic overshoot is produced by a mismatch of the pulse and step components of the motoneuronal control signal, a controller signal in which the pulse portion was larger than the step portion was applied to the model. The modelled eye went beyond its final position and slowly drifted back to the final position as shown in fig. 7. Real eye movements sometimes exhibit similar slow drifts, or glissades [3]. The velocities of actual glissadic eye movements are shown with open circles on the Main Sequence [4] diagrams of fig. 8. The glissadic

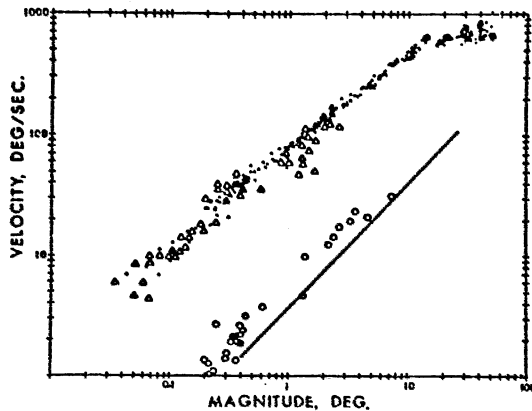


Fig. 8. A Main Sequence diagram showing, as functions of saccadic magnitude, the velocity of: saccades (\bullet), the return phase of dynamic overshoot (Δ), glissades (\circ), and vergence eye movements (—).

velocities are smaller than saccadic velocities and are about the same as vergence velocities. This is reasonable, because glissades are the response of the plant to differences in tonic levels of innervation of the agonist and antagonist muscles. Vergence eye movements, being the response of the plant to approximately a step input (see Krishnan, this issue), have similar dynamics. However, these glissades are definitely not the explanation for dynamic overshoot, for they are much too slow.

The return velocities for dynamic overshoot are indicated with triangles in the Main Sequence diagram of fig. 8. These return velocities are equal to saccadic velocities for saccades of the same size, and therefore, have similar control signals. This yields an important clue to unraveling the origin of dynamic overshoot. If the return phase of dynamic overshoot has saccadic like dynamics, then it must have a saccadic like pulse step controller signal (fig. 9).

To further investigate the cause of dynamic overshoot, the model may be conceptually run in reverse. First, create the desired eye position (fig. 9A) and eye velocity (fig. 9B) as functions of time. Then, derive the active state tensions* of the agonist (fig. 9C) and antagonist (fig. 9D) muscles that are required in

* Active state tension differs from the force of a muscle exerted at the tendon [9]. It generally has faster dynamics and sharper corners, as shown in figs. 9C and 9D.

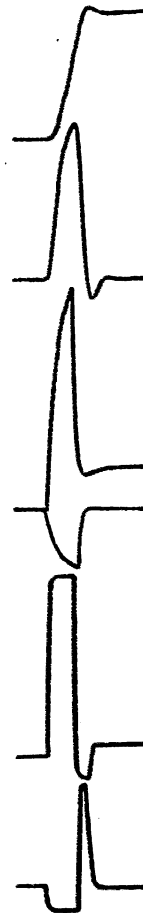


Fig. 9. Model responses for a ten degree saccade with dynamic overshoot, (from top to bottom) as functions of time, eye position, eye velocity, active state tension of the agonist muscle, active state tension of the antagonist muscle, agonist motoneuronal activity and antagonist motoneuronal activity.

order to produce the desired eye position and velocity records. Next, deduce the motoneuronal firing frequencies for the agonist (fig. 9E) and antagonist (fig. 9F) motoneuronal pools that are necessary in order to generate the muscle forces required to realize saccades with dynamic overshoot. This shows that in order to produce dynamic overshoot, the motoneuronal control signals must have reversals near the end of the saccade. That is, the primary saccade agonist must be inhibited, and the primary saccade antagonist must have a high-frequency burst of activity near the end of the saccade. This new pulse-step will develop the

small saccade, or return phase of dynamic overshoot, at the end of the main saccade.

4. Discussion

This model for the extraocular plant and saccadic controller suggests that dynamic overshoot must be caused by neural control signal reversals. These control signal reversals cannot be due to random noise, however, because often as many as a dozen consecutive saccades will have identical overshoot. The reversal at the end of this controller signal is similar to the signal required for time optimal control of an inertial object [13, p. 631], and also the signal used in optimal responses when the forearm moves a load [12].

However, the Central Nervous System (CNS) does not always use this second order time optimal controller for arm movements [12]. We have demonstrated here that about 70% of the time the CNS uses a second order controller for saccadic eye movements. When time optimal control theory was applied to our model, and the Hamiltonian functional was evaluated [7], it was found that this second order controller signal should be used for time optimal control of saccadic eye movements. This controller signal stratagem enables the eye to arrive and stay within one foveal radius (0.25 degrees) of the target in the least possible time.

We might expect the controller signal to be composed of two third order controller signals, because the plant model (fig. 2) is a sixth order system. (One third order controller signal is for the agonist and one third order controller signal is for the antagonist.) Fig. 10 shows experimental evidence that implies that the CNS may use a third order controller signal. For the saccade in this record, the eye is first driven to the left (down in fig. 10), then to the right, as in a normal return phase of dynamic overshoot, and then back to the left. A third order time optimal controller signal would drive the eye in a similar manner. About 1% of our saccadic eye movements exhibited this behavior characteristic of a third order controller signal.

These higher order controller signals require precise synchronization of the individual motoneurons. For instance, thousands of motoneurons in the agonist pool must all pause during the 5–10 msec return phase of the dynamic overshoot. Similarly, there must be a

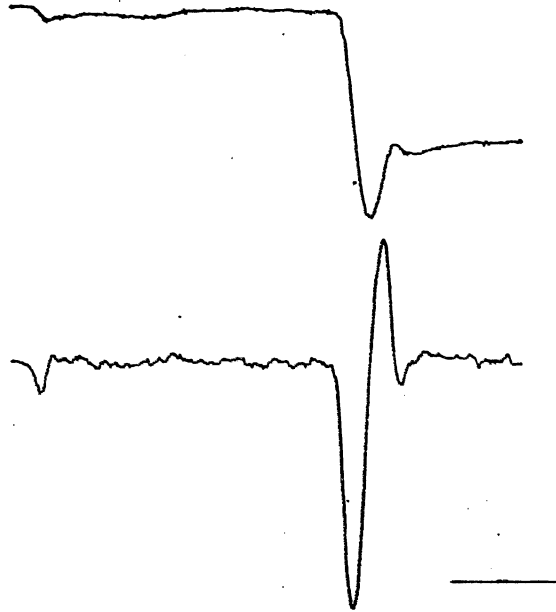


Fig. 10. Eye position and eye velocity for a saccade, presumably driven by a third order time optimal controller signal. The calibrations are as in fig. 5.

synchronized bursting in the antagonist pool during this same interval. Records of the firing of oculomotor neurons often show pauses and bursts near the end of the saccades. We believe these to be responsible for the control signal reversals that produce dynamic overshoot.

The return phase of dynamic overshoot has a saccade-like controller signal. It is feasible that the return phase of dynamic overshoot is actually a second small saccade in the opposite direction from the primordial saccade. This close spacing of saccades is not contradictory to the sampled-data model [16] for the saccadic tracking system, because the sampled-data model was formulated strictly for tracking randomly moving targets. Closely spaced saccades are common and can be produced in response to a variety of stimuli [1, 5]. Dynamic overshoot may represent just one more example of closely spaced saccades.

5. Summary

Most saccadic eye movements have dynamic over-

shoot, but this cannot be explained by classical control system theory for linear second order systems. In the computer stimulation, dynamic overshoot is produced by a second order time optimal controller signal applied to the input of the model of the extraocular plant. The motoneuronal control signals have role reversals immediately before the end of the saccade: the agonist for the main saccade has a brief pause, and the antagonist for the main saccade has a short burst of firing.

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