Eye-Head Coordination During Head-Unrestrained Gaze Shifts in Rhesus Monkeys

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Freedman, Edward G. and David L. Sparks. Eye-head coordination during head-unrestrained gaze shifts in rhesus monkeys. *J. Neurophysiol.* 77: 2328–2348, 1997. We analyzed gaze shifts made by trained rhesus monkeys with completely unrestrained heads during performance of a delayed gaze shift task. Subjects made horizontal, vertical, and oblique gaze shifts to visual targets. We found that coordinated eye-head movements are characterized by a set of lawful relationships, and that the initial position of the eyes in the orbits and the direction of the gaze shift are two factors that influence these relationships. Head movements did not contribute to the change in gaze position during small gaze shifts ($<20°$) directed along the horizontal meridian, when the eyes were initially centered in the orbits. For larger gaze shifts ($25–90°$), the head contribution to the gaze shift increased linearly with increasing gaze shift amplitude, and eye movement amplitude saturated at an asymptotic amplitude of $\sim35°$. When the eyes began deviated in the orbits contralateral to the direction of the ensuing gaze shift, the head contributed less and the eyes more to amplitude-matched gaze shifts. The relative timing of eye and head movements was altered by initial eye position; head latency relative to gaze onset increased as the eyes began in more contralateral initial positions. The direction of the gaze shift also affected the relative amplitudes of eye and head movements; as gaze shifts were made in progressively more vertical directions, eye amplitude increased and head contribution declined systematically. Eye velocity was a saturating function of gaze amplitude for movements without a head contribution (gaze amplitude $<20°$). As head contribution increased with increasing gaze amplitude ($20–60°$), peak eye velocity declined by $>200°/s$ and head velocity increased by $100°/s$. For constant-amplitude eye movements ($\sim30°$), eye velocity declined as the velocity of the concurrent head movement increased. On the basis of these relationships, it is possible to accurately predict gaze amplitude, the amplitudes of the eye and head components of the gaze shift, and gaze, eye, and head velocities, durations and latencies if the two-dimensional displacement of the target and the initial position of the eyes in the orbits are known. These data indicate that signals related to the initial positions of the eyes in the orbits and the direction of the gaze shift influence separate eye and head movement commands. The hypothesis that this divergence of eye and head commands occurs downstream from the superior colliculus is supported by recent electrical stimulation and single-unit recording data.

INTRODUCTION

With the head and body restrained, the direction of the line of sight can be changed by rotating the eyes relative to the head. Under these conditions, movements of the eyes from one visual target to another are, typically, high-velocity, conjugate movements known as saccades. Saccadic eye movements made when the head is restrained have been extensively studied in a variety of species including humans, rhesus monkeys, and cats (cf. Becker 1989). Although there are species differences, the saturating function that describes the relationship between peak eye velocity and eye movement amplitude, and the linear duration-amplitude relationship, are two of the defining properties of saccades (cf. Bahill 1975; Baloh et al. 1975; Collewijn et al. 1988a,b; Robinson 1964; van Gisbergen et al. 1984). As this set of characteristics is extended, new restrictions are imposed on hypotheses of saccadic control. For example, one-dimensional models of the saccadic system (Jürgens et al. 1981; Robinson 1975; van Gisbergen et al. 1981) had to be extended (e.g., Becker and Jürgens 1990; van Gisbergen et al. 1985) as our understanding of oblique saccades, and the interactions between horizontal and vertical components, advanced.

When the head is free to move (unrestrained), the eyes and head can move together to accomplish large redirections of the line of sight (gaze). Most available data on coordination of the eyes and head were obtained from movements directed along the horizontal meridian (Barnes 1979; Bizzi et al. 1971, 1972a,b; Gresty 1974; Guitton and Volle 1987; Guitton et al. 1984, 1990; Morasso et al. 1973; Phillips et al. 1995; Zangemeister and Stark 1981, 1982a,b). These one-dimensional studies revealed several features of eye-head coordination. For instance, different modes of eye-head coordination have been identified (Bizzi et al. 1972a; Moschner and Zangemeister 1993; Roucoux et al. 1981; Zangemeister and Stark 1982b) on the basis of the relative onset of eye and head movements. In some cases head movement precedes eye movement onset, but the vestibuloocular reflex maintains the position of the line of sight until the eyes begin to move. In other cases, eye movements begin and end before the head begins to move, and in other circumstances the head begins to move slightly after eye movement onset and then eyes and head continue to move together toward the target. Depending on the mode of eye-head coordination, the relative contributions of the eyes and head to the accomplishment of the gaze shift will vary. The spatial and temporal predictability of the target, and the amplitude of the movement, have been shown to influence both the relative timing of the onset of eye and head movements and relative eye and head movement amplitudes (Bizzi et al. 1972a; Moschner and Zangemeister 1993; Zangemeister and Stark 1982b).

Although there is no agreement about the set of relationships that characterizes eye-head coordination, a number of

studies in cats (Guitton et al. 1984, 1990), humans (Guitton and Volle 1987; Volle and Guitton 1993), and monkeys (Morasso et al. 1973; Phillips et al. 1995; Tomlinson 1990; Tomlinson and Bahra 1986a) report similar findings. First, gaze velocity is reported to be a saturating function of gaze amplitude, and head velocity is a linear function of head movement amplitude. Second, eye movement amplitude is a saturating function of gaze amplitude and head amplitude is linearly related to gaze amplitude for large gaze shifts (see below). There are several points of disagreement. Some authors report that head movements are first observed when gaze amplitudes exceed ~25° (Phillips et al. 1995; Tomlinson and Bahra 1986a), whereas others report head movements associated with all gaze shifts larger than ~5° or gaze shifts of all amplitudes (Bizzi et al. 1972a; Guitton et al. 1984, 1990). There are still other reports that head movement amplitude depends on the position of the eyes in the orbits at the onset of the gaze shift (Becker and Jürgens 1992; Delreux et al. 1991; Tomlinson 1990; Volle and Guitton 1993). There is also no consensus about the degree of variability in the relative timing of eye and head movements. In cats, head movements generally precede the onset of the gaze shift (Guitton et al. 1984), and movements of the eyes and head appear to be tightly coupled temporally (Guitton et al. 1990). Others report that in humans and rhesus monkeys there is a high degree of variability in eye and head movement onset times (Guitton and Volle 1987; Phillips et al. 1995; Ron et al. 1993; Tweed et al. 1995; Zangemeister and Stark 1981, 1982a,b). This variability could result from comparing movements generated under conditions in which the predictability of target location and/or temporal predictability of the movement initiation cue differ. The position of the eyes in the orbits at the onset of the gaze shift (Becker and Jürgens 1992; Fuller 1996; Volle and Guitton 1993) may also affect the relative timing of eye and head movements. In addition, it has been reported that the head contributes preferentially to the horizontal component of head-unrestrained oblique gaze shifts (Freedman and Sparks 1996; Glenn and Vilis 1992; Tweed et al. 1995), suggesting that gaze shift direction might also influence eye-head coordination. Thus there appears to be at least three factors that influence the coordination of the eyes and head during redirections of the line of sight.

The goals of the present study were to further characterize eye-head coordination in the rhesus monkey performing a single, well-defined task, and to identify factors that may influence these relationships. In addition, because the head was completely free to move both vertically and horizontally, we were able to extend one-dimensional studies to include vertical and oblique gaze shifts, and assess the effects of movement direction on eye-head coordination.

We found that movements of the eyes and head follow certain lawful relationships. It is possible to accurately predict the amplitudes, peak velocities, latencies, and durations of the gaze shift, and of the eye and head components of the gaze shift, given knowledge of the initial positions of the eyes in the orbits and the two-dimensional displacement of the visual targets (initial retinal error). These data help constrain hypotheses of gaze control. In addition, the general principles of eye-head coordination described in this report can be used as the basis for comparison with movements elicited during head-unrestrained microstimulation of the primate superior colliculus (SC), with movements produced under different behavioral or experimental manipulations, with data from other species, and as a foundation for understanding the command signals required for the coordination of eye and head movements.

METHODS

Two female rhesus monkeys (*Macaca mulatta*) served as subjects. A scleral coil for monitoring gaze position was implanted in the left eye of each subject (Fuchs and Robinson 1966; Judge et al. 1980) during aseptic surgeries performed under general anesthesia (isoflourane). In a second aseptic procedure, a receptacle for an *X-Y* positioner (Kopf) was also secured to the heads of both subjects (see below). Postoperative analgesics and prophylactic antibiotics were administered as directed by the attending veterinarian. All surgical and experimental procedures were approved by the University of Pennsylvania Animal Care and Use Committee, and are in accordance with the National Institutes of Health Guide for the Care and Use of Animals.

Experimental apparatus

During training and experimental sessions, animals were seated in a primate chair designed to permit unrestricted movements of the head by restraining the subject with a canvas vest secured loosely around the neck and extending to the inside of the chair. The flexibility of the vest allowed complete head mobility but prevented the subjects from exiting the chair and from reaching equipment mounted on the head. In addition, the chair prevented movements of the hips and restricted upper body rotations to approximately ±20°. Animals were monitored with the use of an infrared video system (Sanyo Electric). Typically, animals sat with hips and shoulders aligned and parallel to the frontoparallel plane. The only impediment to head movements was the mass of the reward delivery system and head coil (~75 g). During some sessions an *X-Y* positioner and microdrive (Kopf; additional mass ~175 g) were also mounted on the head. We observed no differences in gaze or head movements during sessions with and without the additional mass, and data from both types of sessions are pooled in this report.

Subjects were positioned 84 cm from a tangent screen. The center of the screen was aligned with the midsagittal plane. Subjects were positioned vertically so that when they fixated the screen center the line of sight was in a horizontal plane. Visual targets (~10 min diam) could be back-projected at any location (1° resolution) on a tangent screen that subtended ±45° horizontally and ±40° vertically. Positioning of the target was accomplished by deflecting a laser beam (Uniphase) with a pair of mirrors attached to orthogonal galvonometers (General Scanning). Targets were gated on and off with an acoustical-optical shutter (IntraAction). In some experiments, an LED array (2° resolution) positioned in the same location and having the same dimensions was used.

Changes in the direction of the line of sight (defined as the 2-dimensional rotation of the eyes relative to a fixed, external frame of reference: gaze) were measured with the use of the standard scleral coil. Head movements were measured with the use of an identical coil mounted daily on the animal's head. The uniform portion (±2%) of two magnetic fields, in spatial and phase quadrature, was estimated to be a sphere (~20 cm diam) centered within the field-generating coils (85 cm diam). During experiments the gaze and head search coils were approximately centered in this region. Search coil signals are translation invariant within the uniform portion of the magnetic fields, and translations associated with coordinated eye-head movements are not measured with this
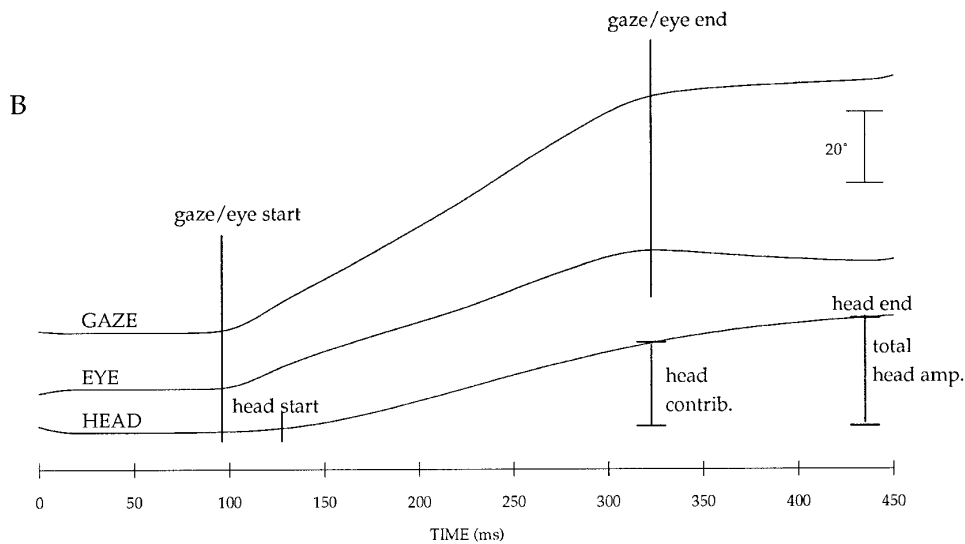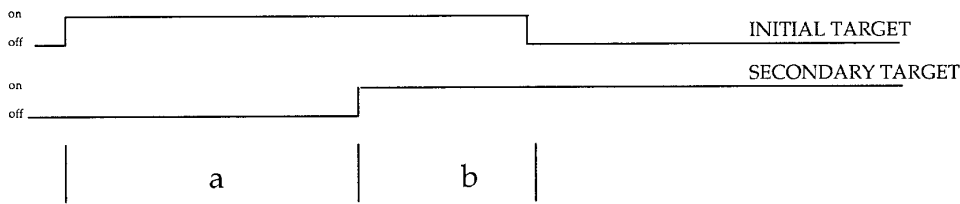
A   DELAYED GAZE SHIFT

FIG. 1. *A*: delayed gaze shift task. Subjects must maintain fixation of the initial target within a computer-defined window (±5°) during the initial interval (*a*) and during the delay interval (*b*) that begins with the onset of the secondary target. The cue to initiate a movement to the location of the secondary target is the extinction of the initial target. See the text for further details. *B*: horizontal gaze, eye, and head positions during a typical gaze shift directed along the horizontal meridian (see text for details).

technique. However, visual inspection of subjects during performance of the task indicated that head translations were not large enough to move the coils out of the uniform portion of the magnetic fields. The gaze coil was calibrated by having the animal fixate different locations on the screen. The head coil was calibrated (on the animal) by manually rotating the head through known angles and adjusting the signal gain appropriately. The two coil signals were sampled at 500 Hz and stored for off-line analysis. The head and gaze signals were corrected for the nonlinearities inherent in the coil system (after Judge et al. 1980), and the eye position relative to the head was calculated off-line by subtracting the head signal from the gaze signal. The center of rotation of the eyes was ~7 cm from the center of head rotation in our subjects (see Huebner et al. 1995 for discussion of measurement errors resulting from different axes of rotation).

Behavioral task

The data in this report were obtained while subjects were performing a delayed gaze shift task (Fig. 1*A*). After fixation of the initial visual target for a variable interval (*a;* 800–1,200 ms, 100-ms increments), a second target was illuminated. The subject was required to maintain fixation of the initial target while the secondary target remained on for an additional delay interval (*b;* 400–800 ms, 50-ms increments). The extinction of the initial target cued the subject to initiate a gaze shift to the location of the secondary target. Reinforcement was contingent on maintaining fixation within computer-defined targeting windows. The size of

the computer window around the secondary target was ~10% of the target displacement. The locations of the initial target and secondary targets were selected randomly from experimenter-defined arrays of potential locations.

The experimenter had no direct control over the initial eye position relative to the head. However, we found that a large range of initial eye positions could be obtained by reducing the initial fixation time and the duration of the delay interval and by randomizing the location of the initial target (see Freedman et al. 1996 for details).

The starting and ending positions of all movements considered in this report fell within ±45° of the midsagittal plane. To present secondary targets displaced by >45° from the initial target, it was necessary to present the initial target close to one edge of the tangent screen and the secondary target on the opposite side of the screen center. Thus large-amplitude movements crossed the body midline. It is not clear how the data in this report extrapolate to movements generated from different initial conditions. The general principles of eye-head coordination described below, for example, may or may not hold for 90° gaze shifts initiated with the eyes and head centered on the body midline, rather than 45° contralateral to the direction of the movement.

Data analysis

Data were analyzed off-line with the use of Sparc1 workstations (Sun Microsystems). The amplitudes of the horizontal and vertical gaze, eye, and head movements (Fick coordinates) were measured

as illustrated for a typical gaze shift in Fig. 1*B*. Velocity criteria[1] were used to automatically define the beginning and end of eye movements, head movements, and gaze shifts. The head contribution to the gaze shift was defined as the amplitude of the head movement that occurred between head movement onset and gaze movement end. Total head movement amplitude was defined as the amplitude of the head movement that occurred between head movement onset and end on the basis of the velocity criterion.

On the basis of the measurements of horizontal and vertical eye, head, and gaze amplitudes, the analysis program calculated the vectorial amplitude and velocity (the amplitude and velocity along the trajectories of the movements) for each component. Movements directed along the horizontal meridian are defined as having direction 0°, movements directed below the horizontal meridian are described as having negative directions, and the angle, in degrees, is expressed relative to the horizontal meridian. Movement amplitudes are also given in degrees.

RESULTS

Data base

We measured >35,000 gaze shifts made by two trained rhesus monkeys with their heads unrestrained. A subset of the gaze shifts made during the delayed gaze shift task was selected for further analysis on the basis of the following criteria. First, trials were excluded if the subject failed to maintain fixation of the initial target during the delay interval (see METHODS), or if the movement that brought the direction of the line of sight within a computer-defined targeting window consisted of more than a single gaze shift. Second, only those trials in which both gaze and head position were stable during the delay interval were included. Trials with slow head movements during the fixation interval were excluded even if gaze position was unaffected because of compensatory eye movements. Because movements of the adducting and abducting eyes are not necessarily identical (cf. Collewijn et al. 1988a), only gaze shifts in which the scleral search coil was in the adducting eye were included for analysis. Over 8,000 gaze shifts (*monkey T,* 4,673; *monkey S,* 3,617) met these selection criteria and are considered below.

General findings

MOVEMENT TRAJECTORIES.   Figure 2*A* illustrates the trajectories of gaze shifts having similar vectorial amplitudes (65°) directed to visual targets along the horizontal meridian (*a*), 45° above (*b*) and below (*c*) the horizontal meridian, and 70° above (*d*) and below (*e*) the horizontal meridian. For comparison, the trajectories of the eye (Fig. 2*B*) and head (Fig. 2*C*) components of these gaze shifts are also shown. The change in direction at the end of each eye movement trajectory reflects the compensatory counterrotation of the eyes that maintains a stable gaze position while the head continues to rotate toward the target. Several features of coordinated eye-head movements are illustrated by these movement trajectories. First, considerable variability in the
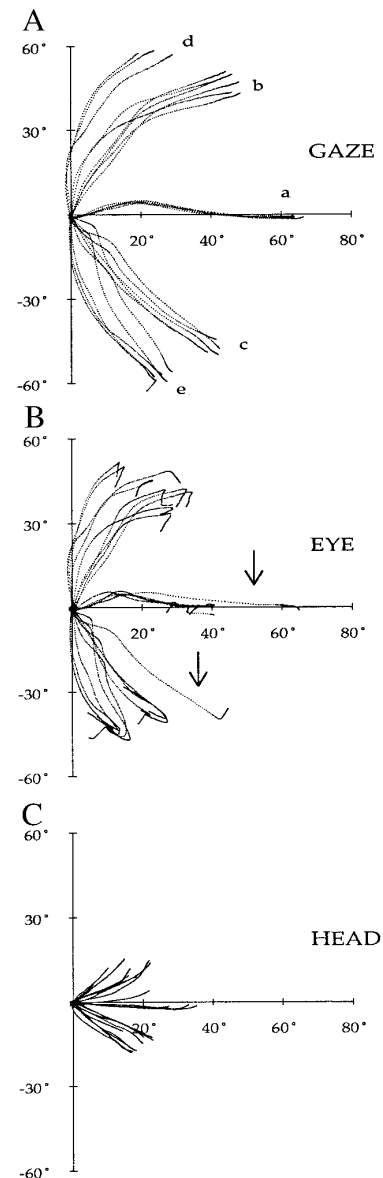
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[1] Gaze and eye onset and offset were defined as the time at which velocities exceeded (onset) or fell below (offset) 35°/s. Velocity criterion for head movement onset was 25°/s; criterion for head offset was 15°/s. Movements were checked automatically and onsets and offsets were marked according to these criteria. All marks were visually inspected on a trial-by-trial basis and could be manually adjusted if necessary.
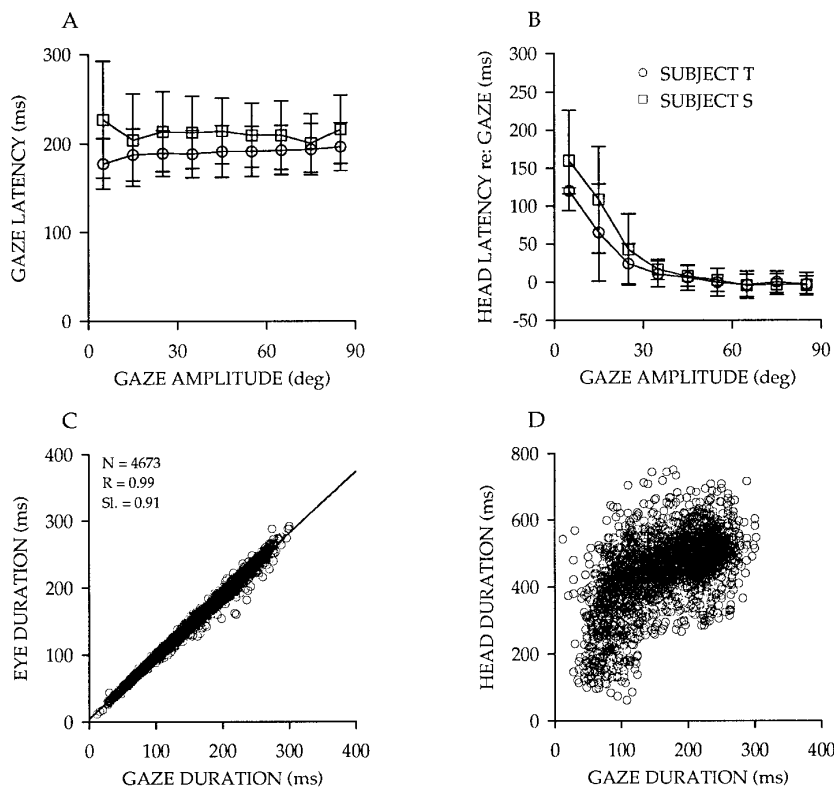

FIG. 2.   Gaze (*A*), eye (*B*), and head (*C*) movement trajectories during gaze shifts of constant vectorial amplitude (65–68°) made in different directions: along the horizontal meridian (*a; n = 4*), 45° up (*b; n = 6*), 45° down (*c; n = 5*), 70° up (*d; n = 3*), and 70° down (*e; n = 5*). All traces are plotted for a duration of 400 ms beginning 50 ms before gaze shift onset. Gaze and head position were sampled at 500 Hz; eye position was calculated off-line as the mathematical difference between head and gaze positions.

relative contributions of eye and head movements to gaze shifts having similar amplitudes and directions was observed. For example, the trials marked with arrows in Fig. 2*B* highlight two eye movements that were significantly larger than the other eye movements made to the same targets (*a* and *c*). Second, the vertical component of the gaze shift was accomplished primarily by vertical eye movements; the head contributed preferentially to the horizontal component of the gaze shift. The difference in vertical eye and head contributions resulted in different eye, head, and gaze trajectories during a single movement. Third, a large proportion of the vertical component of oblique movements

FIG. 3. *A*: gaze latency relative to the movement initiation cue. Latency (mean ± SD) for *monkey T* (○) and *monkey S* (□), for all movements. *B*: head movement latency relative to the onset of the gaze shift for *monkeys T* and *S* (symbols as in *A*). *C*: eye duration as a function of gaze duration for all movements (*monkey T; n = 4,673*), and for comparison, *D*: head duration (head movement amplitude > 2°) plotted as a function of gaze duration [*monkey T: n = 3,972; r = 0.56; monkey S* (not shown): *n = 3,114; r = 0.37*]. N, number of trials; R, correlation coefficient; Sl., slope of line of best fit.

is accomplished early in the gaze shift, before an equal proportion of the horizontal component has been accomplished. Fourth, head movement amplitude was a relatively small fraction of gaze shift amplitude. These and other points are detailed below.

RELATIVE TIMING OF EYE AND HEAD MOVEMENTS. In all instances, changes in the direction of the line of sight were initiated by an eye movement; head movements that occurred before gaze shift onset did not alter gaze position. As a result, eye movement onset and gaze shift onset were identical. During the delayed gaze shift task, gaze latency (Fig. 3*A*) was relatively independent of movement amplitude (*monkey T*: mean = 190.9 ± 28.1 ms, mean ± SD; *monkey S*: mean = 211.1 ± 41.9 ms). In contrast, the time from gaze onset to head movement onset decreased as a function of gaze amplitude (Fig. 3*B*) until, for gaze shifts larger than ~40°, movements of the eyes and head began nearly synchronously (mean latency to head movement onset relative to gaze onset: *monkey T,* 12.2 ± 15.6 ms; *monkey S,* 7.6 ± 15.2 ms). The end of the gaze shift and the end of the eye component of the gaze shift were tightly coupled as illustrated in Fig. 3*C,* which plots eye movement duration as a function of gaze duration for movements of all amplitudes and all directions included in the data base (*monkey T*: *n = 4,673*). Similar results were observed for *monkey S* (*n = 3,617; r = 0.97; slope = 0.82*). Notice that for both subjects the slopes of the lines of best fit are <1. This indicates that eye movement duration is slightly shorter than gaze shift duration; eye movements end before gaze shifts end. This may result from a vestibuloocular reflex gain <1, which would cause the velocity of eye counterrotation to be less than the velocity of the continuing head movement (e.g.,

Fig. 13). Nonetheless, eye movement end and gaze shift end were highly correlated. In contrast, there was not a tight coupling between the end of the head movement and the end of the gaze shift (Fig. 3*D*; see caption for details).

RELATIONSHIPS BETWEEN MOVEMENT AMPLITUDE AND TARGET DISPLACEMENT. The relationship between the horizontal component of primary gaze shifts (corrective movements were excluded from all analyses) and the horizontal displacement of the secondary target, relative to the direction of the line of sight (retinal error), is illustrated in Fig. 4*A* for all movements included in the data base. Similarly, the vertical amplitude of the gaze shift is plotted as a function of the vertical displacement of the target in Fig. 4*B*. Horizontal gaze amplitude was >90% of the target displacement amplitude (note slopes of the lines of best fit), whereas the amplitude of the vertical component was ~80% of the vertical target displacement. Note that the selection criteria (see METHODS) excluded movements that did not fall within the computer-defined targeting window, and less accurate movements that would alter the relationships illustrated in Fig. 4, *A* and *B,* were not analyzed. Total horizontal head movement amplitude (Fig. 4*C*) was ~60% (*monkey T*) and 80% (*monkey S*) of the horizontal target displacement relative to the direction of the line of sight (gaze; see legend to Fig. 4). In contrast, the vertical amplitude of the head movement was considerably smaller than the vertical displacement of the target (*monkey T,* 17%; *monkey S,* 24%). Because gaze position and head position were not necessarily the same at movement onset, the displacement of the target relative to the head and target displacement relative to gaze were not always identical. The relationships between horizontal (Fig. 4*E*) and vertical (Fig. 4*F*) head movement amplitude and
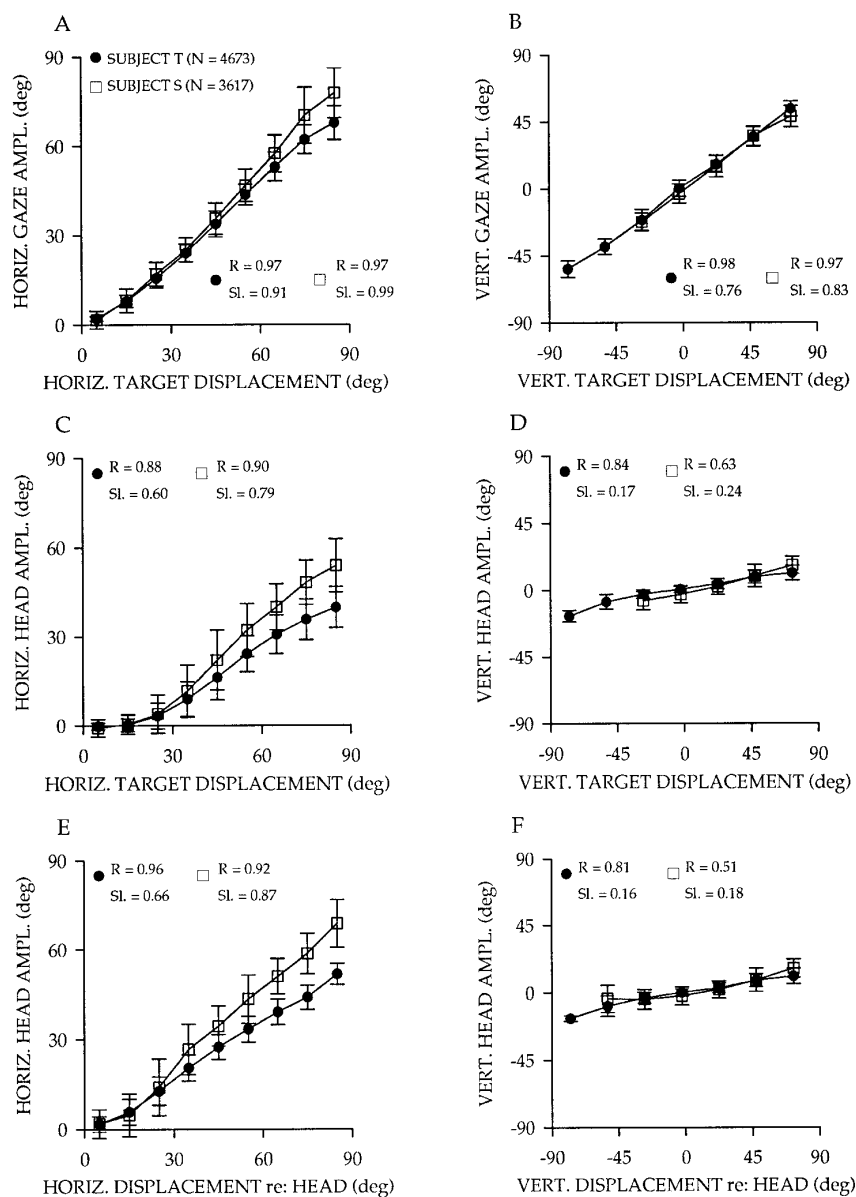
FIG. 4. Horizontal gaze amplitude (*A*) and vertical gaze amplitude (*B*) plotted as functions of horizontal and vertical target displacement (position of secondary target with respect to the direction line of sight; retinal error), respectively, for movements in all directions and amplitudes for *monkey T* (●; *n* = 4,673) and *monkey S* (□; *n* = 3,617). *C* and *D*: total horizontal and vertical head movement amplitude for the same movements as functions of horizontal and vertical target displacement. *E* and *F*: horizontal and vertical head movement amplitude plotted as functions of horizontal and vertical target displacement relative to the head. Data in each panel represent means ± SD with the use of a binwidth of 10°. Only head movements >2° were included in the calculation of lines of best fit.

the horizontal and vertical displacement of the target relative to the head are shown for comparison.

Figure 4 illustrates the high correlation between head movement amplitude and both the target displacement relative to gaze and target displacement relative to the head. Determining whether head movement amplitude is better related to the target displacement relative to gaze or relative to the head requires that these variables be dissociated. To accomplish this we selected trials in which the target displacement relative to the head was relatively constant, but target displacement relative to gaze varied over a wide range. Figure 5, *A–C*, plots horizontal head movement amplitude as a function of horizontal target displacement with respect to gaze for three subsets of trials in which the displacement of the target relative to the head was 65° (*A*), 45° (*B*), and 30° (*C*). As illustrated, the amplitude of the head movement was only weakly related to the displacement of the target relative to gaze, within subsets of trials in which the target displacement with respect to the head was relatively con-

stant. However, comparison across subsets of trials (compare movements in Fig. 5, *A–C*, with target displacement relative to gaze ~60°) illustrates the systematic relationship between head amplitude and target displacement relative to the head; head amplitude was ~15°, ~30°, and ~50° when target relative to the head was 30°, 45°, and 65°, respectively, and target relative to gaze varied over a narrow range between 55° and 60°. For the same subsets of trials illustrated in Fig. 5, *A–C*, eye movement amplitude is plotted as a function of target displacement relative to gaze (Fig. 5, *D–F*). As shown, eye amplitude varied systematically with changes in target displacement relative to gaze during trials in which the target displacement relative to the head was relatively constant. Thus head movement amplitude is better related to the displacement of the target relative to the head than it is to the displacement of the target relative to gaze. However, eye movement amplitude is not well correlated with target displacement relative to the head, but is well correlated with the initial displacement of the target relative to gaze. These

TARGET re: HEAD = 65deg

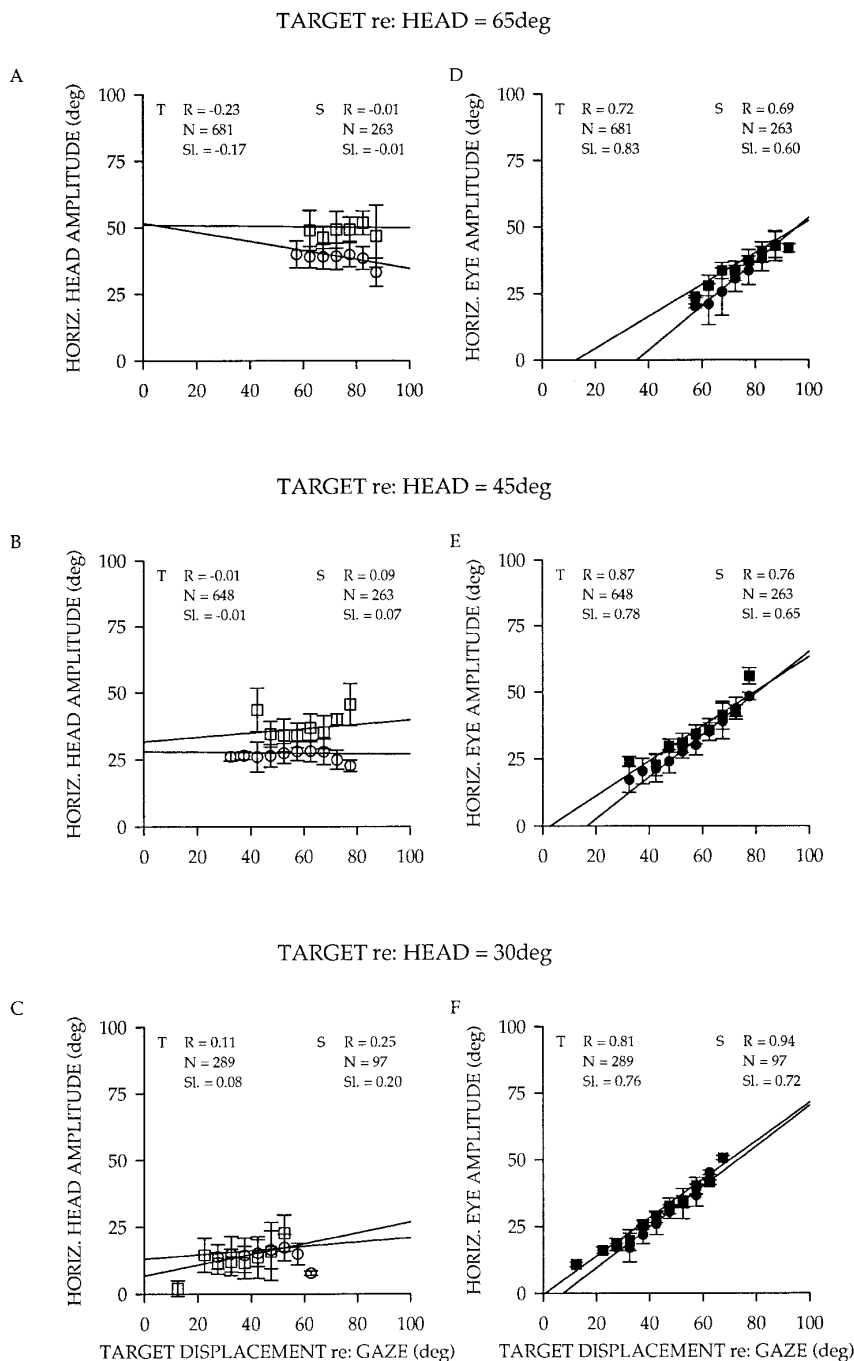A

TARGET re: HEAD = 45deg

B

FIG. 5. Horizontal head movement amplitude plotted as a function of target displacement relative to gaze for 3 subsets of trials in which the target displacement relative to the head was (*A*) 62–70°, (*B*) 42–48°, and (*C*) 28–32°. Data from *monkey T* (○) and *monkey S* (□) are shown. For the same subsets of trials in which target displacement relative to the head was (*D*) 62–70°, (*E*) 42–48°, and (*F*) 28–32°, eye movement amplitude is plotted as a function of target displacement relative to gaze. Filled circles: *monkey T*. Filled squares: *monkey S*. Binwidths of 5° were used to calculate means ± SD.

TARGET re: HEAD = 30deg

C

TARGET DISPLACEMENT re: GAZE (deg)   TARGET DISPLACEMENT re: GAZE (deg)

data are consistent with the hypothesis that a head error signal drives movements of the head, but not the eyes (see DISCUSSION).

The results above are related to general observations concerning the entire data base. Below, details of these and other relationships are described, and several factors that influence the coordination of eye and head movements during gaze shifts to visual targets are described.

Horizontal gaze shifts with eyes centered

AMPLITUDE-AMPLITUDE RELATIONSHIPS. Many previous studies of eye-head coordination in humans, monkeys, and

cats have restricted movements of the head to the horizontal plane either by the use of a vertical head restraint bar or by presenting only targets displaced along the horizontal meridian (see INTRODUCTION). To compare these earlier findings directly with the data in this report, movements along the horizontal meridian initiated with the eyes and head aligned will be considered in this section. For horizontal gaze shifts, directed within ±10° of the horizontal meridian and initiated with the eyes centered in the orbits (initial eye position ±5°), gaze amplitude and the amplitude of the associated head movements were highly correlated (Fig. 6, *A* and *B*). For gaze shifts smaller than ~25°, observed head movements were typically initiated after the gaze shift was
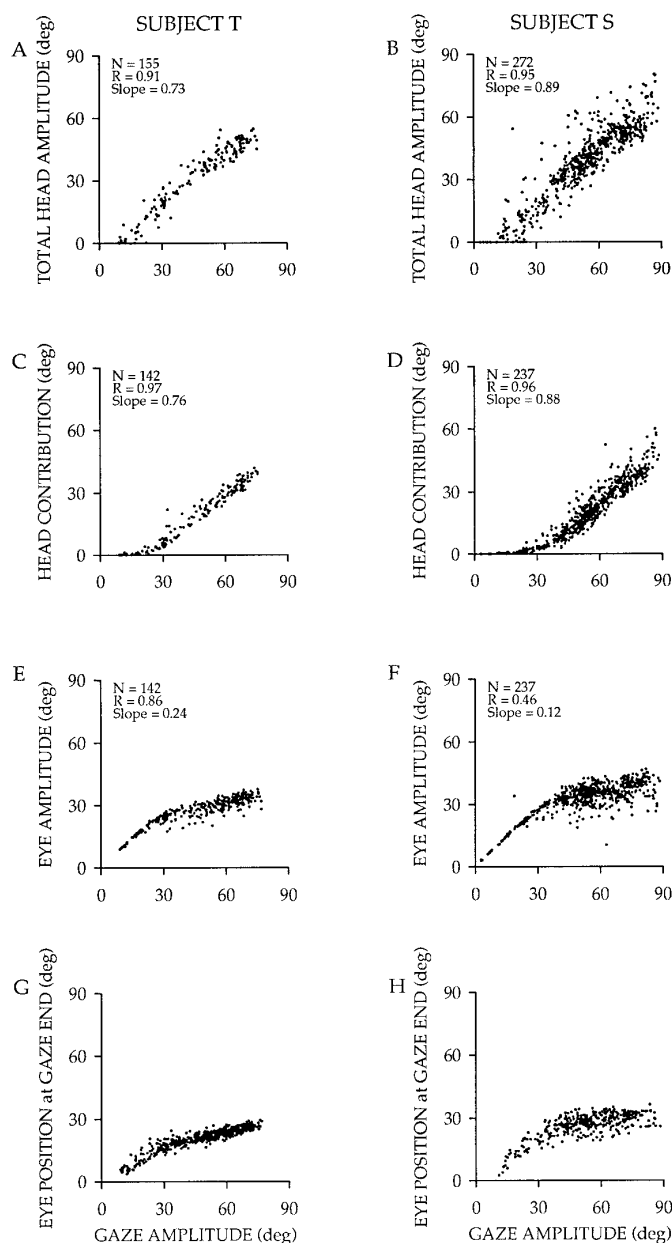
FIG. 6. Total head movement amplitude (*A* and *B*), head contribution (*C* and *D*), eye movement amplitude (*E* and *F*), and eye position at the end of the gaze shift (*G* and *H*) plotted as a function of gaze shift amplitude for movements directed within 10° of the horizontal meridian and beginning with the eyes centered in the orbits (±10°). Correlation coefficients and slopes of the lines of best fit are provided in *A–F*. Only movements in which head contribution was >2° are used to calculate lines of best fit in *C–F*.

completed and therefore did not contribute to the change in gaze position; compensatory counterrotation of the eyes stabilized gaze position during these head movements. The head began to contribute to the gaze shift when gaze amplitudes exceeded ~25° (Fig. 6, *C* and *D*), and the head contribution increased linearly with increasing gaze amplitudes for movements between 25 and 90°.

For gaze shifts larger than ~35°, made with the eyes initially centered in the orbits (within ±5°), eye position at the end of the gaze shift did not exceed ~35° (Fig. 6, *G* and

H), and the maximal contribution of the eyes was limited to <40° (Fig. 6, *E* and *F*). As a result, gaze shifts ranging in amplitude from ~40 to 90° were associated with eye movements having approximately the same amplitudes (see below).

VELOCITY-AMPLITUDE RELATIONSHIPS. The relationships between peak gaze velocity and gaze amplitude, peak eye velocity and eye movement amplitude, and peak head velocity and head movement amplitude are plotted in Fig. 7, *A–C,* respectively. The average velocity-amplitude (Fig. 7, *D–F*) and duration-amplitude (Fig. 7, *G–I*) relationships for each component are also illustrated. A striking feature of the gaze velocity-amplitude relationship was the decline in both peak and average velocity that occurred when gaze amplitudes exceeded ~20°. This decline in gaze velocity occurred in conjunction with a decline in eye velocity (Fig. 7, *B* and *E*) observed during eye movements between ~20° and ~40°. To highlight the differences between the head-restrained and -unrestrained conditions, in Fig. 7*B* the relationship between peak eye velocity and eye movement amplitude when the head is restrained (open symbols) is superimposed on the data from the head-unrestrained subject. As has been well established, when the head is restrained, peak eye velocity is a saturating function of eye movement amplitude (see INTRODUCTION). For movements up to ~20° when the head is unrestrained (during which there were no simultaneous head movements), the relationship between peak velocity and amplitude is identical to the relationship observed when the head is restrained. However, when the head and eyes move together during coordinated gaze shifts, peak eye velocity does not saturate as it does when the head is restrained, but declines for eye movements larger than ~20°. For eye movements of 30°, when the head is restrained, mean peak velocity was ~500°/s, compared with ~300°/s for 30° eye movements made with the head unrestrained.

Gaze duration and amplitude were linearly related (Fig. 7*G*), as were eye duration and amplitude (Fig. 7*H*), for eye movements <25°. But as eye movement amplitude increased, in association with the decline in eye velocity (Fig. 7, *B* and *E*), the eye duration-amplitude relationship became more variable. In contrast to the eye and gaze relationships, head velocity increased linearly as head movement amplitude increased (Fig. 7, *C* and *F*), and head movement duration was a saturating function of head amplitude (Fig. 7*I*).

In Fig. 7, eye velocity is plotted as a function of eye movement amplitude, head velocity as a function of head amplitude, and gaze velocity as a function of gaze amplitude. Although these panels show the relationships characteristic of each component, it is difficult to compare directly eye, head, and gaze velocities on the same trials. To facilitate this comparison, in Fig. 8, gaze (*A*), eye (*B*), and head (*C*) velocities are plotted as a function of time during four individual trials in which the amplitude of the overall gaze shift was 24° (*a*), 35° (*b*), 60° (*c*), or 70° (*d*). Several features that were typical of large-amplitude gaze shifts directed along the horizontal meridian with the eyes initially centered in the orbits are highlighted in these examples. For instance, as gaze amplitude increases, peak and average gaze and eye velocity decline, whereas head velocity increases with increasing gaze (and head) amplitude. Note also that
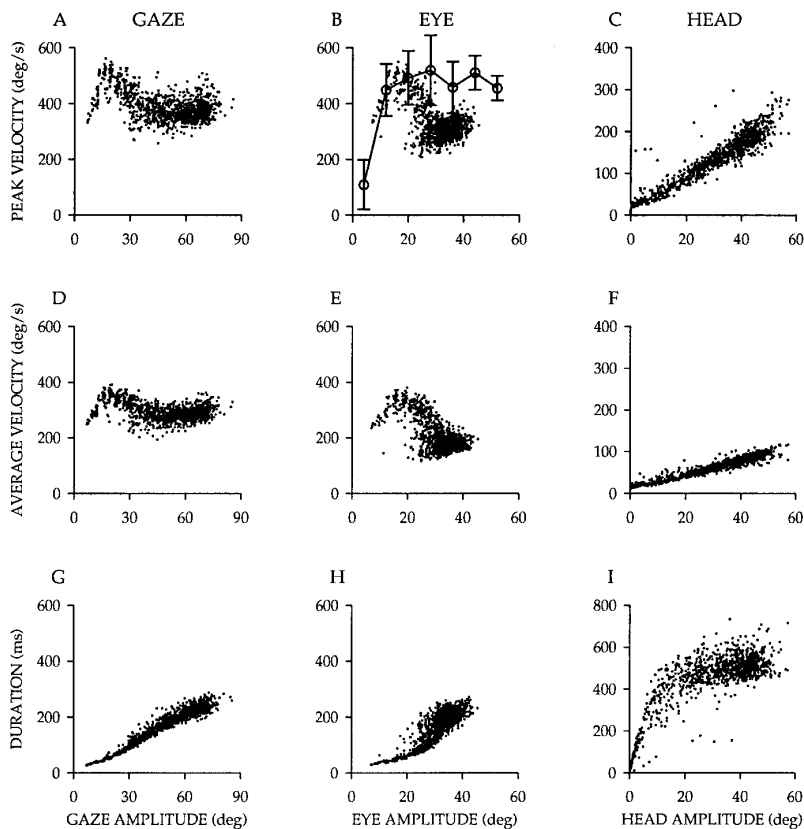
FIG. 7. Relationships between peak gaze velocity and gaze amplitude (*A*), peak eye velocity and eye movement amplitude (*B*), and peak head velocity and head movement amplitude (*C*) illustrated for gaze shifts directed along the horizontal meridian ($\pm 10°$) with the eyes initially centered in the orbits ($\pm 10°$). Average velocity (*D–F*) and movement duration (*G–I*) are plotted, respectively, against gaze amplitude (*D* and *G*), eye amplitude (*E* and *H*), and head amplitude (*F* and *I*). Data from *monkey T, n = 318.* In *B,* relationship between peak eye velocity and eye amplitude when the head was restrained (open symbols) is superimposed. Movements directed along horizontal meridian. Means ± SD. Bin-width: 8°. *n* (Head restrained) = 596.

during large gaze shifts, both eye and gaze velocity have an early peak but decline as head velocity increases and subsequently reaccelerate late in the movement (see Freedman and Sparks 1996).

The qualitative relationships shown in Fig. 8 are extended in Fig. 9, in which average velocity of gaze, eye, and head movements is plotted on the same axes as a function of gaze shift amplitude for *monkey T* (Fig. 9*A*) and *monkey S* (Fig. 9*B*). Average eye and gaze velocities were almost identical for gaze shifts up to ~20°, but for larger amplitudes both eye and gaze velocity declined; during 60–70° gaze shifts, eye velocity was ~50% lower than during 25° movements. Over this range of gaze amplitudes (20–60°), head velocity increased linearly with increasing gaze amplitude. Table 1 compares the mean eye, head, and gaze velocities at 20, 40, 60, and 80° for both subjects.

Effects of gaze direction

The effects of gaze direction on the coordination of the eyes and head are considered in this section. As illustrated in Figs. 2 and 4, the head contributes preferentially to the horizontal component of oblique gaze shifts. In general, there was a linear relationship between total head movement amplitude and gaze movement amplitude (e.g., Fig. 6), but the slope of this relationship decreased as movements were directed away from the horizontal meridian (Fig. 10, *A–D;* Table 2). The slope of the linear relationship between head contribution and gaze amplitude also decreased as gaze directions became increasingly vertical (Fig. 10, *E–H;* Table 2). Similarly, the gaze shift ampli-

tude at which the head began to make a contribution changed as a function of gaze direction; the intersection of the line of best fit with the abscissa systematically increased as the vertical component of gaze shifts increased. In contrast to the decline in head movement amplitude observed as gaze shifts were directed more vertically, eye movement amplitude increased (note the change of slope in Fig. 10, *I–L,* and Table 2). Similar effects were observed in the other monkey (see Table 2).

The effects of gaze direction on eye and head movement amplitude are illustrated further by comparing the relative eye and head contributions to gaze shifts made over a range of directions but matched for vectorial amplitude. During gaze shifts having vectorial amplitudes of 70° (Fig. 11, □), the total amplitude of the head movement (*A* and *D*) decreased from ~50 to 35° as the vertical gaze component increased. Similarly, the head contribution (Fig. 11, *B* and *E*) to gaze shifts 70° in amplitude was reduced by ~50% during movements directed 60° above or below the horizontal meridian compared with those directed along the horizontal meridian. Commensurate with these reductions in head movement amplitude, eye movement amplitude increased during gaze shifts directed 60° above or below the horizontal (Fig. 11, *C* and *F*). Similar effects of gaze direction on head and eye movement amplitude were observed during smaller gaze shifts (Fig. 11: ○, 45°; △, 25°); however, for gaze shifts of 25°, head contributions are small and the effect is reduced (see legend to Fig. 11 for details).

Gaze velocity was also systematically related to movement direction. Horizontal gaze shifts with large head contributions were reduced in velocity compared with more verti-

cal gaze shifts that were accomplished predominantly by movements of the eyes (Fig. 12*A*). The relationship between gaze direction and eye velocity (Fig. 12*B*) highlights the large increase in eye velocity during primarily vertical gaze shifts. Head velocity declined slightly as the vertical component of movements increased (Fig. 12*C*).

To further quantify the effects of direction on eye and head velocity, we selected gaze shifts having vectorial amplitudes of 60° (Fig. 12*D*). For these gaze shifts, eye velocity (filled symbols) increased from ~200 to 390°/s (*monkey T,* squares) and from ~280 to ~450°/s (*monkey S,* circles) as gaze direction changed from horizontal to 60° oblique. A small reduction in head velocity (Fig 12*D*, open symbols) occurred during these 60° gaze shifts, a reduction in velocity consistent with reduced head move-
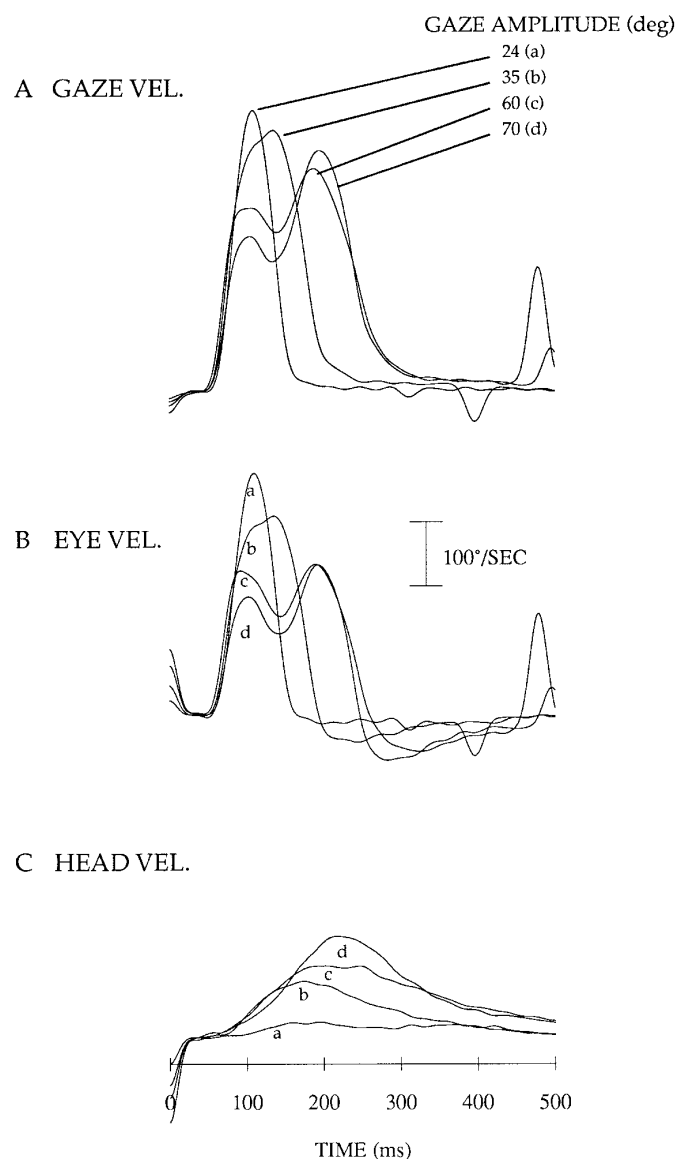
A   GAZE VEL.

GAZE AMPLITUDE (deg)
24 (a)
35 (b)
60 (c)
70 (d)

B   EYE VEL.

100°/SEC

C   HEAD VEL.

TIME (ms)

FIG. 8.   Horizontal gaze (*A*), eye (*B*), and head (*C*) velocities for 4 individual trials. Amplitudes of the gaze shifts are 24° (*a*), 35° (*b*), 60° (*c*), and 70° (*d*). In each case vertical amplitude was <3° and is not shown. Scale for *A*–*C* is shown in *B*. Movements aligned on gaze shift onset. Eye movement amplitude: 21° (*a*), 28° (*b*), 33° (*c*), 28° (*d*). Head movement amplitude: 8° (*a*), 18° (*b*), 37° (*c*), 43° (*d*).
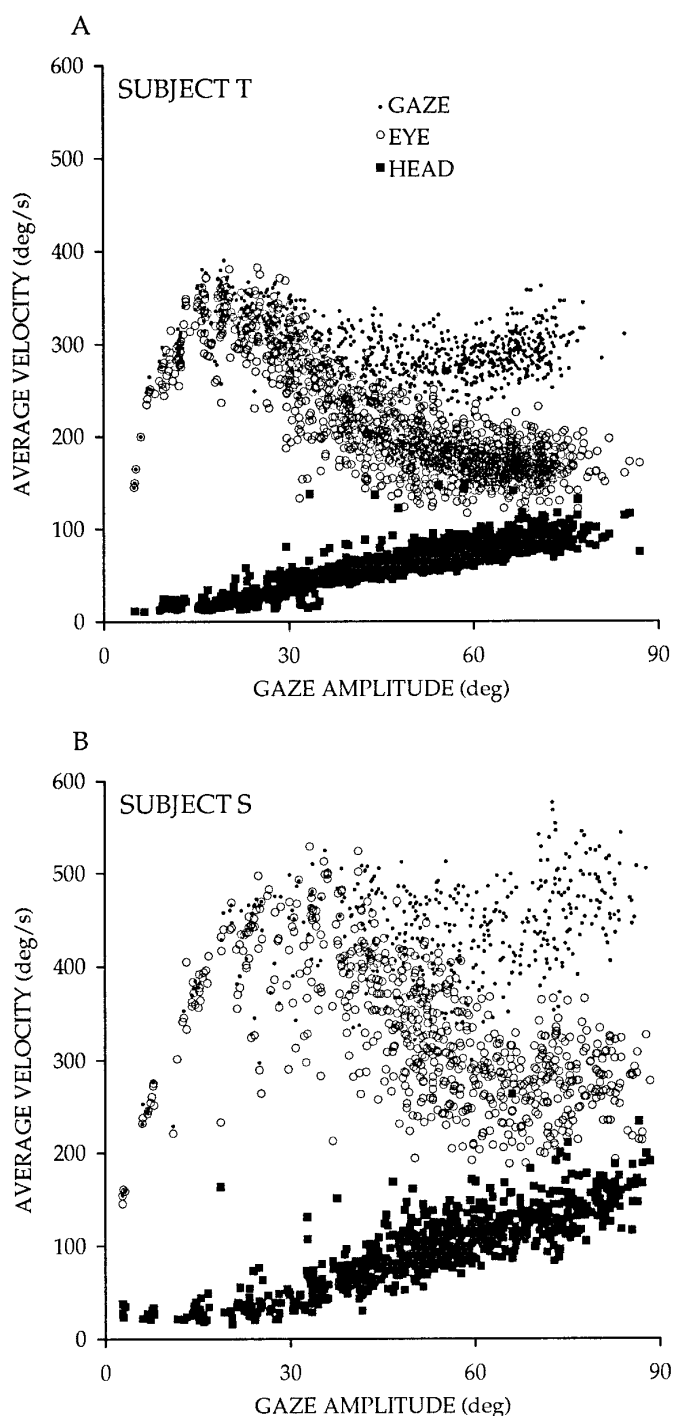
A

SUBJECT T

· GAZE
○ EYE
■ HEAD

B

SUBJECT S

FIG. 9.   Comparison of average gaze (●), eye (○), and head (■) velocities during gaze shifts ranging in amplitude from ~5 to 90° directed along the horizontal meridian (±10°), initiated with the eyes centered (±10°). *A*: data from *monkey T* (*n* = 318). *B*: data from *monkey S* (*n* = 272).

ment amplitude associated with gaze shifts with larger vertical components.

Effects of initial eye position

In addition to the effects of movement direction on the relative amplitudes of eye and head movements, the positions of the eyes relative to the head at the onset of the

TABLE 1. *Statistical test for differences in average gaze, eye, and head velocities at four different gaze shift amplitudes*

	20°	40°	60°	80°
Subject T				
N	27	37	57	57
Average gaze velocity, °/s	365.3 ± 27.9	300.6 ± 27.7*†	283.6 ± 22.6*†	316 ± 23.1*†
Average eye velocity, °/s	344.5 ± 30.1	244.6 ± 35.6*†	185.6 ± 28.3*†	195 ± 29.1*
Average head velocity, °/s	15.6 ± 11.1	50.2 ± 12.6*†	70.1 ± 13.0*†	81.6 ± 22.4*†
Subject S				
N	15	53	37	81
Average gaze velocity, °/s	424.8 ± 34.1	442.3 ± 47.9	416.5 ± 54.7	472.6 ± 34.8*†
Average eye velocity, °/s	410.1 ± 59.8	401.8 ± 56.4	306.9 ± 69.1*†	299.4 ± 39.4*
Average head velocity, °/s	20.6 ± 16.1	64.9 ± 10.9*†	103.9 ± 21.7*†	137.7 ± 20.8†

Values are means ± SD for average gaze, eye, and head velocities during gaze shifts of 20° (18–22°), 40° (38–42°), 60° (58–62°), and 80° (78–82°) for each monkey. Means were compared using a post hoc LSD test. Comparisons were made between the mean velocities at 20° and each of the other amplitudes—40, 60, and 80. *$P < 0.001$. The mean velocity at each amplitude was also compared with the mean velocity at the preceding amplitude. †$P < 0.001$.

gaze shift accounted for much of the observed trial-to-trial variability in the relative amplitudes of eye and head movements. The variability in eye-head contribution arises because gaze shifts of a particular amplitude and direction were not necessarily composed of a constant-amplitude eye movement coupled with a constant-amplitude head movement. Instead, gaze shifts having the same amplitude and direction could be made up of different combinations of eye and head movements depending on the positions of the eyes in the orbits at the start of the movement. In Fig. 13*A* is plotted horizontal gaze position as a function of time for five individual trials (gaze amplitude equals ~70°) directed along the horizontal meridian (vertical position not shown). Two of these five gaze shifts were produced when the eyes were deviated in the orbits 10° contralateral to the direction

of movement, and the horizontal eye and head position traces of these two movements are illustrated in Fig. 13*B*. In these examples, the eyes contributed ~40° and the head ~30° to accomplish the 70° gaze shifts. The remaining three gaze shifts in Fig. 13*A* were produced when the eyes were deviated 30° contralateral to the gaze shift direction, and the eye and head position traces for these trials are shown in Fig. 13*C*. During these 70° gaze shifts the eyes contributed ~50° and the head ~20°.

As illustrated in Fig. 13, the position of the eyes at the onset of the gaze shift can alter the eye and head contributions to the movement. We demonstrate the effects of initial eye position on eye and head movements in this section beginning with Fig. 14. As the eyes began deviated in the orbits, contralateral to the direction of the movement, the
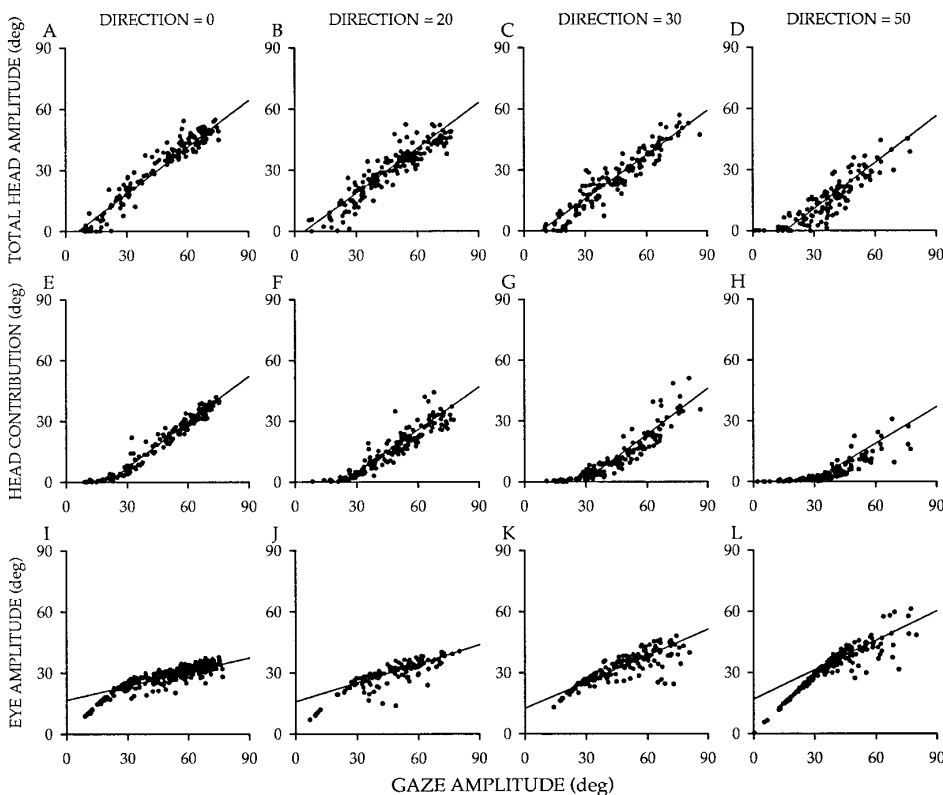

FIG. 10. Total vectorial head movement amplitude (*A–D*) plotted as a function of vectorial gaze amplitude for gaze shifts directed along the horizontal meridian ±10° (direction 0), ±15–20° (direction 20), ±25–35° (direction 30), and ± 45–60° (direction 50). Initial eye position ±5°. Effects of gaze direction on head contribution to the gaze shift (*E–H*) and on the eye component of the gaze shifts (*I–L*) are also illustrated. In *A–D,* lines of best fit for all points are plotted. In *E–L*, only trials in which the head contribution to the gaze was >2° were included in the fit. Table 2 provides details of the fits for *monkey T* (illustrated in this figure) and for *monkey S* (not shown).

TABLE 2. *Effects of direction and initial eye position on eye-head coordination*

		Direction (Initial Eye Position = ±5°)				Initial Eye Position (Gaze Direction = ±10°)			
		0	20	30	50	Cent	Con10	Con20	Con20
Monkey T									
Total head amplitude	N	155	123	147	136	155	375	316	72
	R	0.91	0.95	0.94	0.76	0.91	0.95	0.96	0.95
	Slope	0.73	0.73	0.68	0.62	0.73	0.68	0.67	0.53
	Xint.	7.5	4.7	5.1	13.8	7.5	9.9	15.5	22.2
Head contribution	N	142	115	131	73	142	369	295	60
	R	0.97	0.95	0.90	0.81	0.97	0.99	0.98	0.97
	Slope	0.76	0.69	0.67	0.46	0.76	0.73	0.66	0.58
	Xint	21.6	23.5	25.8	29.5	21.6	24.5	27.8	36.2
Eye amplitude	N	142	115	131	73	142	369	295	60
	R	0.86	0.80	0.80	0.85	0.86	0.91	0.93	0.95
	Slope	0.24	0.31	0.36	0.54	0.24	0.27	0.34	0.42
Monkey S									
Total head amplitude	N	272	82	58	56	272	225	213	98
	R	0.95	0.88	0.90	0.81	0.95	0.95	0.96	0.95
	Slope	0.89	0.85	0.91	0.71	0.89	0.80	0.77	0.60
	Xint.	9.0	9.8	12.6	9.4	7.2	7.4	11.5	13.1
Head contribution	N	237	80	56	35	237	199	187	58
	R	0.96	0.94	0.79	0.76	0.96	0.95	0.97	0.93
	Slope	0.88	0.75	0.58	0.46	0.88	0.82	0.75	0.44
	Xint.	31.1	28.5	25.9	27.0	31.1	31.7	30.9	35.8
Eye amplitude	N	237	80	56	35	237	199	187	58
	R	0.46	0.68	0.69	0.82	0.46	0.53	0.80	0.93
	Slope	0.12	0.25	0.42	0.54	0.12	0.18	0.25	0.44

Number of trials (N), correlation coefficient (R), slope of the line of best fit (Slope), and intersection of the line of best fit with the abscissa (Xint.) are provided for the data in Figs. 10 and 14, and for *monkey S*. Only movements with head contributions >2° were included in the calculation of the line of best fit for both the head contribution and eye amplitude data. Note that the range of initial eye positions for *monkey S* was ±10°, but for *monkey T* it was ±5° for the data demonstrating the effects of movement direction. Direction 0, ±10°; direction 20, 15–20°; direction 30, 25–35°; direction 50, 45–60°. Initial eye positions: Cent, ±5° (*monkey T*) and ±10° (*monkey S*); con10, contralateral 8–12°; con20, contralateral 15–22°; con30, contralateral 25–35°.

gaze amplitude first associated with a head contribution increased (compare the intersections of the lines of best fit with the abscissa in Fig. 14, *E–H,* and Table 2). For example, when the eyes were initially centered, the head began to contribute to gaze shifts of ~20°, but when the eyes began deviated in the orbits by ~35° contralateral to movement direction, the head began to contribute only when gaze amplitude exceeded 30° (Fig. 14*H*). The slope of the linear relationship between gaze amplitude and head contribution (Fig. 14, *E–H;* Table 2) decreased as the eyes began in increasingly contralateral positions. Similarly, the relationship between total head amplitude and gaze amplitude declined as the eyes began in more eccentric positions (Fig. 14, *A–D*). The reduction in the head contribution to gaze shifts was offset by an increase in the eye contribution (Fig. 14, *I–L;* see Table 2 for details).

Figure 15 illustrates the effects of initial eye position on total head movement amplitude (*A* and *D*), head contribution (*B* and *E*), and eye movement amplitude (*C* and *F*), for both subjects, for matched-amplitude gaze shifts of 25° (△), 40° (○), and 70° (□) directed along the horizontal meridian. The amplitude of the eye component increased and the amplitude of the head contribution and total head movement amplitude decreased as the eyes began in more contralateral positions in the orbits (see legend to Fig 15 for details).

Initial eye position also affected eye, head, and gaze velocities. As the eyes began in increasingly contralateral positions, the amplitude of the eye component increased (Figs.

14 and 15), and associated with this increase in eye contribution was an increase in eye velocity (Fig. 16*B*). In Figs. 8 and 9, the decline in eye velocity as head amplitude increased was illustrated (see also Fig. 19). This is reiterated in Fig. 16*B,* which shows that as the eyes begin in less eccentric positions, and associated head movement amplitudes increased, eye velocity decreased. This effect is illustrated for matched-amplitude gaze shifts of 60° in Fig. 16*D*. For these constant-amplitude gaze shifts, eye velocity (filled symbols) increased and head velocity (open symbols) declined as the eyes began in increasingly contralateral initial positions. Figure 16, *A* and *C,* shows the effects of initial eye position on gaze and head velocity, respectively.

EYE-HEAD INTERACTIONS. Head movement amplitude increased as a function of increasing gaze amplitude (Figs. 6, 9, 10, and 14), but eye velocity decreased as gaze amplitude increased. This perhaps surprising relationship is clearly illustrated in Fig. 8, in which four individual trials are superimposed. However, in Fig. 8, head amplitude increases in association with increasing gaze amplitude, and the resulting decline in eye velocity could result from a nonlinear relationship between eye amplitude and velocity (i.e., a nonlinear, nonmonotonic burst generator). Alternatively, the observed decline in eye velocity could result from an interaction between eye and head velocity signals. To distinguish between these alternatives, we selected eye movements matched for amplitude (30–35°) that were associated with a variety of different head movements. In Fig. 17*A* is plotted the average velocity of
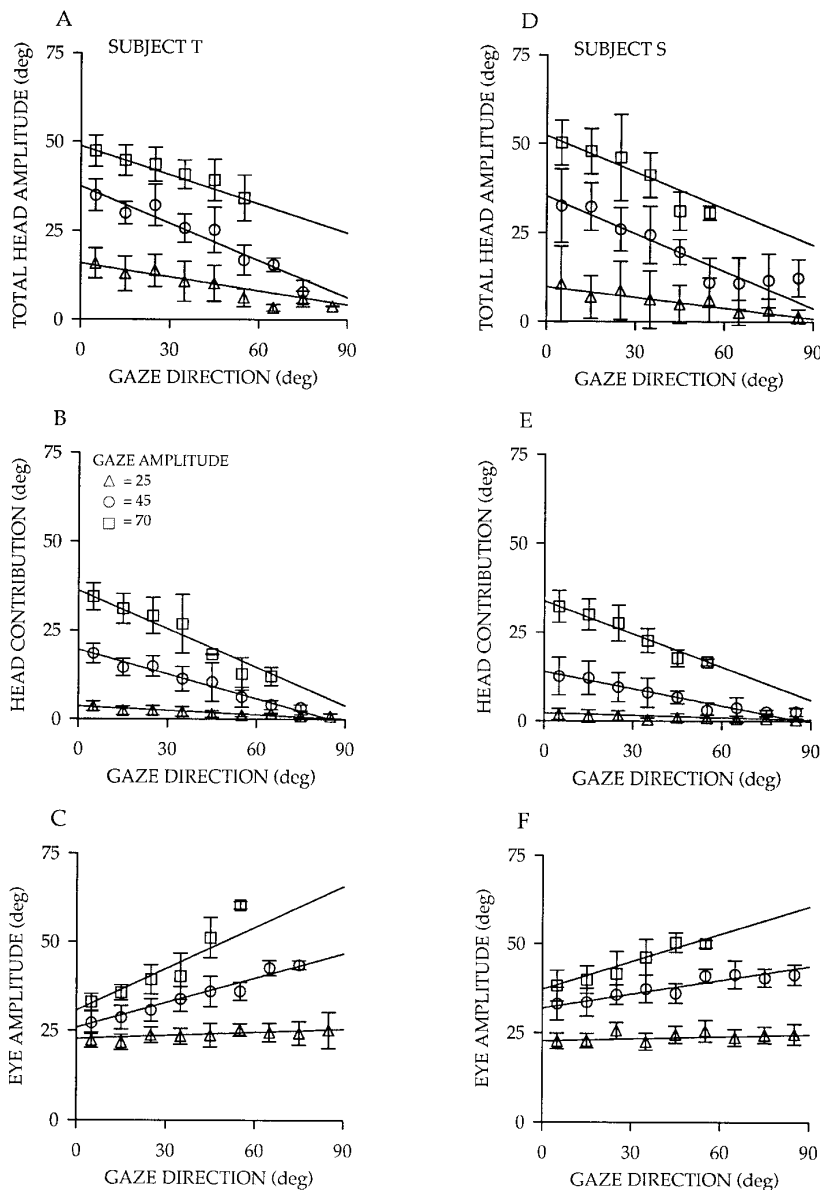
FIG. 11. For gaze shifts with vectorial amplitudes of 25° (△), 45° (○), and 70° (□), total head amplitude (A and D), head contribution to the gaze shift (B and E), and the amplitude of the eye movement (C and F) depend on the direction of the gaze shift. Binwidths of 10° were used to calculate means ± SD and data were fit with least-squares regression lines. Correlation coefficients (r), slopes (sl), and number of trials (n) for each line of best fit were as follows. A—70°: r = −0.6, sl = −0.27, n = 161; 45°: r = −0.81, sl = −0.35, n = 100; 25°: r = −0.57, sl = −0.13, n = 86. B—70°: r = −0.72, sl = −0.36, n = 161; 45°: r = −0.82, sl = −0.23, n = 100; 25°: r = −0.64, sl = −0.04, n = 86. C—70°: r = 0.84, sl = 0.39, n = 161; 45°: r = 0.83, sl = 0.23, n = 100; 25°: r = 0.33, sl = 0.03, n = 86. D—70°: r = −0.47, sl = −0.34, n = 158; 45°: r = −0.70, sl = −0.35, n = 181; 25°: r = −0.4, sl = −0.1, n = 191. E—70°: r = −0.63, sl = −0.31, n = 158; 45°: r = −0.63, sl = −0.16, n = 181; 25°: r = −0.36, sl = −0.02, n = 191. F—70°: r = 0.56, sl = 0.26, n = 158; 45°: r = 0.62, sl = 0.13, n = 181; 25°: r = 0.18, sl = 0.02, n = 191.

these eye movements as a function of the amplitude of the associated head contribution. For eye movements of ~30° made without a coincident head movement, average eye velocity was ~325°/s for *monkey T* (●) and ~475°/s for *monkey S* (■). However, for eye movements of the same amplitude (~30°), made in association with a head movement of 40°, eye velocity was reduced to ~130 and ~230°/s, respectively. The relationships between head contribution velocity (the velocity of the head during the gaze shift) and average eye velocity are shown in Fig. 17B for both monkeys. Eye movement durations for the same movements are plotted as functions of head contribution (Fig. 17C) and concurrent head velocity (Fig. 17D), and as expected for movements of the same amplitude, as eye velocity declined, movement duration increased. Because eye amplitude was essentially the same on these trials, the reduction in eye velocity could not result from a burst generator that converted an eye motor error into a signal proportional to eye velocity. Eye motor error was virtually the same for these amplitude-matched trials, but eye

velocity varied over a wide range and this reduction was correlated with the velocity of the associated head movements (see DISCUSSION).

EYE POSITION AT GAZE SHIFT END. The orbital position of the eyes at gaze shift end is plotted as a function of gaze shift amplitude for both monkeys in Fig. 18, A and B. Regardless of the initial position of the eyes in the orbits (see legend to Fig. 18), eye position at gaze shift end was a saturating function of gaze amplitude; the asymptotic value of this function did not exceed ~35°. Thus, even during the largest movements, eye position at the end of the gaze shift did not exceed this functional (i.e., not mechanical) orbital limit on eye position. On any particular trial, the position of the eyes at the end of the gaze shift necessarily depended on both the initial position in the orbits and the amplitude of the eye component. As gaze shifts were initiated with the eyes deviated in the orbits contralateral to the direction of movement, the amplitude of the eye movement that could be pro-
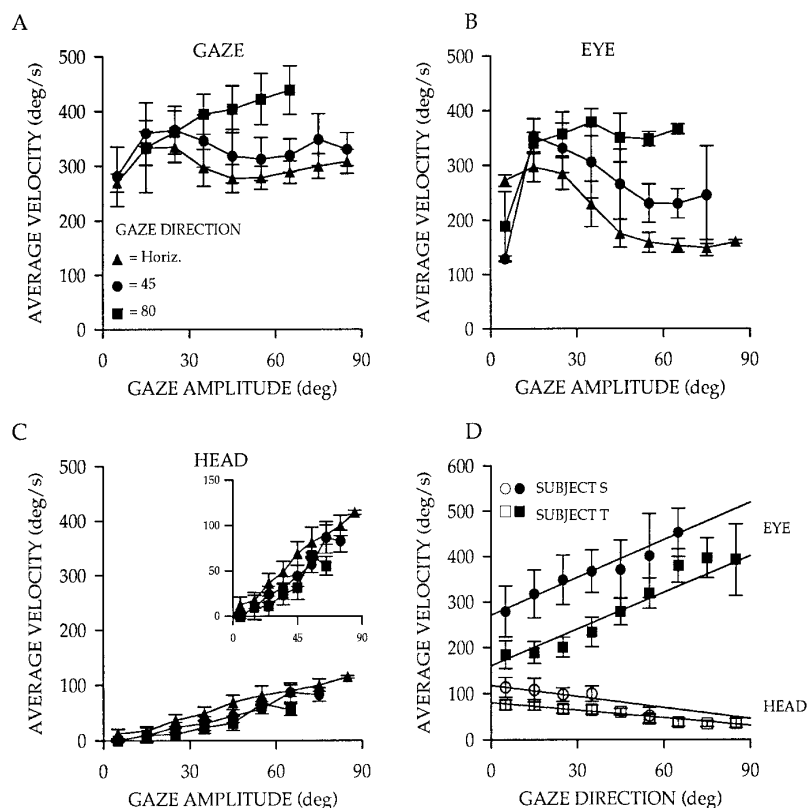
FIG. 12. Average gaze velocity (*A*), average eye velocity (*B*), and average head velocity (*C*) plotted as functions of gaze shift amplitude for movements directed along the horizontal meridian (▲; *n* = 318), between 40 and 50° above or below the meridian (filled circles; *n* = 171), and directed 75–85° above or below the meridian (filled squares; *n* = 87). Movements were made with the eyes initially centered in the orbits (±5°). Binwidths of 10° were used for calculation of means ± SD in *A–C*. *D*: average eye velocity (filled symbols) and average head velocity (open symbols) are plotted as a function of gaze direction during constant-amplitude gaze shifts (60–65°). Squares: *monkey T*. Circles: *monkey S*. Binwidths of 5° were used to calculate the means ± SD, and data are fit with a least-squares regression line. *Monkey T*—filled symbols: *n* = 551, *r* = 0.85, sl = 2.67; open symbols: *n* = 551, *r* = −0.85, sl = −1.36. *Monkey S*—filled symbols: *n* = 175, *r* = 0.73, sl = 2.76; open symbols: *n* = 175, *r* = −0.65, sl = −1.61.

duced before reaching the orbital position limit increased. When the eyes were centered in the orbits, eye movement amplitudes did not exceed ~35°, but when the eyes began deviated 30° contralateral to gaze direction, eye movement amplitudes could be as large as 65°.

RELATIVE TIMING OF EYE AND HEAD MOVEMENTS. In addition to the effects of initial eye position on the relative contributions of eye and head movements, initial eye position accounted for ~20% of the variance in the relative onset times of the eyes and head (Fig. 19*A*). For the constant-amplitude gaze shifts (60°) illustrated in Fig. 19, the interval between eye movement onset and head movement onset decreased linearly as the eyes began in more central orbital positions. Although head latency was more variable as a function of gaze direction, during matched-amplitude gaze shifts (60°), head movement latency increased as the vertical component of the gaze shift increased (Fig. 19*B*). Thus as the head contribution and total head movement amplitude increased (e.g., Figs. 10–15) the time from gaze (or eye) onset to head movement onset decreased.

DISCUSSION

We observed several relationships that characterize eye-head coordination during the delayed gaze shift task in rhesus monkeys: *1*) the direction of the gaze shift and the initial positions of the eyes in the orbits affect the relative amplitudes of the eye and head components during coordinated movements; *2*) for gaze shifts between 25 and 60° eye velocity declines by ~50%, but, over the same range of movements, head velocity increases linearly with gaze amplitude; *3*) for eye movements of similar amplitude, eye velocity

declines as head contribution and head velocity increase; *4*) head movement amplitude is more tightly coupled to the initial displacement of the target relative to the head than to the initial displacement of the target relative to gaze; *5*) as a result of the initial eye position and direction effects on eye and head movements, gaze amplitude and the amplitude of the eye and head components of gaze shifts can be dissociated; and *6*) head movement latency depends on the amplitude of the ensuing head movement and can be dissociated from gaze (eye) latency. Initial eye position and gaze shift direction were factors that influenced the general relationships between eye, head, and gaze metrics, and when these factors are taken into account, the amplitude, velocity, and latency of eye, head, and gaze movements are predictable. These findings, their relationship to previous work, and their implications for hypotheses about the control of coordinated eye-head movements are discussed below.

The relationships described in this report were observed under a particular set of conditions: *1*) targets were presented within ±45° of the midsagittal plane; *2*) only movements made during the delayed gaze shift task and meeting the selection criteria (see METHODS) were considered; *3*) subjects had extensive experience with the task; and *4*) subjects worked in low ambient light. Nonetheless, the relationships are robust, and explicit tests are required to evaluate the sensitivity of these relationships to variations in task and/or test conditions.

Relative amplitudes of eye and head movements

Changes in the direction of the line of sight are often accomplished by combined movements of the eyes and head.
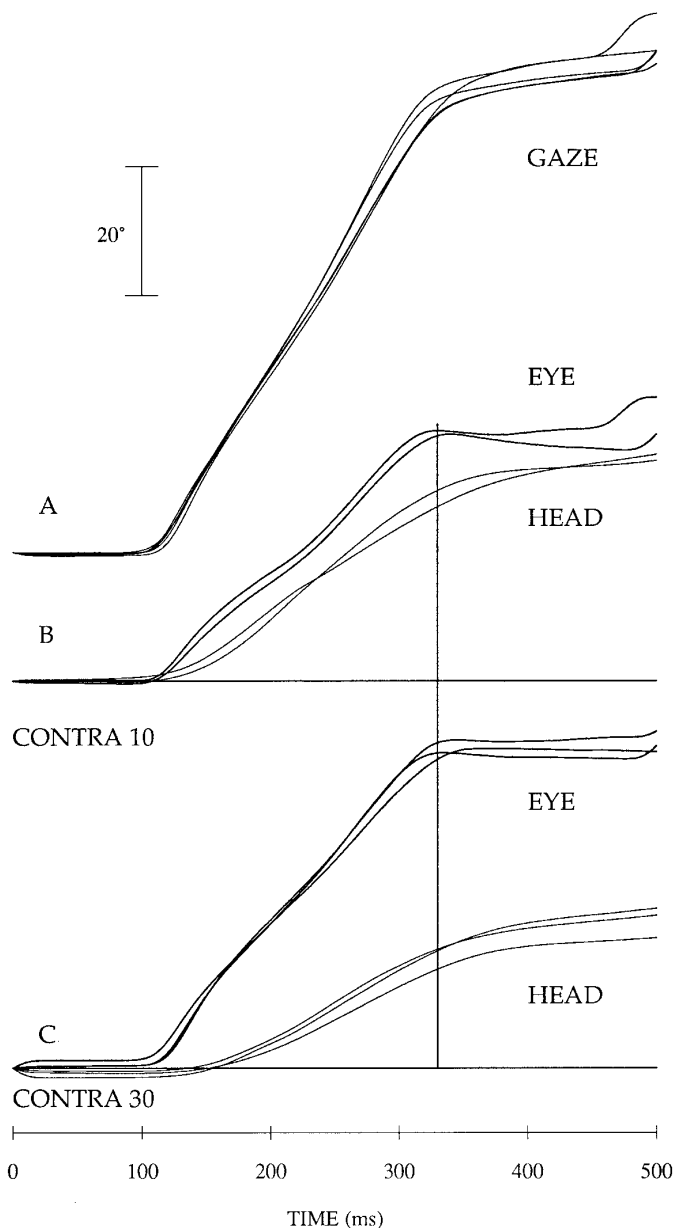
FIG. 13. *A*: horizontal gaze position for 5 individual movements directed along the horizontal meridian. Gaze amplitude = 68–72°. *B*: eye and head position traces for 2 of the 5 movements in *A* initiated when the eyes were deviated in the orbits by 10° contralateral to the direction of movement. *C*: eye and head position traces for the remaining 3 trials initiated when the eyes were 30° contralateral in the orbits. Scale bar in *A* applies to *A–C*.

The relationships observed, using the delayed gaze shift task, between gaze shift amplitude and the amplitude of the eye and head components of gaze define eye-head coordination under these conditions. When the eyes are initially centered in the orbits, the relationship between gaze amplitude and eye amplitude is characterized by a saturating function; eye amplitude increases linearly with increasing gaze amplitude for movements up to ~25°, but for gaze shifts between 40 and 90°, eye movement amplitude is relatively constant. This restriction of eye movement amplitude results from a functional (i.e., not mechanical) limit on the position of the eyes

in the orbits (Guitton and Volle 1987). At the end of a gaze shift, eye position in the orbit does not exceed ~35–40°. Because of this functional limit on orbital position, when the eyes are initially centered, eye movement amplitude does not exceed ~40°. In contrast, when the eyes begin deviated in the orbits by 30° contralateral to the direction of the gaze shift, eye movement amplitudes can be as large as 70° before the functional limit on eye position is reached. The "limit" on orbital position is not an absolute limit against which the eyes are driven during all large gaze shifts; for a particular gaze shift amplitude (e.g., 70°), final eye position varies over a range of ≥10°.

Large gaze shifts (>40°) directed along the horizontal meridian and initiated with the eyes centered in the orbits are accomplished by increasingly large head contributions; eye amplitude is relatively constant for this range of gaze shifts. As a result, a tight linear relationship between head contribution and gaze amplitude is observed during these movements. In general, these results are similar to those reported previously for head-unrestrained gaze shifts in the primate, directed along the horizontal meridian (in monkey: Bizzi et al. 1972a,b; Phillips et al. 1995; Tomlinson 1990; Tomlinson and Bahra 1986a; in humans: Gresty 1974; Guitton and Volle 1987; Tweed et al. 1995; Zangmeister and Stark 1982a,b). In addition, there have been several reports of the effects of initial eye position on the metrics of eye and head movements (Becker and Jürgens 1992; Delreux et al. 1991; Tomlinson and Bahra 1986a; Volle and Guitton 1993). We found that when the eyes are deviated contralaterally in the orbits at the beginning of the gaze shift, the head contribution to gaze and total head movement amplitude are reduced. This had the effect of reducing the ratio between head amplitude and gaze amplitude (i.e., the slope of the linear relationships decreased). The reduction in head contribution is offset by an increase in the amplitude of eye movements and an increase in the slope of the eye-gaze amplitude relationship. As a result of the effects of initial eye position, gaze shifts of a particular amplitude can be accomplished with a variety of different combinations of eye and head movements. For example, the eye and head components of 70° gaze shifts directed along the horizontal meridian can vary over a range of >25°. Within this subset of movements, in which gaze amplitude is relatively constant, there is a high, negative correlation between initial (contralateral) eye position and eye movement amplitude, whereas there is a high, positive correlation between initial (contralateral) eye position and head movement amplitude.

The direction of the gaze shift also affects the relative contributions of the eyes and head; head movement amplitude decreases and eye amplitude increases as gaze shifts are directed away from the horizontal meridian. The ratio of the vertical head movement to the vertical displacement of the target is quite low, and as a result the head contribution to the vertical component of oblique gaze shifts is considerably smaller than the contribution to the horizontal component (see also Glenn and Vilis 1992; Tweed et al. 1995). The low "gain" of vertical head movements, reflected in their predominantly horizontal trajectories, is countered by eye trajectories that are more vertical than the trajectory of the gaze shift. Thus, during oblique gaze shifts, gaze direction and the direction of the eye and head components of gaze are not identical.
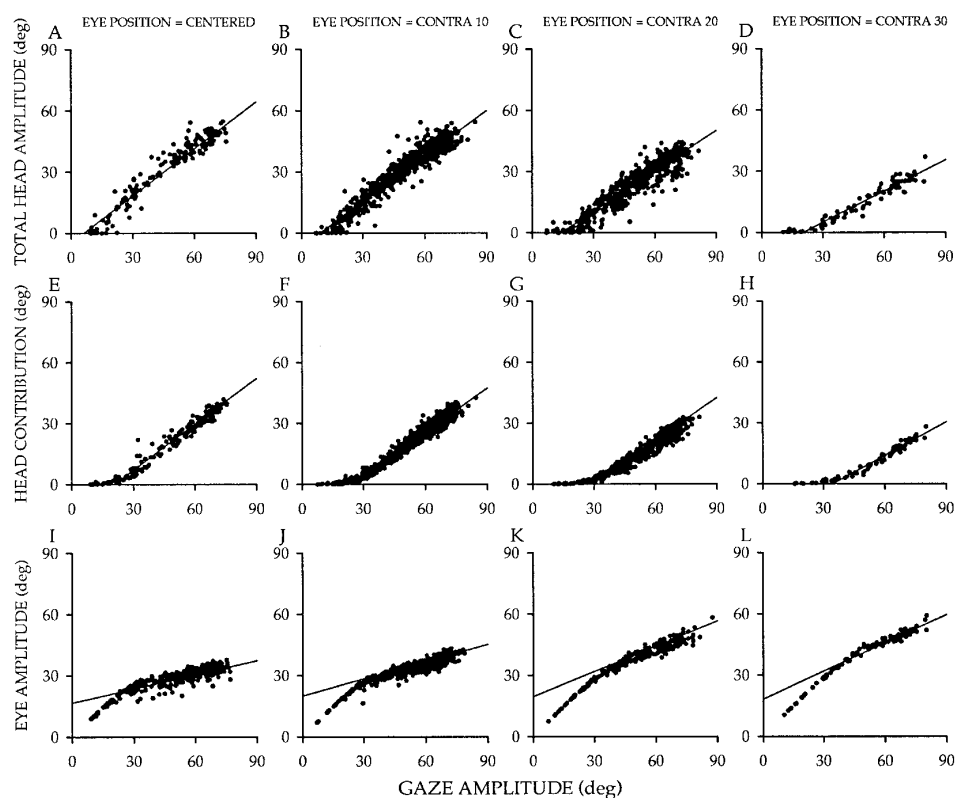
FIG. 14. Total vectorial head movement amplitude (*A–D*) plotted as a function of vectorial gaze amplitude for gaze shifts directed along the horizontal meridian (direction equals ±10) initiated when the eyes were centered in the orbits (±5°), deviated contralateral to movement direction by 8–12° (CONTRA 10), 15–22° (CONTRA 20), and 25–35° (CONTRA 30). Effects of initial eye position on head contribution to the gaze shift (*E–H*) and on the eye component of the gaze shifts (*I–L*) are also illustrated. In *A–D*, lines of best fit for all points are plotted. In *E–L*, only trials in which the head contribution to the gaze was >2° were included in the fit. Table 2 provides details of the fits for *monkey T* (illustrated in this figure) and *monkey S* (not shown).

Amplitude-velocity relationships

When the head is restrained, saccadic velocity is a saturating function of saccade amplitude (Fig. 7*B*) (for example, see Bahill et al. 1975; Baloh et al. 1975; Collewijn et al. 1988a,b). In contrast, for head-unrestrained movements directed along the horizontal meridian, initiated with the eyes centered in the orbits, eye velocity is not a monotonic function of eye movement amplitude; eye velocity increases for eye movements up to ~20° but decreases dramatically as eye movement amplitudes increase up to ~40°. Similarly, the relationship between eye velocity and gaze shift amplitude increases as gaze amplitude increases up to ~25°, but decreases for larger gaze shifts between ~35 and 60°; eye velocity remains at this reduced velocity for gaze shifts between 60 and 90° (Phillips et al. 1995 also illustrate a decline in eye velocity for gaze shifts between 20 and 60°). Head movement velocity is linearly related to head movement amplitude, and also linearly related to gaze amplitude over the entire range of gaze shifts that were associated with head movements in our sample.

Compared with gaze shifts of ~25°, average eye movement velocity is reduced by ~200–250°/s for gaze shifts of 65°. Over this range of gaze amplitudes (25–65°), head velocity increases by ~100°/s. Similarly, for constant-amplitude eye movements, eye velocity is inversely related to concurrent head velocity (Fig. 17). If this eye-head interaction were mediated by the vestibuloocular reflex, the gain of this reflex would have to be high (>2) throughout the movement to account for the observed reduction in eye velocity. However, direct tests of the gain of the vestibuloocular reflex during large-amplitude gaze shifts indicate that the gain is considerably less than 1 for movements larger than

~20° (Guitton and Volle 1987; Laurutis and Robinson 1986; Pelisson and Prablanc 1986; Pelisson et al. 1988; Tomlinson 1990; Tomlinson and Bahra 1986b). It is unlikely, therefore, that a canal-mediated signal of head velocity is solely, if at all, responsible for the reduction in eye velocity associated with increasing head movement velocity. Other signals related to head velocity, either from neck muscle afferents or an internal representation of head velocity (corollary discharge), could be used to reduce the velocity of eye movements. The observed slowing of the eye component of coordinated gaze shifts as head velocity increases (e.g., Figs. 8 and 17) results in the observed tight correlation between eye movement end and gaze shift end. As gaze amplitude and head contribution increase, gaze shift duration increases (see Fig. 7). For many of these large gaze shifts, eye movement amplitude is relatively constant, and if eye velocity were not reduced as head contribution increased, the eyes would reach their final orbital position before the end of the gaze shift. In this case the gaze shift might continue as a result of continued head movement but eye position in the orbits would remain constant. We did not observe, as others have reported (e.g., Guitton et al. 1984), movements in which eye velocity dropped to zero and remained at zero for a large portion of the gaze shift. In contrast, our data show a tight correlation between eye end and gaze end, although the slopes of the lines of best fit for these data are <1 (see Fig. 3 and related text).

Relative timing of eye and head movements

Previous reports provide conflicting data on the degree of temporal coupling between eyes and head during gaze shifts directed along the horizontal meridian. For example, some
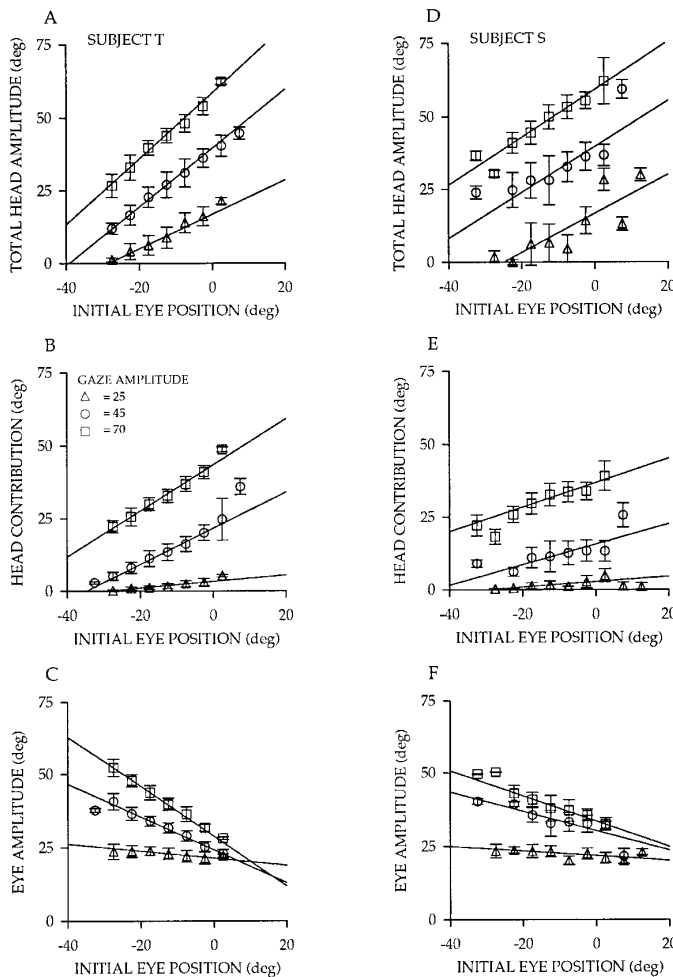
FIG. 15. During gaze shifts with vectorial amplitudes of 25° ($\triangle$), 45° ($\circ$), and 70° ($\square$), total head amplitude (*A* and *D*), head contribution to the gaze shift (*B* and *E*), and amplitude of eye movement (*C* and *F*) are plotted as a function of initial eye position in the orbits. Movements were directed along the horizontal meridian ($\pm 10°$). Negative initial positions: contralateral-to-movement direction. Binwidths of 5° were used to calculate means $\pm$ SD, and data were fit with least-squares regression lines. Correlation coefficients (*r*), slopes (sl), and number of trials (*n*) for each line of best fit were as follows. *A*—70°: $r = 0.92$, sl $= 1.13$, $n = 232$; 45°: $r = 0.85$, sl $= 1.01$, $n = 283$; 25°: $r = 0.71$, sl $= 0.59$, $n = 139$. *B*—70°: $r = 0.88$, sl $= 0.79$, $n = 242$; 45°: $r = 0.82$, sl $= 0.62$, $n = 306$; 25°: $r = 0.61$, sl $= 0.11$, $n = 141$. *C*—70°: $r = -0.92$, sl $= -0.85$, $n = 242$; 45°: $r = -0.90$, sl $= -0.56$, $n = 303$; 25°: $r = -0.36$, sl $= -0.12$, $n = 144$. *D*—70°: $r = 0.80$, sl $= 0.42$, $n = 126$; 45°: $r = 0.66$, sl $= 0.79$, $n = 101$; 25°: $r = 0.69$, sl $= 0.67$, $n = 41$. *E*—70°: $r = 0.59$, sl $= 0.42$, $n = 126$; 45°: $r = 0.51$, sl $= 0.35$, $n = 101$; 25°: $r = 0.48$, sl $= 0.09$, $n = 41$. *F*—70°: $r = -0.62$, sl $= -0.43$, $n = 126$; 45°: $r = -0.57$, sl $= -0.33$, $n = 101$; 25°: $r = -0.35$, sl $= -0.08$, $n = 41$.

report large variability in relative onset times for the eyes and head (e.g., Phillips et al. 1995; Tweed et al. 1995), whereas others report a high degree of temporal coupling (e.g., Guitton et al. 1984). These differences in the relative timing of the eyes and head (reviewed by Fuller 1992) are likely due to comparison of movements made under different behavioral conditions (Barnes 1979; Bizzi et al. 1972a; Gresty 1974; Zangmeister and Stark 1981, 1982a,b). In this report, and consistent with data from human subjects (Becker and Jürgens 1992; Fuller 1996), we demonstrate that the time from gaze onset to head movement onset de-

pends on the initial position of the eyes in the orbits. Note that head movement latency (relative to gaze onset) decreased as the eyes began in more central orbital positions and these gaze shifts were associated with larger head movements. Similarly, as head amplitude decreases for gaze shifts with larger vertical components, head movement latency increases. Head latency appears to be related to the amplitude of the ensuing head movement, and head movement latency and the latency of eye or gaze movements can vary independently. The independence of eye and head movement latencies suggests that signals that initiate head and eye movements may be separate or at least separately influenced by other factors.

Head movement amplitude

There are several reports of the effects of initial eye position on eye and head movement amplitude (Becker and Jürgens 1992; Delreux et al. 1991; Tomlinson 1990; Volle and Guitton 1993). In particular, Delreux et al. (1991) reported that head movement amplitude is equal to a fraction (between 0.4 and 0.8) of target displacement relative to gaze. In contrast, Volle and Guitton (1993) reported that head movement amplitude is approximately equal to the initial displacement of the target relative to the head. These two reports present two different hypotheses for the control of head movement amplitude. The former (Delreux et al. 1991) proposes that head amplitude is controlled by a gaze error signal produced by comparing signals of desired gaze displacement and actual gaze displacement. Alternatively, the correlation between head amplitude and the displacement of the target relative to the head (e.g., Volle and Guitton 1993) is consistent with the hypothesis that head movement amplitude is controlled by a head error signal produced by comparing signals of desired head displacement and actual head displacement. We observed tight correlations between head amplitude and both displacement of the target relative to the head (Fig. 4*E*) and displacement of the target relative to gaze (Fig. 4*C*). When target displacements relative to gaze and relative to the head are dissociated (Fig. 5), however, head movement amplitude is better correlated with target displacement relative to the head than relative to gaze, whereas eye amplitude is better correlated with initial retinal error. Assuming that both eye and head movement amplitude are controlled by local feedback controllers, these data suggest that head and eye amplitude are controlled separately; head amplitude seems to be driven by a head error signal but eye amplitude is driven by a signal related to the displacement of the target relative to gaze.

Evidence for independent control of eye and head movements

The data in this report support the hypothesis that the control signals used to drive the eye and head components of coordinated gaze shifts diverge, and at some level (see below) are independent. First, the opposite effects of initial eye position on the eye and head components of amplitude-matched gaze shifts indicates that a signal related to eye position affects independent signals driving the eyes and the head. Second, the trajectories of eye and head movements
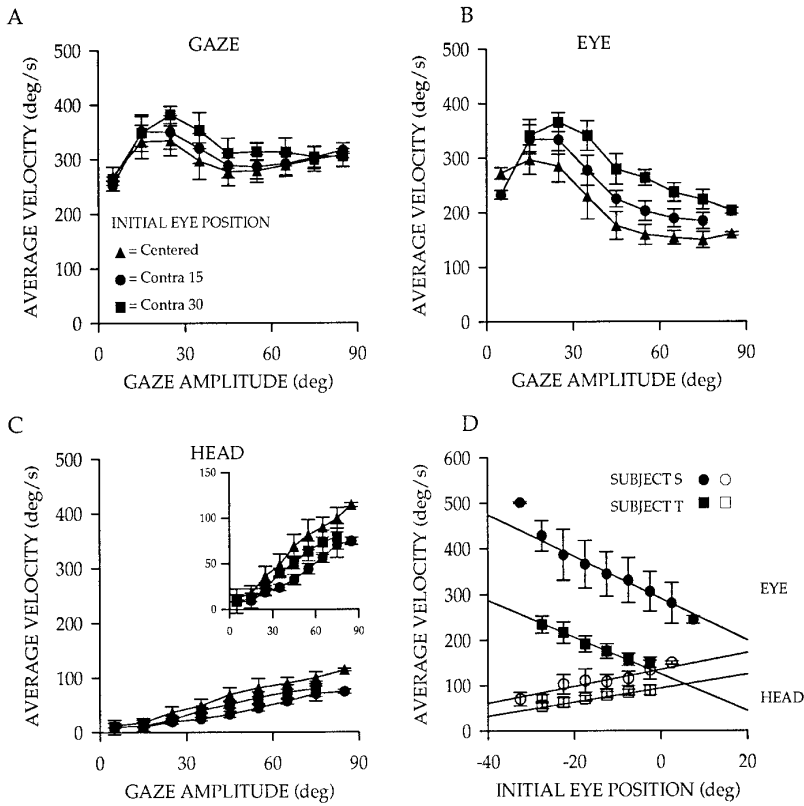
FIG. 16. Average gaze velocity (*A*), average eye velocity (*B*), and average head velocity (*C*) plotted as a function of gaze shift amplitude for movements initiated with the eyes centered ($\pm 5°$; ▲), deviated contralaterally by $12-18°$ (Contra 15; filled circles), or deviated contralaterally by $25-35°$ (Contra 30; filled squares). Binwidths of $10°$ were used for calculation of means $\pm$ SD in *A–C*. *D*: average eye velocity (filled symbols) and average head velocity (open symbols) plotted as a function of initial eye position for constant-amplitude gaze shifts ($60-65°$) directed along the horizontal meridian ($\pm 10°$). Squares: *monkey T*. Circles: *monkey S*. Binwidths of $5°$ were used to calculate the means $\pm$ SD, and data are fit with a least-squares regression line. *Monkey T*—closed symbols: $n = 229$, $r = -0.80$, $sl = -4.06$; open symbols: $n = 229$, $r = 0.79$, $sl = 3.98$. *Monkey S*—closed symbols: $n = 224$, $r = -0.57$, $sl = -4.58$; open symbols: $n = 224$, $r = 0.76$, $sl = 5.57$.

during oblique gaze shifts are not identical, suggesting that the signals driving the horizontal and vertical eye and head components are not identical. Third, the linear head velocity-

amplitude relationship and nonlinear, nonmonotonic eye velocity-amplitude relationship suggest either independent velocity signals or interactions between two independent eye
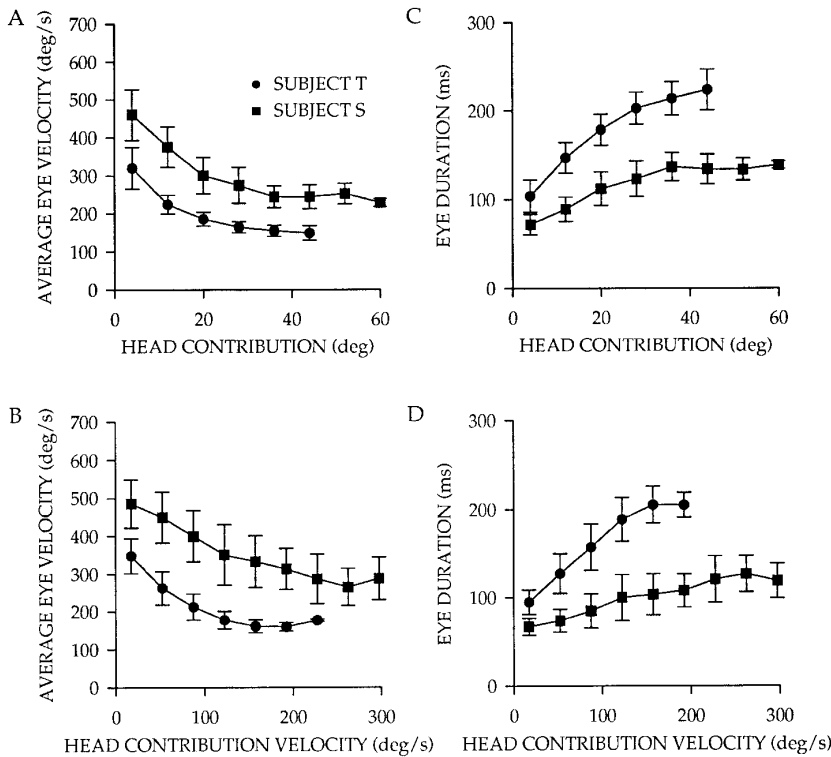
EYE MOVEMENT AMPLITUDE = 30deg

FIG. 17. Relationships between amplitude of the head contribution and eye velocity (*A*) and duration (*C*) during constant-amplitude eye movements (range $30-35°$). Relationships between the average velocity of the head movement during the gaze shift (head contribution velocity) and average eye velocity and duration are plotted in *B* and *D*, respectively. Means $\pm$ SD are plotted for each monkey (*monkey T*, ●; *monkey S*, ■). Binwidths for calculation of means: $8°$ (*A* and *C*), $30°/s$ (*B* and *D*).
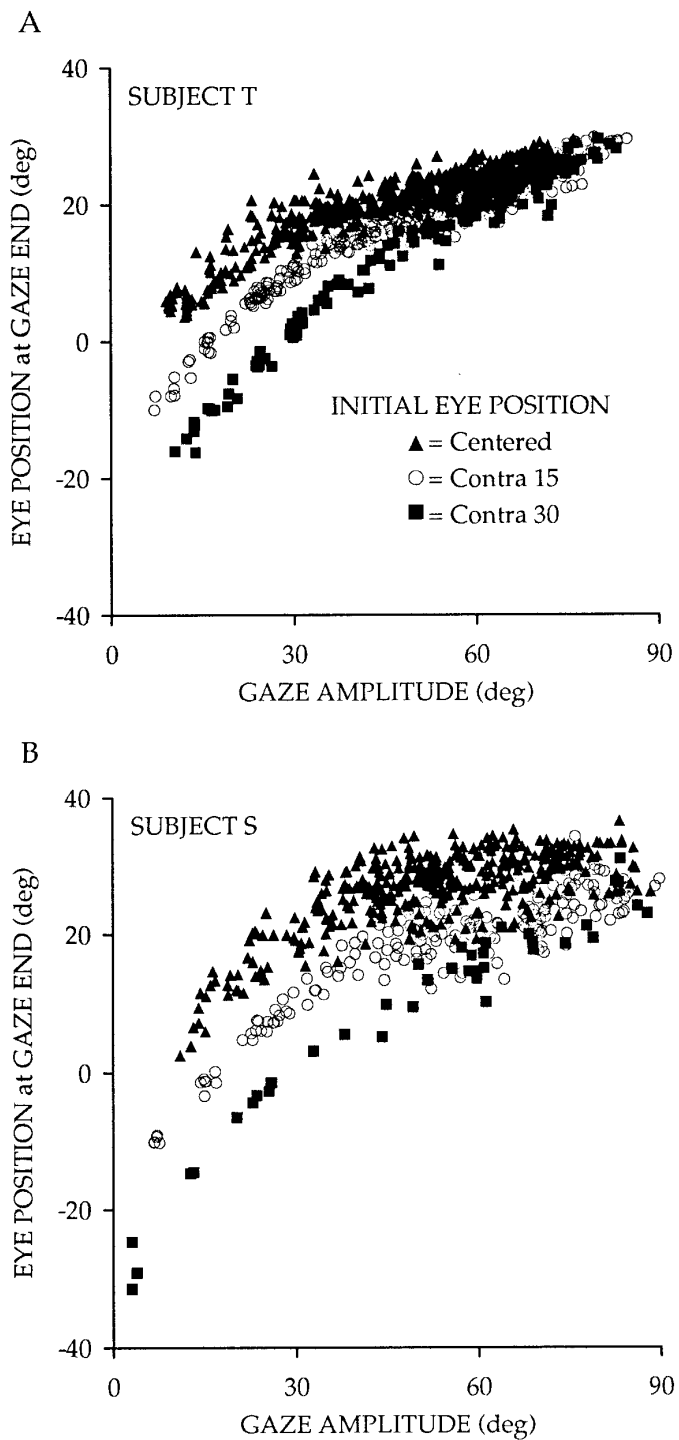
A

B

FIG. 18. Eye position at the end of the gaze shift plotted as a function of gaze amplitude for movements initiated with the eyes in different initial positions: centered = ±5° (▲); 12–18° contralateral to movement direction (○); and 25–35° contralateral to movement direction (■). Movements were directed along the horizontal meridian (±10°). Data from *monkey T* (*A*) and *monkey S* (*B*). Negative positions: eyes did not cross primary position.

and head signals. Fourth, head movement amplitude is better correlated with the displacement of the target relative to the head than to target displacement relative to gaze, but eye amplitude is only weakly correlated with target displacement relative to the head. This suggests that the signals driving
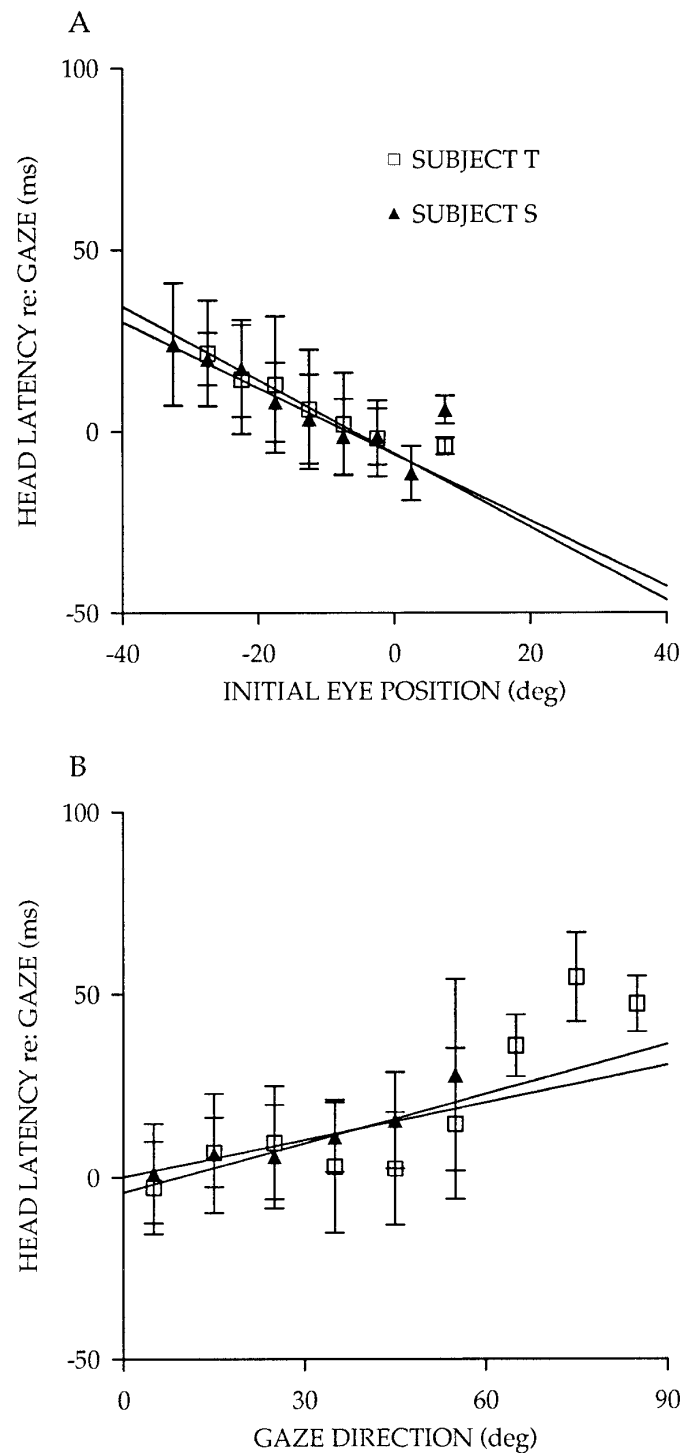
FIG. 19. *A*: effect of initial eye position on the relative timing of eye and head movements for *monkey T* (□) and *monkey S* (▲) for constant-amplitude gaze shifts (60–65°). Binwidth for calculating means ± SD was 5°, and data are fit with a least-squares regression line. *Monkey T*: $n = 218$, $r = -0.45$, sl = −1.0. *Monkey S*: $n = 122$, $r = -0.47$, sl = −0.94. *B*: effects of movement direction on the latency of head movements relative to gaze onset for gaze shifts between 60 and 65°. Binwidth for calculating means ± SD was 10°. *Monkey T*: $n = 219$, $r = 0.58$, sl = 0.45. *Monkey S*: $n = 201$, $r = 0.45$, sl = 0.34. Negative initial eye positions are contralateral to movement direction. Negative head latencies relative to gaze onset: head movement onset preceded gaze onset. Gaze directions are relative to the horizontal meridian and include movements with both upward and downward vertical components.

eye and head movements are not identical. Finally, head movement latency is related to the amplitude of the ensuing head movement, and is therefore related to initial eye position and movement direction; however, gaze (eye) latency relative to the movement initiation cue is unaffected by either initial eye position or movement direction. This suggests that the processes involved in triggering eye and head movements may be separate. Each of these observations is inconsistent with the hypothesis that an identical gaze-related signal drives both eye and head plants (e.g., Guitton et al. 1990), and we interpret these findings as evidence supporting the hypothesis that, at some level, eye and head movement control signals are separate (see Freedman et al. 1996; Phillips et al. 1995; Tweed et al. 1995).

Role of the SC in gaze control

When the head is unrestrained, electrical stimulation of the primate SC evokes coordinated eye-head gaze shifts (Freedman et al. 1996; for comparable data in cat, see Paré et al. 1994). The relative amplitudes of the eye and head components and the velocity-amplitude relationships of these stimulation-induced movements are similar to the relationships observed during visually guided movements with the use of the delayed gaze shift task (described in this report). In addition, during electrical stimulation at a single SC site, with fixed stimulation parameters, evoked gaze shifts had similar amplitudes and directions. These ''fixed-vector'' gaze shifts could be composed of many different combinations of eye and head movements depending on the position of the eyes in the orbits at stimulation onset (Freedman et al. 1996), just as relative eye and head contributions depend on eye position during the delayed gaze shift task. Thus the coordination of the eyes and head during gaze shifts evoked by electrical stimulation of the SC is remarkably similar to the coordination observed during the delayed gaze shift task. This similarity suggests that the relationships between eye, head, and gaze amplitude, velocity, and duration described in this report may be characteristics that delineate eye-head coordination in general, and not only during the task used in this experiment.

We interpreted the results of SC stimulation as consistent with the hypothesis that a signal of desired gaze displacement (not separate eye and head displacement commands) is derived from the locus of collicular activity (see Freedman 1996; Freedman et al. 1996 for extended discussion). The results of microstimulation and the analyses described above indicate that the desired gaze displacement command observed at the level of the SC is decomposed into separate eye and head displacement signals at a site (or sites) downstream from the SC. The decomposition of the desired gaze displacement command does not depend exclusively on the synaptic weighting functions of collicular efferents; the same collicular gaze command can be decomposed differently depending on the initial position of the eyes in the orbits. This suggests that a signal, related to eye position in the orbit, affects the decomposition of the gaze command; contralateral eye position signals increase the desired eye displacement signal and decrease the head displacement signal. In addition to this decomposition as a function of initial eye position, a cross-coupling of separate eye and head velocity

commands could account for the inverse relationship between eye and concurrent head velocities.

The hypothesis that the desired gaze displacement command, present in the SC, is subsequently decomposed into separate eye and head signals is a parsimonious explanation of data obtained from microstimulation of the SC, physiological recording from the primate SC, and the behavioral relationships reported in this paper. For a particular desired gaze displacement command, the ratio of eye and head contributions to the gaze shift will depend on eye position in the orbit and direction of movement. This analytic framework for the generation of coordinated eye-head gaze shifts need not be altered to account for species differences in the range of mobility of the eyes relative to the head (oculomotor range) or the range of head mobility relative to the body, if the decomposition of the gaze command into separate eye and head movement signals incorporates information about species-specific mechanical (or functional) constraints. Thus control of redirecting the line of sight in the barn owl, cat, rhesus monkey, and human may be mediated by similar neural mechanisms even though the specific ways in which the eyes and head are coordinated during orienting behaviors may be quite different across species.

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