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Saccades in extremes of lateral gaze.

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Saccades (between targets at 30° and 40°) were recorded with DC electro-oculography in 10 normal subjects. Velocity-amplitude relationships were examined on the basis of abduction vs. adduction and centering vs. eccentric movement. In these small peripheral saccades the former pairing showed no consistent differences in peak velocity, whereas centering saccades were consistently faster than both eccentric movements and those made around primary position.

The peak velocities of saccadic eye movements increase with amplitude and gradually saturate for larger saccades.[1-3] The effect of direction and field of gaze upon this velocity-amplitude relationship has been addressed repeatedly but with contradictory conclusions. Temporal (abducting),[4] nasal (adducting),[5] and centering[6] saccades have all been reported as faster, whereas other investigators have found no consistent directional variations in velocity,[1, 3] although centering movements have tended to be occasionally faster. Most studies have used different methodologies, which makes comparison of the data difficult. The present study was undertaken to attempt to resolve and explain the disparate findings in the literature.

Methods. Ten subjects, seven male and three female, all free of neurologic or ophthalmologic disease (except for corrected refractive error) ranging in age from 22 to 47 years, were studied. Eye movements were recorded electro-oculographically with electrodes placed in the inner and outer canthi of each eye. The eye position signals were electronically differentiated to provide velocity information. Written records were made on a rectilinear Beckman Type R Dynograph. The system bandwidth was DC-100 Hz. Records were continuously monitored for drift, which was corrected when observed. Linearity was assured by calibrating within the 20° to 40° range of gaze angles, so that 0.5 cm was equal to 10° throughout the range. Subjects sat in a modified dental chair with a chin rest and head brace. The fixation targets were red light-emitting diodes mounted on an arc 1.14 m

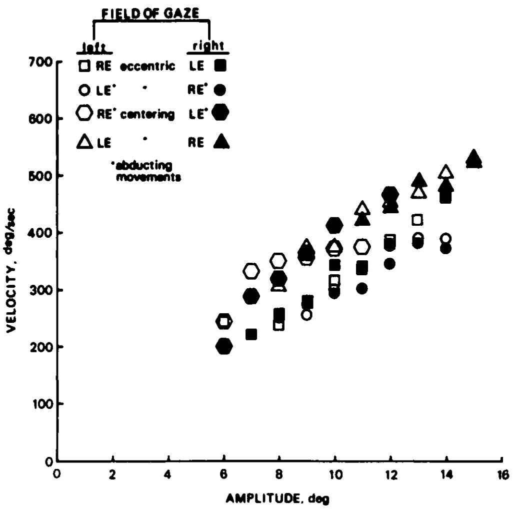

Fig. 1. Averaged saccadic velocity-amplitude relationships for 10 subjects, as functions of side of gaze, eye, and direction of movement. Each graph point represents from four to 10 data points.

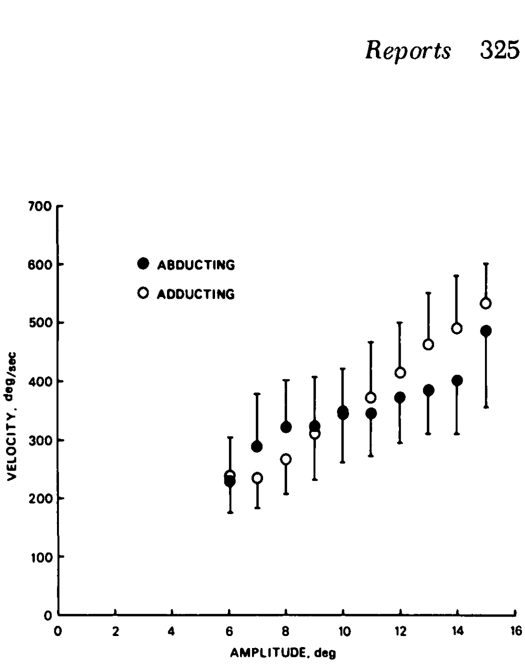

Fig. 2. Abduction vs. adduction effects on saccadic velocity. Bars in this and following figure indicate ±1 S.D.

from the subject. After calibration, subjects were directed to refixate between lights at 20°, 30°, and 40° in the left and right fields of gaze. There were four refixation sequences between these points; each was repeated 10 times in random order. Only those movements between 30° and 40° targets were measured for this study; 20° served as the starting point for each sequence. We reasoned that the study of saccades in the periphery would accentuate any possible velocity disparities related to the two directions.

Results. The velocity-amplitude data were grouped according to left or right eye, side of gaze, and movement direction for each subject. Although the saccades were nominally 10° in amplitude (i.e., the targets were spaced 10° apart), the movements actually ranged from 5° to 15°. The majority of saccades were near 10° in amplitude, and decreasing numbers were of larger and smaller amplitudes.

There were no peak velocity differences between movements in the left and right fields of gaze or between the two eyes moving in the same direction. A possible velocity difference between eccentric and centering movements was noted but was far from significant statistically.

The data from all 10 subjects were averaged together and the cumulative results plotted (Fig. 1), in an effort to isolate any possible trends. Again, there was considerable scatter, with the only trend

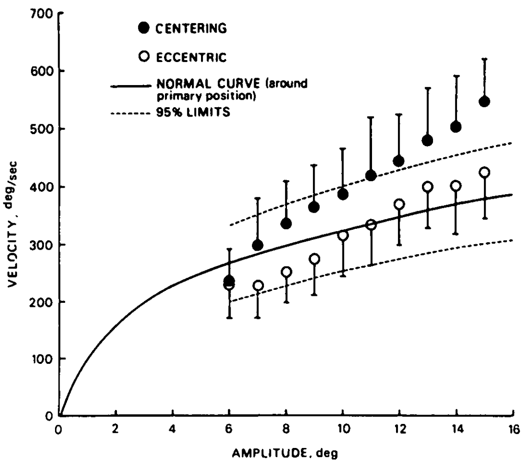

Fig. 3. Centering vs. eccentric movement effects on saccadic velocity. Solid curve is a best mean-square fit to velocity data of saccades made by six subjects around primary position.

being a tendency for centering movements to be faster than eccentric movements. When the data were pooled so that abduction and adduction were the only classifying features (Fig. 2), adduction was statistically significantly faster ($p < 0.01$) but only at 12°, 13°, and 14°; for 7° and 8° saccades, abduction was significantly faster. At five points there was no difference between velocities. Thus no overall trend emerged with this pooling.

When the same data were regrouped according to centering (off-direction) or eccentric (on-direction) saccades (Fig. 3), the centering saccades were consistently faster than the eccentric for all movements greater than 6°. The difference was significant at better than the $p < 0.01$ level.

Also shown in this figure are a best mean-square power law curve ($PV = 134.6A^{0.38}$, $r^2 = 0.95$) fitted to peak velocity-amplitude data obtained from six normal subjects for saccades made around primary position and the range around this curve (dashed lines), which includes 95% of the population. The eccentric saccades lie around the curve, whereas the centering movements rise more steeply, exceeding the upper 95% limit for large movements. The normal curve is similar to others in the literature and slightly higher in velocity than the original data of Boghen et al.[1] due to our higher bandwidth (100 vs. 25 Hz).

Discussion. Grouping our data to isolate the directional differences, previously claimed as affecting saccadic velocity, disclosed only that centering, as opposed to eccentric, saccades had a consistently higher velocity.

There is considerable uncertainty about the complex central and neuromuscular mechanisms responsible for centering and eccentric saccades. Our results conceivably could be explained by several of the proposed but, unfortunately, mutually contradictory mechanisms. The basic innervational pattern responsible for the generation of saccades is the pulse-step increase in the activity of the agonist muscle with the concomitant inhibition of antagonist firing. This has been known since the early studies of ocular electromyography (EMG) during the initiation of saccadic eye movements, which disclosed facilitation of agonist and simultaneous total inhibition of antagonist activity.[7] This reciprocal pattern was confirmed and quantitated by recordings from monkey brainstem motoneuronal units, where pulses of increased firing frequency and inhibition were found in agonist and antagonist cells, respectively.[8-10] Scott[11] reported a different EMG innervational pattern for saccades from eccentric positions toward primary position, i.e., in the "off" field of the agonist but in the "on" direction. Small saccades from the far periphery resulted almost entirely from antagonist relaxation (from the previously highly innervated steady-state holding pattern required to maintain the eye eccentrically) with little or no excitation in the agonist muscle. The saccade seemed driven by the passive elastic force of the stretched agonist muscle, which during the holding pattern was minimally innervated because it was in its "off" field. These observations, however, were recently disputed by Sindermann et al.[12] who recorded single-unit EMG activity in the horizontal recti of normal volunteers and found considerable muscle activity for saccades made in the on-direction from the off field. Although the activity was less than for similar saccades made closer to primary position, the nonlinearity of muscle length-tension characteristics demonstrated by Collins[13] raises the possibility that the agonist may be generating nearly the same forces in both cases.

The definitive explanation of our observations of faster centering saccades must await critical and relevant EMG and muscle force studies on small saccades made in far lateral gaze.

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