Oblique Saccadic Eye Movements

Independence of Horizontal and Vertical Channels

A. Terry Bahill, PhD, Lawrence Stark, MD

● Horizontal and vertical components of oblique saccadic eye movements are dynamically independent. That is, they have independent dynamic trajectories determined by either the presence, or the absence, as well as the magnitudes of dynamic overshoot, glissades, overlapping saccades, and closely spaced saccades. Temporally, oblique movements manifest varying degrees of independence, for the two components can begin and end either together or separately. Purely horizontal saccades (ie, between two points on a horizontal line) usually show crosstalk demonstrated by extraneous, transient, vertical components. Therefore, saccades are very seldom linear or straight; the trajectories are usually curved.

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Horizontal and vertical eye movements are implemented by separate, distinct neural channels: they employ different muscles, different motoneurons, and different brain stem staging areas. There is anatomical,[1] physiological,[2] and clinical[3] evidence for the independence of these two channels. We propose that this independence is maintained during individual saccadic eye movements as well; for if it were not, saccades could be straight. In reality, human saccadic eye movements are seldom straight; they are usually curved.[4-7] One of the reasons for this is that, in general, the horizontal and vertical components cannot be of the same duration. For example, a five-degree oblique saccadic eye movement at a 53° inclination to the horizontal typically has a three-degree, 30 msec horizontal component, and a four-degree, 40 msec vertical component. Therefore, it is not possible for the two components to begin and end simultaneously. The shorter component may occur at the start, in the middle, or at the end of the larger component. Occasionally there is no temporal overlap between the horizontal and vertical components.

In a previous study,[7] we analyzed the interdependence of the horizontal and vertical components of oblique saccadic eye movements. Since then, we have studied new clinical literature, reanalyzed our data, performed new experiments, and made new observations. This present brief report explores the dynamic and temporal independence of the two components of oblique saccadic eye movements, provides insight about the neurological control signals, and suggests possible clinical uses of these observations.

METHODS

Saccadic eye movements were recorded with the photoelectric method of eye movement recording.[7] Saccades as small as three minutes of arc have been recorded with this equipment.[8] Head movements were minimized by use of a head rest and bite bar. Records with head or eyelid arti-

facts were easily recognizable and were disregarded.

The bandwidth for eye position recording extended from DC to over 500 Hertz (Hz); the X-Y trajectory was computed from the X and Y positions by a digital computer and also had a 500 Hz bandwidth. This large bandwidth was necessary for recording saccadic dynamics. If the data were low-pass filtered, as is usually done with electro-oculography (EOG) data in order to remove the inherent noise, then the dynamic overshoots and most of the nonlinear trajectories would have been removed.[9] Thus, the saccades of this report are much more curved than those of other reports, wherein the data had been low-pass filtered. Each velocity trace shown in Fig 1 and 2 begins before and ends after its associated position trace, because these velocity traces were derived from the position traces by a digital computer differentiation algorithm with a 50 Hz bandwidth. This algorithm utilized the five points before and the five points after each point of interest. Thus, digital filtering, being insensitive to time's arrow, spreads the velocity trace both before and after the actual start of the saccade.

The registration between the two instrumental channels was within 0.5 msec, as determined by flashing a light from a light emitting diode simultaneously into the two channels and plotting the response after it had passed through the diodes, the amplifiers, the tape recorder, the computer, and the X-Y plotter.

The statistical data of this report were derived from tracings like those shown in Fig 3 wherein the bandwidths were 500 Hz for the eye position and 250 Hz for the eye velocity traces. The beginnings and endings of the eye movements were defined as the points where the velocity records crossed 10° per second.

The noise in the records of Fig 1 and 2 is artifactual and is due to the computer algorithm and to noise in the tape recorder. The smaller amount of noise in the records of Fig 2 is of biological origin (ie, the eye is not perfectly stationary during fixations).

Instrumental crosstalk was less than 5% over the entire target range. This was determined by having the subject make about 50 fixations on the outline of a 90° sector of a circle with a radius of five degrees.[7] Most of our recorded oblique saccades were five degrees or less in magnitude. We believe that it is more realistic to study small saccades than large saccades, because most naturally occurring human saccades have magnitudes of 15° or less.[10] These photoelectric data of oblique saccadic eye movements were corroborated with EOG, with the Stanford Research Institute first and fourth Purkinje image eye tracker,[11] and with the ODD Tracker,[12] a new system which uses a minicomputer to control the scanning of a camera with an image dissector tube. We have used this ODD Tracker, as well as von Helmholtz's psychophysical after image technique,[4] to show that large oblique movements are also highly nonlinear and curved.

The saccadic eye movements shown in this report were made on a verbal command between small points marked on a screen that was 29 cm in front of the subject. No differences were noted for other stimuli, such as light emitting diodes, or a spot of light reflected off a mirror galvanometer. The left eye was occluded with a black patch during the experiments reported here. Our four subjects had various corrected refractive states. Informed consent was obtained from them after the experiment had been explained.

RESULTS

The temporal independence of the horizontal and vertical channels was illustrated by the L-shaped trajectory of Fig 1. The horizontal saccade of Fig 1 was almost completely finished before the vertical saccade commenced. Thus, in the X-Y trajectory, the movement began with the fast, leftward, saccadic motion, then had a fast, upward saccadic motion. The temporal desynchronization and non-overlapping of the horizontal and vertical saccades showed the temporal independence of the two channels.

The dynamic independence of the two channels was illustrated by the curved trajectory shown in Fig 3: the horizontal saccade had dynamic overshoot, and the vertical channel did not

have. This trajectory further demonstrated partial temporal dependence of the components: the horizontal and the vertical eye movements ended at about the same time. The components of other oblique saccadic eye movements also ended at about the same time, thus exhibiting partial temporal dependence, because of the lengthening of the shorter component due to either closely spaced saccades, or glissades. Glissades, which were named by Weber and Daroff,[13] are the slow, drifting, monocular eye movements sometimes appended to the end of saccadic eye movements. They result when there are mismatches between the pulse and step components of the motoneuronal controller signal. Closely spaced saccades are two or more saccades with very short intersaccadic intervals.[14] They are often indicative of fatigue. They produced particularly bizarre trajectories. For instance, when there were two closely spaced saccades in the horizontal component, the resulting trajectory was composed of an oblique portion, followed by a purely vertical portion, which in turn was followed by another oblique portion (Fig 6a in Bahill and Stark[7]).

The fishhook shaped trajectory of the oblique saccadic eye movement shown in Fig 3 was produced by dynamic overshoot in both the horizontal and vertical saccades. Fishhook saccades may also be produced if one component is much smaller than the other, with the small component occurring at the end of the large component, and the large component having dynamic overshoot.

The saccades of Fig 1 through 3 were selected to clearly illustrate curved trajectories; many oblique saccadic eye movements were not as curved as these. However, linear or straight oblique trajectories were very rarely seen. Even purely horizontal saccades (ie, between two points on a horizontal line) were seldom linear, because a transient, extraneous, vertical component was typically spawned in response to a purely horizontal target movement. The magnitude of this orthogonal component averaged about 10% of the magnitude of the horizontal compo-
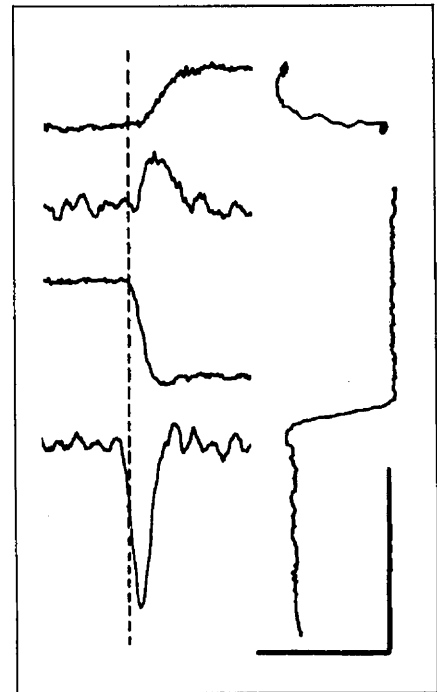

Fig 1.—Temporal independence illustrated with L-shaped saccadic trajectory due to lack of simultaneity of horizontal and vertical components of oblique saccadic eye movements. Display shows the following: in left column (from top to bottom), vertical eye position, vertical eye velocity, horizontal eye position, and horizontal eye velocity; at top of right column, X-Y trajectory, which shows two fixation points and path of eye between them; at bottom of right column, horizontal position vs time record rotated on its side, and aligned with X-Y trajectory above. Calibrations shown represent 4°, 150°/sec, and 100 msec. For the functions of time, rightward (temporal) and upward eye movements are represented by upward deflections. Vertical dotted line shows that horizontal movement begins before vertical movement, and also that each velocity trace begins before its associated position trace, due to computational algorithm for differentiation (see "Methods").

nent; however, there was tremendous variability in this magnitude. Successive saccades between the same two points had dramatically different trajectories.

A statistical breakdown of our data revealed that dynamic independence characterized oblique saccadic eye movements: the horizontal and vertical components had different dynamics. As a result, straight saccadic trajectories were very rare. Complete temporal independence was also common for oblique saccadic eye move-
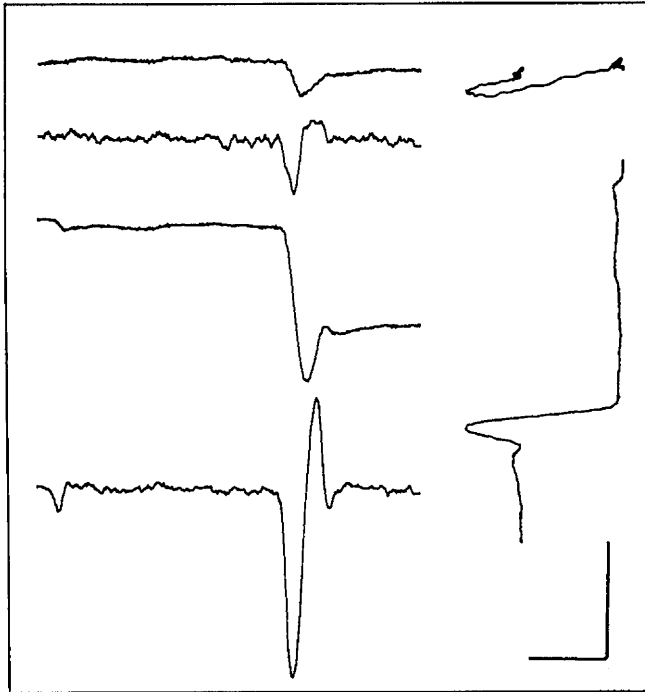
Fig 2.—Fishhook-shaped oblique saccadic trajectory produced by dynamic overshoot in both horizontal and vertical components. Calibration and display are same as in Fig 1.

Fig 3.—Dynamic independence exemplified with curved saccadic trajectory due to dynamic overshoot in only horizontal component of oblique saccadic eye movement. Peak velocity of each saccade is shown. Indicated durations are between zero velocity points at start of saccades and first zero velocity points at end of saccades. Indicated saccadic magnitudes are between foot and peak of saccades, ie, maximum change in eye position. Otherwise, display is same as in Fig 1.
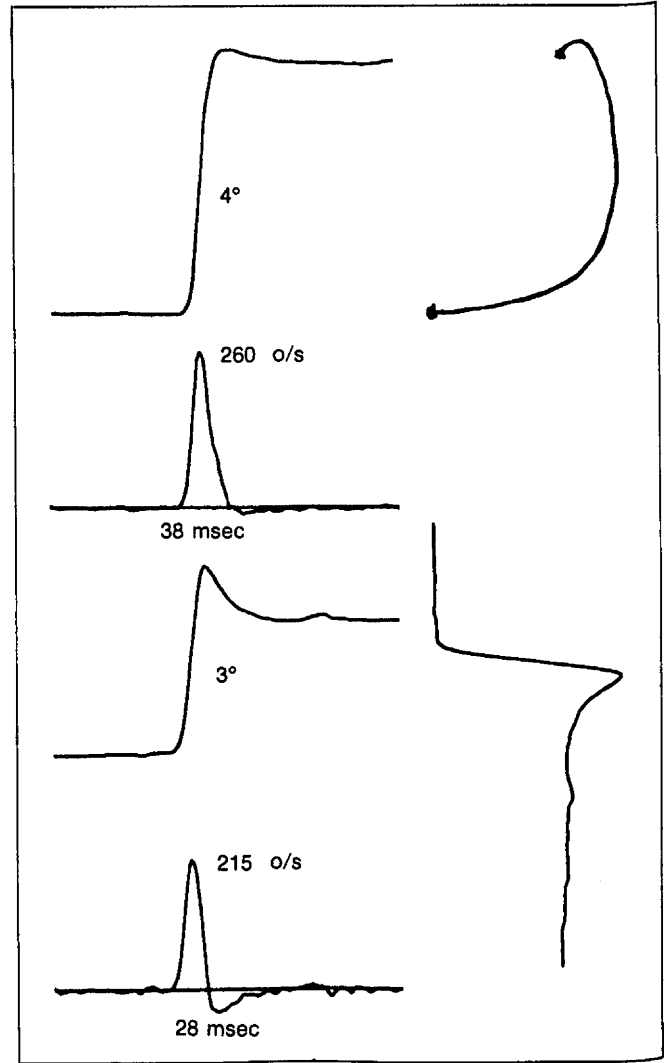
ments, because 15% had horizontal and vertical components that neither began, nor ended together. One fifth of these did not even overlap and, thus, produced "L" shaped trajectories. Partial temporal independence was frequently demonstrated with 30% of the obliques having horizontal and vertical components that only ended independently, and 15% having components that only began independently. Lack of temporal independence was seen in 40% of the obliques. In these movements, the horizontal and vertical components began and ended within 3 msec of each other. However, this did not necessarily reflect true dependence. This apparent synchronization was caused by lengthening of the shorter component and by the fact that the 3 msec time

intervals were large enough to encompass much of the obligatory duration differences due to amplitude disparities in the horizontal and vertical components. These statistical data can be summarized as follows:

Dynamic independence	100%
Temporal independence	
With no overlap	3%
With overlap	12%
Partial temporal independence	
Independent beginnings	15%
Independent endings	30%
No temporal independence	40%

COMMENT

The data of this report demonstrated the independence of the hori-

zontal and vertical channels for human saccadic eye movements. However, crosstalk usually existed between the two channels: an extraneous, orthogonal component was usually produced in response to either a purely horizontal, or vertical target movement. However, the presence or absence of an orthogonal component did not affect the component of the eye movement that was collinear with the target displacement. For example, a typical three-degree horizontal saccade had a maximum velocity of 215° per second, and a duration of 28 msec, whether it was either the horizontal component of an oblique saccadic eye movement, as shown in Fig 3, or the horizontal component of a purely horizontal saccade (ie, a saccade between two points on a horizon-

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tal line) with a small orthogonal vertical component,[14] or the horizontal component of a purely horizontal saccade with a large orthogonal vertical component. Therefore, the firing patterns of neurons associated with muscles producing the horizontal components should be the same for purely horizontal saccades with large or small vertical components and for similarly sized horizontal components of oblique saccadic eye movements.

Although they did not show any actual oblique eye movement trajectories, Henn and Cohen[15] hypothesized that monkey oblique saccadic trajectories would be straight lines. A great deal of computational effort would be necessary to create this very tight crosslinking of the horizontal and vertical channels: the duration of the smaller component would have to be stretched out by a very precise amount, and the two components would have to have identical dynamics. We have only found two linear saccades out of 2,000 saccadic eye movements that included some purely horizontal, and purely vertical saccades. Dodge[16] stated that all of the saccades he recorded (which were all purely horizontal saccades) had transient, vertical components. Therefore, these saccades had curved trajectories. Yarbus[5] has also shown oblique saccadic eye movements with highly curved trajectories and some purely horizontal saccades that were only slightly curved. Over a century ago, Von Helmholtz[4] realized that although oblique saccadic eye movements were highly curved, horizontal saccades could be made "only slightly curved" with practice and biofeedback. The curvature of purely horizontal saccades is reflected in the extraocular muscle and oculomotoneuron firing patterns. The electromyographic activity[17] and the firing patterns of the oculomotoneurons[18] associated with the vertical recti and oblique muscles show a transient burst during purely horizontal saccades, but no alternation of tonic activity.

Successive saccadic eye movements between two fixed points seldom had identical trajectories. Some pairs of movements had identical horizontal components and identical vertical components, but the dynamic and temporal interrelationships of the channels (and inferentially of the motoneuronal controller signals) were different for the two movements. Dynamic overshoot, glissades, overlapping saccades, and closely spaced saccades are monocular phenomena and, thus, are dynamic violations of Hering's law.[19] For this reason, the two eyes rarely follow the same trajectory during oblique saccadic eye movements. The variability in the saccadic trajectories appears to be visually unimportant, partly because saccadic suppression and retinal image smearing during the high velocity saccade reduce visual acuity. However, if the trajectories become extreme, perhaps some adaptive control (probably emanating from the cerebellum) would enter to modulate these saccadic trajectories, which are open loop, and make them less bizarre.

The hyperfine structure of saccadic eye movements results from the variability in the pulse-step controller signals that are created independently in the brain stem staging areas for the horizontal and vertical channels. This independence accounts for the varied trajectories seen in oblique saccadic eye movements. However, neurophysiological studies suggest that higher levels of the central nervous system do not treat the two channels independently.[20,21]

Neuro-ophthalmologic clinical studies seldom report oblique disorders. For example, nystagmus is usually either horizontal or vertical. This paucity of oblique disorders is corroborative data supporting the independence of the horizontal and vertical channels. Once again, however, cortical and cerebellar circuits probably do not treat the two channels independently. The chaotic conjugate opsoclonus syndrome is an example, indicating that when similar involvement of both the horizontal and the vertical channels is a prominent feature of the abnormality, then higher levels of control are usually involved. Thus, examination of the dynamics of the horizontal and vertical components of oblique saccadic eye movements may provide clinicians with finer details to aid in localizing lesions in patients.

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