Exp Brain Res (2000) 131:22–32
Digital Object Identifier (DOI) 10.1007/s002219900296

RESEARCH ARTICLE

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Coordination of the eyes and head: movement kinematics

Received: 20 July 1999 / Accepted: 9 November 1999 / Published online: 1 February 2000

Abstract When the head is restrained, saccades are characterized by lawful relationships between movement amplitude, peak velocity, and duration. In addition, the spatiotemporal progression of saccades (i.e., movement kinematics) is predictable if saccade amplitude and direction are known. However, when the head is free to move, changes in the direction of the line of sight (gaze shifts) often involve saccades associated with simultaneous head movements. The metrics (duration, amplitude, peak velocity) and kinematics of saccades occurring in conjunction with head movements cannot be predicted on the basis of saccade amplitude and direction alone. For example, when the head is unrestrained, velocity profiles of 35° eye movements can be symmetrical and might have peaks ~600°/s. But, 35° eye movements can also have peak velocities of ~300°/s and have velocity profiles with two pronounced peaks: an initial peak followed by a reduction and subsequent increase in velocity. Saccade amplitude and direction are insufficient to predict the shape of the velocity profile. However, as illustrated in this report, if the amplitude of the concurrent head movement is taken into account, saccade kinematics *are* predictable even during gaze shifts with large head components. The data presented here are indicative of an interaction between eye and head motor systems in which head movement commands alter the execution of concurrent saccades.

Key words Gaze shifts · Kinematics · Eye-head interactions

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Introduction

Visual orienting movements bring the images of objects onto specialized regions of the retina by changing the direction of the line of sight (gaze). When the head does not move, changes in the direction of gaze can be accomplished using high velocity, conjugate eye movements known as saccades. Saccades are defined by a set of relationships between movement amplitude, duration, and peak velocity (Bahill et al. 1975; Baloh et al. 1975; Van Gisbergen et al. 1984). In addition to these stereotyped relationships, saccade kinematics (the spatiotemporal progression of movements) are predictable (e.g., Van Gisbergen et al. 1984) given information about movement amplitude and duration. Movements which do not meet these criteria are often indications of neuromechanical deficits (cf. Westheimer and Blair 1973; Zee et al. 1976).

When the head is free to move, gaze shifts are often accomplished with combinations of saccades and simultaneous movements of the head (Barnes 1979; Bizzi et al. 1971, 1972; Freedman and Sparks 1997b; Guitton et al. 1984; Phillips et al. 1995; Tweed et al. 1995; Volle and Guitton 1993). One might expect that the neural control of saccadic eye movements remains unaltered during combined eye-head movements. If this were the case, the behavioral relationships observed when the head is restrained might also be observed in the saccadic portion of the coordinated gaze shift. Alternatively, movements of the head might affect the ongoing saccade. This could result in saccades with features that varied as a function of the properties of the ongoing head movement. One example of this kind of interaction is observed in the relationship between eye velocity and amplitude during large gaze shifts made when the head is unrestrained. Unlike the velocity-amplitude relationship observed during head restrained saccades, which increases monotonically, when the head is unrestrained eye velocity initially increases as a function of saccade amplitude, but subsequently declines as movement amplitudes increase further (cf. Freedman and Sparks 1997b; Phillips et al. 1995).

To date, descriptions of the coordination of the eyes and head have generally relied upon assessment of movement metrics: measurements of gaze, eye and head movement amplitudes, directions, peak velocities and latencies (Freedman and Sparks 1997b; Guitton et al. 1984; Phillips et al. 1995; Tomlinson and Bahra 1986a). This report extends these observations to descriptions of gaze, eye and head movement kinematics, and demonstrates that gaze and eye movement kinematics *cannot* be accurately predicted given knowledge of the amplitude and direction of the gaze and/or eye movements. Additional information about the amplitude of the concurrent head movement is required to predict gaze and eye kinematics. In contrast, head movement kinematics are predictable solely on the basis of information about head movement amplitude. These data provide further support for the hypothesis that, at some level, eye and head movements are controlled separately (Freedman and Sparks 1997b; Goossens and Van Opstal 1997; Phillips et al. 1995; Tweed et al. 1995) and that there are interactions between these separate systems.

Materials and methods

Data from three juvenile rhesus monkeys (3–6 kg) are presented. Data from two monkeys (S and T) were collected at the University of Pennsylvania, and data from the third subject (U) were collected at the University of Washington. Methods differed slightly and will be presented separately.

Monkeys S and T

Preparation of monkeys S and T for data collection and analysis, training procedures, and behavioral tasks have been described in detail (Freedman and Sparks 1997a, 1997b). All surgical and experimental protocols were approved by the University of Pennsylvania Animal Care and Use Committee, and are in accordance with the NIH Guide for the Care and Use of Animals.

Direction of gaze was measured using standard scleral search coil techniques (Judge et al. 1980; Robinson 1963). Head movements were measured using an identical coil mounted daily on the animal's head. Signals from the two search coils were collected at a rate of 500 samples/s and stored for offline analysis. Eye position relative to the head was calculated offline by subtracting the head signal from the gaze signal.

Subjects S and T performed the delayed gaze shift task illustrated in Fig. 1A. The initial target (target1) was illuminated for a variable interval (800–1200 ms, 100-ms increments). The location of this initial target was randomly selected from a set of up to eight potential locations. If the subject maintained fixation of this target throughout the interval, a second target (target2) was illuminated at a randomly selected location. Both targets remained on for a variable interval (400–800 ms, 50-ms increments) while the subject maintained fixation of target1. The primary target was extinguished after the delay interval, cueing the subject to change the direction of the line of sight to fixate the secondary target. Fixation of the secondary target had to be maintained for at least 500 ms. Upon successful completion of the trial, all targets were extinguished for a variable intertrial interval (1000–2000 ms, 200-ms increments) and the subject was given a liquid reward via a tube that moved with the head.

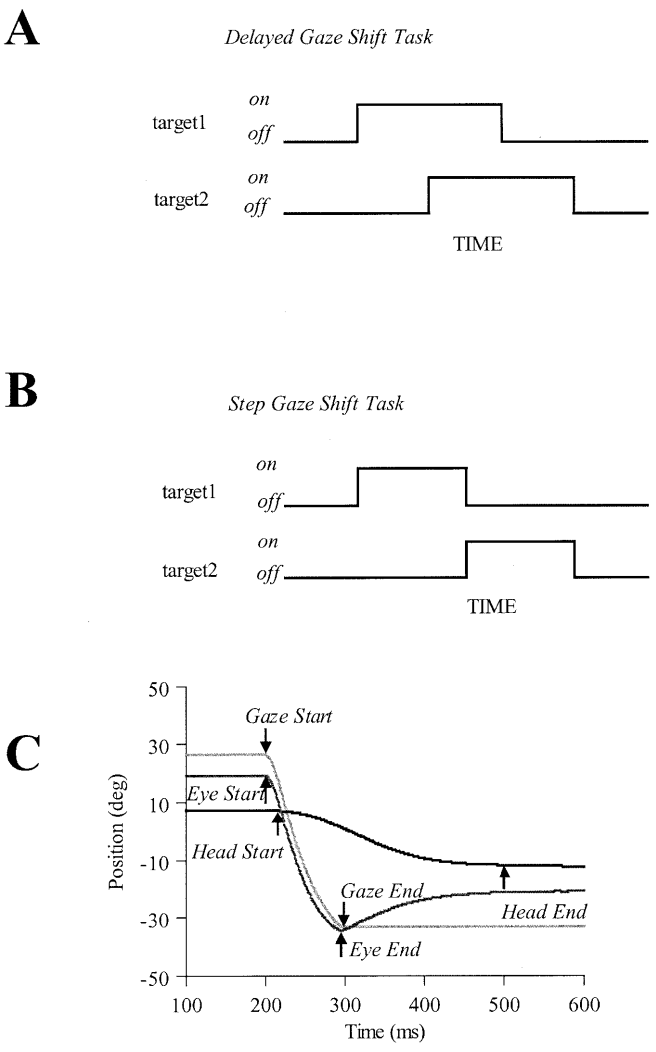

Fig. 1A–C Methods. **A,B** illustrate the tasks used in these experiments. **C** illustrates the locations of gaze, eye and head movement beginning and end. See "Materials and methods" for details

Monkey U

The methods used for preparation of this subject were similar to those described by Phillips et al. (1995). All surgical and experimental protocols, as well as routine care (provided by the veterinary staff of the Regional Primate Research Center) and housing procedures, were approved by the University of Washington Animal Care and Use Committee, and are in accordance with the NIH Guide for the Care and Use of Animals. A scleral coil implanted under the extraocular muscles (Fuchs and Robinson 1966) was used to measure the position of the line of sight (gaze). Head position was measured through a potentiometer attached daily to the subject's head via a rigid post (see Phillips et al. 1995). The post restricted movements of the head to the horizontal plane.

Training, target presentation, and data analysis differed from that previously described (Phillips et al. 1995). Monkey U was trained to perform the step-gaze task illustrated in Fig. 1B. An initial target (LED) was illuminated. The location of this initial target was selected randomly from a set of five potential locations (between 20° and 40° to the right of the center, 5° increments). After continuous fixation (600–1000 ms, 50-ms increments), the initial target was extinguished and a second target was simultaneously illuminated at a randomly selected location. Reward was contingent upon fixation of the second target for at least 800 ms. If success-

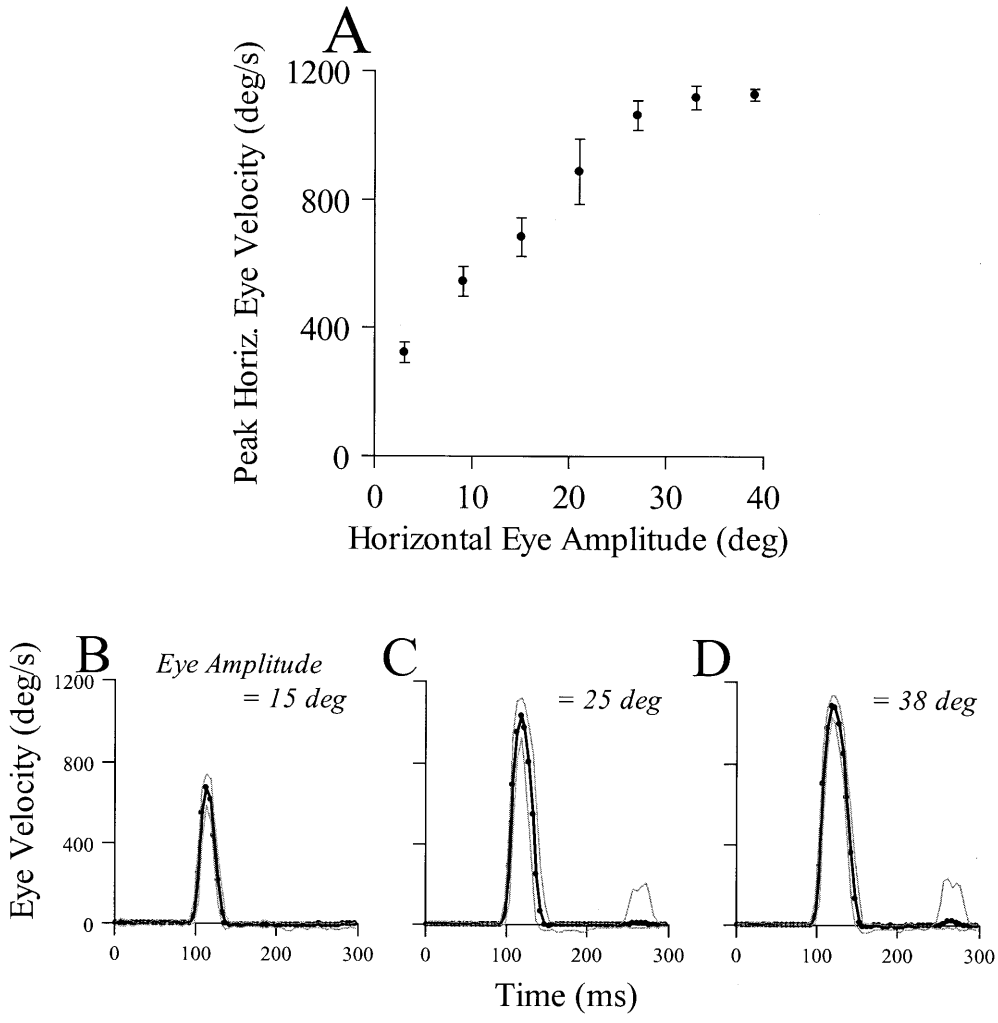

Fig. 2A–D Head restrained saccades. **A** plots peak horizontal eye velocity as a function of horizontal saccade amplitude during head restrained saccades made by monkey S (*N*=295). Each panel **(B–D)** plots mean (*black lines*) eye velocity (±SD: *gray lines*) as a function of time for head restrained saccades (*N*=15). All movements were initiated with the eyes in the center of the orbits. Saccade amplitudes were in the ranges 13–18° **(B)**, 23–27° **(C)**, and 35–40° **(C)**

fully completed, all targets were extinguished for a variable intertrial interval (1300–1700 ms, 50-ms increments) and the monkey was given a food reward via a tube that moved with the head. Horizontal gaze and head positions were digitized online (1 kHz sampling) and stored for offline analysis. Eye position was calculated offline.

Data analysis for all subjects was performed on a PC, using a custom software package. Velocity criteria for marking the beginnings and ends of movements were typically 35°/s for eye and gaze and 15°/s for head movements. However, because of the variety of velocity profiles observed, no single set of criteria could accurately mark every movement. As a result, every movement was inspected to insure that cursors were properly placed as indicated in Fig. 2C. Gaze, eye and head velocities and accelerations were calculated from positions and velocities, respectively.

In all cases, the search coil technique as implemented was insensitive to rotations of the eyes around axes parallel with the line of sight or rotations of the head about axes parallel to the facing direction. This technique was also insensitive to translations of the coils within the uniform portion of the magnetic fields. All movements occurred within 45° of the midsagittal plane and large amplitude movements crossed the midline. Subjects sat in a chair which prevented movements of the hips, which were positioned parallel to the target array. For subjects S and T, there were no restrictions on either horizontal or vertical movements of the head. As stated above, head movements of monkey U were restricted to the horizontal stereotaxic plane. In all figures, positive velocities and accelerations indicate rightward movements (monkeys T and S); negative deflections indicate leftward movements (monkey U).

Results

When the head is prevented from moving (restrained), saccade metrics (e.g., peak velocity) can be accurately predicted based only on information about the amplitude and direction of movements. For example, peak saccade velocity is a monotonic, saturating function of saccade amplitude (Fig. 2A; Bahill et al. 1975; Baloh et al. 1975). Saccade kinematics (in this case the two-dimensional spatiotemporal progression of movements) are also predictable when the head is restrained (Van Gisbergen et al. 1984). Figure 2B–D illustrates mean eye velocity (±SD) as a function of time during head-restrained saccades of 15°, 25° and 38°, respectively. These saccades were directed along the horizontal meridian (vertical amplitudes were less than ±5°) and were initiated with the eyes in the center of the orbits (±5°).

As illustrated in Fig. 2B–D, there is little variability in velocity profiles of saccades of similar amplitudes when the head is restrained. This is not the case when the head is free to move. Figure 3A–C plots mean (black lines) eye velocity (±SD: gray lines) as a function of time for each of three subjects (T, S and U, respectively).

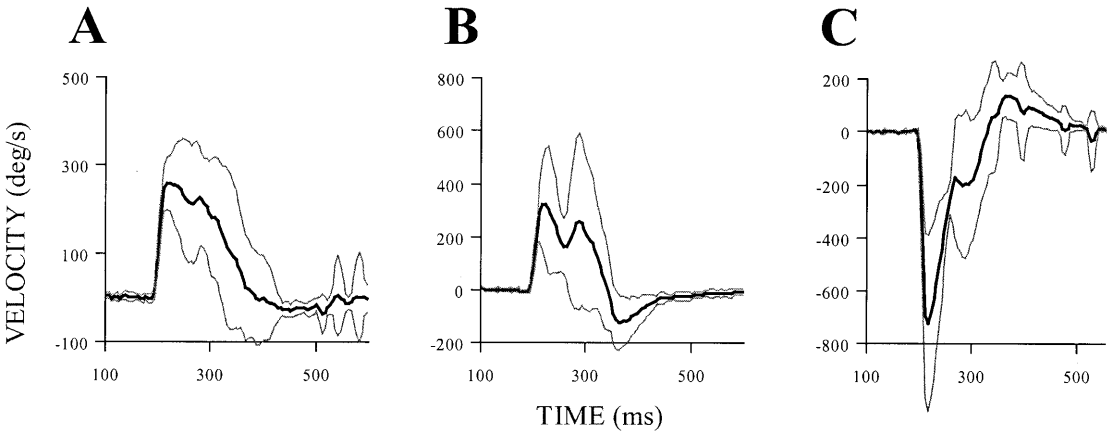

Fig. 3A–C Saccades associated with head movements. Mean (*black lines*) eye velocity (±SD: *gray lines*), calculated at each time sample, is plotted as a function of time for eye movements directed along the horizontal meridian, initiated with the eyes in the center of the orbits and having amplitudes between 35° and 40°. Movements from subjects T **(A)**, S **(B)**, and U **(C)** are shown. Head movements associated with these saccades varied from 0° to 50°

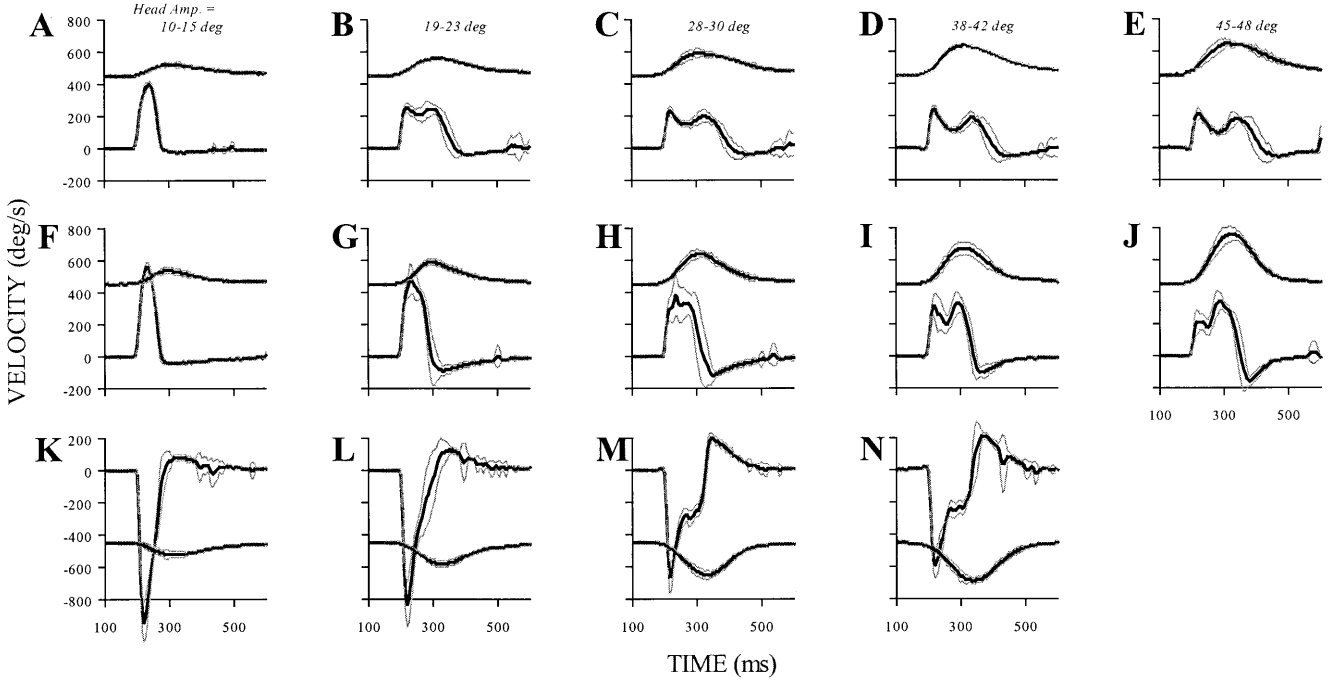

Fig. 4A–N Constant eye amplitude. Horizontal eye and head (displaced 450°/s along the ordinate) velocity profiles during constant amplitude (35–40°) eye movements; vertical amplitudes were ±5°. Data illustrate means (*black lines*) ± SD (*gray lines*), calculated at each time sample. Eye movements were associated with different amplitude head (and gaze – not shown) movements; head amplitudes are given *at the top of each column*. Data from monkeys T **(A–E)** and S **(F–J)** were rightward movements; data from monkey U **(K–N)** were leftward. There were insufficient data from monkey U, in which ~38° eye movements were associated with ≥45° head movements

In all cases these were horizontal (±5°) saccades of ~38°, initiated with the eyes centered in the orbits (±5°): the same conditions as in Fig. 2D. The difference between the movements in Fig. 2D and those in Fig. 3A–C is that the latter are saccades occurring during head unrestrained gaze shifts. As illustrated, the variability of saccades which occur during simultaneous head movements is greatly increased, and neither metric nor kinematic features of these movements is predictable based on knowledge of saccade amplitude (cf. Freedman and Sparks 1997b).

As shown, the kinematics of saccades are only weakly related to saccade amplitude when they occur in association with head movements. However, saccade kinematics made under these conditions *are* predictable (i.e., stereotyped) if the amplitude of the concurrent head movement is also known. This point is illustrated in Fig. 4, which plots saccade velocity profiles from each of the three subjects. Each panel shows eye movements having similar amplitudes and directions (35–40° horizontal; ±5°

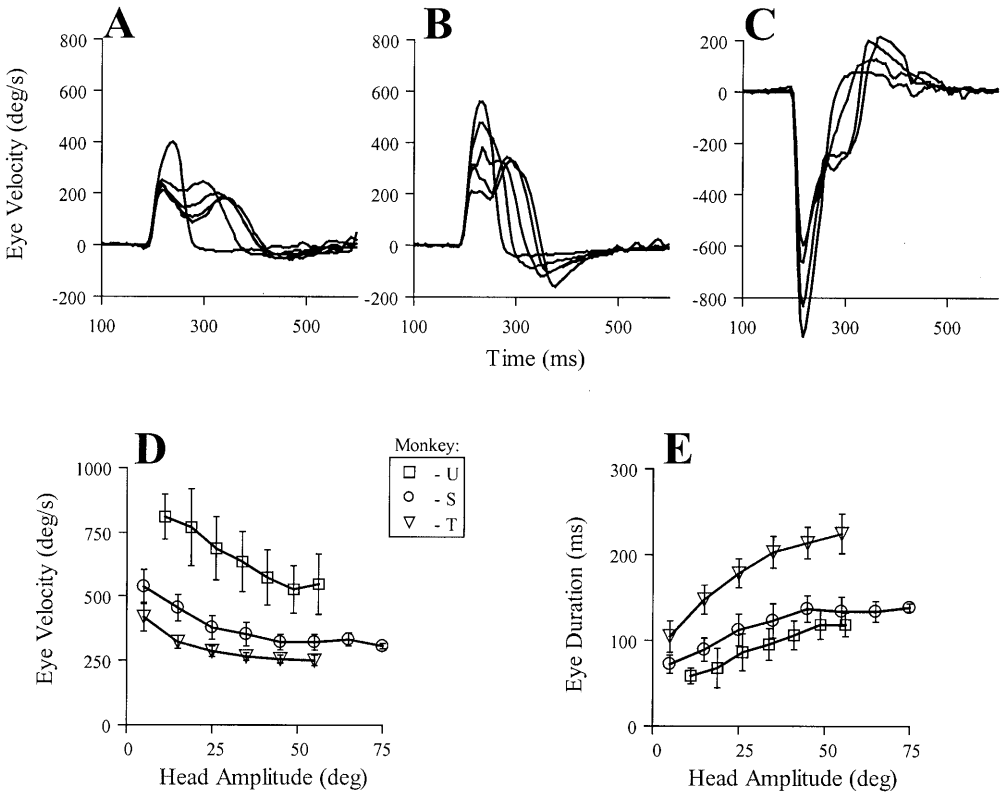

Fig. 5A–E Eye velocity comparison. In **A–C** the mean velocity profiles from Fig. 4 are replotted and superimposed. Monkeys T **(A)**, S **(B)**, and U **(C)**. See text for details. Peak eye velocity **(D)** and duration **(E)** are plotted as functions of head movement amplitude. Saccade amplitudes ranged from 35° to 40°

vertical) associated with head movements of a particular amplitude (in each panel corresponding head velocity profiles are displaced along the ordinate by 450°/s). All movements were initiated with the eyes centered in the orbits. Average velocities (black lines) of between 12 and 20 movements are plotted (±SD: gray lines). Head movement amplitudes are indicated at the top of each column. (Note: for monkey U, there were insufficient saccades of this amplitude, initiated with the eyes in the center of the orbits, associated with head movements of between 45° and 48°. Therefore, what would be panel O is absent.) During constant amplitude (~38°) eye movements associated with ~12° head movements (panels A, F and K), eye velocity profiles were relatively symmetrical and had a single peak. These velocity profiles are similar to the velocity profiles observed during saccades made when the head was restrained (Fig. 2). However, when saccades of this amplitude (and direction) were associated with larger head movements, peak eye velocity declined, duration increased, and velocity profiles changed dramatically. For example, compared to saccades associated with 12° head movements (A, F and K), when 38° saccades are associated with ~40° head movements (panels D, I, and N), peak eye velocities were reduced by nearly 45%, durations increased by ~50%, and velocity profiles were altered: after an initial peak in the eye velocity profile, there was a pronounced deceleration and subsequent reacceleration (in the case of monkey U, for movements of this amplitude velocity profiles had a marked shoulder but no reacceleration; see below). The result was saccadic velocity profiles with two peaks.

Note in Fig. 4 that eye velocity profiles do not develop two peaks during head movements of the same amplitude for each subject. For monkey T (A–E), profiles with two peaks were present during ~38° eye movements associated with relatively small head movements (~20°; panel B). For subject S, head movements needed to be larger than 30° before the second velocity peak was clearly present. For subject U, during eye movements of ~38°, the second “peak” appeared only as a shoulder in the velocity profile even when head movements were nearly 45° (note that eye velocity profiles for this subject clearly had two peaks during larger amplitude movements – Fig. 6I). These differences between subjects highlight several points. First, it is not only head movement amplitude but also the relative timing of eye and head movements which produce two peaks in the velocity profiles; head movements of monkey U lagged eye movement onset by as much as 10 ms more than comparable movements made by monkeys T or S. Second, in monkeys U and S eye velocities were much higher than in monkey T. As a result when head movements were not very large, 38° eye movements made by these monkeys could be finished before head velocity exceeded ~50°/s. Two velocity peaks were not observed until eye movements were associated with faster head movements. Some of these differences may be subject-specific idiosyncrasies; some subjects are more likely to make large head movements than others (Fuller 1992a, 1992b). In addition, recall that the vertical head rotation axis for monkey U was fixed, whereas monkeys T and S were unrestrained.

Table 1 Peak head velocities occurring at the time of the initial peak in eye velocity

Figure 4 – panel (monkey)	Mean (±SD) initial peak eye velocity (°/s)	Mean (±SD) head velocity (°/s) at time of initial peak eye velocity
A (T)	397.5 (20)	35.2 (8)
B (T)	250.0 (30)	31.1 (9)
C (T)	229.3 (26)	41.0 (14)
D (T)	224.6 (25)	50.2 (15)
E (T)	210.4 (36)	47.7 (15)
F (S)	560.3 (29)	36.9 (16)
G (S)	476.3 (35)	42.3 (13)
H (S)	377.2 (47)	42.8 (13)
I (S)	311.9 (61)	48.6 (23)
J (S)	207.5 (52)	42.6 (18)
K (U)	–954.4 (82)	–13.9 (15)
L (U)	–836.9 (91)	–16.3 (10)
M (U)	–664.1 (93)	–29.1 (8)
N (U)	–593.9 (82)	–33.8 (17)

In order to facilitate comparison of saccade velocity profiles for movements of similar amplitudes, the mean velocity profiles for each subject (from Fig. 4) are superimposed in Fig. 5A–C. Note in all cases that eye movement trajectories follow similar initial paths. However, velocity profiles diverge as initial peak velocities are reduced and movement durations increase. Note, too, that when associated with large head movements, the initial peak in the saccade velocity profile can be reduced by as much as a factor of 3 (Fig. 5B). In this example (Fig. 5B), the initial "peak" is a velocity plateau ~200°/s, and after nearly 50 ms at this velocity there is a pronounced increase in velocity producing a large secondary peak in the velocity profile. This variability in initial peak saccade velocities occurs while the head is moving less than 50°/s. Furthermore, the differences in head velocities at the time of the initial peak in saccade velocity are quite small. For example, mean head velocity (±SD) at the time of peak eye velocity for movements in Fig. 4F (and Fig. 5B: highest peak velocity) was 36.9°(±16°)/s. Compare this with movements in Fig. 4J (and Fig. 5B: lowest initial peak) in which mean head velocity was 42.6°(±18°)/s. Whereas head velocities differed by ~6°/s, concurrent eye velocities differed by as much as 200°/s (see Table 1).

To summarize the effects of head movements on saccades which were directed along the horizontal meridian, initiated with the eyes centered in the orbits, and which had horizontal amplitudes between 35° and 40°, peak eye velocity (Fig. 5D) and saccade duration (Fig. 5E) are plotted as functions of head movement amplitude. As the amplitude of the associated head movement increased, eye velocity declined and eye movement duration increased.

As shown above, saccade metrics do not determine saccade kinematics when the head is free to move. Note that in order to select saccades having similar amplitudes, initiated with the eyes centered in the orbits, *and* that are associated with head movements having a variety of amplitudes, gaze shift amplitudes must also vary. For the data in Figs. 4 and 5, gaze amplitude is linearly related to head amplitude. Therefore, for these trials, knowledge of gaze amplitude could also provide the additional information needed to accurately predict eye movement kinematics. One possibility is that when the head is free to move, gaze and eye movement kinematics depend only on the amplitude of the *gaze shift*, and as a result would be predictable if gaze amplitude and direction were known.

Figure 6 demonstrates that gaze shift metrics are, in fact, *not* adequate to accurately predict either gaze or eye movement kinematics. In Fig. 6A, gaze velocity is plotted as a function of time for ten single trials made by monkey T. The amplitude of these gaze shifts was between 34° and 36°, and all movements were directed within 5° of the horizontal meridian. The amplitude of head movements associated with these gaze shifts varied from 3° to 28°; head velocity profiles are shown in 6B. This large range of head movement amplitudes during constant amplitude gaze shifts is a result of initiating movements with the eyes in different orbital positions. For the trials illustrated, initial eye position ranged from 25° contralateral (relative to the direction of movement) to 5° ipsilateral. Head movement amplitude decreased as the eyes began in increasingly contralateral positions. Although the initial portion of all gaze and eye velocity traces followed the same trajectory, striking differences in velocity profiles were observed (Fig. 6A). Similar to saccade velocity profiles observed during eye movements of the same amplitude (Fig. 4), when gaze shifts having the same amplitude are associated with larger head movements, gaze (and the associated eye) velocity profiles develop two peaks. The shift from gaze and eye velocity profiles with one peak to those having two peaks was correlated with the amplitude (and velocity) of the concurrent head movement. This is further illustrated in panels D and G. In panel D (monkey S), each gaze velocity profile is the average of between three and seven individual trials. All gaze shifts had horizontal amplitudes between 63° and 67° (vertical amplitudes were less than ±5°) and were associated with head movements of 25°, 35°, 48° or 55°. When head movements were 25° (darkest line), gaze shifts had one peak and relatively symmetrical velocity profiles. However, as head move-

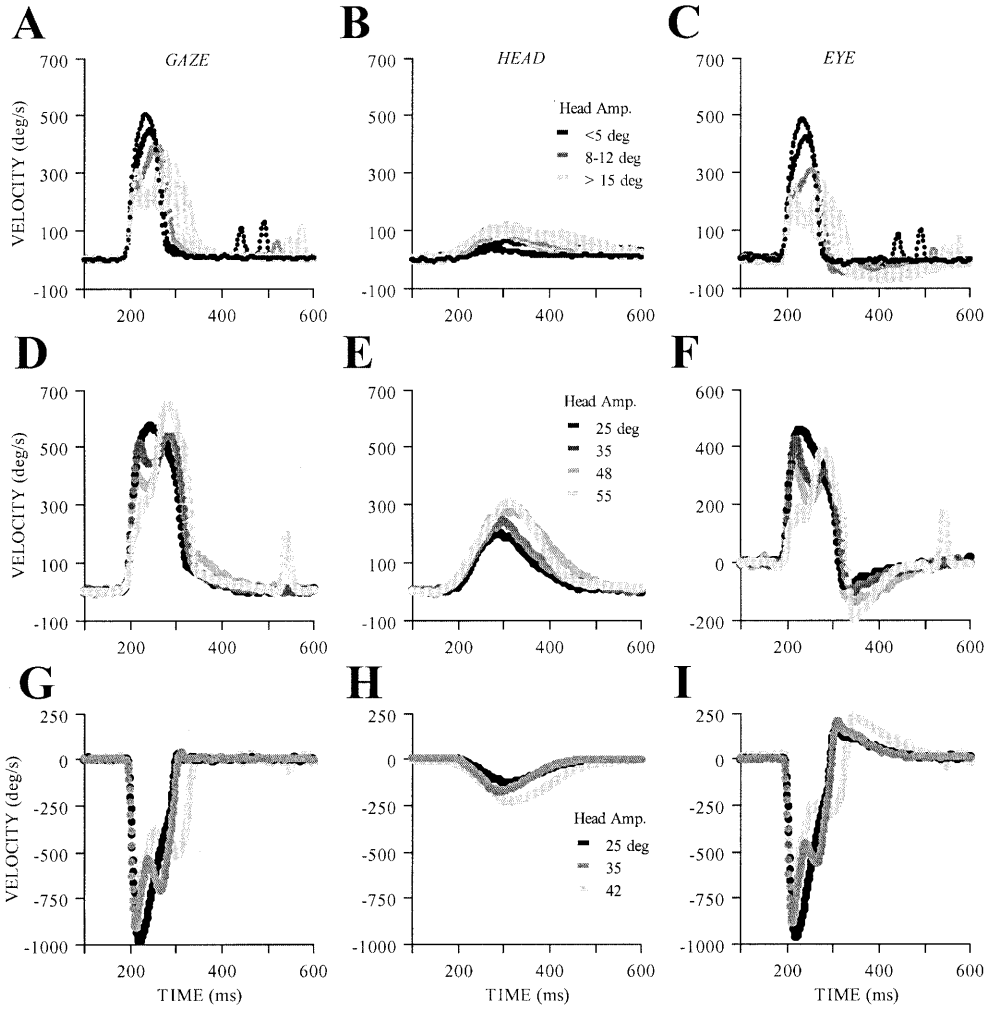

Fig. 6A–I Constant gaze amplitude. Gaze **(A)**, head **(B)**, and eye **(C)** velocities plotted as a function of time for ten individual trials (monkey T). Horizontal gaze amplitudes were between 34° and 36°; vertical amplitudes were between ±5°. In **A–C**, head movement amplitudes varied <5° (*black*), 8–12° (*dark gray*), and >15° (*light gray*). **D–F** (monkey S) and **G–I** (monkey U) illustrate average gaze, head and eye velocity profiles during constant amplitude gaze shifts. Mean head amplitudes are given in the legend. For data in **D–F**, initial eye positions ranged from 5° ipsilateral to 20° contralateral relative to movement direction. Initial eye positions ranged from 30° contralateral to centered for movements in **G–I**. Standard deviations of the mean, calculated at each time sample, did not exceed 100°/s for any of the profiles illustrated. Between three and seven trials were used for each average profile. Movements are aligned at gaze onset (time = 200 ms)

ment amplitude and velocity (Fig. 6E) increased, two velocity peaks were observed and movement duration increased. In addition, as head amplitude increased the magnitude of the initial peak in the gaze velocity profile was further reduced and the magnitude of the secondary peak increased. Similar effects of increasing head movement amplitude on the velocity profiles of constant amplitude gaze shifts are illustrated in panels G and H (monkey U).

Eye velocity profiles (Fig. 6C,F,I) were qualitatively quite similar to gaze velocity profiles. Profiles associated with smaller head movements had one peak whereas profiles of movements associated with larger head movements had two. The magnitude of the initial peak declined and the duration of movements increased as head movement amplitude increased. When the head is unrestrained, gaze and eye movement kinematics and metrics are only predictable if the amplitude of the associated head movement is known; gaze and eye movement kinematics *depend* on the associated head movement.

Head movement kinematics

The kinematics of gaze shifts and their eye components cannot be predicted accurately given knowledge only of gaze or eye movement amplitude. In contrast, head movement kinematics *are predictable* based only on knowledge of head movement amplitude. For each subject (Fig. 7), head movement acceleration (means ± SD) is plotted as a function of time for head movements having amplitudes in the ranges 8–10° (A,F,K), 18–22° (B,G,L), 28–32° (C,H,M), 38–42° (D,I,N), and 50–55° (E,J). At least 20 and as many as 45, individual movements were averaged to generate each panel in this figure. For head movements of a particular amplitude, there was little variability in head acceleration profiles for a given subject. In general, a large acceleration phase was followed by a slightly smaller and longer deceleration phase. As head movement amplitude increased, the acceleration and deceleration phases increased proportionally. We did not observe triphasic acceleration profiles as have been predicted by several models of the head plant (Zangmeister and Stark 1981, 1982a, 1982b). However, movements made in the present tasks were not necessarily “time-optimal,” and this might account for the absence of the third acceleration peak.

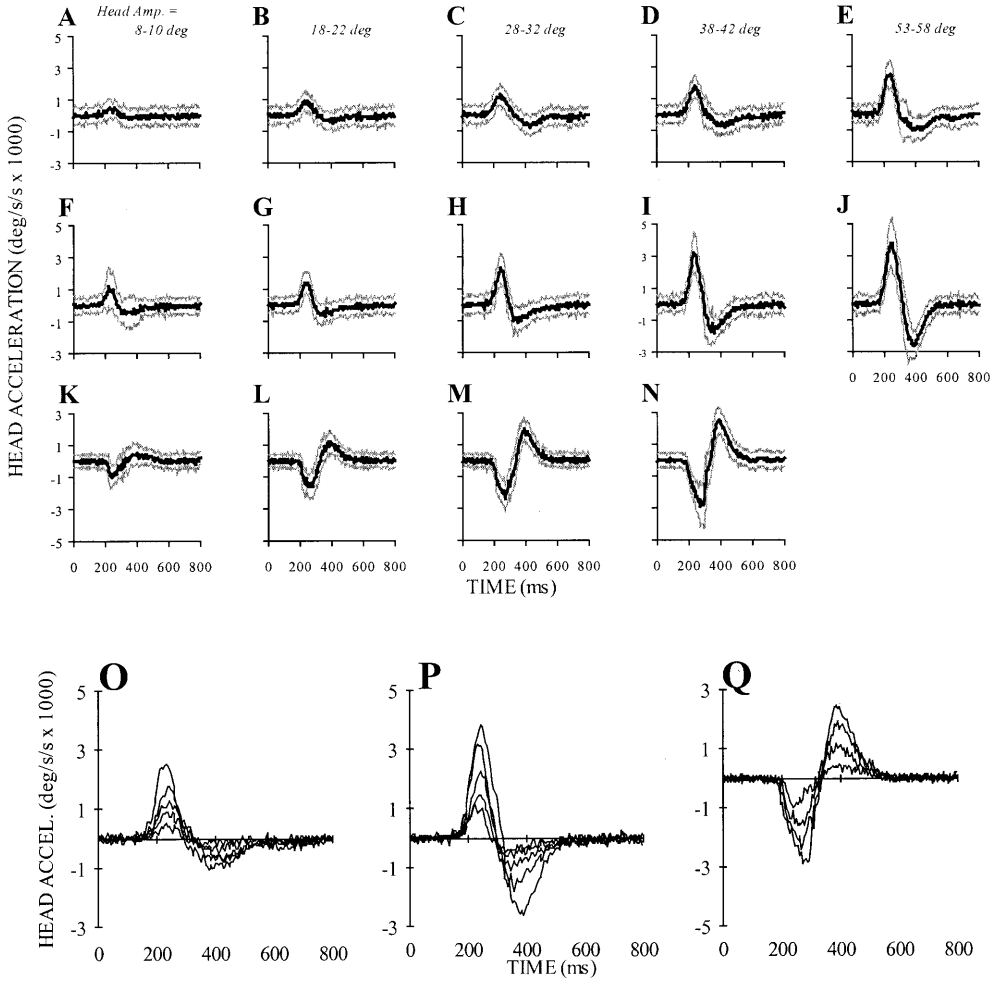

Fig. 7A–Q Head kinematics. Head accelerations (means ± SD) plotted as a function of time for head movements of different amplitudes (indicated *at the top of each column*). Data from monkeys T **(A–E)** and S **(F–J)** were rightward movements; data from monkey U **(K–N)** were leftward. There were insufficient data from monkey U to illustrate head movements >50°. Mean head acceleration profiles from **A–E** are superimposed in **O**; means from **F–J**,**K–N** are superimposed in **P** and **Q**, respectively

An interesting feature of head movements is illustrated in panels O–Q, which superimpose each subjects' mean acceleration profiles. For a particular subject, the durations of the acceleration and deceleration phases of head movements were relatively constant. Thus, the transition from acceleration to deceleration (zero-crossing) occurred at approximately the same time (for all subjects, standard deviations of the mean zero-crossing times were <23 ms) despite large differences in movement amplitude. In addition, peak acceleration and deceleration occurred at approximately the same times regardless of movement amplitude (for all subjects, standard deviations of the mean times to peak acceleration and deceleration were <17 ms).

Head acceleration profiles for movements of different amplitudes appear to be scaled versions of each other and, for any particular amplitude, head kinematics are independent of concurrent eye or gaze kinematics. For example, during the head movements plotted in Fig. 7D, horizontal gaze amplitudes ranged from 33° to 85°, vertical gaze amplitudes ranged from 30° down to 25° up, horizontal eye movements ranged from 20° to 52° and initial horizontal eye positions ranged from 24° contralateral to 5° ipsilateral. Similarly for the movements shown in Fig. 6I, horizontal gaze amplitudes ranged from 40° to 83°, while vertical gaze amplitudes ranged from 30° down to 38° up. Similar broad ranges of gaze and eye movements and initial eye positions were associated with the other head movements shown in Fig. 7 (see legend for details). These large differences in eye and gaze movements have no observable effects on head kinematics.

Discussion

Behavioral data from human and non-human primates suggest that eye and head movements are controlled independently. One indication of this is that the relative contributions of the eyes and head to gaze shifts of a particular amplitude depend upon the initial positions of the eyes in the orbits (Becker and Jürgens 1992; Freedman and Sparks 1997b; Volle and Guitton 1993). For example, during a 60° gaze shift, the eyes may contribute 55° if they are initially deviated away from the direction of movement but contribute only 35° if they are initially centered in the orbits. Similarly, the timing of eye and head movement onset can vary over a wide range, and depend upon initial conditions (Becker and Jürgens 1992; Freedman and Sparks 1997b; Fuller 1996). Other

tasks have revealed several striking dissociations of eye and head movements (cf. Goossens and Van Opstal 1997; Ron and Berthoz 1991). Taken together these data are a strong indication that, at some point, the motor commands which result in movements of the eyes and head are separate, and can be differentially influenced by the current conditions of the effectors.

In this report, we describe the two-dimensional kinematics of eye and head movements during coordinated orienting movements to visual targets. These data provide further evidence that eye and head motor commands are separate and in addition provide evidence that there are interactions between these separate signals. In particular, eye and gaze shift kinematics are altered as a function of the concurrent head movement. During eye or gaze movements of similar amplitudes and directions, there is a pronounced reduction of initial eye/gaze velocity which is correlated with the amplitude of the ensuing head movement. In addition, there is a dynamic decrease and subsequent increase in eye/gaze velocities resulting in velocity profiles with two peaks. The degree to which velocities are reduced, and the amplitude and timing of the reacceleration of the eyes, also depends upon the concurrent head movement. This dynamic interaction between eyes and head appears to be unidirectional: head movements influence eye movements but eye (or gaze) metrics and kinematics have little or no influence on associated head kinematics. This eye-head interaction must occur at a point where the eye and head control signals are separate.

Note that observing eye or gaze velocity profiles with two peaks does not depend upon a specific training paradigm, or on a specific task (monkey U was trained on a different task than were monkeys S and T). It is observed whether the vertical head rotation axis is fixed or not, and can be found in reports from several different groups (Freedman and Sparks 1997b; Munoz et al. 1991; Phillips et al. 1995; Roy and Cullen 1998; Tomlinson and Bahra 1986a; Tweed et al. 1995). Although rarely discussed explicitly, the occurrence of two velocity peaks during large amplitude gaze shifts is a consistent finding across species and tasks and, as shown in this report, is predictable if the relative amplitudes and the relative timing of eye and head movements are known.

Vestibulo-ocular reflex

Several gaze control hypotheses propose eye-head interactions that are mediated by the vestibulo-ocular reflex (VOR) (Bizzi et al. 1972; Morasso et al. 1973; Phillips et al. 1995), and the eye-head interactions illustrated above might appear to be consistent with these models. However, referring to Fig. 6F, note that during gaze shifts associated with 35° head movements, peak eye velocity (410°/s) is attained ~20 ms after eye movement onset and decays to 275°/s over the next 35 ms. During the same movements and over the same time interval, head velocity increased from 90°/s to 200°/s. During similar gaze shifts made by another monkey (panel I), increases in head velocity of 150°/s were associated with decreases in eye velocity of 400°/s (see also Freedman and Sparks 1997b). These data suggest that the gain of any putative reflex interactions would have to be greater than one. However, a number of experiments (Guitton and Volle 1987; Laurutis and Robinson 1986; Pelisson and Prablanc 1986; Pelisson et al. 1988; Roy and Cullen 1998; Tabak et al. 1996; Tomlinson 1990; Tomlinson and Bahra 1986b) suggest that the gain of the VOR is significantly reduced during large amplitude gaze shifts.

Other aspects of the data are also inconsistent with the hypothesis that the VOR mediates the observed eye-head interactions. For instance, initial eye velocity can be reduced from >400°/s during 12° head movements (Fig. 4A), to <200°/s when associated with 48° head movements. In both examples, however, concurrent head velocities were nearly identical and <30°/s. It seems improbable that the VOR can operate on identical inputs (head velocities of ~30°/s) and, in one case, have no effect on eye movements and in another reduce eye velocity by 200°/s. Some other mechanism seems likely. Finally, eye-head interactions mediated by the VOR are generally postulated to occur downstream from the local feedback loop controlling eye movement amplitude. In this type of model (Bizzi et al. 1972; Morasso et al. 1973; Phillips et al. 1995), as head velocity increases, eye velocity will decline. However, these models do not predict the observed increase in duration of the horizontal eye movement since the signals produced by the horizontal eye burst generator, the feedback integrator, and the comparator are not influenced by downstream (below the feedback loop) interactions. Also, although these models might predict the reduction in eye (and gaze) velocity as head velocity increases, they have difficulty accounting for the observed reacceleration of the eyes (or gaze). If sensory signals (from semicircular canals or neck afferents) mediate the observed interactions, these signals must exert their influence at the level of the burst generator.

One possibility is that the eye-head interaction occurs at the level of the burst generator via burster-driver neurons (BDNs). These neurons are located in and near the nucleus prepositus hypoglossi (NPH), and show type II vestibular responses to horizontal rotations (Kitama et al. 1995; Ohki et al. 1988). They also fire a burst of action potentials before and during contraversive quick phases of nystagmus. Furthermore, these cells have monosynaptic, excitatory connections with elements of the saccade burst generator (excitatory burst neurons: EBNs). These cells are thought to be involved in production of quick phases in response to vestibular input. While this type of signal could result in the reacceleration of the eyes when saccades are associated with large head movements, BDN activity is inappropriate for producing the observed changes in the initial portion of eye velocity profiles, since these changes can occur before the head has begun to move. Furthermore, these cells were searched for but not found in monkeys (Kaneko and Fukushima 1998). It

is not clear what, if any, role these cells have in mediating the eye-head interactions illustrated in this report.

Neither the VOR nor BDN activity can account for all of the observed effects of head movement on eye (and gaze) kinematics. However, there is a mechanism that can account for the initial reduction in eye velocity as well as the occurrence of two velocity peaks and also account for the changes in eye movement duration as a function of the associated head movements (Freedman 1999). In this scheme, a copy of a head velocity command inhibits the *gain* of the saccadic burst generator. Thus, before the head movement begins, the gain of the burst generator (and therefore the initial velocity of the eye movement) is reduced as a function of the velocity of the ensuing head movement. As the head velocity command begins to decline, the gain of the eye burst generator increases, causing a reacceleration of the eyes. Because this interaction is within the postulated feedback loop controlling saccade amplitude (cf. Robinson 1975), reductions in eye velocity are compensated by increased saccade duration. Unlike the interactions discussed above (VOR and BDN activity), this scheme does replicate eye, gaze, and head movement kinematics (Freedman 1999). The predictions of this hypothesis must now be tested.

Acknowledgements The authors thank A.F. Fuchs for permitting inclusion in this report of data collected in his laboratory and for his continuing support and encouragement, and K. Pearson for development of analysis and graphics software. The study was supported by National Institute of Mental Health training grant T32-MH-17168 (E.G.F.) and National Eye Institute grant R37-EY01189 (D.L.S.).

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