

Neurological Control of Horizontal and Vertical Components of Oblique Saccadic Eye Movements

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ABSTRACT

The horizontal and vertical components of oblique saccadic eye movements are not always tightly crosslinked; often they are completely independent. Most of the time the two components do not start and end simultaneously. The neurological bursting and pausing of the extraocular motoneurons that underlie the generation of these oblique movements will, correspondingly, not be synchronized. Evidence for some crosstalk between the horizontal and vertical systems comes from observations that pure horizontal or pure vertical saccades are rarely straight but are almost always curved. The hooks seen frequently in oblique trajectories are caused by dynamic overshoot in one or both components. Vertical saccades are slower than horizontal saccades, with downward saccades being the slowest. Oblique saccades, being the result of the summation of forces of the horizontal and vertical systems, can be faster than either purely horizontal or vertical saccades of the same amplitude.

INTRODUCTION

Saccadic eye movements are very seldom linear. For example, human saccades almost always have curved trajectories [7, 16, 15, 13]. However, Henn and Cohn [11] reported linear trajectories for oblique saccades in monkeys. If oblique saccadic eye movements were in straight lines, then the bursts of neural firing controlling the horizontal and vertical muscles would be tightly linked and synchronized. Our experimental results, however, show a wide variety of nonlinear trajectories of oblique saccadic eye movements corresponding to a wide variety of interrelationships of the neural firing in the motor nuclei.

The anatomy and saccadic dynamics of the horizontal and vertical

movement systems are different. The brain stem nuclei responsible for the production of horizontal and vertical saccades are unique [6], and classical syndromes exist which interfere separately with horizontal and vertical eye movements [18, 15]. Vertical saccades are slower than horizontal saccades [17, 9], and downward saccades are the slowest.

This report will show how the variations in interdependence of the horizontal and vertical saccadic systems can produce the variety of shapes in the trajectories of oblique saccades and permit inferences about the neurological signals that are occurring in the different extraocular motor nuclei during oblique eye movements.

METHODS

The infrared photodiode method of eye movement monitoring [4] was used for recording the horizontal components of the eye movements. To measure the vertical components, a second pair of photodiodes was added to the instrument. These photodiodes were aimed at the lower border of the iris, as shown in Fig. 1, and the sum of their photocurrents was computed and used as a measure of vertical eye position. This sum increased for upward eye position and decreased for downward eye movements. For horizontal eye movements, the photocurrent of one photodiode increased,



FIG. 1. Photodiodes were aimed so that they received light from the stippled areas.

while the current of the other diode decreased, thereby keeping the sum constant. The fields of view of the vertical photodiodes did not encompass the lower eyelid, for this lid moved with vertical eye movements, but moved slower and with a longer latency than the eyeball. Thus, the motion of the lower eyelid could confound the eye position measurement. The lower eyelid was often taped down, in order to remove it from the photodiode fields of view.

A typical calibration record is shown in Fig. 2. Here the subject followed a horizontal line to the right for 5 degrees, then followed a circular path with a radius of 5 degrees, and then moved down the vertical line back to the starting point. This particular calibration record was chosen to illustrate instrumental crosstalk, which can be seen at the lower right hand corner of this figure. The subject was looking at a point on the horizontal line 5 degrees to the right of center, but crosstalk from the horizontal channel caused the vertical channel to erroneously indicate 0.3 degrees of elevation. When this type of crosstalk existed, all saccades that began or ended in the range from 4.8 to 5 degrees right were discarded.

Several thousand oblique saccades executed by three subjects were recorded. The statistics of this report are for the 200 randomly selected oblique saccades analyzed in detail.

The bandwidth of the complete system was measured by exciting the photodiodes with light from a light emitting diode (LED) and was found to be in excess of 1 kilohertz under all circumstances. Square wave excitation of the LED showed the registration between the horizontal and vertical channels to be within 0.5 msec.

Oblique eye movements were also recorded using electro-oculography (EOG) and the Stanford Research Institute eye tracking machine, which utilizes the first and fourth Purkinje images. All three methods yielded similar results, but the saccades of this report are from the photodiode data.

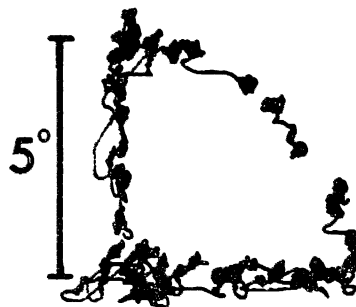


FIG. 2. Calibration chart showing eye position as the subject looked at points along a 5-degree quarter circle.

RESULTS

TIMING AND SHAPE OF OBLIQUE SACCADES

Small saccades have shorter durations than large saccades. So, for an oblique eye movement in which the horizontal saccadic component and the vertical saccadic component are not equal, one component will begin or end before the other. Several variations on this theme are shown in Fig. 3, which shows the position of the eye in X - Y space, and, as functions of time, the vertical eye position, vertical eye velocity, horizontal eye position, and horizontal eye velocity. The smaller component, and thus the oblique portion of the movement, can occur at the start, in the middle, or at the end of the eye movement, as shown in Fig. 3(a), (b) and (c), respectively. It is even possible for one component to be finished before the other component begins. Fig. 3(d) shows an oblique eye movement in which the horizontal and vertical saccades have very little temporal overlap. This results in an L shaped movement. 60% of our saccades are asynchronous. This asynchronism in the start and stop timing of the two components can best be seen in the eye velocity records for each component, while its effect on the shape of the eye movement is best seen in the X - Y trajectory in the upper right hand corner of each diagram.

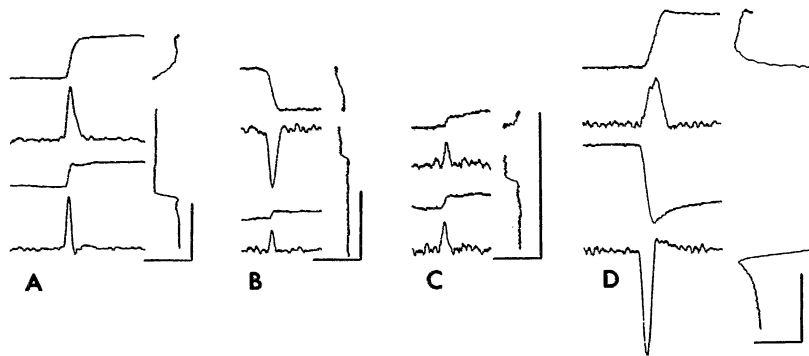


FIG. 3. Asynchronous oblique saccadic eye movements where the oblique portion occurs at the start (a), in the middle (b), at the end (c), and not at all (d). Each display shows: in the left column, from top to bottom, vertical eye position, vertical eye velocity, horizontal eye position, and horizontal eye velocity; at the top of the right column, eye position in space, or the X - Y trajectory; at the bottom of the right column, horizontal position versus time record rotated on its side, and aligned with the X - Y trajectory above. The calibrations shown represent 4 degrees, 150 degrees/sec, and 100 msec for all figures. For the functions of time rightward (temporal) and upward eye movements are represented by upward deflections in all figures.

The horizontal and vertical components of oblique saccadic eye movements sometimes commenced and ceased simultaneously (40% of the records of our data). In these cases each component had the same duration. This resulted when the durations were naturally equal, e.g., the 3.4 degree, 35 msec horizontal saccade, and the 1.6 degree, 35 msec downward saccade of Fig. 4(a); and also from artificial lengthening of the smaller component due to a glissade at the end of the saccade [Fig. 4(b)], lowering of the saccadic velocity [Fig. 4(c)], dynamic overshoot (Fig. 5), and double saccades (Fig. 6).

When the eye goes beyond its final position and returns very rapidly, its movement has dynamic overshoot. Most horizontal saccades have dynamic overshoot, while most vertical saccades do not [3]. This dynamic overshoot

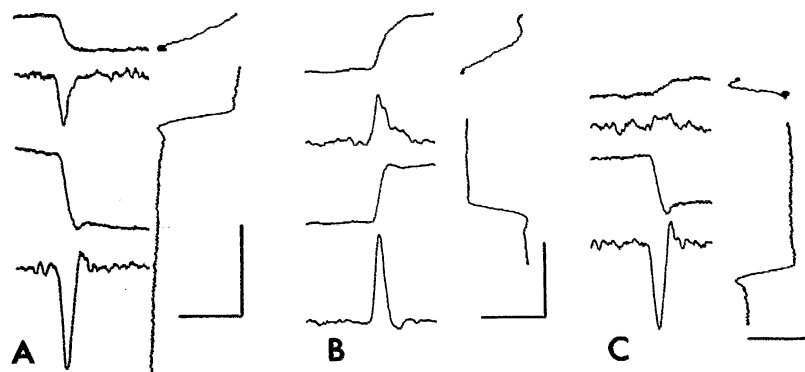


FIG. 4. Synchronous saccades: (a) both saccadic components naturally have equal durations; (b) vertical component is lengthened by a glissade; (c) non-main-sequence vertical saccade with unusually low velocity and long duration.

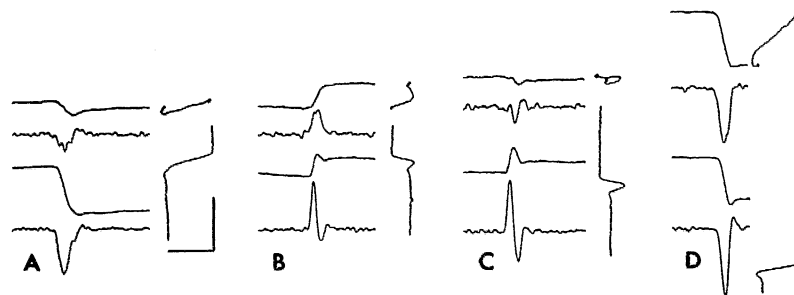


FIG. 5. Dynamic overshoot in one or both components producing synchronous hooks (a, b), loops (c), and asynchronous hooks (d).

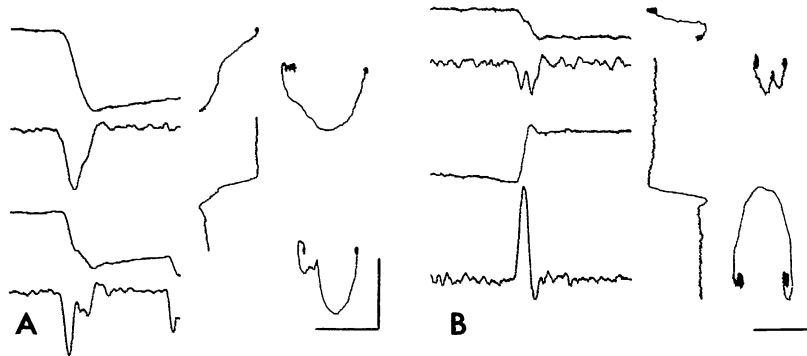


FIG. 6. Oblique eye movements with double saccades in the horizontal (a) and vertical (b) components. The plots on the right of each diagram are the vertical and horizontal phase planes.

can produce a wide variety of synchronous and asynchronous oblique saccadic eye movements. In the oblique eye movement of Fig. 5(a) both the horizontal and the vertical saccades have dynamic overshoot, and a synchronous hook is produced. Only the horizontal saccade of Fig. 5(b) has dynamic overshoot, so a differently shaped hook results. The oblique eye movement of Fig. 5(c) has dynamic overshoot in both components, producing a loop where the eye circles its final position. In the eye movement of Fig. 5(d) the primary saccades of both the horizontal and the vertical channels end at the same time, and the return phase of the horizontal channel's dynamic overshoot occurs while the vertical channel is stationary, thus producing an asynchronous hook.

Occasionally a saccadic eye movement is not executed as one large saccade, but rather it is broken down into two small, very closely spaced saccades, where the velocity profiles may overlap [2]. This can produce either synchronous or asynchronous oblique eye movements, in which either the horizontal saccade [Fig. 6(a)] or the vertical saccade [Fig. 6(b)] is broken up into a pair of smaller saccades. In this figure the left sides are the same as in the previous figures; however, horizontal and vertical phase planes are added which show, respectively, horizontal velocity as a function of horizontal position, and vertical velocity as a function of vertical position. When double saccades appear in oblique eye movements, they usually appear in the smaller of the horizontal and vertical components, although we have records with double saccades in the larger component, and also in both components simultaneously.

When the natural durations of the horizontal and vertical components are equal, as in Fig. 4(a), the oblique saccade will probably be synchronous. In order to determine the relative frequency of occurrence of each type of

oblique saccadic eye movement, we have analyzed all of the oblique eye movements that did not have components with naturally equal durations. We have found the following approximate percentages:

Asynchronous (60%):

- oblique portion at start, 30%,
- Oblique portion in the middle, 12%,
- oblique portion at the end, 15%,
- non-overlapping components, 3%.

Many asynchronous movements had dynamic overshoot and double saccades: they were included in the most appropriate of the above categories.

Synchronous (40%), caused by artificial lengthening of the smaller component due to:

- glissades, 13%,
- low velocity small components, 2%,
- dynamic overshoot, 20%,
- double saccades, 5%.

The asynchronism in the start and stop of each component was not related to any particular combination of muscles or motor nuclei, because there are records where the horizontal components started and ended both before and after the vertical components for saccades in all directions and at all inclinations. Furthermore, all three methods of eye movement measurement have produced saccades in all categories.

VELOCITY OF SACCADES

In order to analyze oblique saccades, it was often expedient to compare the horizontal and vertical components with pure horizontal and vertical saccades. Figure 7 is a main sequence diagram [4] which shows the maximum saccadic velocity as a function of saccadic magnitude. Vertical saccades have smaller maximum velocities, with downward saccades having the smallest velocities. Their durations are correspondingly longer.

Typical downward [Fig. 8(a)] and upward [Fig. 8(b)] saccades illustrate, respectively, static overshoot and static undershoot. A saccade has static overshoot when it takes the eye beyond the target, and a subsequent corrective saccade brings the eye back. Downward saccades had static overshoot in 64% of the cases; upward saccades had static undershoot in 52% of the cases. For the records of Fig. 8 the subject was saccading between two points: one at the center of the target, and the other 6 degrees directly above it. The downward movement was composed of a 6.15 degree primary saccade and a 0.45 degree corrective saccade. The upward movement was composed of a 5.45 degree primary saccade plus a 0.59 degree corrective

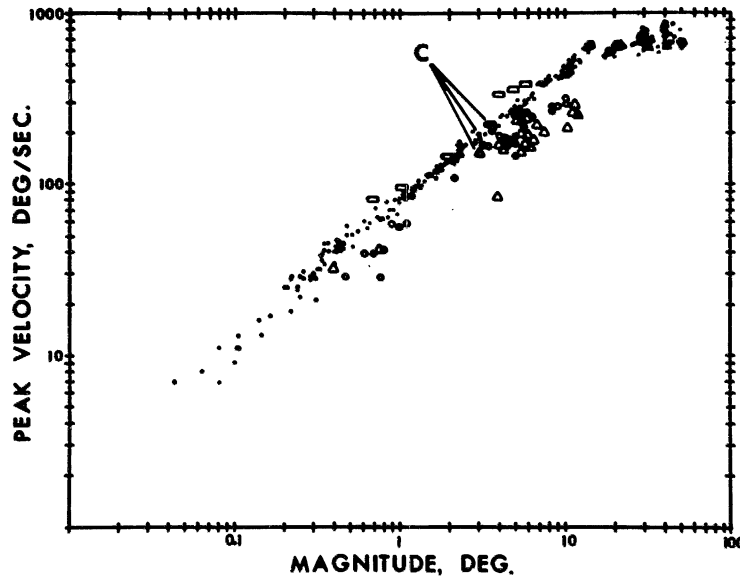


FIG. 7. Main sequence diagram showing maximum velocity as a function of saccadic magnitude for horizontal (\bullet), upward (Δ), downward (\circ), and a few fast oblique (\square) saccades.

saccade. Neither movement was linear. That is, both of the large vertical saccades had transient, orthogonal horizontal components. When the horizontal component was only transient and the initial and final horizontal positions were identical, then the saccade was called "purely vertical". Our data show that 90% of all purely horizontal or purely vertical saccades had transient orthogonal components with magnitudes at least 10% of the magnitude of the main saccade. Most of the observed linear saccades were less than 2 degrees in magnitude.

The presaccadic velocity plateau seen in Fig. 8(b) is occasionally seen in horizontal saccades, but it is more common in vertical saccades.

Horizontal saccades fit on the horizontal main sequence diagrams shown in Fig. 7. The horizontal components of most oblique saccades also fit on the horizontal main sequence diagrams. This means that if the eye is to move 5 degrees to the right, it will make that horizontal movement with the same speed, whether it is a pure horizontal saccade or part of an oblique movement. The horizontal component is not speeded up or slowed down by either the presence or the absence of a vertical component. Similarly, vertical components of oblique eye movements lie on the vertical main sequence diagrams and are not affected by horizontal components. This is illustrated in Fig. 7 by the points connected to the letter C, which represent the components of the oblique saccade shown in Fig. 8(c).

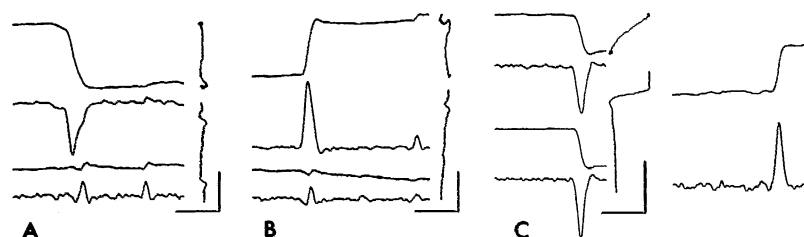


FIG. 8. Purely downward (a) and upward (b) saccades showing typical nonlinearity of the X - Y trajectory; (c) a nearly linear oblique saccade. The records on the right are the odometer and speedometer displays.

If each component is main sequence, then the oblique saccade can be super-main-sequence: for the horizontal muscles are exerting maximum force, and the vertical muscles are also exerting maximum force, and these forces are added vectorially to yield a superforce that can make oblique saccades superfast. The oblique saccade of Fig. 8(c) is one example of this, for the horizontal component is a 3 degree, 190 degree/sec main sequence saccade, and the vertical component is a 3 degree, 150 degree/sec upward main sequence saccade: but the resultant is a 3.7 degree, 215 degree/sec super-main-sequence saccade, as shown in the odometer and speedometer displays on the extreme right of Fig. 8. The odometer and speedometer displays show, respectively, the cumulative distance traveled as a function of time, and the instantaneous eye velocity as a function of time. The computer algorithm for generating these displays compensates uniformly for noise in the records. However, the biological noise (tremor) is not uniform; it is smaller during the saccade, because the muscles are active and the tremor is reduced. As a result, the odometer and speedometer displays indicate values that are too small. If the resultant oblique saccade is computed by a sum of squares technique, its magnitude becomes 4.2 degrees and its maximum velocity is 242 degrees/sec, which is also super-main-sequence.

Although there are two pairs of muscles affecting vertical eye movements, they are tightly cross-linked, and we found no evidence that they did not act as one unit.

When the eyes are abducted 39 degrees from primary position, the superior and inferior oblique muscles will not contribute any force to pure vertical eye movements; all of the force will be developed by the superior and inferior recti. In this position, 5 degree upward and downward saccades had the same maximum velocities—150 degrees/sec (28 saccades, standard deviation 20 degrees/sec). This is lower than the maximum velocity for vertical saccades in primary position of 186 degrees/sec (standard deviation 39 degrees/sec).

DISCUSSION

Detailed examinations of hooked, oblique saccades, such as shown in Fig. 5, enabled us to conclude that the hooks were caused by dynamic overshoot in one or both of the components. Thomas and O'Beirne [16], having access to less detailed information, suggested that hooks may have been caused by a delay created by the extra length of the sixth cranial nerve. A delay in activating any set of muscles would cause asynchronous saccades, but not hooked saccades. For instance, in Fig. 3(c) and (d) the vertical components are delayed, so the eye movements start in horizontal directions. Hooked saccades are created when the eye goes too far in one direction and returns in the opposite direction, due to dynamic overshoot.

For the simultaneous operation of two systems there are three possibilities; first, they may be completely independent; second, they may have crosstalk, because one system couples unwanted information into the other; and third, they may have cross-linking, because synchronizing information passes between the two systems. At various times, the horizontal and vertical eye movement systems exhibit each of these. Independence is exhibited in Fig. 3(d), crosstalk in Fig. 8(a) and (b), and cross-linking in Fig. 4(a).

This paper is concerned with the interdependence of the systems that produce the horizontal and vertical components of individual oblique saccadic eye movements. The larger, more encompassing horizontal and vertical eye tracking systems — including sensory, central nervous system (CNS), and motor components — have also been investigated for interdependence. It is possible for the horizontal channel to be in a saccadic tracking mode, and the vertical channel simultaneously in a smooth pursuit tracking mode, in order to do either of the following: maintain fixation of a stationary target [9], or maintain fixation of a target with complex motion [8]. These horizontal and vertical eye tracking systems are two independent channels with mutual crosstalk [10].

Over a century ago, Hughlings Jackson studied the spread of grand mal epileptic seizures and surmised that the human cerebral cortex controls movement not muscles [12].

Evidence that the primate cortex controlled oblique eye movements seemingly came from Robinson and Fuchs [14], who electrically stimulated the frontal eye fields with large current pulses [100 to 2,000 microamperes (μA)] and produced oblique saccadic eye movements, where the magnitude and direction of the movement depended solely upon the region stimulated. However, Asanuma [1] has found that by reducing the stimulating current to 5 μA , a small volume of the cortex can be excited, which will produce an effect on only one muscle; it will not even effect the antagonist muscle. The variability in the trajectories of oblique saccadic eye movements demon-

strates that, at least at the level of the pons and the midbrain, muscles are controlled; for when an oblique saccadic eye movement is made, the horizontal system produces a horizontal saccade and the vertical system produces a vertical saccade. These two saccades need not be synchronized and may even be discontinuous. Therefore, if a movement command exists at any level, it specifies only the end points of the horizontal and vertical components of the movement and does not specify the trajectory of the movement. The neurological circuits which would translate this movement command into the muscle commands would have to be unique for the horizontal and vertical channels and would often operate asynchronously.

We cannot state with assurance whether the lack of synchronism between the horizontal and vertical components of oblique eye movements is due to either inability or indifference on the part of the CNS. Considering only one eye, all saccadic eye movements involve at least two extraocular motor nuclei. Furthermore, vertical eye movements always require both sides of the brain stem, because the superior rectus and superior oblique muscles are innervated by contralateral motor nuclei, whereas their yoke muscles are ipsilaterally innervated. Thus, for oblique eye movements communication must be established between many motor nuclei on both sides of the brain. This communication may tax the system and produce asynchronous behavior. On the other hand, the systems may be capable of precise synchronism (as required for dynamic overshoot), but for convenience and ease of computation a certain amount of inaccuracy may be tolerated.

SUMMARY

The horizontal and vertical components of oblique saccadic eye movements are not always tightly cross-linked; often they are completely independent. Most of the time the two components do not start and end simultaneously. The neurological bursting and pausing of the extraocular mononeurons that underlie the generation of these oblique movements will, correspondingly, not be synchronized.

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