Coupling Between Horizontal and Vertical Components of Saccadic Eye Movements During Constant Amplitude and Direction Gaze Shifts in the Rhesus Monkey

Edward G. Freedman
Department of Neurobiology and Anatomy; University of Rochester Medical Center; University of Rochester; Rochester, New York

Submitted 12 June 2008; accepted in final form 15 October 2008

Freedman EG. Coupling between horizontal and vertical components of saccadic eye movements during constant amplitude and direction gaze shifts in the rhesus monkey. J Neurophysiol 100: 3375–3393, 2008. First published October 22, 2008; doi:10.1152/jn.90669.2008. When the head is free to move, changes in the direction of the line of sight (gaze shifts) can be accomplished using coordinated movements of the eyes and head. During repeated gaze shifts between the same two targets, the amplitudes of the saccadic eye movements and movements of the head vary inversely as a function of the starting positions of the eyes in the orbits. In addition, as head-movement amplitudes and velocities increase, saccade velocities decline. Taken together these observations lead to a reversal in the expected correlation between saccade duration and amplitude: small-amplitude saccades associated with large head movements can have longer durations than larger-amplitude saccades associated with small head movements. The data in this report indicate that this reversal occurs during gaze shifts along the horizontal meridian and also when considering the horizontal component of oblique saccades made when the eyes begin deviated only along the horizontal meridian. Under these conditions, it is possible to determine whether the variability in the duration of the constant amplitude vertical component of oblique saccades is accounted for better by increases in horizontal saccade amplitude or increases in horizontal saccade duration. Results show that vertical saccade duration can be inversely related to horizontal saccade amplitude (or unrelated to it) but that horizontal saccade duration is an excellent predictor of vertical saccade duration. Modifications to existing hypotheses of gaze control are assessed based on these new observations and a mechanism is proposed that can account for these data.

INTRODUCTION

The transformation of sensory information into motor actions is a critical function of the nervous system, and one that is not yet fully understood. The oculomotor system continues to be a model for the study of the neural control of behavior in large part because of the stereotyped nature of saccadic eye movements and because the neural elements controlling these high-velocity, conjugate movements of the eyes are accessible for experimentation. Careful studies of saccadic behavior have constrained hypotheses concerning their neural control and led to direct tests of the predictions of various oculomotor control models. Analyses of gaze shifts made when the head is free to move will similarly constrain hypotheses concerned with the coordination of the eyes and head during visual orienting behaviors.

Saccadic eye movements change the direction of the line of sight and permit new images to fall on the receptor rich foveal region of the retina. They are defined by a set of characteristic relationships between amplitude, duration, and peak velocity. These stereotyped relationships (sometimes referred to as the “main sequence”) have been described in detail during horizontal, vertical, and oblique movements in a variety of species (Bahill et al. 1975; Baloh et al. 1975; Becker and Jürgens 1990; Collewijn et al. 1988a,b; Evinger et al. 1981; Fuchs 1967; Guitton and Mandl 1980; King et al. 1986; Smit et al. 1990; van Gisbergen et al. 1985; Yee et al. 1985). For example, the positive correlation between saccade duration and amplitude during horizontal saccades is illustrated in Fig. 1A. In this panel, the durations of horizontal saccades made to targets displaced by 5, 15, 35, and 50° are plotted. In the diagram below (Fig. 1C), these movements are represented schematically by arrows of different lengths along the abscissa. As shown in A, horizontal saccades (made by this non-human primate subject) having amplitudes of 35° take around 75 ms to complete. The durations of vertical saccades with amplitudes of 20° (shown schematically in Fig. 1C by the black arrow along the ordinate), were ~50 ms (Fig. 1B, unfilled circles). If horizontal and vertical saccade components were independently generated, when oblique movements had 20° vertical components and 35° horizontal components, movements could be dramatically curved (Fig. 1C, gray trajectory) because the 20° vertical component would be completed 25 ms before the completion of the 35° horizontal component. However, during oblique saccades, the horizontal and vertical components tend to begin and end at nearly the same times and trajectories of oblique saccades tend to be straight (Fig. 1C, dotted lines). As shown in Fig. 1B, this is a result of the temporal stretching of the smaller-amplitude component (the vertical component in this example). Instead of taking 50 ms for the eyes to move vertically 20°, when part of an oblique saccade with 35 or 50° horizontal components, the 20° vertical component took 75 or 100 ms to complete: about the same amount of time it took to complete the 35 or 50° horizontal component. The duration of the vertical component is increased to match closely the duration of the horizontal component even though the amplitude of the vertical component is not changing. This results in a positive correlation between vertical saccade duration and the amplitude of the horizontal saccade component (Fig. 1B).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

Address for reprint requests and other correspondence: Dept. of Neurobiology and Anatomy; University of Rochester Medical Center; University of Rochester; Box 603, Rochester, NY 14642.
In models of the head-restrained saccadic system, component durations are not explicitly determined or controlled. Instead, movement durations are determined by the desired size of the movement and by the exponential function that converts motor error into a signal proportional to velocity (known as the saccadic burst generator). In these models, the tight link between saccade duration and amplitude stems from the presumed stability of the burst generator function for movements in a given direction. As the relative amplitudes of the horizontal and vertical components change (i.e., movement directions differ), there are two ways to alter the durations of saccade components. The input to the burst generator or the burst generator function itself can be altered as a function of saccade direction. Both methods can change the duration of a constant amplitude saccade component such that the smaller-amplitude component is stretched in time to match the duration of the larger component (see Fig. 1B). As indicated, matching the durations of the horizontal and vertical components is necessary if saccade curvature is to be avoided. However, curved saccades like that shown schematically in Fig. 1C (gray line) will also result if the horizontal component is delayed with respect to the vertical. An example of this is illustrated in Fig. 1D, which shows a schematic diagram of vertical velocity (black) plotted as a function of time. Consider the movements that would result if this velocity profile was paired with a horizontal movement that began after a delay (gray dashed velocity profile) or if it was paired with a horizontal movement that accelerated and decelerated along a different trajectory.

**FIG. 1.** A: saccade duration plotted as a function of amplitude for movements directed along the horizontal meridian when the head is restrained. B: vertical saccade duration plotted as a function of horizontal component amplitude during oblique, head restrained saccadic eye movements. Vertical saccade amplitude did not vary and was 20°. For comparison (unfilled circles) duration of vertical saccades of 20° during pure vertical movements are also shown. C: arrows along the abscissa represent movements of various amplitudes directed along the horizontal meridian. Arrow along the ordinate represents vertical movements of constant amplitude. Gray line indicates the curved trajectory of a hypothetical movement that might occur if vertical component duration were not increased to match that of the horizontal component. Dashed lines represent more realistic saccade trajectories during oblique movements that combine varying horizontal amplitudes with constant vertical amplitude. D: schematic diagram of velocity profiles of vertical (black) and horizontal (dashed, gray) components that lead to curved saccade trajectories. E: vertical velocity is plotted as a function of horizontal velocity for two oblique saccades. This panel presents a method for assessing saccade curvature. Low curvature (black) results in high VAF; high curvature (gray) results in low VAF.
(gray solid line). In both of these hypothetical cases, the majority of the vertical component of the saccade would be accomplished before an equivalent amount of the horizontal component was completed, leading to dramatically curved saccades (Fig. 1C, gray line). The lack of dramatically curved oblique saccades when the head is restrained suggests that the horizontal and vertical saccade components begin and end together and component velocity profiles differ only in scale. In Fig. 1E, a method for comparing curvature of different saccades is presented. Vertical velocity is plotted as a function of horizontal velocity for a head restrained saccade (black). Ninety-nine percent of the variance in vertical velocity is accounted for by the horizontal velocity; an indication that vertical and horizontal velocity differ only in scale. The variance accounted for (VAF) will be much lower if movements are curved (Fig. 1E, gray trace). This method will be revisited when the straightness of oblique gaze shifts is addressed.

Several mechanisms have been proposed to account for the coupling of horizontal and vertical components of oblique saccades (Becker and Jürgens 1990; Grossman and Robinson 1988; Nichols and Sparks 1996; Quaia and Optican 1997; Smit et al. 1990; van Gisbergen et al. 1985; van Opstal and Kappen 1993). Although there are differences among them, each of these hypotheses (except the proposal of Grossman and Robinson 1988) uses the direction of the saccade (or equivalently the relative amplitudes of the horizontal and vertical components) to scale the component velocities. Two classes of model have been proposed. Common source models (Quaia and Optican 1997; van Gisbergen et al. 1985; van Opstal and Kappen 1993) rely on a single saccadic burst generator that produces a signal proportional to vectorial velocity. Because both components arise from a common velocity command, a critical prediction of this hypothesis is that horizontal and vertical velocities will differ only by a scaling factor, thus guaranteeing that movements will be straight (in a variant of this type of model, Quaia and Optican 1997 suggest that common source models may be consistent with direction-specific curvature). To accomplish appropriate velocity scaling, common-source models calculate movement direction and adjust both the gain (asymptotic value) and the time constant of the exponential function that defines the relationship between saccade component size and peak velocity (see van Gisbergen et al. 1985, Eq. 3). A critical prediction of common-source models is that the slopes of the duration-amplitude relationships will be determined by the direction of movement. Note that all the above-referenced models were designed to account for head-restrained saccade data. Eye-head interactions are irrelevant under these conditions. The predictions of these models might differ if they were extended to include movements of the head.

Cross-coupling models assume that a vectorial command is first decomposed into separate horizontal and vertical components and that these serve as inputs to separate, interacting burst generators (Becker and Jürgens 1990; Grossman and Robinson 1988). To account for component stretching of oblique saccades, the cross-coupling model of Becker and Jürgens (1990) scales the inputs to the burst generators according to movement direction. This hypothesis proposes that the input to the horizontal burst generator is given by the following equation

$$H_{me}/(1 + c^* V_{me})$$

(1)

Where $H_{me}$ is horizontal motor error, $V_{me}$ is vertical motor error, and $c$ is a coupling constant (on the order of 0.05). This approach has proven to be reasonably successful because of the seemingly immutable relationship between saccade duration and amplitude; the degree to which the horizontal velocity must be reduced so that its duration matches that of the vertical component can be calculated given the amplitude of the vertical component and knowledge of the duration-amplitude relationship. The same can be said about common-source models with the caveat that the duration-amplitude relationship for movements made in a particular direction must be known to accurately predict the angular constant that scales component velocities.

When the head is free to move, changes in the direction of the line of sight can be accomplished using coordinated movements of both the eyes and head. Two observations concerning head unrestrained gaze shifts are pertinent. The first is that during gaze shifts having similar amplitudes, the relative contributions of the eyes and head vary inversely and depend on the starting positions of the eyes in the orbits (Delreux et al. 1991; Freedman and Sparks 1997a,b, 2000; Stahl 1999, 2001; Tomlinson 1990; Volle and Guitton 1993). The second is that as head-movement amplitudes and velocities increase, the velocities of the associated saccadic eye movements decline (Freedman 2001, 2005; Freedman and Sparks 2000; Tomlinson 1990; Tomlinson and Baha 1986). A direct consequence of these two observations is that during gaze shifts of the same amplitude, initiated with the eyes in different orbital positions, the relationship between saccade duration and amplitude can be reversed: the linear relationship has a negative slope (see RESULTS). Given this uncoupling of the usually tight link between saccade amplitude and duration, it is possible to test the hypothesis that it is the relative amplitudes of horizontal and vertical components of oblique saccades that leads to the observed component stretching. Under the conditions outlined in the preceding text, the effects of saccade component duration and amplitude on the orthogonal component duration can be separately assessed. In the following text, it is demonstrated that the duration of the constant amplitude vertical component of oblique saccades does not depend on the amplitude of the horizontal component. These data will help constrain hypotheses that propose mechanisms for the control of coordinated eye-head movements.

METHODS

Two female rhesus monkeys weighing between 4.5 and 6 kg (Macaca mulatta) served as subjects. Each had a scleral eye coil implanted in one eye (Judge et al. 1980) and a small head-restraint post secured to the skull. Surgical procedures were carried out using general inhalation anesthesia (isoflurane) and aseptic techniques. After full recovery, subjects were trained to make gaze shifts to visual targets for a juice reward. All surgical and experimental procedures were approved by the University of Rochester Committee on Animal Resources and comply with the National Institutes of Health guide for the Care and Use of Laboratory Animals.

Subjects sat in a primate chair that prevented movements of the hips and shoulders but permitted unrestricted horizontal and vertical movements of the head. The chair was positioned such that the head of the monkey was located at the center of a 1.2-m cube that housed 3 pairs
of magnetic field coils (CNC Engineering, Seattle, WA). The four vertical faces of the cube (front-back and left-right) contained two pairs of Helmholz coils in spatial and phase quadrature (Collewijn 1977). The two horizontal faces of the cube (top and bottom) contained a third pair of Helmholz coils for measurement of the vertical angle of the scleral and head-mounted coils. A five-pole low-pass Bessel filter with a cutoff frequency of 3 kHz was used to remove the coil system carrier frequency. A second low-pass filter (time constant = 0.3 ms) conditioned coil signals before digitizing. This filter will introduce no more than a 0.2-ms delay in signals with frequency content between 0 and 530 Hz.

A lightweight cam-lock device was secured to the implanted head post. This device carried a coil similar to that implanted in the eye to measure head position. In addition, three small laser diodes (red: 650 nm) were secured to the head daily. The central laser was aligned with the midsagittal plane of the subject’s head, the second laser was directed −18° to the left of center, and the third was directed −18° to the right. Illumination of the head-mounted laser was controlled via custom behavioral control software.

Visual target presentation

Visual targets were presented by pointing green laser diodes (532 nm) at the inside of a 1.5-m-diam hemisphere painted 18% gray. The hemisphere (0.5-in acrylic; Capital Plastics, Beltsville, MD) was positioned so that the center of its vertical face was aligned with the geometric center of the field coil frame. Positioning of the lasers was carried out by two independent, two-axis, motorized gimbals (custom designed using pairs of RGV 100 rotation stages; Newport, Irvine, CA). Each pair of rotation stages, arranged in a Fick gimbal, could direct a laser spot at any location within the hemisphere with better than 0.01° accuracy and precision rated at 0.0003°. Switching lasers on and off was controlled via custom data acquisition and behavioral control software running on a PC with an extended PCI bus (National Instruments; Austin TX).

Behavioral tasks

Subjects were trained to perform the following task. Before the onset of each trial, both two-axis gimbals were positioned such that the lasers were pointed at locations randomly selected from a set of potential target locations. At this stage, neither target was illuminated. Trials began with the illumination of the first target [in these data, this was always located at (0,0)—a target aligned with the mid-sagittal plane of the subject’s body and equidistant from the upper and lower bounds of the display]. In conjunction with the illumination of the first target, one of the three head-mounted lasers was randomly selected by computer and also turned on. Subjects were trained to look at the green fixation target while simultaneously aligning the red head-mounted laser with this target spot (within a computer defined window: radius 4°). When the central head-mounted laser was selected, the eyes were positioned in the center of the orbits (the eyes and head were aligned). When the left-pointing head laser was illuminated, alignment of the head laser and the target spot required the subject to fixate the central target while rotating the head to the right—positioning the eyes to the left in the orbits. Similarly when the right-pointing head laser was lit, the eyes began deviated to the right in the orbits.

After fixating the first target and aligning the head appropriately for a variable interval (250–1,250 ms; 50-ms increments), a second green target was turned on. This spot could be in any of 24 locations and was randomly selected before the beginning of each trial. After a variable delay interval (250–1,000 ms; 50-ms increments) when head alignment and fixation of the first target had to be maintained, the first target and the head mounted laser were turned off (the secondary green laser spot was left on). This served as the cue for the subject to initiate a gaze shift to the location of the still illuminated target. Subjects had 500 ms to initiate and complete gaze shifts to the second target and were required to fixate this location within a computer defined window (2.5–5° radius). Task contingencies were implemented in real time with 1-ms resolution. Only trials during which subjects met the spatial and temporal requirements of the task are included in this report.

Figure 2 illustrates in schematic form the positions of the 24 targets (filled circles) and the initial fixation target location (central square). Several additional target locations were added along the horizontal meridian and will be discussed explicitly in the text. In addition, the three possible positions of the head are also shown. It is important to remember that the task required the head-mounted laser to be aligned with the central fixation target; only the head-mounted laser and the central target were illuminated at the beginning of each trial. However, because the head-mounted lasers were pointed in three different directions; to align these targets, the head had to be rotated in the horizontal plane. As a result, the head began directed toward one of the three locations indicated in Fig. 2 (for display purposes head alignment positions are slightly elevated in this figure; actual rotations of the head were along the horizontal meridian). The eyes were not deviated vertically in the orbits and always began in a central position. The vertical component of gaze shifts reported below was restricted in amplitude to be within 35° of the horizontal meridian. Because the eyes began in a vertically centered orbital position, vertical head contributions did not exceed 5° (head movements were primarily horizontal). A consequence of this arrangement was that for each presented target, the vertical components of oblique gaze shifts and saccadic eye movements were relatively constant, whereas the horizontal eye- and head-movement components varied.

Data

Horizontal and vertical gaze and head position data were sampled at 1 kHz and eye position relative to the head was calculated by subtracting head from gaze at each time sample. Eye position is defined as the position of the eyes relative to the head and rapid eye movements relative to the head are referred to as saccadic eye movements or saccades throughout the text. Gaze and head positions are defined relative to an external/spatial reference. Data were stored and analyzed off-line using Matlab (Natick, MA). Velocities were

---

**FIG. 2.** The locations of the majority of visual targets used during head unrestrained data collection (other targets specified in the text). The initial fixation target was always located centrally (0,0), and 1 of 3 head-mounted lasers was required to be aligned with this central target. As a result the head could be pointed initially in one of 3 directions (starred locations). Initial head locations are displaced vertically for display only.
calculated using a five-point parabolic function (see Freedman (2005) for description). The beginning and end of horizontal and vertical gaze, head and eye movements were calculated using velocity and acceleration criteria. To be marked as the onset of a movement, samples had to have velocities that exceeded 30°/s or accelerations that exceeded 5,000°/s² for each of three consecutive samples. Movement end was marked when velocity and acceleration fell below these levels. Each movement was individually inspected and criteria marked correctly nearly 98% of all gaze, eye, and head movements. Our criteria failed to mark movements when both horizontal and vertical gaze (or eye) velocities fell to 0 and then resumed to complete the trial within the time requirements of the task. These trials consisted of essentially two movements separated by a very short interval and were not analyzed. Beginning and end of horizontal and vertical gaze, eye, and head movements were calculated separately; however, both the beginning and end of eye movements and gaze shifts differed very little using the criteria in the preceding text. To be specific, gaze shift end rarely (<1% of trials) exceeded eye movement end by more than ~10 ms; eye movements that reached position plateaus and maintained constant position for extended periods while gaze shifts continued were not observed. Durations were calculated as the time from beginning to end, amplitudes were calculated as the change in position during the movement. Head contribution is defined as the change in position of the head that occurs during the gaze shift.

Statistical null hypotheses [Kolmogorov-Smirnoff (K-S) or Student’s t-test] were rejected when \( P < 0.05 \). Slopes of duration-amplitude relationships were determined to be statistically different from 0 by calculating 95% confidence intervals and determining whether these excluded the 0-slope line.

**RESULTS**

Data for this report include 12,672 head-restrained gaze shifts from subject \( P \) and 10,334 from subject \( S \). Additional head-restrained data from each subject were collected separately and are included for comparison as indicated in the text. Because leftward and rightward as well as upward and downward movements were made, unless explicitly stated in the text, data are presented as the absolute value of movement amplitude. Negative amplitudes and velocities indicate leftward (or downward) movements.

When the head is free to move, gaze shifts of a particular amplitude and direction can be composed of movements of the eyes and head. During repeated gaze shifts to the same target, eye- and head-movement amplitudes vary inversely as a function of the starting positions of the eyes in the orbits (Delreux et al. 1991; Freedman and Sparks 1997b, 2000, 2001, Volle and Guitton 1993). For example, a 35° gaze shift might be accomplished by making a 35° saccade. The head movement, if any, would occur after the gaze shift was completed, so on such a trial, the head contribution would be 0°. However, the same 35° gaze shift might be made up of a 10° saccade coupled with a large (and fast) head movement that contributes 25° to the overall change in gaze position. The former movement is likely to be observed when the eyes begin deviated in the orbits away from the direction of the gaze shift, whereas the latter example might occur when the eyes were initially deviated in the direction of the ensuing gaze shift.

**Gaze shifts along the horizontal meridian**

Before presenting data from oblique gaze shifts, it is important to consider the effects of head movements on the amplitude and duration of saccadic eye movements when repeated gaze shifts are directed to the same visual target displaced along the horizontal meridian. Because gaze amplitudes are similar when movements are made between the same two visual targets, as head contribution to gaze shifts increases, the amplitude of saccadic eye movements necessarily declines. Figure 3 plots data from gaze shifts made to a target displaced 35° to the left of fixation. Using the head-pointing task (METHODS), initial eye positions varied from 19.6° in the direction of the gaze shift to 23.2° away from movement direction. During 526 gaze shifts (Fig. 3A; subject \( P \)) the amplitude of saccades varied over a fairly large range (5°-35°), even while gaze shift amplitude varied very little (absolute value of mean horizontal gaze amplitude = 35.2 ± 1.6°; mean vertical gaze amplitude = 1.5 ± 1.1°). For this set of movements, small saccadic eye movements were part of gaze shifts with large, fast head movements, whereas larger saccades were coupled with smaller, slower head movements. As demonstrated previously for both horizontal (Freedman and Sparks 2000) and vertical (Freedman 2005) gaze shifts, as head velocity and head contribution to the gaze shift increase, saccadic velocity declines. A direct consequence of these observations is that during constant amplitude gaze shifts in which the amplitude of the saccade varies, the duration-amplitude relationship for saccadic eye movements is reversed. In Fig. 3, horizontal saccade duration is plotted as a function of the amplitude of the saccade (note that movements were to the left, but data are plotted as the absolute value of saccade amplitude). As shown the relationship between saccade duration and amplitude has a negative slope.

To provide some insight into the reversal of the duration-amplitude relationship during horizontal gaze shifts having similar amplitudes, horizontal gaze (black), eye (dark gray), and head (light gray) velocities are plotted as functions of time for three sets of movements (\( n = 5 \)). Each set of trials was selected from a different section of the data shown in Fig. 3A (arrows indicate regions). In Fig. 3B, head-movement amplitudes were large (total head-movement amplitudes were between 45 and 49°; head contributions ranged from 28 to 30°), trials in Fig. 3C were associated with head movements between 24 and 26°, and movements in \( D \) had head movement amplitudes between 5 and 10°.

Figure 3E plots data similar to that shown in \( A \) but for the second subject (\( S \)). In each case, smaller saccades associated with large head contributions were slower than larger saccades associated with small head contributions, reversing the relationship between saccade duration and amplitude observed when the head is restrained (e.g., Fig. 1B). The slopes of the lines of best fit for these data were −2.5 (Fig. 3A) and −2.7 (B).

During horizontal gaze shifts to targets located to the left and right, displaced 25, 30, 35, 40, or 50° from the fixation target (Fig. 4), the slopes of the duration-amplitude relationships were negative for both \( S \) (gray) and \( P \) (black). During movements to targets displaced >20°, slopes ranged from −2.4 to −4.7. Figure 4B provides the data in tabular form in the \( r^2 \), slope and number of trials for both subjects. Also shown in Fig. 4 are the lines of best fit for the duration-amplitude relationships observed during gaze shifts to a 20° target. In this case, the slopes were not significantly different from zero and positive. Note that during 20° gaze shifts with the eyes deviated in the direction of the movement, head contribution remained quite small (0.19 ± 0.3°). As a result, horizontal saccade amplitudes did not vary over a large range (18.9 ± 2.3°) and the duration
of saccades changed very little. This results in lack of correlation between duration and amplitude during movements to 20° targets. If the range of initial eye positions had been increased so that saccade amplitudes varied over a wider range, it is likely that the slope of the duration-amplitude relationship would have been negative during movements to these targets as it was during gaze shifts to the targets displaced by ≥25°.

Oblique gaze shifts

Before describing the overall effects of head movements on horizontal and vertical saccade components, several single trial examples are illustrated in Fig. 5 to provide an overall impression of the results. In Fig. 5A, vertical gaze (A), eye (B), and head (C) positions are plotted as functions of horizontal positions during each of these three movements; note that head positions are plotted for the duration of the gaze shift (head contribution is shown, not the entire movement of the head during these trials). In each case, gaze shifts were initiated from the central target location and were made to the same target displaced down and left 35°. The eyes began in different horizontal positions relative to the head (Fig. 5B). One movement was initiated with the eyes deviated away from the horizontal direction of the ensuing movement and in this case the eyes began deviated to the right (black). A second movement began with the eyes and head aligned (dark gray), and the third began with the eyes deviated to the left (in the direction of the movement: light gray). In all three examples, the horizontal gaze shift amplitudes were nearly identical (37°) as were the vertical amplitudes (33°). When the eyes began deviated initially to the right (black) horizontal component amplitude was >30°. Compare this to the 25° eye movement made when the eyes and head were aligned initially (dark gray) and 12.5° when the eyes began deviated to the left (light gray). Horizontal and vertical gaze (D), eye (E), and head (F) positions are plotted as functions of time. Inspection of the horizontal eye position traces from these three example trials (E) makes it clear that the
duration of the horizontal component of the movement initiated with the eyes deviated to the right (black)—the saccade with the largest horizontal component amplitude—had a shorter duration than did the movement initiated with the eyes deviated to the left (light gray). And although the amplitudes were the same, the duration of the vertical saccade component associated with the smallest amplitude horizontal component had the longest duration of these three movements. To complete the overview of these oblique gaze shifts, horizontal and vertical velocities are plotted as functions of time in Fig. 6. Compared with the movements made when the eyes were deviated either to the right or centered in the orbits, there is a clear reduction in peak velocity and increase in duration of the vertical eye movement component during the movement associated with the smallest horizontal component (light gray).

Several observations are illustrated in the examples shown in Fig. 5. First, as it was during movement along the horizontal meridian, there is a reversal of the duration-amplitude relationship for the horizontal component of eye movements that are part of constant amplitude and direction gaze shifts. Second, the duration of the vertical component of eye movements increases along with the duration of the horizontal component. This occurs despite the progressively smaller horizontal component amplitude coupled with constant amplitude vertical movements. Third, the curvature of saccades and gaze shifts appears to be correlated with the contribution of the head. In the figures that follow, details of each of these observations will be provided.

During movements along the horizontal meridian, the linear relationship between saccade duration and amplitude had a negative slope (Figs. 3 and 4). Figure 6 shows the relationship between duration and amplitude of horizontal saccade components of oblique gaze shifts. Movements were made to a target displaced 35° to the left and 35° down. In A, saccade duration is plotted as a function of amplitude for 214 movements made by subject P. The duration-amplitude relationship for similar movements to the same target (subject S) is plotted in B. In each case, the slopes of the lines of best fit are negative. This provides an opportunity to assess separately the effects of amplitude and duration of the horizontal saccade component on the duration of the constant amplitude vertical saccade component.

As stated in the preceding text, the initial fixation location was always a target positioned straight ahead of the subject (0,0). Over the course of many gaze shifts to the same target, gaze shifts had very similar horizontal and vertical amplitudes. However, due to the head-alignment requirements of the task, the contribution of the head to the horizontal component of movements, and similarly the horizontal amplitude of saccadic eye movements varied. Recall that current hypotheses of the coupling between vertical and horizontal components generally rely on a calculation of movement direction to scale the velocities of the two components. Thus these models of the head-restrained saccadic system predict a positive correlation between the duration of the constant amplitude component and the varying amplitude of the orthogonal component. None of these models predict that the duration of the vertical component will be unrelated to the amplitude of the horizontal component nor do they predict that the relationship will have a negative slope.

During repeated gaze shifts to a target 35° to the left and 35° down (Fig. 7), with the eyes in different initial horizontal positions, vertical saccade amplitudes were relatively constant (Fig. 7A: mean ± SD vertical saccade amplitude = −33.97 ± 1.3°; B: = −33.58 ± 1.5°). The amplitudes of the horizontal saccade components varied from 10 to 38°. When the horizontal saccade amplitude was ~10°, the vertical component amplitude was about three times larger than the horizontal. During other movements (when the eyes began deviated away from the direction of movement), the horizontal and vertical components had approximately equal amplitudes. Figure 7 plots the duration of the vertical saccade component as a function of the amplitude of the horizontal component for subjects P (A) and S (B). In each case, the duration of the 34° vertical saccades was longer (~175 ms) when coupled with a small (10°) horizontal saccade component. In contrast, when horizontal and vertical components were of equal amplitude, the duration of the vertical component was ~50 ms shorter. Although the amplitude of the vertical saccade component was not changing, the duration was increased by 50 ms when the vertical component was three times larger than the horizontal component amplitude. Note in Fig. 7, A and B, the mean (±SD) duration of pure vertical saccades to a target 35° down is indicated along the ordinate (Fig. 6A: mean = 72.6 ms; B: mean = 77.5 ms).

For comparison, in Fig. 7B, data from a second target (down 35° and to the right 35°) are shown (gray filled symbols). It is clear that during movements to this target the range of horizontal eye movements was significantly smaller (<10°) than...
during movements made to the target located down and to the left 35° (black symbols). These data reflect an asymmetry in the amplitude of head contributions during movements to some targets. Head contributions varied over a wide range for movements to the target 35° to the left but varied over a much smaller range during symmetrical movements to the right. Over the range where they can be compared, the data from the two targets were quite similar; however, the variance in vertical movement duration accounted for by horizontal eye-movement amplitudes during this set of rightward movements was much less than that accounted for during movements to the target down and left (see text following text and Table 1).

During repeated gaze shifts to the same target, gaze amplitude and direction were relatively constant as were the amplitudes of the vertical components of the saccadic eye movements. The relationship between vertical saccade duration and horizontal saccade amplitude could have a negative slope as shown in Fig. 7. In contrast, there was a positive correlation between vertical component duration and horizontal component duration. Figure 8 plots vertical duration as a function of horizontal duration for the same movements shown in Fig. 7. As shown, the lines of best fit to these data had positive slopes and horizontal component duration accounted for 73% (A) and 94% (B) of the variance in vertical saccade duration. Although the duration of small-amplitude horizontal saccades was longer than the duration of larger-amplitude movements, the vertical component duration was stretched in time so that its duration matched closely the duration of the horizontal component.
shifts to 16 oblique target locations (see METHODS). The horizontal (Xpos) and vertical (Ypos) locations of the targets, the number of gaze shifts made to that target and meeting the selection criteria (N), and the variance ($r^2$) of the line of best fit for the relationship between vertical saccade duration and horizontal saccade amplitude are given in the first two columns of Table 1. For each subject, data are rank ordered from highest to lowest $r^2$. Bold type indicates the data illustrated in Fig. 7.

The third column provides the slope of the line of best fit and the 95% confidence interval on the slope. The values of $r^2$ for the vertical saccade duration versus horizontal duration data (Fig. 8) and the slopes and 95% confidence intervals are shown in columns 4 and 5 of the table. As shown, the slopes of the lines of best fit for the duration-amplitude data were statistically different from 0 for movements to 23 of the 32 target-subject pairs. For all cases in which statistical significance was reached, the slopes of the duration-amplitude data were negative. It should be noted that existing hypotheses designed to account for component stretching predict a tight positive correlation between vertical saccade duration and horizontal saccade amplitude. The data from the 9/32 target-subject pairs for which the 95% confidence intervals on the slopes included 0 are not consistent with the predictions of these hypotheses; there was no statistically significant relationship between vertical duration and horizontal amplitude during movements to these targets. In stark contrast to the amplitude-duration data, across all 16 oblique target locations, horizontal saccade duration accounted for much of the variance in the duration of the vertical component [mean variance accounted for: 78.5% ($S$), and 71.0% ($P$)]. The slopes of the duration-duration relationships were all positive, and all were statistically different from 0 (Table 1).

There was clearly temporal stretching of the vertical component of oblique saccades made under the conditions of this experiment. This is demonstrated in Figs. 7 and 8, each of which show that although the vertical amplitude was not changing, the duration varied from 75 to nearly 200 ms. However, the vertical component duration was longest when it was coupled with the horizontal saccade components having the smallest amplitudes (Fig. 7). This stretching of the $\sim 34^\circ$ vertical component by a horizontal component that was 1/3 the size arises from the prolonged duration of these small-amplitude horizontal components. Component stretching appears to be based not on the relative amplitudes of the horizontal and vertical saccade components, but rather on increasing the duration of the “shorter” component so that it matches closely the duration of the “longer” component.

For each subject, data of this type were collected during gaze shifts to 16 oblique target locations (see METHODS). The horizontal (Xpos) and vertical (Ypos) locations of the targets, the number of gaze shifts made to that target and meeting the selection criteria ($N$), and the variance ($r^2$) of the line of best fit for the relationship between vertical saccade duration and horizontal saccade amplitude are given in the first two columns of Table 1. For each subject, data are rank ordered from highest to lowest $r^2$. Bold type indicates the data illustrated in Fig. 7.

The third column provides the slope of the line of best fit and the 95% confidence interval on the slope. The values of $r^2$ for the vertical saccade duration versus horizontal duration data (Fig. 8) and the slopes and 95% confidence intervals are shown in columns 4 and 5 of the table. As shown, the slopes of the lines of best fit for the duration-amplitude data were statistically different from 0 for movements to 23 of the 32 target-subject pairs. For all cases in which statistical significance was reached, the slopes of the duration-amplitude data were negative. It should be noted that existing hypotheses designed to account for component stretching predict a tight positive correlation between vertical saccade duration and horizontal saccade amplitude. The data from the 9/32 target-subject pairs for which the 95% confidence intervals on the slopes included 0 are not consistent with the predictions of these hypotheses; there was no statistically significant relationship between vertical duration and horizontal amplitude during movements to these targets. In stark contrast to the amplitude-duration data, across all 16 oblique target locations, horizontal saccade duration accounted for much of the variance in the duration of the vertical component [mean variance accounted for: 78.5% ($S$), and 71.0% ($P$)]. The slopes of the duration-duration relationships were all positive, and all were statistically different from 0 (Table 1).

FIG. 6. Oblique gaze shifts to a target 35° left and 35° down relative to the fixation target. Horizontal saccade component duration is plotted as a function of horizontal saccade component amplitude for 214 movements made by subject P (A) and 161 by subject S (B). Lines of best fit shown in each panel. ○ in A are the 3 movements presented in Fig. 5.

FIG. 7. For the same set of oblique movements shown in Fig. 6, the duration of the constant amplitude vertical saccade component is plotted as a function of the amplitude of the horizontal saccade component. Lines of best fit, slopes, number of trials, and variance are shown in each panel. For comparison, the mean ($\pm SD$) duration of pure vertical saccades (made when the head was unrestrained) to a target displaced 35° downward is shown along the ordinate in each panel. ○ in A are the 3 movements presented in Fig. 5. In B, data from subject S are presented. ○ in B plot vertical eye movement duration as a function horizontal eye movement amplitude for 209 movements made to the target located 35° down and 35° to the right. See also related text and Table 1.
Because the horizontal and vertical components of gaze shifts were similar for these movements, to achieve the reversal in the duration-amplitude relationship for the horizontal saccade components, movements had to be initiated with the eyes in a variety of orbital positions. One might think that the increased duration of the horizontal component seen when the eyes begin deviated in the direction of the ensuing movement (e.g., light gray in Fig. 5) is a result of orbital mechanical effects and not due to interactions between the saccade and the ongoing head movement. To allay these concerns, head-restrained movements were analyzed. During 3,117 head-restrained saccades made to the same 24 target locations (16 oblique, 4 along the horizontal meridian and 4 along the vertical) used during the head-unrestrained trials and initiated from the same orbital eye positions, 137 successful movements were made to the target located 35° to the left and 35° down relative to the central fixation location. These conditions are identical to those illustrated in Fig. 7 except that in this case the head was prevented from moving. Figure 9 plots the durations of the vertical eye movements as a function of the amplitudes of the horizontal saccade components. When the eyes began centered in the orbits, horizontal movement amplitudes were on the order of 32°. However, when the eyes began deviated away from the direction of movement and the head remained restrained and pointing straight ahead, saccade amplitudes increased to ~48°. When the eyes began deviated in the direction of movement, saccade amplitudes were ~15°. In the head-restrained case as shown here, the changes in movement amplitudes are consistent with the altered displacements required to bring the image of the target onto the fovea.

TABLE 1. Duration-amplitude and duration-duration relationships during oblique gaze shifts

<table>
<thead>
<tr>
<th>Target Location (Xpos, Ypos)</th>
<th>( r^2 ) Vertical Duration vs. Horizontal Amplitude</th>
<th>Slope (± 95%)</th>
<th>( r^2 ) Vertical Duration vs. Horizontal Duration</th>
<th>Slope (± 95%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>((-20, -35) (220))</td>
<td>0.55</td>
<td>-4.30 (1.85)*</td>
<td>0.93</td>
<td>1.00 (0.15)*</td>
</tr>
<tr>
<td>((-35, -35) (161))</td>
<td><strong>0.39</strong></td>
<td><strong>-2.96 (0.58)</strong>*</td>
<td><strong>0.95</strong></td>
<td><strong>0.94 (0.04)</strong>*</td>
</tr>
<tr>
<td>((-35, -20) (132))</td>
<td>0.33</td>
<td>-2.60 (0.62)*</td>
<td>0.82</td>
<td>0.95 (0.08)*</td>
</tr>
<tr>
<td>((-20, -20) (167))</td>
<td>0.27</td>
<td>-4.90 (1.22)*</td>
<td>0.94</td>
<td>0.99 (0.06)*</td>
</tr>
<tr>
<td>((-20, 20) (174))</td>
<td>0.24</td>
<td>-3.40 (1.10)*</td>
<td>0.85</td>
<td>0.92 (0.06)*</td>
</tr>
<tr>
<td>((-35, 35) (264))</td>
<td>0.18</td>
<td>-1.30 (0.48)*</td>
<td>0.74</td>
<td>0.76 (0.12)*</td>
</tr>
<tr>
<td>((-35, 20) (131))</td>
<td>0.15</td>
<td>-1.12 (0.43)*</td>
<td>0.80</td>
<td>0.81 (0.04)*</td>
</tr>
<tr>
<td>(20, 20) (385))</td>
<td>0.07</td>
<td>-1.12 (0.43)*</td>
<td>0.80</td>
<td>0.81 (0.04)*</td>
</tr>
<tr>
<td>(35, -20) (267))</td>
<td>0.02</td>
<td>-1.52 (1.32)*</td>
<td>0.72</td>
<td>1.02 (0.08)*</td>
</tr>
<tr>
<td>((-20, 35) (312))</td>
<td>0.02</td>
<td>-0.58 (0.46)*</td>
<td>0.51</td>
<td>0.49 (0.06)*</td>
</tr>
<tr>
<td>(20, 35) (269))</td>
<td>0.014</td>
<td>0.55 (0.57)</td>
<td>0.57</td>
<td>0.82 (0.10)*</td>
</tr>
<tr>
<td>(20, -35) (235))</td>
<td>0.008</td>
<td>0.80 (1.12)</td>
<td>0.96</td>
<td>1.07 (0.03)*</td>
</tr>
<tr>
<td>(-20, 20) (338))</td>
<td>0.006</td>
<td>1.26 (2.18)</td>
<td>0.81</td>
<td>0.85 (0.07)*</td>
</tr>
<tr>
<td>(35, 35) (175))</td>
<td>0.004</td>
<td>0.25 (0.62)</td>
<td>0.77</td>
<td>0.76 (0.06)*</td>
</tr>
<tr>
<td>(35, 20) (125))</td>
<td>0.004</td>
<td>-0.35 (0.93)</td>
<td>0.78</td>
<td>0.79 (0.08)*</td>
</tr>
<tr>
<td>(35, -35) (209))</td>
<td>0.000</td>
<td>-0.20 (1.73)</td>
<td>0.86</td>
<td>1.01 (0.06)*</td>
</tr>
</tbody>
</table>

| \(-20, -35) (39)\)          | 0.66                               | -3.70 (0.80)*| 0.98                               | 0.98 (0.04)* |
| \(-35, -20) (101)\)         | 0.44                               | -2.59 (0.60)*| 0.57                               | 0.82 (0.24)* |
| \(-35, -20) (139)\)         | 0.40                               | -2.67 (0.57)*| 0.76                               | 1.02 (0.09)* |
| \(-35, -35) (214)\)         | **0.33**                           | **-2.00 (0.42)*** | **0.73**                           | **0.93 (0.08)*** |
| \(-20, 35) (54)\)           | 0.30                               | -3.00 (1.30)*| 0.63                               | 0.59 (0.13)* |
| \(35, -20) (135)\)          | 0.23                               | -2.80 (0.90)*| 0.66                               | 0.76 (0.10)* |
| \(-20, 20) (124)\)          | 0.20                               | -2.00 (0.70)*| 0.93                               | 0.85 (0.04)* |
| \(35, 20) (135)\)           | 0.18                               | -2.60 (1.00)*| 0.82                               | 0.81 (0.09)* |
| \(-35, 35) (205)\)          | 0.14                               | -1.60 (0.56)*| 0.83                               | 1.05 (0.06)* |
| \(35, 35) (209)\)           | 0.07                               | -1.63 (0.77)*| 0.47                               | 0.66 (0.09)* |
| \(20, -35) (76)\)           | 0.06                               | -1.09 (0.95)*| 0.77                               | 0.78 (0.10)* |
| \(20, 20) (77)\)            | 0.06                               | -1.54 (0.74)*| 0.59                               | 0.67 (0.07)* |
| \(-20, 20) (269)\)          | 0.05                               | -1.17 (0.60)*| 0.79                               | 0.84 (0.06)* |
| \(-20, -20) (70)\)          | 0.02                               | -0.79 (1.51) | 0.88                               | 0.79 (0.07)* |
| \(35, 35) (202)\)           | 0.03                               | 0.38 (1.10)  | 0.56                               | 0.64 (0.08)* |
| \(35, -35) (168)\)          | 0.000                              | 0.08 (0.81)  | 0.84                               | 0.67 (0.05)* |

For subject S and P, horizontal and vertical locations of the target (Xpos, Ypos) and number of trials (n) are presented in the leftmost column. Vertical saccade duration was plotted as a function of horizontal saccade amplitude, and lines were fit using least-squares methods. The variance in vertical duration accounted for by changes in horizontal amplitude (\( r^2 \)) is shown in column 4. The slope of each line of best fit and the 95% confidence interval on the slopes are shown in column 5. Column 6 shows the \( r^2 \) values for the duration-duration data, and column 5 presents the slopes and 95% confidence intervals on these slopes. *, slopes significantly different from 0. Bold text indicates data illustrated in Figs. 6 and 7. Bold gray text indicates data shown using gray-filled symbols in Fig. 6b. Data are ordered from highest to lowest duration-amplitude \( r^2 \) for each subject.
COUPLING DURING OBLIQUE GAZE SHIFTS

Fig. 8. For the same trials illustrated in Figs. 6 and 7, vertical saccade duration is plotted as a function of horizontal saccade duration. Lines of best fit, slopes, number of trials, and variance are shown in each panel. Mean (±SD) amplitude of the vertical saccade components are shown in each panel.

and horizontal amplitude are tightly coupled and positively correlated.

Straightness of oblique gaze shifts

Straightness is a well-documented characteristic of head-restrained saccades. Straight saccades are produced when horizontal and vertical components begin and end together and when their velocity profiles differ only by a scaling factor (see Fig. 1 and related text). Figure 10A illustrates gaze (black), eye (dark gray, and head contribution (light gray) trajectories for a set of movements made to a target displaced leftward 35° and downward 35°. Total head-movement amplitudes were between 35° and 50° during these movements, all traces are aligned at zero. As is clear from the eye and gaze trajectories, movements were dramatically curved. Head movements during another set of trials to the same target location were much smaller (between 0 and 15°), and gaze, eye and head contribution trajectories for this set of movements are illustrated in Fig. 10B. Note that the amplitudes of the horizontal and vertical components of these gaze shifts were nearly identical to movements shown in A. Despite the similarities in gaze shift amplitude and direction, these movements appear to be much straighter. This statement is reinforced by plotting vertical as a function of horizontal velocity and calculating the VAF for each trial. Velocity-velocity plots for the gaze (black) and eye (eye) movements corresponding to trajectories plotted in Fig. 10A are shown in D. Horizontal velocity accounted for 45% of the variance in vertical velocity during these movements. During the movements shown in Fig. 10B, horizontal velocity accounted for 92% of the variance (D). During gaze shifts of the same amplitude and direction, gaze trajectory curvature depended on the amplitude of the associated head movements; gaze shift curvature is direction-independent. This direction independence of gaze shift curvature is demonstrated by comparing the curvature of gaze shifts (black) in A to those shown in B. The directions are identical, but curvature depends on the associated head movement. Similarly, the curvature of the eye movement component of gaze shifts can be shown to be direction-independent. Compare the eye movements in A (gray) with those shown in C. The movements shown in C were selected so that the amplitude and direction of the saccadic eye movements matched those made during the trials shown in A. Trajectories of these eye movements are shown along with the trajectories of the gaze shifts and associated head movements. Comparison of eye movements in A and C illustrates that curvature of eye movements does not depend on movement direction; it is, however, correlated with the contribution of the head. In F, vertical velocity is plotted as a function of horizontal velocity for these eye movements and as shown, horizontal velocity accounted for 89% of the variance in vertical velocity. As with gaze shifts, eye-movement curvature appears to be direction-independent and correlated with the contribution of the head.

Table 2 summarizes the curvature data for gaze shifts and eye movements to 10 different target locations for subjects S and P. Target locations correspond to the locations given in Table 1 for each subject (the 1st 10 locations in order). Movements to each target were divided into groups having head movements larger than 35° (large head contribution in Table 2), and movements having head movements smaller than 15° (small). Mean and SD for gaze and eye movements are shown for each group. K-S tests were used to compare the variance during movements having large and small head contributions. In every case, gaze shifts and eye movements...
associated with large head movements were more curved (variance accounted for was statistically significantly lower: $P < 0.05$) than during matched movements associated with small head contributions. Curvature of both gaze shifts and eye movements depends on the amplitude of the associated head movement, not on the direction of movement.

**Discussion**

The horizontal and vertical components of oblique saccades made when the head is prevented from moving are not independent (Bahill et al. 1975; Baloh et al. 1975; Becker and Jürgens 1990; Collewijn et al. 1988a,b; Evinger et al. 1981; Fuchs 1967; Guitton and Mandl 1980; King et al. 1986; Smit et al. 1990; van Gisbergen et al. 1985; Yee et al. 1985). Several mechanisms for the coupling of components have been proposed (Becker and Jürgens 1990; Grossman and Robinson 1988; Nichols and Sparks 1996; Quaia and Optican 1997; Smit et al. 1990; van Gisbergen et al. 1985; van Opstal and Kappen 1993). Extending these hypotheses to include coordinated movements of the eyes and head has yet to be adequately addressed. By systematically manipulating the positions of the eyes in the orbits at the onset of constant amplitude and direction gaze shifts, it is possible to probe the nature of the coupling of horizontal and vertical saccade components in ways that are not possible when the head is prevented from moving.

Using this approach several key points have been demonstrated in this report. First, during gaze shifts to the same target location along the horizontal meridian, when the initial positions of the eyes in the orbits vary, the relationship between saccade duration and amplitude has a negative slope. This observation has not been made explicitly before; however, it is a direct consequence of two aspects of eye-head coordination both of which have been previously described. The first is that during constant amplitude gaze shifts the amplitudes of the eye and head components of movements vary inversely; small
saccadic eye movements are coupled with large (and fast) head movements, whereas large saccades are coupled with small head movements (Freedman 2005; Freedman and Sparks 1997a,b; Stahl 1999, 2001; Tomlinson 1990). The second important observation is that as the amplitude and speed of head movements increase, the velocity of the eyes declines (Freedman and Sparks 2000). During gaze shifts initiated with the eyes deviated away from the direction of movement, the head contribution and speed of the head will be small, and the large concomitant saccade will have a high peak velocity. However, when the eyes are deviated in the direction of the ensuing movements, a fast (and large) head movement will be associated with a small-amplitude saccade that has a reduced velocity. This results in the reversed duration-amplitude relationship seen during constant amplitude gaze shifts initiated with the eyes in different initial positions (Figs. 3 and 4).

During oblique gaze shifts of similar amplitude and direction, when the eyes begin in the same vertical positions but in different horizontal positions, the amplitude of the saccade component was relatively constant, but the amplitude of the horizontal saccade component varied. Under these conditions, it was possible to assess the effects of varying horizontal component amplitude on the duration of the constant amplitude vertical saccade component. In addition, under these conditions, it was possible to test the assumption that the constant amplitude vertical component is temporally stretched as a function of the amplitude of the horizontal component. As shown here, the relative amplitudes of horizontal and vertical components were not a good predictor of the duration of the vertical component. Instead the duration of the horizontal component (regardless of amplitude) appears to determine the duration of the vertical component. This occurred even when the vertical component was three times larger than the amplitude of the horizontal component.

During coordinated eye-head movements, the eyes and head move in the same direction. The operation of the vestibulocular reflex (VOR) during these movements might be expected to reduce the velocity of the eyes in proportion to the ongoing velocity of the head. This assumes that the VOR remains fully functional during eye-head movements. The role of the VOR during gaze shifts remains unclear with data from a number of experiments producing a variety of conclusions including complete absence of the VOR during gaze shifts, modulation of VOR along a time course related to gaze motor error, and no modulation of VOR during gaze shifts (Cullen et al. 2004; Dichgans et al. 1974; Guitton and Volle 1987; Guitton et al. 1984; Lauritis and Robinson 1986; Pelisson and Prablanc 1986; Tabak et al. 1996; Viirre et al. 1986). The pertinent issue is whether or not operation of the VOR could account for the data in this report. To address this concern, Fig. 11 plots eye (thick lines) and head (thin lines) velocities as functions of time for three example movements taken from data shown in Fig. 8A. As shown, one of these saccades was associated with a small (light gray: 4°), one with a medium (dark gray: 28°), and one with a large (black: 45°) head movement. Dashed lines indicate the time at which the early peak in eye velocity occurs for each trial. Head velocity for the smallest head movement is near zero at the time of peak saccade velocities. During the two movements with larger head movements, head velocity was <30°/s at the time that peak eye velocities occurred. However, eye velocities differed by as much as 500°/s when comparing the movement with the largest and smallest head contributions. For the VOR to account for this dramatic decrease in saccade velocity, the gain of the reflex would need to exceed 16. Note that this analysis of the VOR depends on the assumption that

![Image](http://jn.physiology.org/)

**FIG. 11.** Eye (thick lines) and head (thin lines) velocities are plotted as functions of time for 3 movements. Movements selected from data presented in Fig. 7. The time at which peak eye velocity occurs is marked (dashed vertical lines). *Inset:* the negative slope of the duration-amplitude relationship for these 3 example trials. See text for discussion of the role of the VOR during gaze shifts of this type.

### TABLE 2. Curvature of gaze shifts and eye movements when head movements are large or small

<table>
<thead>
<tr>
<th>Gaze r² Head Contribution</th>
<th>Eye r² Head Contribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large</td>
<td>Large</td>
</tr>
<tr>
<td>Small</td>
<td>Small</td>
</tr>
<tr>
<td><strong>A. Subject S</strong></td>
<td></td>
</tr>
<tr>
<td>0.37 ± 0.18*</td>
<td>0.93 ± 0.03</td>
</tr>
<tr>
<td>0.40 ± 0.25*</td>
<td>0.85 ± 0.08</td>
</tr>
<tr>
<td>0.38 ± 0.12*</td>
<td>0.84 ± 0.12</td>
</tr>
<tr>
<td>0.36 ± 0.14*</td>
<td>0.88 ± 0.13</td>
</tr>
<tr>
<td>0.59 ± 0.17*</td>
<td>0.89 ± 0.06</td>
</tr>
<tr>
<td>0.70 ± 0.10*</td>
<td>0.95 ± 0.03</td>
</tr>
<tr>
<td>0.54 ± 0.10*</td>
<td>0.91 ± 0.07</td>
</tr>
<tr>
<td>0.75 ± 0.09*</td>
<td>0.96 ± 0.02</td>
</tr>
<tr>
<td>0.70 ± 0.13*</td>
<td>0.98 ± 0.01</td>
</tr>
<tr>
<td>0.65 ± 0.07*</td>
<td>0.97 ± 0.01</td>
</tr>
<tr>
<td><strong>B. Subject P</strong></td>
<td></td>
</tr>
<tr>
<td>0.45 ± 0.16*</td>
<td>0.84 ± 0.17</td>
</tr>
<tr>
<td>0.45 ± 0.14*</td>
<td>0.92 ± 0.03</td>
</tr>
<tr>
<td>0.61 ± 0.04*</td>
<td>0.89 ± 0.04</td>
</tr>
<tr>
<td>0.53 ± 0.11*</td>
<td>0.95 ± 0.03</td>
</tr>
<tr>
<td>0.56 ± 0.15*</td>
<td>0.96 ± 0.01</td>
</tr>
<tr>
<td>0.51 ± 0.13*</td>
<td>0.98 ± 0.01</td>
</tr>
<tr>
<td>0.53 ± 0.09*</td>
<td>0.94 ± 0.04</td>
</tr>
<tr>
<td>0.74 ± 0.11*</td>
<td>0.95 ± 0.04</td>
</tr>
<tr>
<td>0.64 ± 0.12*</td>
<td>0.97 ± 0.01</td>
</tr>
<tr>
<td>0.60 ± 0.10*</td>
<td>0.95 ± 0.03</td>
</tr>
</tbody>
</table>

For subjects S and P, the table provides mean r² (±SD) values calculated from plots of vertical versus horizontal velocity for gaze shifts (2 columns on left) and eye movements (2 columns on right). Data are from the first 10 target locations listed in Table 1 (chosen because of the large range of head movements made during these trials). Movements having associated head movements >35° are in the “large head contribution” columns. Movements having small head movements (0–15°) are shown in the “small head contribution” columns. Bold entries indicate data from Fig. 11, A and B. Bold italicized entry shows data from Fig. 11, C. r² values during large head movements were all statistically smaller than corresponding r² values during small head movements (Kolmogorov-Smirnov test P < 0.05).
the gain of the VOR is similar during gaze shifts having the same amplitudes and directions. While the available data suggest that this is a reasonable assumption, this is an issue that requires further attention.

In addition to the comparison in the preceding text, if the two movements with larger head contributions are considered, there is a difference in peak saccade velocity of \( \sim 250^\circ/s \), but at this same point in time, there was no difference in the velocities of the head. The reacceleration of the eyes seen in both of the movements associated with larger head contributions is also difficult to account for using a VOR-based mechanism. Whether the VOR remains partially or completely operational during large-amplitude gaze shifts remains an open question, but it is not adequate to account for the data presented here. Yet the reduced velocity of small-amplitude saccades seen during constant amplitude gaze shifts leads to the reversal of the saccadic duration-amplitude relationship (inset) and must be accounted for in any attempt to model the gaze control system.

**Implications for neural control of gaze shifts**

The reversal of the saccadic duration-amplitude relationship observed during head unrestrained gaze shifts, and the impact that this has on the duration of the constant amplitude vertical component of oblique movements may be surprising. It might also seem that some of the core assumptions that have formed the basis for our understanding of the oculomotor system are more tenuous than previously thought. For instance, the hypothetical saccadic burst generator has been presumed to convert signals of dynamic motor error into a motor command proportional to saccade velocity (cf. Becker and Jürgens 1990; Jürgens et al. 1981; Robinson 1973; van Gisbergen et al. 1987). This function (in conjunction with the feedback control loop) enables models of the saccadic system to reproduce the monotonic, saturating relationship between peak saccade velocity and movement amplitude as well as the linear, positive correlation between saccade duration and amplitude observed when the head is restrained. But the reversal of the duration-amplitude relationship raises questions about the nature of the burst generator and the exponential function that has been used to model the transformation of motor error into a velocity command.

Hypotheses designed to capture the main features of the saccadic system assume that the observed amplitude of a saccade is a veridical representation of the input to the burst generator; models assume that the desired displacement of the eyes equals the amplitude of the observed movement. However, when the head contributes to the accomplishment of gaze shifts, multiple subsystems (e.g., saccadic system, vestibulo-ocular and cervicoocular reflexes) may all be contributing simultaneously to the movements of the eyes. The observed saccadic eye movement may no longer be a good predictor of the desired displacement signal that serves as the initial input to the saccadic burst generator. If this is the case, knowledge of the state of the saccadic, or in some models gaze, burst generator cannot be inferred from either the amplitude or from the temporal progression of the observed movements. As a result it could be the case that the reversal in the duration-amplitude relationship during head unrestrained gaze shifts does not reflect a dramatic change in the nature of the burst generator function but reveals an uncoupling of the saccade burst generator from the observed behavior. This “neural uncertainty” (Frens et al. 1998; Sparks 1999; Stanford and Sparks 1994) could prevent development of hypotheses based on the observed amplitude-duration-velocity relationships when the head is free to move. Without a clear understanding of all of the inputs that contribute to the movements of the eyes and head, and the ways in which they interact to produce the observed movements, it may not possible to generate useful hypotheses. In fact, to the extent that there is uncertainty about the state of the burst generator during eye-head movements, *all existing gaze control models may be rendered moot.*

To progress, this conundrum must be circumvented. One solution is to understand and experimentally isolate all of the input signals to the burst generator, thereby determining its state during gaze shifts. Until this is accomplished, making the assumption (albeit a potentially problematic one) that the observed movements reflect the state of the burst generator permits continued progress toward understanding the neural control of coordinated eye-head movements. As yet untested, this assumption is not implausible; observed saccades may be good predictors of the state of the saccadic burst generator even during eye-head movements. For instance, tests of the gain of the VOR during large-amplitude movements indicate a significant reduction in reflex efficacy during gaze shifts, thus reducing any impact of this subsystem on observed movement amplitudes and kinematics. It is also possible that reflexes during active movements operate only on unexpected movements of the head and that as long as head movements progress according to the head motor command, the vestibular system does not alter ongoing saccades. Again if this was the case, the amplitude and kinematics of the observed saccade would indeed reflect the comparator and burst generator inputs. Given the possibility that the assumption is valid, it is worth considering what modifications to existing hypotheses are required to account for the results described in this report.

**Extending current models**

There are numerous gaze control models (e.g., Bizzi et al. 1971, 1972; Freedman 2001; Galiana and Guitton 1992; Goossens and van Opstal 1997; Guitton and Volle 1987; Guitton et al. 1990; Phillips et al. 1995; Tomlinson 1990; Tweed 1997; Volle and Guitton 1993). In general they differ in their assumptions about the order of linear and nonlinear elements such as the burst generator, the separation of gaze into eye and head commands, the decomposition of vectorial into horizontal and vertical component signals, and the position of these hypothetical elements within or outside of the dynamic feedback control loop. The vast majority of these hypotheses are concerned only with movement along the horizontal meridian. The means by which these models are extended to include movements in two dimensions will depend on assumptions about the uncoupling of horizontal and vertical components (is there a single vectorial burst generator or separate, interacting horizontal and vertical burst generators?), the position of this uncoupling (is there a vectorial gaze burst generator? Separate vectorial eye and head burst generators? Separate eye and head, horizontal and vertical burst generators? And how do these interact?). A detailed exposition of each of these possible hypotheses, its predictions, and its compatibility with existing
behavioral data is beyond the scope of this report. Instead the focus here will be to extend one hypothesis (Freedman 2001) and show that this model can account for the amplitude-duration reversal, and by extending the Becker and Jürgens (1990) cross-coupling scheme to include the eye-head interaction mechanism described previously, it is possible to account for the data presented in this report.

Simulations using the model first proposed by Freedman (2001) are shown in Fig. 12, A—C, and demonstrate the ability of this model to account for the reversal of the duration-amplitude relationship observed during constant amplitude gaze shifts initiated with the eyes in different orbital positions. Note that with the exception of the two inputs (desired gaze displacement and initial eye position), nothing in the original model was changed to produce these simulations; all parameters were identical to those described in the published account. In A, simulated horizontal eye positions are plotted as functions of time for seven movements. In each case, desired gaze displacement was 40°. Eye position at the onset of movements ranged from 25° in the direction opposite to the movement direction (−25°) to 25° in the direction of the movement. When the eyes began deviated in the orbits −25°, peak saccade velocity (B, black trace) was high and duration short. Saccade amplitude during this simulated movement was 37° and movement duration was <90 ms (Fig. 12C, right-most black filled symbol). As the eyes began in more central positions, and then as the eyes began deviated in the direction of movements, eye-movement amplitudes declined. As shown in B, as initial eye positions changed, peak velocity declined and durations increased. The duration-amplitude data for these simulated horizontal gaze shifts having different amplitudes are shown in C. For each set of simulations, gaze shift amplitudes were constant. As simulated saccade amplitude declined, duration increased and the slopes of the lines of best fit were negative. Compare these simulations with the data presented in Fig. 4.

An extension of the Freedman (2001) hypothesis to include movements in two dimensions is illustrated schematically in Fig. 13A. In this scheme, a vectorial desired displacement command is derived from the active population of motor-related neurons in the superior colliculus. In the model, this command is decomposed into horizontal and vertical desired displacement commands (gray filled square). Then using information about the positions of the eyes in the orbits, horizontal and vertical gaze commands are separated into desired eye (horizontal and vertical) and desired head (horizontal and vertical) displacement signals (Freedman 2001, 2005). At this stage, the desired eye displacement signals serve as the input to a standard cross-coupled 2D model of saccadic eye movements (Becker and Jürgens 1990). Finally, to account for the reduction in both horizontal and vertical saccade velocities as a function of increasing horizontal head contribution, in an extension of the Freedman (2001) gaze control model, it is suggested that a signal proportional to horizontal head velocity reduces the gain of both the horizontal and vertical saccadic burst generators. Similarly a vertical head velocity signal is assumed to reduce the saccadic burst generator gains. Using a model having this basic design, it was possible to simulate...
oblique gaze shifts of constant amplitude (40°) and direction (45° above the horizontal) with the eyes in different horizontal initial positions. In Fig. 14B, vertical eye movement duration is plotted as a function of horizontal saccade amplitude for simulations using a Becker and Jürgens cross-coupling factor of 0.1. As illustrated the slope of the linear correlation of these data were negative (−2.7; compare with data in Fig. 7). For the same simulations, the durations of the horizontal and vertical components of saccades were positively correlated (Fig. 14C; slope = 1.0; compare with data in Fig. 8).

As shown, the eye-head interaction suggested by Freedman (2001) reduces the gain of the horizontal burst generator as a function of the head velocity command. This enables this model to account for the reversal of the duration-amplitude relationship. There are other methods that might also reduce the gain of the horizontal burst generator. For instance, partial inactivation of neurons if the PPRF might accomplish the same thing, even if the head were restrained. Barton and colleagues (2003) have used this approach to assess component stretching during oblique head-restrained saccades. Saccades became increasingly curved after PPRF inactivation, and this implies that movements of the same amplitude and direction took longer to complete. Comparison of the duration-amplitude relationships after lidocaine injection does not provide clear evidence for a reversal in the expected head-restrained relationship. It is difficult to determine whether these results are similar to those reported here. And it should be mentioned that lidocaine injections in the PPRF may not reduce the gain of the saccadic burst generator without also altering other related functions. It remains to be shown that burst generator gain reductions caused by other mechanisms will result in similar duration-amplitude relationship reversals.

In addition to being compatible with the reversal of the slope of the duration-amplitude relationship during horizontal gaze shifts, and accounting for the effects on both horizontal and vertical component duration during oblique movements, the model presented schematically in Fig. 13, can also account for the direction-independent curvature of gaze and eye movements observed during gaze shifts. In Fig. 14, vertical gaze (A) and eye (B) positions are plotted as functions of horizontal gaze and eye position during three simulated movements. The eyes and head began aligned (black) or the eyes began deviated in the direction of the gaze shift (light gray) or in the opposite direction (dark gray). Vertical and horizontal velocities for gaze shifts (D) and the eye-movement components of gaze (E) are shown plotted as functions of time. Note as head contribution increases, there are dramatic changes in horizontal velocity profiles of these simulated gaze shifts. To assess movement curvature, vertical velocity is plotted as a function of horizontal velocity for the gaze shift with the largest (G) and smallest (H) head contribution. When head contribution was small, 99% of
the variance was accounted for by horizontal velocity for both gaze shift and associated eye movements (H); movements were straight (dark gray in A and B). In contrast, during gaze shifts of the same amplitude and direction, both eye and gaze shift curvature was much larger when the head contribution was large (G). These simulations demonstrate the ability of the model outlined in Fig. 13 to account for gaze shift curvature that is independent of gaze shift direction; in the model as in the behavioral data, curvature of both gaze shift and saccade depends on head contribution.
To achieve gaze shifts having similar amplitudes and directions with small and large head contributions, the simulated initial positions of the eyes had to vary. It is also important to consider curvature of saccades that have the same amplitude and direction, initiated from the same positions. In Fig. 14C, position trajectories of three such simulations are shown. In each case, eye movements had vertical components of 35° and horizontal components of 38°. Horizontal head-movement amplitudes varied from 4° (black) to 25° (dark gray) to ±40° (light gray). Vertical and horizontal velocity profiles for each eye movement are shown in F, and in I, vertical velocity is plotted as a function horizontal velocity for each simulated movement. As demonstrated, the model simulates both straight and curved saccade trajectories. The degree of curvature is direction-independent but correlated with the contribution of the head. These simulations are consistent with the observed behavioral results described in the preceding text.

The purpose of the simulations in the preceding text is to show that the reversal (somewhat surprising in itself) need not force us to reject head restrained ideas about the saccadic burst generator or about the coupling of the horizontal and vertical components of saccadic eye movements. By incorporating the Becker and Jürgens (1990) cross-coupling model into an existing gaze control model, it is possible to account for the effects of head movements on saccades during constant amplitude and direction gaze shifts. This does not preclude other formulations from also accounting for these observations. Deciding among various alternatives requires continuing to test differential predictions of various hypotheses. Development of new or extensions of existing models is necessary as new findings are uncovered. It is now incumbent on proponents of other schemes to see how their models can be altered and what assumptions are necessary to account for the data presented here. It seems unlikely that there will be a general consensus on a single hypothesis of gaze control in the near future (nor should there be). But it is critical that there is agreement on the data that models need to simulate to be considered viable alternatives. Once all alternatives achieve the same output, they can be distinguished by testing their differential predictions.

**Summary**

During repeated gaze shifts to the same target displaced along the horizontal meridian, when the eyes begin in different orbital positions, there is a reversal of the expected relationship between saccade duration and amplitude. When movements are made to a target displaced both horizontally and vertically, there is a similar reversal in the duration-amplitude relationship for the horizontal component of saccades. Under these conditions, it was possible to assess the relative roles of horizontal saccade amplitude and horizontal saccade duration on the duration of the constant amplitude vertical saccade component. The data presented here demonstrate that the duration of the vertical saccade component is poorly related to the horizontal amplitude of saccades and the linear relationship between vertical duration and horizontal amplitude can have a negative slope. However, vertical duration is positively correlated with the duration of the horizontal saccade component—independent of the horizontal component amplitude. It is not clear how most extant models of the gaze control system will be able to account for these findings. However, the Freedman (2001) model without alterations can account for the reversal of the duration-amplitude relationship during horizontal gaze shifts, and by extending this model to two dimensions (using the cross-coupling of Becker and Jürgens 1990), it is possible to simulate the results in this paper. It is now important to test the critical predictions of this scheme and determine the neural mechanisms with which it may be implemented.

**ACKNOWLEDGMENTS**

The author thanks Aaron L. Cecala for assistance with data collection and, along with Drs. S. Quessy, M. Walton, and J. Quinet, for comments on an earlier version of the manuscript. Thanks also to G. Parker for technical assistance.

**GRANTS**

This work was supported in part by National Eye Institute Grant EY-13239.

**REFERENCES**


