

Unequal Saccades during Vergence

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Abstract

An examination of saccades during vergence eye movements (accommodative and disparity) reveals that binocular saccades have unequal magnitudes in each eye, the smaller saccade of each pair opposing the vergence movement. Furthermore, this inequality cannot be explained by linear summation of the saccadic amplitudes onto the ongoing vergence. Saccadic inequalities are usually greater at the start of the vergence; the amplitude of the smaller saccade may be reduced 70% from that of the larger.

Using a sixth-order nonlinear model of the eye movement plant and linear summation of saccadic (pulse-step) and vergence (step) control signals to drive the plant, we have produced a reduction in saccadic amplitudes between the two eyes during vergence that is similar to those found in our subjects. These results suggest that the reduction of saccadic amplitudes is due to an interaction in the muscular system moving the eye, not to a nonlinear neuronal interaction more centrally located.

Key Words: saccades, accommodative vergence, disparity vergence, nonlinear eye movement model

Patients with strabismus and/or amblyopia have been shown to exhibit a predominance of accommodative vergence over disparity vergence when tracking targets moving in three-dimensional space.¹⁻³ Apparently, sensory information presented to

the nondominant eye is not used effectively, transforming a binocular stimulus into a monocular one. Specifically, in tracking three-dimensional targets the disparity information is lost while the accommodative blur information is retained. Furthermore, if such targets are placed symmetrically between the two eyes, a prominent binocular saccade, apparently driven by the eccentricity of the target in the dominant eye, is used to place the dominant eye on the new target. Fig. 1 shows a typical response to symmetric targets from patients with strabismus and/or amblyopia. Since these patients consistently perform saccades during vergence, they proved to be a good population for studying the interactions between saccades and vergence.

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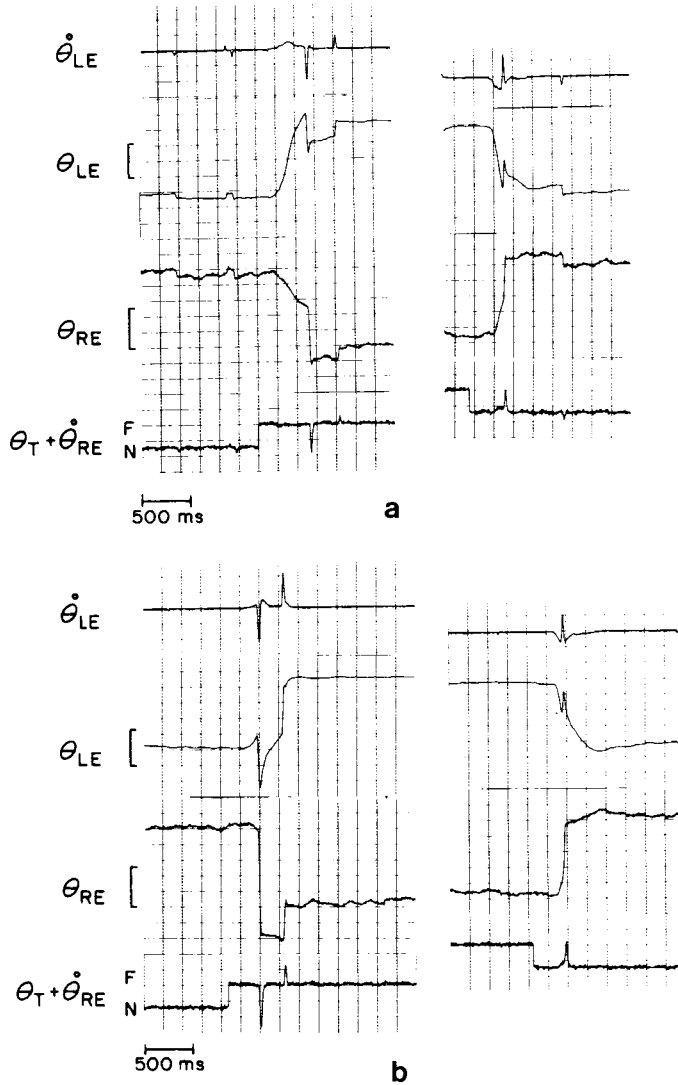


FIG. 1. A Patient's eye movements while changing fixation between near and far symmetric targets under binocular conditions. The following conventions are used unless otherwise indicated: θ_{LE} = left eye position, θ_{RE} = right eye position, $\dot{\theta}_{LE}$ = left eye veolcity, $\dot{\theta}_{RE}$ = right eye veolcity, θ_T = target position, and $\theta_T + \dot{\theta}_{RE}$ = linear summation of θ_T and $\dot{\theta}_{RE}$ in one trace. The time marker represents 500 msec and the calibration bars equal 2 deg. The deflections up are left and down are right. The saccades that occur during the vergence have unequal amplitudes. In each saccadic pair, the smaller saccade opposes the vergence movement. Saccades that occur before and after the vergence have equal amplitudes, indicating that these unequal saccades are not an artefact of the recording system. In this series of responses the saccades occur during the vergence at 300 msec (top left), 100 msec (top right), 100 and 300 msec (bottom left), and 80 msec (bottom right) after the start of the vergence.

As Fig. 1 shows, saccades that occur in our strabismus/amblyopia patients summate with the accommodative vergence such that one saccade (of the pair) opposes the vergence while the other saccade (of the pair) moves along with the vergence.

Since accommodative vergence has been shown to be a binocular response,⁴ these binocular pairs of saccades have the opportunity to summate with as well as oppose the ongoing accommodative vergence. Many times this interaction results in

markedly unequal saccades in the two eyes. For example, in Fig. 1a the divergence movement contains saccades of 2.1 deg in the left eye that opposes the vergence and 3.0 deg in the right eye that is in the same direction as the vergence movement. In Figure 1b, the divergence contains saccades of 1.4 deg in the left eye opposing the vergence and 2.1 deg in the right eye going with the vergence. Notice that in each saccadic pair the smaller saccade opposes the vergence movement. This is a characteristic of unequal saccades during vergence.

Unequal saccades were first reported by us⁴ during accommodative vergence in normal subjects and by Ono et al.⁵ during disparity vergence in normal subjects. In this report we examine saccades during vergence produced when targets are placed symmetrically between the two eyes. Usually such targets induce smooth, equal disjunctive vergence movements, as seen in Fig. 2a (left). Occasionally saccades occur during the vergence movement, most often during divergence. Occurrence of these saccades provided us the opportunity to study

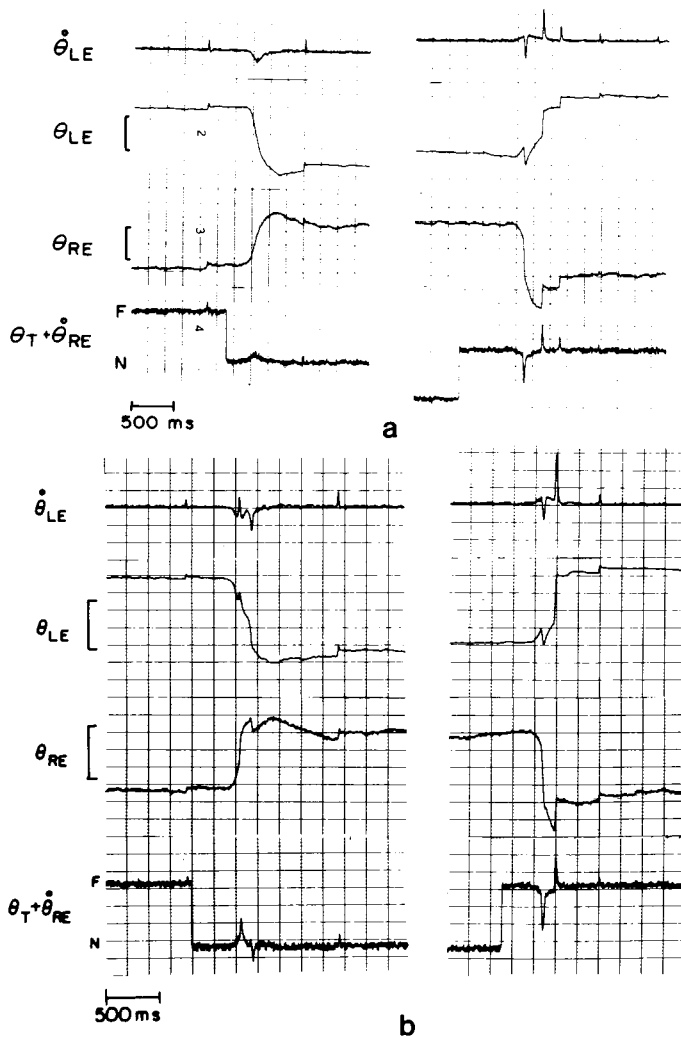


FIG. 2. Eye movements from normal control subject, showing the same unequal saccades during disparity vergence found in the patient in Fig. 1 during accommodative vergence. Therefore, the inequality of the saccades is not related to the ocular condition of the patient or to accommodation or disparity vergence movements.

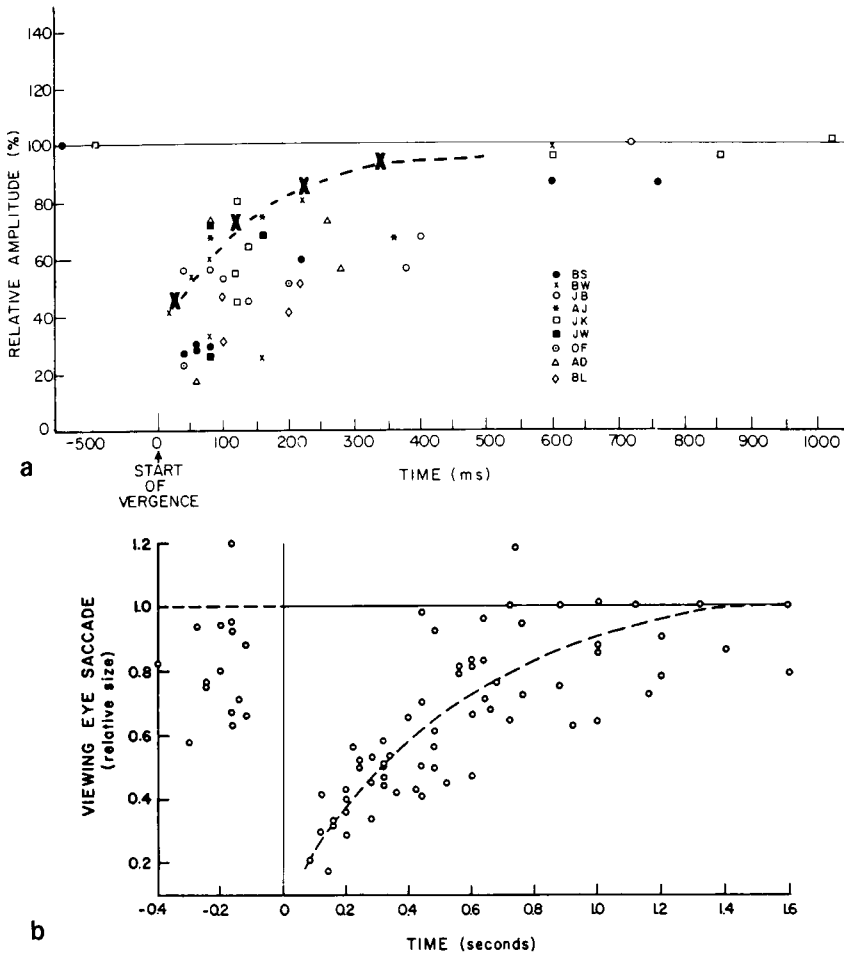


Fig. 3. Plot of the relative amplitudes of saccadic pairs during vergence at various times after the start of the vergence response. a: The ratio of smaller saccade to larger saccade is plotted on the ordinate for nine subjects. The X and the solid line represent data from the simulations using the sixth-order nonlinear plant with linear summation of the vergence (step) and the saccadic (pulse-step) neurological control signals. The data resemble the attenuation found for the subject with smaller x symbol. The horizontal line represents saccades of equal amplitude. b: Plot of relative saccadic amplitude vs time after vergence for saccades during accommodative vergence from four normal subjects. As in a, the largest inequality occurs at the start of the vergence, where the velocity of the eye is greatest for vergence. The dashed line was fitted by eye.

the saccade/vergence interaction in normal subjects. The presence of saccades during disparity vergence movements in Fig. 2 indicates that these saccades are affected by the vergence in a similar fashion as those in our patients. In the divergence response of Fig. 2a, the saccadic pair 100 msec after the start of the vergence equals 1.0 deg for the saccade that opposes the vergence (LE) and 3.0 deg for the saccade moving with the vergence (RE). In the same response, the next saccadic pair has amplitudes of 1.8 deg

with the vergence (LE) and 1.4 deg against the vergence (RE). Notice that the smaller saccade in this second pair is now in the right eye and opposes the vergence. Furthermore, the inequality of these saccades is greater when these saccades occur early in the vergence movement, in both patients and normal subjects. These observations suggest that a better understanding of the summation mechanism might be obtained by a quantitative analysis of saccadic amplitudes in each eye as a function of the

occurrence of the saccades during the vergence.

QUANTIFICATION OF SACCADE INEQUALITIES

For each saccadic pair occurring near the beginning, near the end, or in the midst of the vergence movement, a ratio was calculated by dividing the amplitude of the smaller saccade by that of the larger saccade. This ratio was plotted as a function of time. In Fig. 3a, the amplitude of the smaller saccade is less than 30% of the amplitude of the larger saccade near the beginning of the vergence movement. However, by the time the vergence movement has ended, about 600 msec later, the ratio approaches unity. As will be discussed later, it may be that some internal state variable, such as velocity, more closely relates the interaction between the saccadic inequality and the ongoing vergence than time does. Studies investigating this question are in progress in our laboratory.

When saccades during accommodative vergence in normal subjects are examined by this same procedure, the resulting function has the same general characteristics. In Fig. 3b, saccades occurring early in the accommodative vergence movement are more unequal than those occurring toward the end of the vergence.

SIMULATION STUDIES

The saccadic inequalities shown above may be a product of a nonlinear interaction between neurological control signals for saccades and vergence eye movements. A nonlinear summation of these neurological control signals would need to occur prior to the motoneurons, since Keller and Robinson⁶ have shown that saccade and vergence control signals travel along the same motoneuron in the final common pathway. However, the neurophysiological records of the eye movement control signals at the final common pathway have not been able to show a nonlinear interaction between saccades and vergence signals.⁶

Another region of possible interaction is at the periphery, where these summated vergence and versional control signals produce excitation and contraction of the ex-

traocular muscles, which in turn act on the globe. This biomechanical region seemed to us to be the first place to study possible interactions between saccades and vergence. Our initial assumption was that saccadic and vergence control signals summate linearly to drive the muscles. Accordingly, linearly summated saccadic and vergence control signals were used to drive a nonlinear sixth-order model of the globe and its reciprocally innervated horizontal recti muscles.⁷⁻¹¹ Results from these simulations are shown in Figs. 4 and 5.

A saccadic pulse-step control signal representing 2.1 deg and a vergence step control signal representing 4.0 deg were linearly combined to produce reciprocal pairs of control signals to drive each muscle in the model (NR and NL). In Fig. 5a, saccades occur 25 msec after the vergence starts, and the saccade opposing the vergence has an

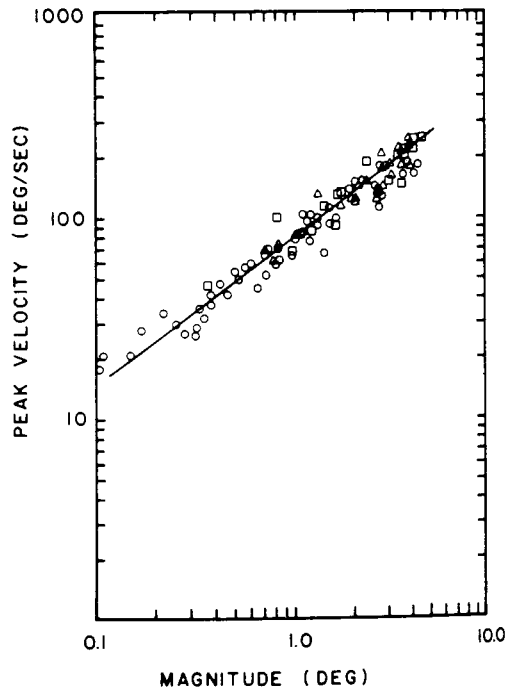


FIG. 4. Relation between peak velocity and amplitude of saccades. The solid line represents the locus of points upon which normal saccadic velocity/amplitude function should fall. The symbols represent the unequal saccadic pairs performed during vergence eye movements by normal subjects and patients. The clustering of these data around the solid line indicates that these saccades do not have abnormal dynamics in spite of their inequality.

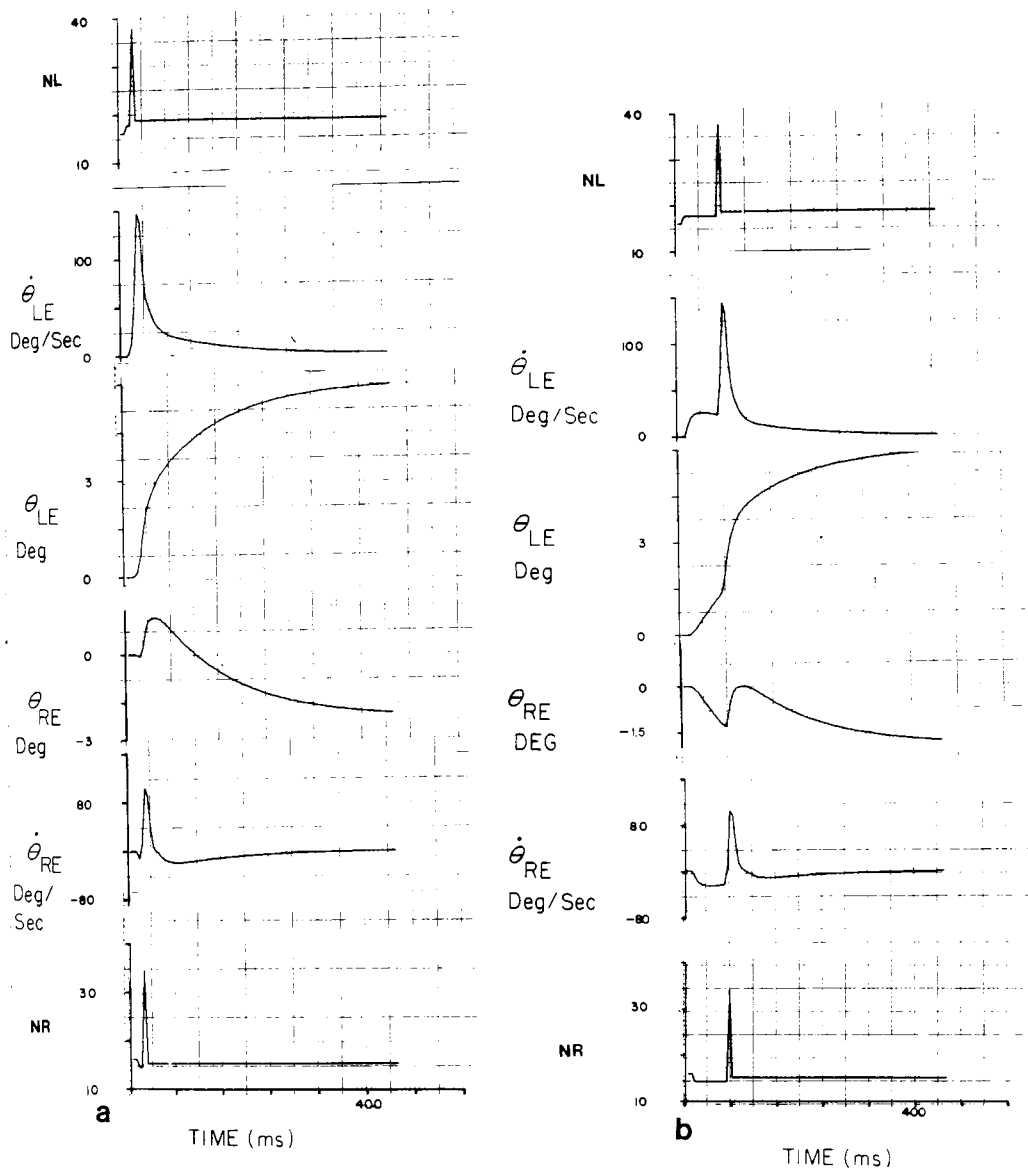


FIG. 5. Simulations of vergence and saccadic interactions using linear summation of the motoneuronal control signals. NR = antagonist control signal (arbitrary units); NL = agonist control signal (arbitrary units); θ_{RE} = right eye position; $\dot{\theta}_{RE}$ = right eye velocity; θ_{LE} = left eye position; $\dot{\theta}_{LE}$ = left eye velocity. Upward deflections are left and down are right. Each simulation has control signals to produce an initial vergence of 4 deg and a 2.1-deg saccade. a: Saccadic pulse step occurs 25 msec after the start of the vergence step. The saccadic amplitudes are 0.9 and 2.2 deg for the left and right eye saccades, respectively. The left eye saccade opposes the vergence. b: Saccadic pulse step occurs 60 msec after the vergence step. The saccadic amplitudes are 1.1 and 2.2 deg.

amplitude of 0.9 deg instead of the 2.1 deg the control signal programmed; the saccade moving with the vergence has an amplitude of 2.5 deg. Saccades occurring later in the vergence movement begin to approach the

programmed 2.1 deg in each eye (Fig. 5b). For example, 375 msec after the vergence, the saccade opposing the vergence equals 1.5 deg and with the vergence 2.1 deg. The gradual approach to equality of saccades as

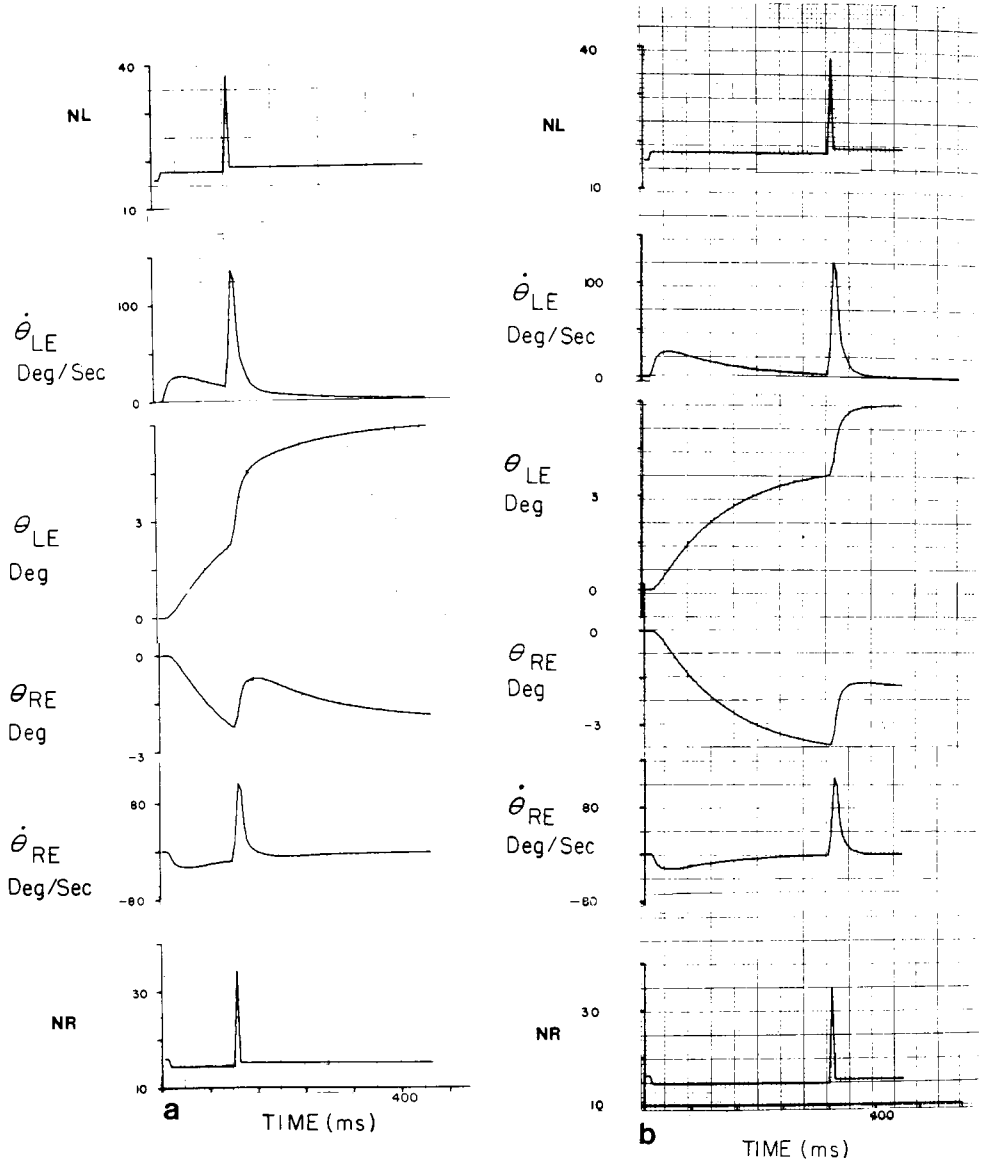


FIG. 6. Simulations of saccadic and vergence interactions as the saccades occur later in the vergence movement. a: The saccadic pulse-step control signal is summated on the motor control signal 130 msec after the start of the vergence control signal. The saccade opposing the vergence in this movement is larger than the opposing saccades in the previous two simulations. The saccadic amplitudes are 1.5 and 2.2 deg in the right and left eyes, respectively. b: The saccadic pair occurs 325 msec after the vergence in this simulation. The saccadic amplitude in the right eye continues to increase and approach the amplitude of the fellow eye's saccade.

they occur progressively later in the vergence shows that the saccadic inequalities act similar to those seen in both patients and normal subjects. An analysis of these simulated saccades' relative amplitudes as a function of time shows good agreement with those from our subjects. The bold X

symbols and the solid line in Fig. 3a represent the simulated saccades' ratio at varying times during the simulated vergence. The same quasi-exponential function is produced from these simulations as from our subjects. It can be readily seen that the saccades in the simulation show inequali-

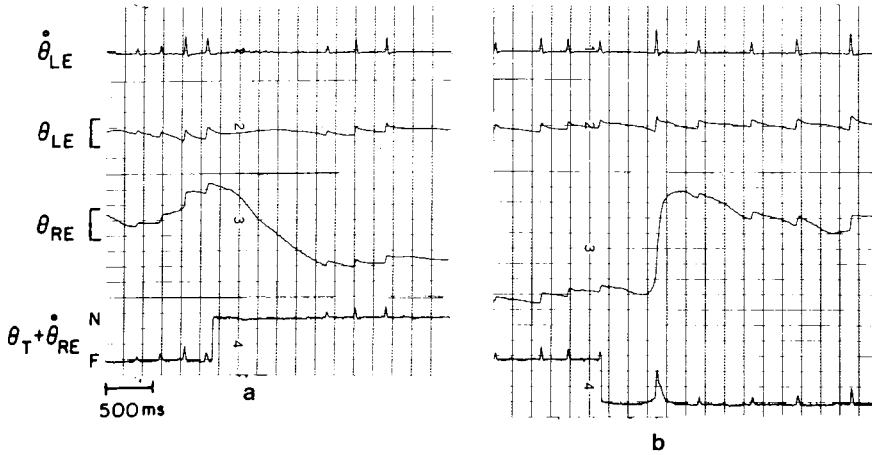


FIG. 7. Interaction of slow-phase nystagmus with accommodative vergence (Müller paradigm) in the viewing eye. a: When the viewing eye begins to diverge, the interaction with the slow phase of nystagmus is such that the eye remains steady and on the target. Without a retinal error to correct, there is no saccade, and thus the nystagmus is absent for the amount of time the two movements cancel. b: When the accommodative vergence and the nystagmus in the viewing eye are in the same direction, the drift increases and so does the amplitude of the saccade correcting for the drift.

ties similar to those seen in our patient group and in normal subjects with ongoing disparity vergence or ongoing accommodative vergence. The same qualitative rule applies: saccades directed opposite the vergence are truncated in amplitude and velocity, and the opposite occurs for saccades going in the same direction as the vergence. Since the model uses only linear summation of controller signals, nonlinear summation of saccadic amplitudes with the ongoing vergence seen in these simulations must occur as the result of interactions within the biomechanical mechanisms of the plant model. It may be appropriate here to mention that the most prominent nonlinearity in the muscle-globe plant is the nonlinear force-velocity relation of muscle, which is a consequence of conversion of chemical energy to mechanical work.¹² Thus, this essential feature of muscle is well captured by our model.

CHARACTERISTICS OF PATIENTS' SACCADES

Fig. 6 represents the relation between velocity and amplitude of a saccade and serves an important diagnostic purpose in evaluating eye movement recordings in patients.¹³ The fact that our patients' saccades fall on this curve indicates that the changes in amplitude and velocity are similar, so

that divergence from this relation does not occur within the limits of experimental precision. This suggests that the pulse-shaping functions of the brainstem and the neuromuscular elements of the oculomotor system are all functioning normally. It further suggests that the complex nonlinear interactions that lead to the inequality of the saccades do not alter the normal relation between saccadic velocity and amplitude.

NYSTAGMUS INTERACTION WITH VERGENCE

One of our patients exhibited manifest nystagmus,¹⁴ which typically has a saccadic phase and a slow phase, as shown in Fig. 7. When the patient makes vergence eye movements, it appears that the slow phase of the nystagmus summates algebraically with the vergence.¹ In the divergence movement of Fig. 7a, the slow phase of the nystagmus and the accommodative vergence in the viewing eye oppose each other. This interaction counteracts the slow phase of the nystagmus, keeping the viewing eye stationary and on the target. With no drift of the eye off the target, the saccadic phase of this nystagmus was absent. This shows that the slow phase in this patient's nystagmus is primary and that the saccade is used to correct for the retinal error produced by the drift. In the convergence response (Fig.

7b), the vergence and the slow phase move in the same direction, thus increasing the drift and the amplitude of the saccade used to correct for the drift.

UNEQUAL SACCADES AND HERING'S LAW

Hering's law is a law of *innervation*.^{15, 16} It states that corresponding muscles receive equal innervation, and it applies to both conjugate and disjunctive eye movements. Our simulations were designed so that they too obeyed Hering's law. Since the simulations showed the same inequality of saccades when superimposed on vergences as our patients' eye movements, the simulation suggests that our patients' eye movements obeyed Hering's law, i.e., each saccade of a binocular pair getting the same innervation.

We conclude that the inequality of saccades is due not to a violation of Hering's law but to a biomechanical interaction in the muscle globe plant.

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