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Closely spaced saccades. A. TERRY BAHILL,
KAREN A. BAHILL, MICHAEL R. CLARK,
AND LAWRENCE STARK.

The relationships between saccadic velocity, duration, and magnitude have been used to prove the normalcy of saccades with intersaccadic intervals of less than 200 ms. Pairs of normal saccades with small intersaccadic intervals will have the second saccade larger or smaller and going in the same or the opposite direction than the first saccade. These normal saccades may be horizontal, vertical, or oblique.

Saccades are the fast, staccato eye movements characteristically exhibited by people who are reading or looking about a scene. These saccades are usually spaced about 200 ms. apart; however, Fig. 1 shows normal saccades with smaller intersaccadic intervals. The important and consistent relationships between duration, maximum saccadic velocity, and saccadic amplitude, called the main sequence¹ and shown in Fig. 2, are used to prove the normalcy of contiguous saccades.

Young and Stark² realized that most saccades are separated by about 200 ms. so they modeled the saccadic eye movement system as a sample data system with a sampling interval of 200 ms.

Many experimenters have observed infrequent saccadic pairs with smaller intersaccadic intervals. There are reports of saccades with intersaccadic intervals as small as 160 ms.,³ 120 ms.,⁴ 100 ms.,⁵ 75 ms.,⁶ 70 ms.,⁷ 50 ms.,⁸ 40 ms.,⁹ 10 ms.,¹⁰ and 0 ms.¹¹⁻¹³ To elicit closely spaced saccades, some experimenters^{4, 12, 13} used pulse-step stimuli—for example, the target could jump five degrees right, pause for 50 ms., then jump another three degrees right. Other experimenters recorded more natural saccades during reading,⁹ fixation,⁸ or in response to a step change in target position.^{3, 10} A variety of other effects can evoke closely spaced saccades: for instance, fatigue,⁶ flickering illumination,⁵ voluntary pauses,⁷ and abrupt decelerations of a moving target.¹¹ In all of these reports, the second saccade was usually smaller, and in the same direction as the first saccade. One reporter¹¹ emphasized that the second saccades of his pairs were abnormal, while the others made no mention of normalcy. Our present findings indicate that no refractory period is necessary in order for the subsequent saccadic eye movement to be normal.

Methods. The infrared photodiode method of eye position measurement^{1, 2} was used to record the saccades of this report. The photodiodes were mounted on a pair of spectacle frames worn by the subject. The subject's head was stabilized with a head rest and a bite bar covered with dental impression compound. Saccades as small as three minutes of arc have been measured with this equipment.¹ The bandwidth of the complete system, including photodiodes, direct current, (DC) amplifiers, computerized velocity algorithm, computerized slow-down plotting routine, and the X-Y plotter was in excess of 1,000 Hz. The data of Fig. 3 are for five normal unfatigued subjects. The saccades of Fig. 1 were made while tracking a spot of light that jumped periodically, with a frequency of 0.33 Hz., between various predetermined pairs of points. The oblique saccadic eye movements of Fig. 4 were made while repetitively saccading between two continuously observable targets. We have also recorded closely spaced saccades using electro-oculography (EOG). Corneal reflection,^{4, 6, 8, 9} EOG,^{3, 10, 12, 13} suction contact lens,⁵ photodiode,¹¹ and psychophysical⁷ techniques have been used by others to record closely spaced saccades.

Results. Fig. 1 shows naturally occurring, normal, human saccades with successively smaller intersaccadic intervals (ISI). ISI is defined as the time between saccadic eye movements; more specifically, the time between the end of the first saccade, until the beginning of the next saccade. This definition of ISI is illustrated in the idealized drawing of closely spaced saccades near the vertical axis of Fig. 3. We have recorded many saccadic pairs with small intersaccadic intervals;

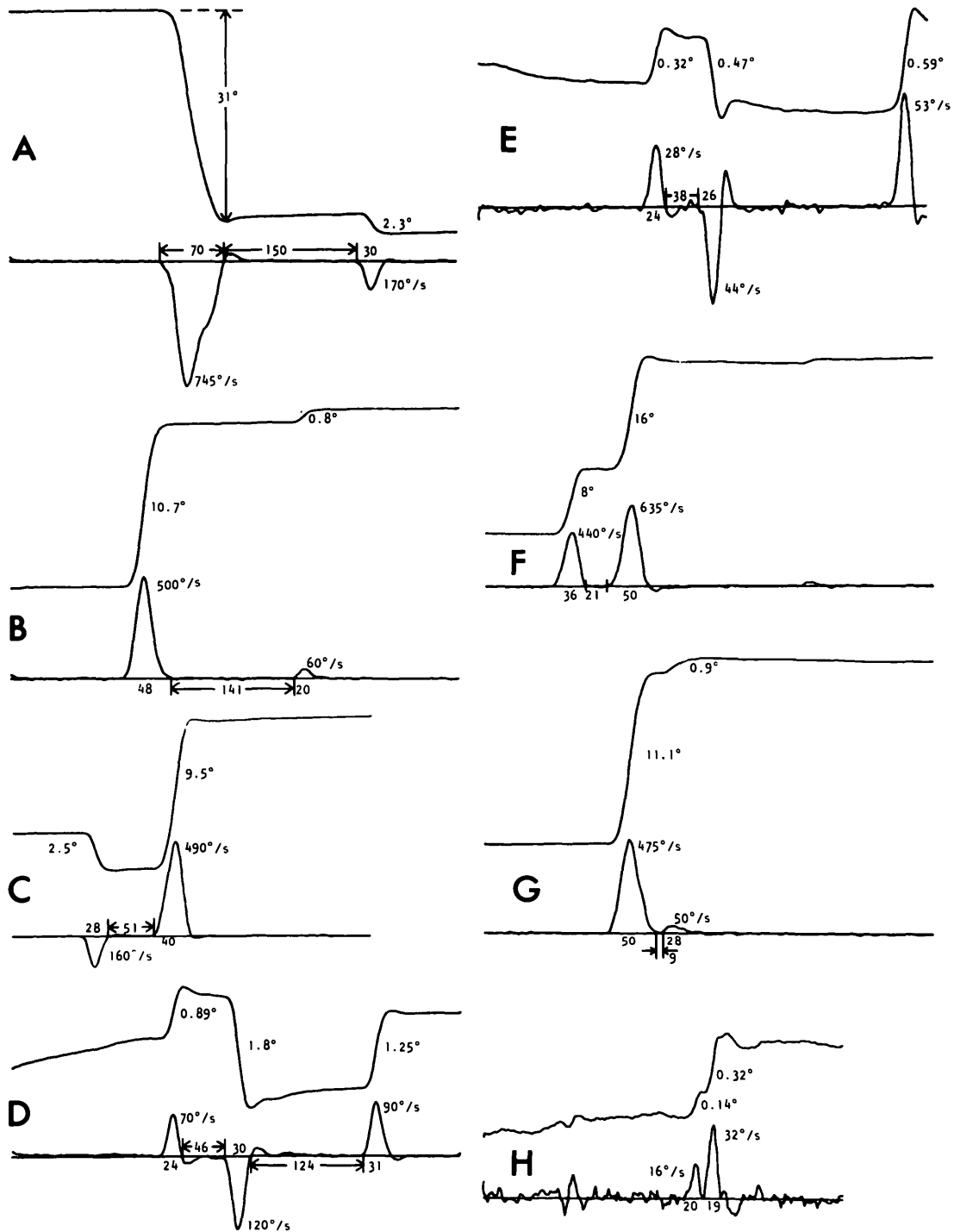


Fig. 1. Closely spaced saccades with decreasing intersaccadic intervals. In each record the position versus time trace is above the velocity versus time trace. Magnitude (in degrees), peak velocity (in degrees/second), duration (in milliseconds), and intersaccadic interval (in milliseconds) are shown for each record and are sufficient for calibration. The magnitude scale is different for each record in order to accommodate the three-hundred-fold difference in magnitudes; however, the time scale is the same in all records. Left, temporal is up.

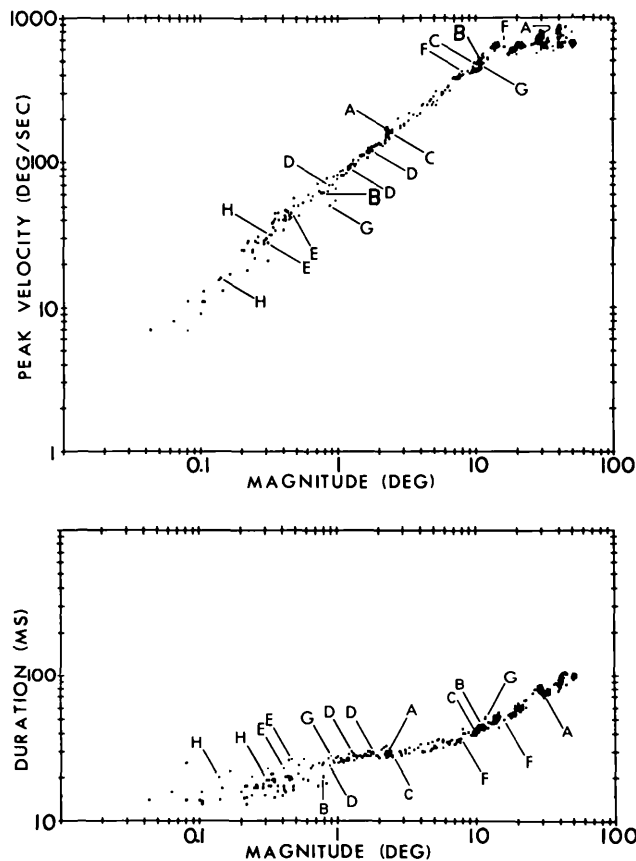


Fig. 2. Main sequence diagrams with the saccades of Fig. 1 indicated. The saccades of Fig. 1, A are marked with an "A," those of Fig. 1, B with a "B," etc.

only a few demonstrative, closely-spaced saccades are shown in Fig. 1. Saccades in this small selection graduate from eight minutes of arc to 31 degrees. Records appear with the second saccade being larger or smaller and in the same or in the opposite direction than the first saccade. Saccades are even shown through points other than primary position; those of Fig. 1, E were recorded with the eye gazing at a point 35 degrees temporal of primary position.

The peak velocities and durations of these saccades are indicated on the main sequence diagrams of Fig. 2. Main sequence diagrams are plots of peak velocity and duration versus saccadic magnitude for normal unfatigued human saccadic eye movements.¹ These closely spaced saccades all fall on the main sequence, verifying that they are all indeed normal saccades. The existence of these closely spaced saccades precludes absolute refractoriness in the extraocular muscles or motoneurons (other than the neuronal refractoriness of a few milliseconds).

Fig. 3 is a plot of ISI, the time between the end of the first saccade and the start of the second saccade, versus saccadic initiation interval

(SII), the time between the start of the first saccade and the start of the second saccade, for saccadic pairs falling in the closely spaced saccadic range. The closely spaced saccadic range is defined as that region of Fig. 3 where SII is less than 200 ms. and ISI is greater than zero milliseconds. Under normal circumstances, about 0.5 per cent of human saccadic pairs fall into this range. This percentage can be increased, as stated above, by using pulse-step stimuli,^{4, 12, 13} by fatigue,⁶ and for a variety of other reasons.^{3, 5, 7-11} Although the data of Fig. 1 are for horizontal saccades, closely spaced saccades also occur for vertical and oblique saccadic eye movements. Fig. 4 shows a closely spaced saccadic pair of oblique saccadic eye movements having an intersaccadic interval of 69 ms. and a saccadic initiation interval of 110 ms.*

Discussion. It is difficult to apply concepts from engineering theory, such as sampled data control, to such an incompletely understood neurologic

*Closely spaced saccades are often monocular. For example, one eye may utilize a closely spaced saccadic pair to get to the new eye position, while at the same time the other eye may use one large smooth saccade.

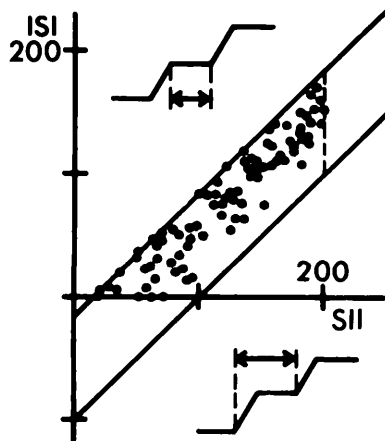


Fig. 3. Intersaccadic interval (ISI) versus saccadic initiation interval (SII) for saccadic pairs in the closely spaced saccade range.

mechanism as the control of saccadic eye movements. For example, although sampling in early radar systems occurred at the input, this is not a fixed feature of engineering sampled data systems. Any system with digital computation in the control loop is a sampled data or discrete system, where the sampling clearly goes on in the controller. The sampling can be uniform, random, clocked, or signal dependent.

Closely spaced saccades, seemingly an exception to the sampled data model,² throw light on the nature of the sampler, by requiring that the sampler, whatever it may be, exists in the feed-forward pathway before the controller that produced these main sequence saccades. Thus, the sampling cannot occur either in the output, or in the input portions of the visual system.

The saccadic control system is a discrete system. The sampling occurs neither at the input, nor at the output. Sequential, closely spaced saccades may occur with no intersaccadic interval. The second saccade may be larger or smaller and in the same or opposite direction as the first saccade. Closely spaced saccades have been proved to be normal by using the main sequence concepts. These experimental facts must be accounted for in future models of the saccadic eye movement system. Closely spaced saccades should yield clues in elucidating the neurophysiologic substrates underlying the eye movement control system.

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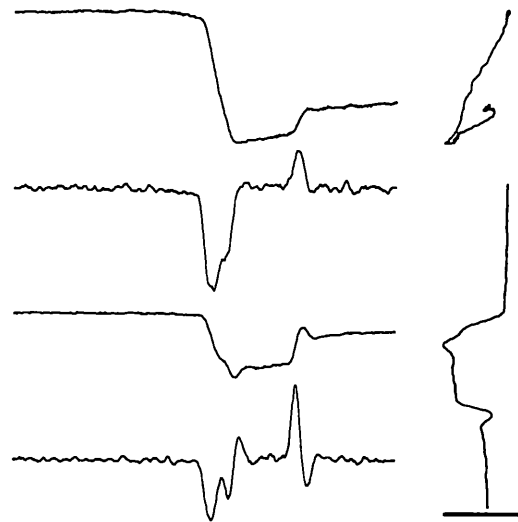


Fig. 4. Closely spaced oblique saccadic eye movements. In the left column, from top to bottom, are shown vertical eye position, vertical eye velocity, horizontal eye position, and horizontal eye velocity, all as functions of time. The right column shows (top) the eye position in space, or the X-Y trajectory, and (bottom) the horizontal position record rotated 90 degrees and aligned with the X-Y trajectory above. The calibrations represent four degrees, 150 degrees per second, and 100 ms. In the left column rightward (temporal) and upward eye movements are represented by upward deflections.

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Total retinal degeneration in apparent anophthalmos of the Syrian hamster.

CHAT H. YOON.

Anophthalmia in the Syrian hamster was found to result from an extensive degeneration of retinal tissue and tissues derived from the retina. Eyes of affected animals were normal at the twelfth day of gestation (the average gestation period in the Syrian hamster is 16 days). However, the retina of these eyes showed rapid and extensive degeneration during the first two weeks after birth. In adults, the sclera-choroid complex was the only prominent structure of the original eye, with an occasional remnant of deteriorated lens.

Anophthalmia has been reported in every class of vertebrates.¹ Some of these forms are known to be hereditary, but the number of well established forms of hereditary anophthalmia, in which the eyes are the primary target of mutations, is relatively small. Mammalian species, where the hereditary nature of anophthalmia has been established, include mice,¹ hamsters,² and guinea pigs.³ Some forms of anophthalmia reported in man are apparently hereditary. Of these, the developmental process of the anomaly has been worked out only in mice. Chase and Chase¹ concluded, after their investigation of the embryology of anophthalmia in mice, that there was an inhibition of growth of the eye vesicle and that a failure of the eye vesicle to induce the lens led to the anophthalmic condition. However, anophthalmia in the Syrian hamster was found to have a completely different etiology.

Anophthalmia in the Syrian hamster was first

described by Knapp and Polivanov.² The condition is transmitted by a pair of incompletely dominant genes (gene symbol, *Wh*).⁴ Affected homozygotes never open their eyelids, although they are not fused. Also, these animals appear to be deaf. In adults, a mass of muscular tissues and Harderian glands are seen inside a thin and transparent conjunctiva. The fur of the affected animal is invariably white. Thus, the effects of the genes are apparently pleiotropic. Heterozygotes are normal except for their light-colored bellies.

It was found that affected animals do have normal eyes at the twelfth day of gestation, when the development of the eye proper is practically complete. However, the retinal components of these animals undergo rapid and extensive degeneration from around the time of birth. In adults, the sclera-choroid complex is the only recognizable sign of the eye, with an occasional remnant of deteriorated lens. Changes are brought about by a total degeneration of the retina and the tissues that are immediately derived from the retina. Thus, anophthalmia in the Syrian hamster resembles the retinal degeneration found in various species of animals and man rather than the anophthalmia in mice.

Materials and methods. Hamsters carrying the *Wh* gene in a heterozygous condition were obtained from an inbred line, BIO 72.29. In order to increase reproductivity, these animals were outcrossed to another inbred line, BIO 4.24 (wild type). Both lines are maintained at Bio-Research Institute, Cambridge, Mass. Matings were made between heterozygotes obtained from this outcross to produce anophthalmic animals, which are poor breeders.

In order to obtain embryos of known age, mass matings were made between heterozygotes. When embryos were removed, anophthalmic animals were identified by lack of pigment in their eyes. In the mating system used, anophthalmic animals were always white, and white animals were always anophthalmic.

Embryos and young animals were killed with chloroform and fixed in 10 per cent formalin. In the case of fully grown animals, only the eye and its accessory organs were removed and fixed. Some specimens were frozen in a cryostat after chloroforming. Both longitudinal and cross-sections were cut either at 8 μ or 16 μ . They were stained with cresyl echt violet.

Results. At the twelfth day of gestation, when most of the major components of the eye proper were present, the mutant hamsters were found to have normal eyes, except for the reduced number of pigment granules in the pigment layer. No apparent differences were detected between the normal and affected eyes.

However, significant differences were clearly