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VOLUNTARY NYSTAGMUS IS SACCADIC: EVIDENCE FROM MOTOR AND SENSORY MECHANISMS

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The true saccadic nature of voluntary nystagmus is demonstrated by analysis of eye movements using wide/bandwidth photocell instrumentation. Features of the high velocity saccadic trajectories are displayed in Main Sequence diagrams of velocity, acceleration and duration as functions of amplitude. The sensation of oscillopsia accompanying voluntary nystagmus relates to Helmholtz' frame-of-reference brain calculation that ordinarily stabilizes the visual world during saccadic eye movements.

Voluntary nystagmus is a very rapid to-and-fro oscillation of the eyes produced at will in some healthy subjects. Although many aspects of this interesting phenomenon have been noted,[1] its saccadic nature has only recently been shown.[2] This report describes use of an eye movement recording system, of an on-line digital computer, and of a 'Main Sequence' analysis that permitted precise definition of the saccadic structure of voluntary nystagmus. The oscillopsia experienced during voluntary nystagmus is interpreted in terms of Helmholtz's frame-of-reference computation for saccades.

The development of large bandwidth instruments for recording human eye movements permits definition and differentiation of the structure of the various types of eye movements---saccades, smooth pursuit, vergences, glissades. Infra-red photocell recording has a bandwidth of 400 Hz. and a noise level equivalent to 1 minute of arc of eye rotation.[3] Frequent calibration guarantees the recorded eye movements faithfully reflect retinal rotation. Measurements are linear within a range of plus or minus 10 degrees. On-line digital computer sampling 5,000 or 10,000 times per second and computer algorithms for differentiation and summing or smoothing eliminates the phase distortion that is an unavoidable part of electronic differentiation.

Six normal subjects recruited for this study were university students and laboratory visitors including two of sixty scientists participating in a University of California, Berkeley, symposium on saccadic eye movements. The subjects carried out various maneuvers in order to elicit their voluntary nystagmus, strong convergence usually being most effective.

Amplitudes and durations of nystagmus varied considerably from time to time and from subject to subject. One subject, D.W., was able to control the amplitude of nystagmus. Eye positions, velocity, and acceleration, all as functions of time, are shown in Fig. 1A. Note the apparent "pendular" quality of the position trace, even when undistorted by the smoothing and filtering that is usually associated with other lower bandwidth recording systems. This pendular appearance is the reason that previous investigators have overlooked the saccadic composition of voluntary nystagmus. The velocity traces of Fig. 1A document the defining feature of saccades ----the high velocity.

Display of peak velocities and durations as functions of the amplitudes of saccades, the Main Sequence plot in Fig. 1B, shows an empirical relationship studied since the time of Dodge.[4] All saccades---schematic, refixation, nystagmus, corrective, and micro-fixational[5]---show this relationship, suggesting similarity in generating mechanism. Saccades have normal trajectories even when fractionated into double saccades,[7] when saccadic dynamic overshoot occurs,[8] or when saccades follow sequentially in opposite directions as in voluntary nystagmus. The Main Sequence plot, Fig. 1B, shows the velocity, acceleration, and duration values of the saccadic trajectories of voluntary nystagmus, thus providing clear evidence from the motor output of its saccadic identity.[9]

Recent studies,[6] including simulations and experimental findings, show the time-optimal, pulse-step, nonlinear control of the saccadic trajectory underlies the Main Sequence relationship. A saccadic controller signal consists of a pulse of high frequency of neuronal firing and a step of maintained tonic discharge. The pulse-step signal is thus the envelope of oculomotor neuronal activity. Time-optimal studies[6] showed the width of the pulse to code dynamic saccadic amplitude. That is, the larger the width of the driving pulse, the larger the amplitude of the saccade. The pulse lasts about one-half the duration of the saccade itself, driving velocity to the maximum possible in that period. Physiologically, the normal peak velocities are a sign that there is normal reciprocal innervation, an agonist 'burst' and a concomitant antagonist 'pause.'[10] Thus we can deduce that in voluntary nystagmus successive alternating bursts occur in motoneurons of the horizontal recti and for each phase generate a high velocity saccade.

The generation of such a rapid sequence of saccades exceeds the limits of discrete, intermittent eye movement control, since this sampled data mechanism requires 150-200 msec in order to process the visual error signal, during which period it is refractory to other signals.[11] Thus, voluntary nystagmus cannot be generated through the normal visual, sampled-data mechanism but rather later in the sequential control process; because of the Hering's Law conjugacy and normal trajectories, it must be introduced before the final signal generating mechanism for the pulse-step discharge in the motoneurons.

Supporting this deduction, there is another line of evidence involving sensory input that contributes to the understanding of the level of saccadic control in voluntary nystagmus. The subjects during their voluntary nystagmus experience oscillopsia,[12] a symptom of jiggling of the visual environment. Visual space around us ordinarily does not shift when we make a normal saccade because the movement of the retinal image is anticipated in the 'Helmholtzian frame-of-reference comparator'.[13] If we externally jiggle the eyeball, the world appears to jiggle. If we attempt a voluntary saccade, but are restrained by an external force or a paretic eye muscle, the world appears to jump in the opposite direction. A sensorially directed signal which Helmholtz related to 'effort of will,' VonHolst and Mittelstaedt called 'efferent copy', and Sperry named 'corollary discharge' is generated by the normal sampled data mechanism for every saccade it initiates,[14] and it is this signal that prevents illusory environment movement from occurring. Westheimer speculated on the neurological level of 'origin' of voluntary nystagmus that would permit oscillopsia: "One would accordingly place the immediate origin of the impulses producing voluntary nystagmus at a level between the cerebral cortex and the motor nuclei of the extra-ocular muscles."[15] We suggest that the motor generating signal for voluntary nystagmus might be injected into the eye movement control system after the corollary discharge path had diverged from the efferent signal pathway. It thus does not activate the frame-of-reference computation and oscillopsia ensues. We cannot provide foundation for this argument. First, we point out recent studies showing only saccades are associated with the frame-of-reference computation.[13] Second, we add our discovery that voluntary nystagmus is composed of saccades. With these significant additions, the reason for occurrence of oscillopsia in voluntary nystagmus becomes tightly linked to its saccadic structure. Furthermore, the point of introduction of the signal for voluntary nystagmus that this argument for oscillopsia requires---after the sampled data mechanism and the bifurcation of its corollary discharge pathway and before the sequential generator mechanism for conjugate and reciprocally innervated pulse-step signals---is precisely the same point deduced from motor evidence in Fig. 1 on the saccadic structure of voluntary nystagmus.

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9. Peak velocities and accelerations of the saccades of voluntary nystagmus are somewhat higher and the durations somewhat shorter than normal Main Sequence values, suggesting that the succession of alternating saccades is so rapid that full amplitude of the saccade is not achieved. Thus the peak velocities we find are appropriate for larger saccades than occur and are larger than normal for the saccadic amplitudes we measure. Support for this suggestion comes from study of the velocity traces of Fig. 1A which reveal the decelerating velocity of one saccade smoothly continuing into the accelerating velocity of the next saccade. This point is important in considering the pulse-step generation of sequential alternating saccades. Absence of a shelf, that is a peripherally visible pause, indicates that shortening of step-phases is occurring between successive pulses, and thus that the full amplitude of the saccade may not eventuate.

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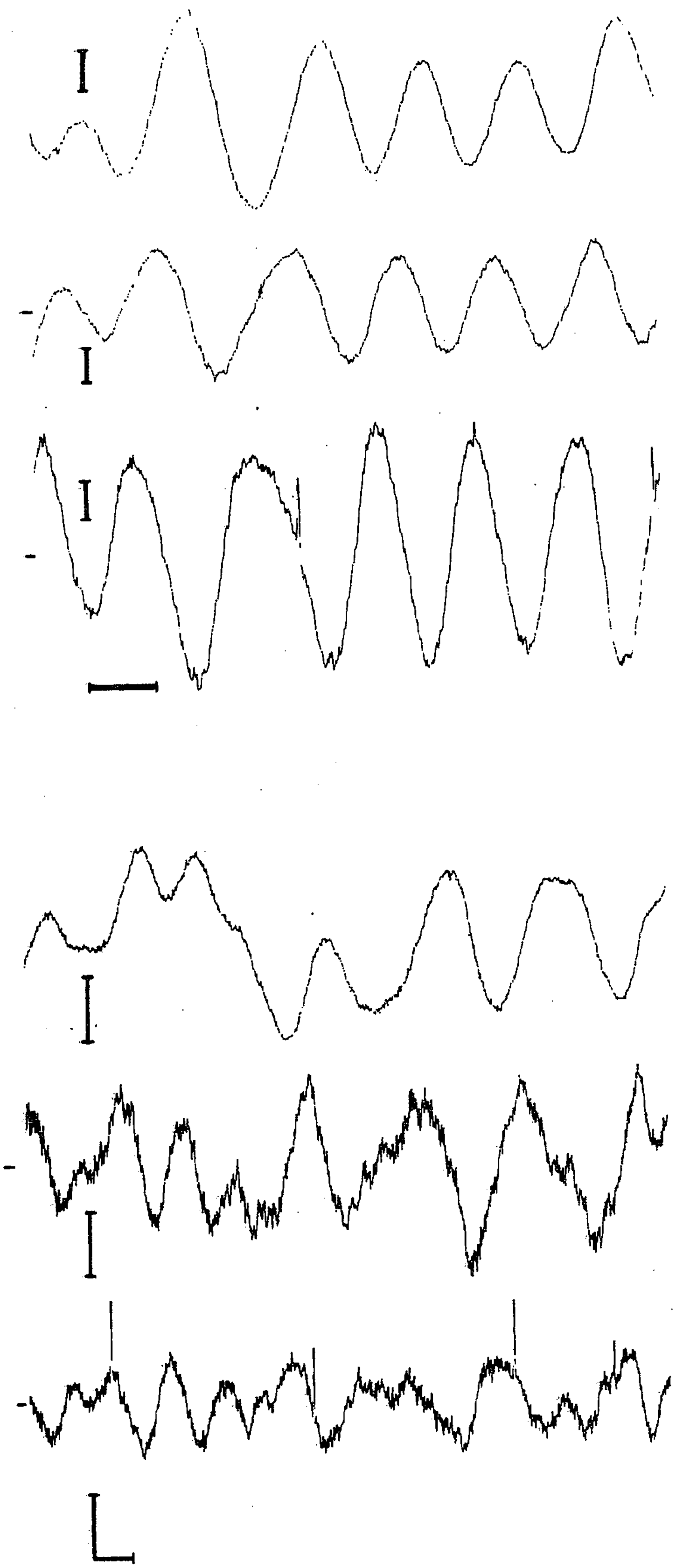

Figure 1A shows eye position, velocity, and acceleration time functions for two subjects. Note especially very high velocity which is defining feature of saccadic eye movements. Absence of zero velocity and zero acceleration regions appearing as 'shelves' suggests some attenuation in duration of at least part of step-phase of normal pulse step saccades. Acceleration trace shows noise limitations in eye movement recording. Calibration marks indicate 0.51 degrees, 103 degrees/second, and 20,000 degrees/second/second for upper traces and 0.57 degrees, 62 degrees/second, and 30,000 degrees/second/second for lower traces; time calibration equals 100 milliseconds for both.

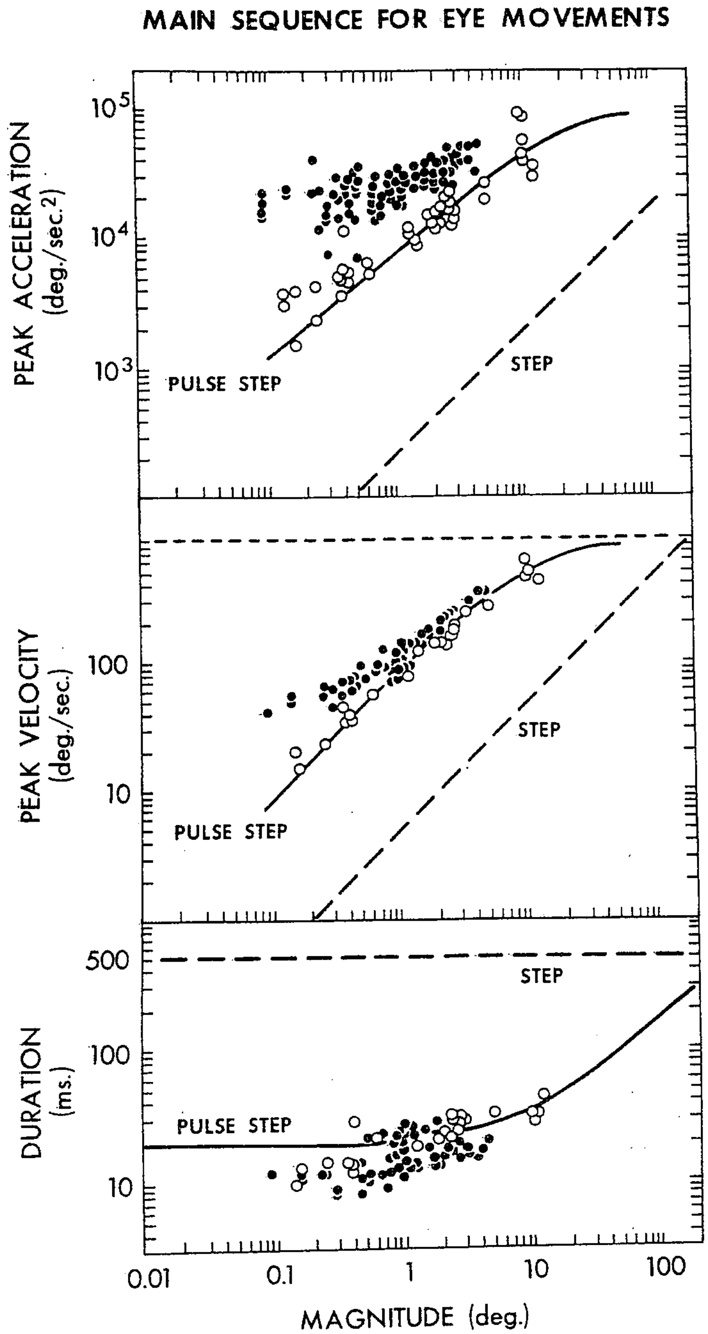

Figure 1B shows Main Sequence of acceleration, velocity, and duration as functions of amplitude. Normal saccadic experimental data is shown as well as model simulation results, both as solid lines. These confirm presicion of representation of both pulse-step controller signal and eye movement plant model. Voluntary nystagmus saccades (filled circles)are somewhat above velocity position of the Main Sequence diagram and somewhat below duration portion, demonstrating their very rapid saccadic nature. Minor deviations can be assessed with respect to Main Sequence relationships for vergence and glissadic eye movements generated by step controller signal shapes; voluntary nystagmus saccades are somewhat faster than normal saccades (open circles) of our subjects suggests some attenuation in amplitude by rapid succession of next alternating saccade (9).