

Robert V. Kenyon

Man-Vehicle Laboratory
 Department of Aeronautics and Astronautics
 Massachusetts Institute of Technology
 Cambridge, MA 02139

Lawrence Stark, M.D.

School of Optometry
 University of California
 Berkeley, CA 94720

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Introduction

In 1868, Ewald Hering¹ hypothesized a control mechanism to explain the synchronous movements of the eyes. His hypothesis, now known as Hering's Law of Equal Innervation, states that muscles of each eye are yoked in their actions to rotate the eyes by receiving equal innervation patterns. This relationship has become one of the most widely used relationships in analyzing eye movements. The validity of this relationship has been shown through electromyographic recordings of the innervation activity in the extra ocular muscles during saccadic, smooth pursuit, and

vergence eye movements². Saccades are a particularly strong example of where Hering's Law of Equal Innervation produces eye movements that have equal magnitude in each eye. Large inequalities in saccadic eye movements are often interrupted as signs of pathology in the oculomotor system³.

Until recently, violations of Hering's Law by saccadic eye movements (as expressed as unequal saccadic amplitudes in each eye) in normals were usually sporadic and of small magnitude⁴. However, recent reports^{5,6} have shown that saccades occurring during vergence eye movements consistently have greatly different amplitudes in each eye.

This report focuses on these unequal saccades by analyzing their inequalities as functions of time and velocity during the vergence. Our analysis showed a systematic reduction in saccadic amplitudes that suggested an interactive rather than non Hering's Law effect. A 6th order nonlinear model of the eye and orbit was used to investigate this hypothesized interactive effect that vergence eye movements may have on the size of these saccades.

Eye Movement Recordings

Binocular eye movements from 14 subjects were recorded using a photocell method that had a bandwidth of 150 HZ, a noise level of 2 min arc, and a linear range of $\pm 7^\circ$. The vergence and saccadic eye movements were produced by having the subject change fixation between two targets, one at 57 cm and the other at 25 cm from the centers of rotation of the eyes.⁸ Calibration of the eye monitoring equipment was performed before, during, and after each experiment; data between changed calibrations was excluded from analysis.

Inspection of the eye movement record in Figure 1 reveals the unequal saccadic amplitudes commonly found when saccades occur during vergence eye movements. The

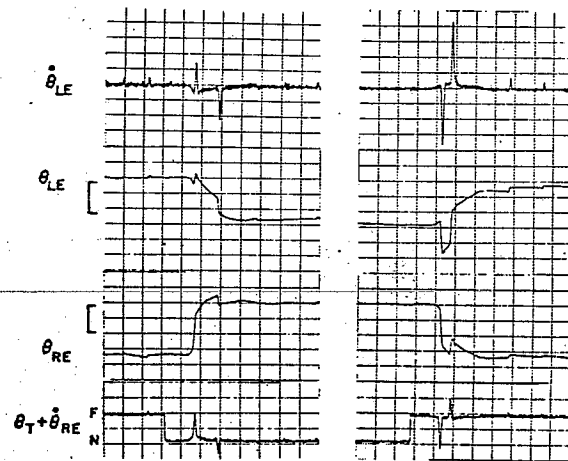


Fig. 1 Binocular eye movement recordings show unequal saccades during vergence. Saccades during the early portion of the vergence show greater inequalities than those that occur later in the vergence movement. θ_{re} and θ_{le} represent right and left eye position respectively. Calibration bars represent 2 degrees and time is 200ms/Div. $\dot{\theta}_{le}$ is the velocity of the left eye. $\dot{\theta}_{re}$ represents the velocity of the right eye linearly summated with the target position change marker: F= far target illuminated, N= near target illuminated.

saccades displayed in this sample record show the two main features that characterize unequal saccades during vergence. Firstly, the smaller saccade of the pair always opposes the vergence movement, and secondly, the saccadic inequalities are larger for saccades at the start of the vergence than at the end. The applicability of these observations to data obtained across subjects is evidenced when the degree of saccadic inequality is plotted as a function of time after the vergence (Figure 2). The plot of saccadic relative amplitudes (see Figure Legend) versus time shows an exponential-like trend in the data reminiscent of the instantaneous velocity of vergence eye movements. This suggested a velocity rather than a time related affect on the saccadic amplitudes. Therefore a portion of the data in Figure 2 was replotted as a function of the velocity of the eye prior to the saccade (Figure 3). These data show that increases in eye velocity prior to the saccade are related to increases in saccadic inequality. Initially one might expect a linear

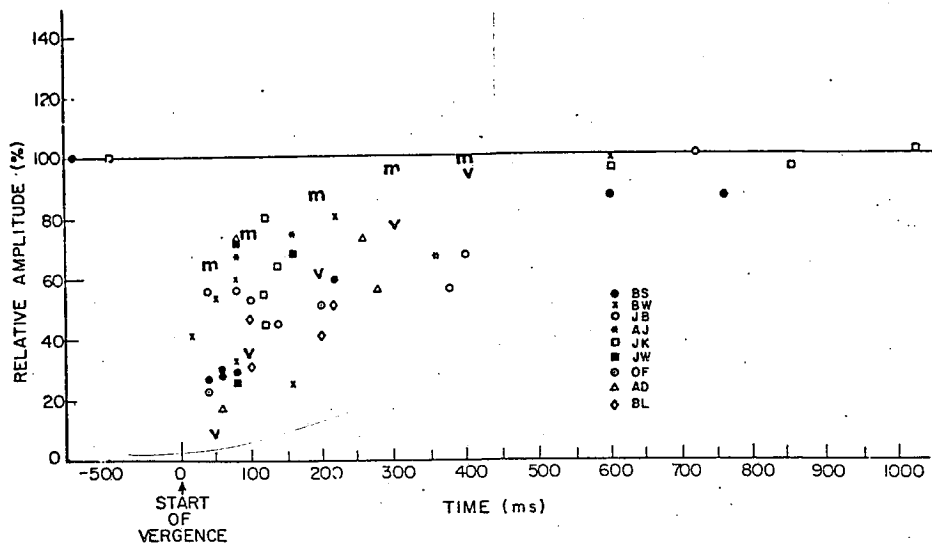


Fig. 2 Degree of saccadic inequality plotted as a function of time following the vergence movement. Relative Amplitude is defined as the ratio, in percent, of the saccadic amplitude opposing the vergence to its counterpart in the fellow eye. This plot shows the consistency of the opposing saccade always resulting in an amplitude that is less than that in the fellow eye, since the data points all fall below the 100% line in the graph. Also, notice how saccades occurring early in the vergence have greater inequalities than those occurring later in the vergence movement. Letters 'm' and 'v' represent data from simulations using our model of the oculomotor plant. The 'm' data points show relative amplitudes that result from a 4 deg. vergence and a 2.1 deg. saccadic interaction. The 'v' data points were generated using a 6 deg. vergence interacting with a 2.1 deg. saccade.

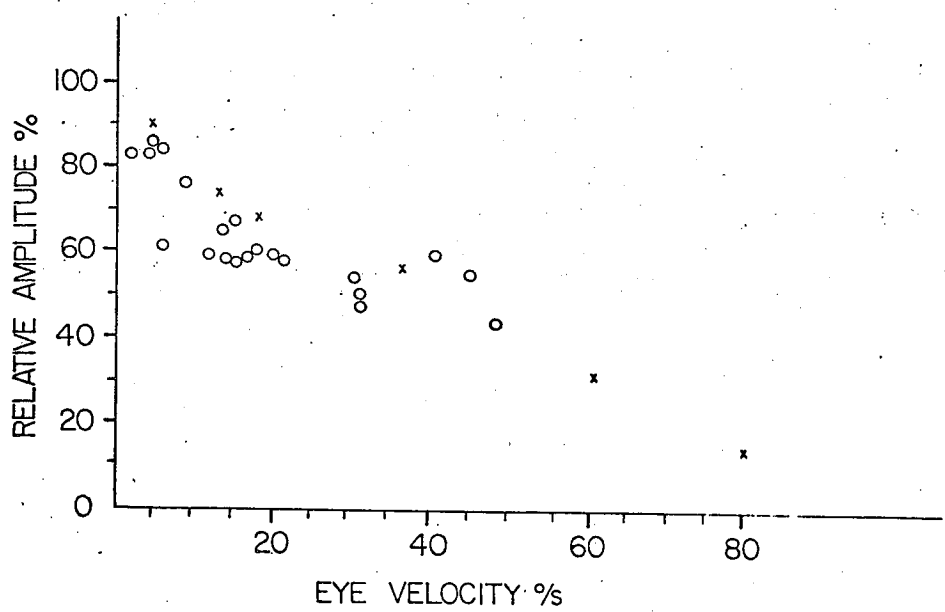


Fig. 3 Degree of saccadic inequality, in Relative Amplitude as defined above, is plotted against the velocity of the eye prior to the saccade. The open circles represent experimental data from our subject population. The crosses 'x' are data from our model results using both the 4 and 6 deg. vergence data to span the range of velocities from 5 deg./sec. to 80 deg./sec.

additive relationship between vergence and saccades to explain these saccadic inequalities. However, Ono

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et al. have shown that this simple additive case can not explain this saccade-vergence interaction. Thus we must look elsewhere for an explanation of this effect.

Modeling Results

The systematic attenuation of saccades during vergence shown in Figures 2&3, suggested that a passive rather than an active mechanism may be responsible for these inequalities. We first questioned the assumption that these unequal saccades were the result of independent saccadic innervation signals to each eye and thus violations of Hering's Law of Equal Innervation. Instead we assumed that Hering's Law was observed but that the velocity of the eye prior to the saccade influenced the size of the saccades. We investigated the validity of this hypothesis by using a 6th order nonlinear model of the eye and orbit to model these subjects' responses.

The model contained a nonlinear force-velocity relationship and reciprocal innervation. Control signals used to drive the model were linear summated vergence step and saccadic pulse-step control signals, where the traditional yoked muscles of Hering's Law received equal innervation patterns.

The model responses shown in Figures 4 and 5 are the result of linearly summating control signals for a 4 degree vergence and a 2.1 degree saccade. In Figure 4, where the saccade follows 25ms after the vergence, the saccade opposing the vergence velocity is only 40% the amplitude of the saccade in the fellow eye. When the saccade occurs 320ms after the vergence the amplitude of the saccade opposing the vergence velocity is 80% that of the saccade in the fellow eye.

A series of these simulations were performed where the timing of the saccade varied from 50 to 400ms after the start of the vergence. A plot of these simulated saccade-vergence interactions are plotted in figure 2 as a function of time (points 'm' and 'v'), and in Figure 3 as a function of the velocity of the eye prior to the saccade (point 'x'). The model responses besides displaying similar features as those from our subject population, also show a similar exponential-like relationship to the timing of the saccade during the vergence. The agreement between experimental and model data as functions of velocity is also quite close.

This qualitative agreement between experimental and model data is an encouraging sign that our initial assumption that these unequal saccades are not the result of violations of Hering's Law but due to a nonlinear interaction in the oculomotor plant was justified. The exact nature of the plant mechanism responsible for this interactive effect is still being investigated; our primary candidate for this effect is the nonlinear Force-velocity relationship of muscle. We hope to see continued interest in this hypothesis by neurophysiologist and model builders alike. Electrophysiological data from both humans and animals along with better and more sophisticated models of the oculomotor plant are needed to investigate this effect further.

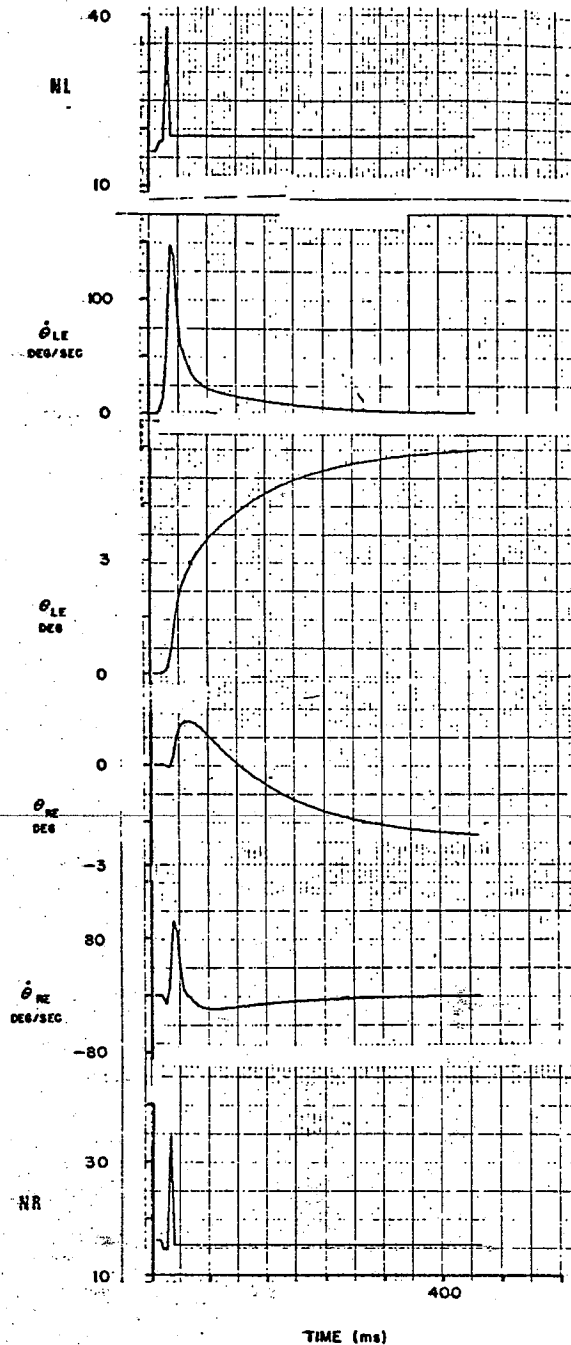


Fig. 4 Model responses to linearly summated 4 deg. vergence step and 2.1 deg. saccadic pulse-step control signals. Saccade occurs 25 ms after the start of the vergence control signal. As in our experimental data, our model data shows a reduction in the size of the saccade that opposes the vergence movement. Instead of the 2.1 deg. saccade programed, 1 deg. saccade is seen. NL and NR represent the neuronal control signal envelope that is used to drive the model for the yoked saccadic agonist muscle of the left and right eyes respectively. Other notations same as in Figure 1.

Arbitrary units

Acknowledgements

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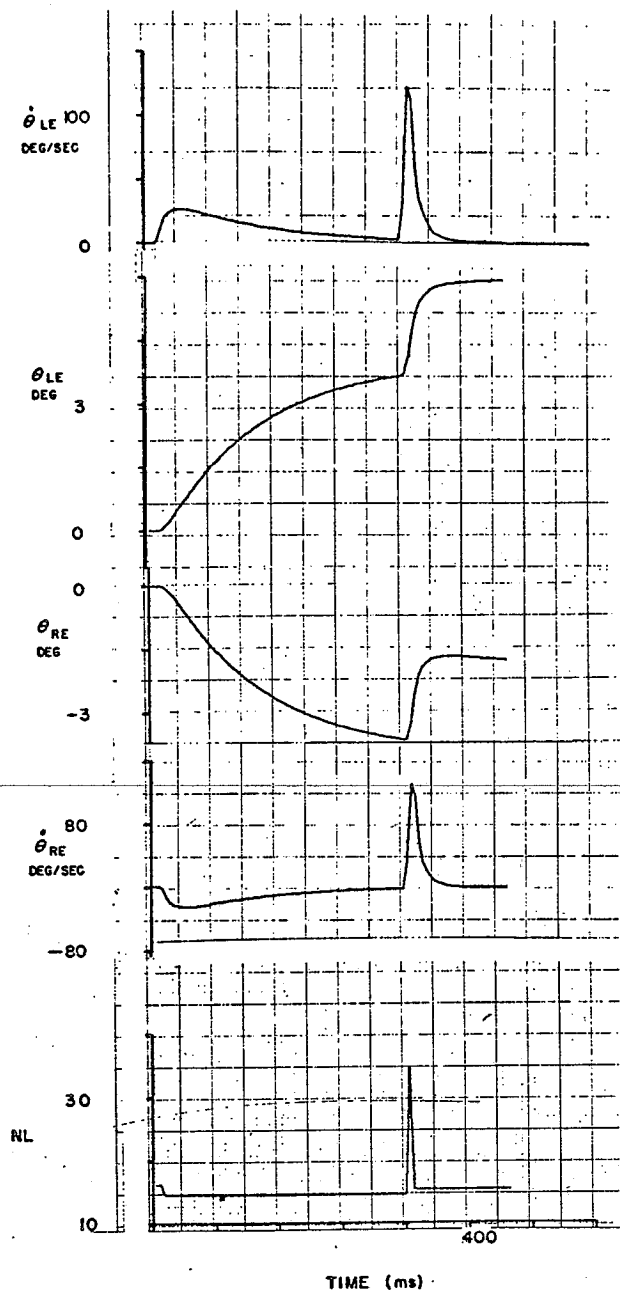


Fig. 5 Model responses to linearly summated 4 deg. vergence step and saccadic pulse-step control signals. Saccade occurs 320ms after the start of the vergence step signal. Notice that the size of the saccade opposing the vergence is larger than the same saccade in the previous figure. The same notation as described in Figure 4 applies to this figure.