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Oblique Gaze Shifts: Head Movements Reveal New Aspects of Component Coupling

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Abstract

When the head is prevented from moving, it has been clearly demonstrated that the horizontal and vertical components of oblique saccades are not independently produced. The duration of the smaller of the two components is stretched in time to match the duration of the larger component. Several hypotheses have been proposed and each can account for the observed interaction between horizontal and vertical saccade components. When the head is free to move, gaze shifts can be accomplished by combining eye and head movements. During repeated gaze shifts of the same amplitude, as head contribution increases, saccade amplitude declines but saccade duration increases. Thus, the expected relationship between duration and amplitude of saccadic eye movements can be reversed. We have used this altered relationship to determine whether the duration of the vertical saccade component is affected by the amplitude or the duration of the horizontal component. We find that the relative amplitudes of horizontal and vertical saccades cannot account for the observed temporal stretching: vertical component duration increases despite a decrease in the amplitude of the horizontal component. These results are likely inconsistent with models that rely on calculating the vector or relative component amplitudes to account for component stretching.

Introduction

When the head is prevented from moving, saccades are characterized by a set of stereotyped relationships between peak velocity, duration and amplitude. 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; Guitton and Mandl 1980; Evinger et al. 1981; vanGisbergen et al. 1985; Yee et al. 1985; King et al. 1986; Collewyn et al. 1988b; Collewyn et al. 1988a; Becker and Jürgens 1990; Smit et al. 1990). During oblique saccades, the duration of the smaller of the two components is stretched in time to match closely the duration of the larger component (Guitton and Mandl 1980; Evinger et al. 1981; vanGisbergen et al. 1985; King et al. 1986; Becker and Jürgens 1990). Although various mechanisms accounting for component stretching have been proposed, nearly all hypotheses rely on a calculation of the relative amplitudes of the vertical and horizontal components (or equivalently saccade direction) in order to scale the velocity of the two components (vanGisbergen et al. 1985; Grossman and Robinson 1988; Becker and Jürgens 1990; Smit et al. 1990; vanOpstal and Kappen 1993; Nichols and Sparks 1996; Quaia and Optican 1997).

When the head is free to move, and gaze shifts are made to targets displaced both vertically and horizontally, the question of component coupling remains. However, although the eyes and head move together to accomplish large changes in the direction of the line of sight, the trajectories along which they proceed are not necessarily the same. In general the eyes

accomplish a larger proportion of the vertical component of oblique gaze shifts compared to their contribution to the accomplishment of the horizontal component (Tweed et al. 1995; Freedman and Sparks 1997b). This raises questions about component coupling and the type of neural interactions that lead to the temporal stretching of saccade components. For instance, are horizontal and vertical components coupled at the level of gaze control signals? Or are gaze commands separated into eye and head signals before the coupling of horizontal and vertical components? Few of these issues have been addressed and the majority of gaze control models have been restricted to simulation of gaze shifts along the horizontal meridian. Nonetheless, just as understanding the interactions of horizontal and vertical saccades constrained hypotheses related to the neural control of saccadic eye movements (vanGisbergen et al. 1985; Grossman and Robinson 1988; Becker and Jürgens 1990), so too will a clearer understanding of oblique gaze shifts constrain hypotheses designed to describe the neural control of coordinated eye-head movements in two dimensions.

Investigating oblique gaze shifts provides insight into the neural control of eye-head coordination. In addition, because of the ways in which accompanying head movements alter ongoing saccades, some of the fundamental assumptions regarding the brainstem control of saccadic eye movements may need to be reassessed. In this report, conditions are identified in which the usual saccadic duration-amplitude relationship is reversed; saccade duration *declines* as amplitude *increases*. This violation of one of the fundamental rules defining saccades is a direct consequence of two previous observations. The first is that during gaze shifts of similar amplitude made to the same target location, the relative amplitudes of the eyes and head vary inversely as a function of the starting positions of the eyes in the orbits (Delreux et al. 1991; Volle and Guitton 1993; Freedman and Sparks 1997b; Freedman 2001; Stahl 2001; Freedman 2005). For example, a 35° gaze shift can be accomplished by combining a 10° saccadic eye movement and a head movement that contributes 25° to the change in the direction of the line of sight. A 35° gaze shift can also be accomplished with a 35° saccadic eye movement. Head movements occurring on trials like this begin after the gaze shift is complete and therefore do not contribute to its accomplishment. The second important observation is that as head movement amplitude and velocity increases, the velocity of the concurrent saccadic eye movement declines (Tomlinson and Bahra 1986; Phillips et al. 1995; Freedman and Sparks 1997b; Freedman and Sparks 2000). Thus, during a series of 35° gaze shifts, when the eyes begin deviated away from the direction of the movement, the head movement will be small. The resulting saccadic eye movement will be large and fast. In contrast, when the eyes begin deviated in the direction of the gaze shift, the head contribution will be large. The concurrent saccadic eye movement will be smaller and due to the effects of the large, fast head movement the velocity of this saccade will be reduced. We will show that under these conditions the duration-amplitude relationship for saccades has a negative slope. This uncoupling of saccade duration and amplitude allows us to address the question of component coupling during oblique saccades in a new way. It is now possible to assess the differential effects of horizontal component duration and amplitude on the duration of a constant amplitude vertical saccade component. Previously, as horizontal component amplitude increased, component duration also increased. The resulting hypotheses about the nature of component coupling rely on calculation of the relative amplitudes (or direction) of saccades and use this to scale the velocities of the two components. As shown in this report, the duration of the constant amplitude vertical saccade component is not altered as a function of the amplitude of the horizontal component. Temporal stretching of the vertical component duration is correlated with changes in horizontal component duration and is independent of amplitude. These data may require a new set of hypotheses to account for the interaction of horizontal and vertical components during oblique saccades.

Methods

Data from one female rhesus monkey (*Macaca mulatta*; 5kg) are reported here. A scleral eye coil was 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 (isoflourane) and aseptic techniques. After full recovery, the subject was 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 NIH guide for the Care and Use of Animal.

The subject 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 1.2m 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 Helmholtz coils in spatial and phase quadrature (Colleijn 1977). The current induced in the implanted scleral coil (and similar head-mounted coil) varied linearly (within 2%, over $\sim 360^\circ$) as a function of horizontal angle between the search coils and the front vertical face of the cube. The two horizontal faces of the cube (top and bottom) contained a third pair of Helmholtz coils for measurement of the vertical angle of the scleral and head-mounted coils. A 5-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 (1-pole, $\tau = 0.3$ 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 – 530 Hz.

A lightweight cam-lock device was secured to the head restraint post. This device carried a coil similar to that implanted in the eye in order to measure head position. In addition, 3 small laser diodes (red: 650 nm) were daily secured to the head. The central laser was aligned with the mid-sagittal plane of the subject, the second laser was directed $\sim 18^\circ$ to the left of center, and the third was directed $\sim 18^\circ$ to the right.

Each trial began with the illumination of one of the three head-mounted lasers and a central fixation light. The subject was trained to look at the central light and also to align the head-mounted laser spot with the central fixation spot. When the central head-mounted laser was illuminated, this served to align the eyes and head. When one of the other head-mounted lasers was illuminated the eyes began deviated either in the direction of the ensuing gaze shift or in the opposite direction. Initial eye positions ranged from 19.6° in the direction of the movement to 23.2° in the opposite direction. After a variable delay the gaze shift target was illuminated. The subject was required to maintain fixation and head-laser alignment for a variable delay period that ended with the turning off of both the central fixation spot and the head-mounted laser. This was the cue to initiate a gaze shift to the still illuminated target. Movements to many different target locations were randomly interleaved. For this report only movements to two targets are presented. Data along the horizontal meridian directed at a target displaced 35° to the left, and oblique gaze shifts directed at a target displaced 35° left and 35° down.

Coil signals were digitized at 1kHz and stored for off-line analyses (Matlab, Natick, MA). All behavioral contingencies were executed in real time with 1 ms resolution using custom data acquisition and behavioral control software.

Results

As stated in the Introduction, during gaze shifts of similar amplitude and direction, when the eyes begin in different orbital positions, the linear relationship between saccade duration and amplitude can be reversed. An example of this type of reversal is shown in Figure 1. This figure

plots the duration of horizontal saccades as a function of their amplitude. Gaze shifts were made from the fixation target (0,0) to a target 35° to the left (note that absolute value of horizontal saccade amplitude is plotted along the abscissa in this figure). During 526 gaze shifts (these data were extracted from multiple data collection sessions; a variety of target locations were randomly interleaved during any particular session) the initial orbital positions of the eyes varied from ~20° in the direction of the gaze shift to ~20° in the opposite direction. As a result the amplitude of the saccadic eye movements that made up these gaze shifts varied from 5° to > 35°. Because gaze shift amplitude varied very little during these movements (mean (SD) = 35.2° (1.6)), when saccade amplitudes were small the associated head movements were necessarily large. Because saccade velocities are reduced when associated with large, fast head movements (Freedman and Sparks 2000), as saccade amplitude declined, head amplitude and velocity increased leading to a decline in saccade velocity. This results in the negative slope of the line of best fit for the duration-amplitude relationship for saccades made under these conditions (Fig. 1; slope = -2.5).

During oblique gaze shifts to a target located 35° to the left and 35° down relative to the central fixation target, the vertical positions of the eyes at the beginning of movements did not vary. However, as a result of the head-alignment requirements of the task, the horizontal positions of the eyes varied over the central 40° relative to the head. The vertical amplitude of eye movements made during gaze shifts to these targets varied very little. However, under these conditions, the amplitude of the horizontal component of saccades varied as did the duration of the horizontal component. And, as in Fig. 1, the slope of the duration-amplitude relationship was negative. The effects of this altered duration-amplitude relationship are illustrated in Figure 2, during 3 example movements. Horizontal and vertical saccade positions are plotted as functions of time for 3 gaze shifts (Fig. 2A). One of these movements began with the eyes and head nearly aligned (dark gray), a second movement began with the horizontal positions of the eyes deviated away from the direction of the movement (black) and the third began with the eyes deviated in the direction of the ensuing saccade (light gray). Note that the initial vertical positions of the eyes were zero in each case. In Fig. 2B the corresponding component velocities are plotted as functions of time. It is clear from these examples that when the eyes began deviated in the direction of the movement, the amplitude of the horizontal component was small (~12°; light gray) and the velocity was low (peak horizontal velocity <200 °/s). In contrast, when the eyes began deviated in the opposite direction (black) the horizontal component amplitude was large (33°) and velocity was high (peak velocity 500°/s). Although the amplitudes of the vertical saccade components were similar during each of these trials, the duration increased when the 35° vertical component was associated with a 12° horizontal component (light gray) compared to the vertical component duration when coupled with a larger horizontal component (black).

During 214 similar movements to the same target location, the duration of the constant vertical component is plotted as a function of the horizontal component amplitude (Fig. 3A). As illustrated the slope of the line of best fit for these data was negative. When the vertical component was 3 times larger than the associated horizontal component, the duration of the vertical component was increased by a factor of ~2.5 compared to movements of the same amplitude directed along the vertical meridian (mean and SD indicated along the ordinate of Fig. 3). Vertical component duration was also increased when horizontal saccade amplitudes were about one third the amplitude of the vertical component, compared to other oblique movements when the horizontal component was approximately the same amplitude as the vertical. This stretching of the vertical component results in the major saccade component being stretched in time to match the duration of the minor component. In Fig. 3B, the duration of the vertical component is plotted as a function of the horizontal component, and as shown, the horizontal component duration accounts for 73% of the variance in vertical duration.

Discussion

Several mechanisms have been proposed to account for the coupling of horizontal and vertical components of oblique saccades (vanGisbergen et al. 1985; Grossman and Robinson 1988; Becker and Jürgens 1990; vanOpstal and Kappen 1993; Quaia and Optican 1997). With the exception of the model proposed by Grossman and Robinson (1988), each of these hypotheses scales the velocity of horizontal and vertical components as a function of the relative component amplitudes (or direction) of the saccade. In the absence of head movements, when oblique saccades are made and the amplitude of one of the components (for example, the vertical) remains constant while the other (e.g. the horizontal component) varies, the duration of the vertical is positively correlated with the amplitude of the horizontal. Because the amplitude and duration of the horizontal component (in this example) are tightly linked and positively correlated, the duration of the vertical component is also correlated with the duration of the horizontal component. Nonetheless, nearly all extant models of oblique saccades use information about the relative amplitudes of the two saccade components to appropriately scale component velocities.

The assumption that component coupling is determined by the relative amplitudes (and not duration) of the two components is not readily testable when the head is restrained because of the seemingly immutable duration-amplitude relationship observed under these conditions. However, when the head is free to move and under specific conditions, the duration-amplitude relationship for saccadic eye movements can be reversed: as saccade amplitude increases, duration decreases. This separation of saccade duration and amplitude allow for reconsideration of the assumption that relative amplitudes of saccade components govern component coupling.

During repeated gaze shifts to the same target location, when the eyes begin in different orbital positions, eye and head movement amplitudes vary inversely as a function of the initial orbital positions of the eyes (Delreux et al. 1991; Volle and Guitton 1993; Freedman and Sparks 1997b; Freedman and Sparks 1997a). In addition, as head movement amplitude and velocity increase, the velocity of concurrent saccades decreases (Freedman and Sparks 2000; Freedman 2005). A direct consequence of these two observations is that under the conditions stated above, as saccade amplitude decreases, duration increases (Fig. 1). When repeated oblique gaze shifts to the same target location are made with different initial horizontal positions of the eyes, the duration-amplitude relationship for the horizontal saccade component has a negative slope. The duration of the constant amplitude vertical component varies under these conditions, but variations in vertical component duration are not correlated with the amplitude of the horizontal saccade; in fact horizontal saccade amplitude and vertical saccade duration are anti-correlated (Fig. 3A). The duration of the constant amplitude vertical saccade component is, however, positively correlated with the duration of the horizontal saccade component (Fig. 3B).

The data presented in this report suggest that the hypothesized mechanisms resulting in coupling of horizontal and vertical saccade components may need to be reconsidered. It appears that the duration of the constant amplitude component is stretched in time when associated with a long duration orthogonal component regardless of the amplitude of that component. For instance, even when the vertical component is 3 times larger than the associated horizontal component, vertical saccade duration is significantly prolonged. It is difficult to reconcile existing coupling hypotheses with these data. Understanding the ways in which the eyes and head are coordinated during gaze shifts continues to alter our thinking about the saccadic system and the neural control of saccades. The data presented here constrain existing and future hypotheses attempting to account for component coupling during oblique saccades, and may force a reconsideration of the primacy of relative component amplitudes in governing the scaling of component velocities.

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Figure 1.

Horizontal saccade duration plotted as a function of the absolute value of horizontal saccade amplitude. This set of movements occurred during head unrestrained gaze shifts to the same target displaced 35° to the left along the horizontal meridian. Initial orbital positions of the eyes varied as a result of the head-alignment requirements of the task. Consequently the amplitude of saccades varied (from 5° – 37°) during constant amplitude gaze shifts. As shown the line of best fit to these data has a negative slope; the duration-amplitude relationship was reversed.

Figure 2.

Three single trial examples of oblique saccades made during constant amplitude gaze shifts to a target displaced to the left 35° and down 35° . A: eye position plotted as functions of time for horizontal and vertical components of saccades. The initial vertical positions of the eyes in the orbits were 0 (centered). Initial horizontal positions varied and was 15° to the right (away from the direction of movement (Black)), 17° to the left (light gray), and aligned with the head (centered in the orbits: dark gray). Horizontal and vertical velocities are plotted as functions of time in panel B.

Figure 3.

Summary data for 214 oblique gaze shifts (35° left, 35° down). A: vertical saccade duration plotted as a function of the absolute value of horizontal saccade amplitude. The slope of the line of best fit was negative (-2.0), and horizontal saccade amplitude accounted for only 33% of the variance in vertical saccade duration. B: for the same set of 214 movements, vertical saccade duration is plotted as a function of horizontal saccade duration. The line of best fit had a positive slope (0.93) and horizontal saccade duration accounted for 73% of the variance in vertical saccade duration. For comparison, the mean (SD) duration of 35° movements directed along the vertical meridian is shown along the ordinate.