

# Eye, Head, and Body Coordination During Large Gaze Shifts in Rhesus Monkeys: Movement Kinematics and the Influence of Posture

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**McCluskey MK, Cullen KE.** Eye, head, and body coordination during large gaze shifts in rhesus monkeys: movement kinematics and the influence of posture. *J Neurophysiol* 97: 2976–2991, 2007. First published January 17, 2007; doi:10.1152/jn.00822.2006. Coordinated movements of the eye, head, and body are used to redirect the axis of gaze between objects of interest. However, previous studies of eye-head gaze shifts in head-unrestrained primates generally assumed the contribution of body movement to be negligible. Here we characterized eye-head-body coordination during horizontal gaze shifts made by trained rhesus monkeys to visual targets while they sat upright in a standard primate chair and assumed a more natural sitting posture in a custom-designed chair. In both postures, gaze shifts were characterized by the sequential onset of eye, head, and body movements, which could be described by predictable relationships. Body motion made a small but significant contribution to gaze shifts that were  $\geq 40^\circ$  in amplitude. Furthermore, as gaze shift amplitude increased ( $40\text{--}120^\circ$ ), body contribution and velocity increased systematically. In contrast, peak eye and head velocities plateaued at velocities of  $\sim 250\text{--}300^\circ/\text{s}$ , and the rotation of the eye-in-orbit and head-on-body remained well within the physical limits of ocular and neck motility during large gaze shifts, saturating at  $\sim 35$  and  $60^\circ$ , respectively. Gaze shifts initiated with the eye more contralateral in the orbit were accompanied by smaller body as well as head movement amplitudes and velocities were greater when monkeys were seated in the more natural body posture. Taken together, our findings show that body movement makes a predictable contribution to gaze shifts that is systematically influenced by factors such as orbital position and posture. We conclude that body movements are part of a coordinated series of motor events that are used to voluntarily reorient gaze and that these movements can be significant even in a typical laboratory setting. Our results emphasize the need for caution in the interpretation of data from neurophysiological studies of the control of saccadic eye movements and/or eye-head gaze shifts because single neurons can code motor commands to move the body as well as the head and eyes.

## INTRODUCTION

Coordinated eye-head movements are made during everyday activities to rapidly redirect the axis of gaze between two targets of interest (humans: André-Deshays et al. 1988; Barnes 1979; Guitton and Volle 1987; Pélisson et al. 1988; Zangemeister and Stark 1982a,b, and monkeys: Bizzi et al. 1971, 1972; Dichgans et al. 1973; Freedman and Sparks 1997; Lanman et al. 1978; Morasso et al. 1973; Tomlinson 1990; Tomlinson and Bahra 1986a,b). When the head is immobilized, gaze is redirected by high-velocity saccadic movements for which the relationship between gaze shift amplitude and eye velocity as well as movement duration is predictable (Bahill et

al. 1975; Baloh et al. 1975; Van Gisbergen et al. 1984). Similarly, when the head is unrestrained, primates make coordinated eye-head gaze shifts for which movements of the eyes and head both demonstrate robust relationships with gaze amplitude (humans: Guitton and Volle 1987; Volle and Guitton 1993; and monkeys: Freedman and Sparks 1997; Morasso et al. 1973; Phillips et al. 1995; Tomlinson 1990; Tomlinson and Bahra 1986a). To date, these prior studies of gaze shift kinematics have, for the most part, focused on horizontal movements. For such movements, there is considerable agreement across studies that gaze and eye velocities saturate as a function of gaze amplitude at  $\sim 400^\circ/\text{s}$  and that eye position saturates at  $\sim 35^\circ$  eccentricity relative to the orbit, whereas head velocity and displacement both increase as a linear function of gaze amplitude.

The head movements that are produced during gaze shifts are not only related to gaze shift amplitude but are also influenced by other factors. For example, the starting position of the eyes relative to the orbits has an important influence on the coordination of eye and head movements during gaze shifts. Head-movement amplitude increases when the eyes are initially deviated in the orbit relative to the direction of the target to be fixated for a given amplitude of gaze shift (Becker and Jurgens 1992; Delreux et al. 1991; Freedman and Sparks 1997; Tomlinson 1990; Volle and Guitton 1993), and thus measured head-movement latencies are shorter (Becker and Jurgens 1992; Fuller 1996; Volle and Guitton 1993). Electrical stimulation of the superior colliculus (SC) (reviewed in Sparks 1999) evokes coordinated eye-head gaze shifts that are kinematically indistinguishable from natural gaze shifts; they are characterized by the same velocity relationships and the relative amplitudes of the eye and head contributions depend on eye position at stimulation onset. Similarly, stimulation of the supplementary eye fields (SEFs) (Martinez-Trujillo et al. 2003, 2005) and frontal eye fields (FEFs) (Monteon et al. 2005; Tu and Keating 2000) can evoke combined movements of the eye and the head that are similar to natural gaze shifts. These findings have been taken as evidence that each of these structures play an important role in planning and/or controlling the head as well as the saccadic components of gaze shifts.

An assumption that is inherent to most prior studies of gaze shifts in head-unrestrained rhesus monkeys, including those reviewed in the preceding text, is that head motion is exclusively generated by the movement of the head relative to body (i.e., activation of the neck musculature). Generally, the design of the primate chair and/or presence of a loosely tethered vest

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have been considered sufficient to prevent significant body movement. Outside of the laboratory setting, however, the visual axis of gaze is often reoriented not only by movements of the eyes and head but also by movements of the body and even of the feet. Thus during eye-head-body gaze shifts, for example, head in space motion results from the activation of the shoulder, abdominal, and back, as well as neck, musculature. The goals of the present study were to characterize eye-head-body coordination during gaze shifts in the rhesus monkey and to determine if movements of the body-in-space, head-on-body, and eye-in-head are governed by predictable relationships. We used a simple well-defined task to establish which factors influence eye-head-body coordination within a typical laboratory setting. Trained rhesus monkeys with unrestrained heads and bodies performed a voluntary gaze shift task in which they were rewarded for aligning their gaze, and not their body per se, with a visual target.

We first established whether body rotation contributes to gaze shifts (amplitudes ranging from 20 to 120°) in a systematic manner so that its movement is part of the coordinated series of motor events that determine how gaze is redirected between objects of interest. In particular, we addressed whether body motion contributes significantly to gaze shifts even in a typical laboratory setting where a monkey is seated in a standard primate chair. Movement kinematics and their relationship to the starting position of the eye relative to the orbit, and head relative to body were assessed. Second, we compared eye-head-body coordination when monkeys made gaze shifts while sitting upright in a standard primate chair with those made when they were allowed to adopt a more natural sitting posture to determine whether coordination of movements was influenced by body posture. Finally, our third objective was to assess the effect of target predictability on eye-head-body coordination during gaze shifts. Predictability of the timing and/or location of target presentation are known to influence the relative timing of eye and head movements as well as their relative amplitudes (Bizzi et al. 1972; Guitton and Volle 1987; Moschner and Zangemeister 1993; Phillips et al. 1995; Zangemeister and Stark 1982a,b), and eye-head coupling is affected when the subject knows that gaze is to be directed in the vicinity of the new visual target for a relatively long period of time or will be followed by further shifts in the same direction (Oommen et al. 2004). Thus we tested the influence of target predictability on body-in-space as well as head-on-body movements made during eye-head-body gaze shifts. Experiments focused on gaze shifts made when the location, but not timing, of the next target was known.

Taken together our findings directly challenge the common assumption of most prior studies of gaze shifts in head unrestrained rhesus monkeys: namely that head motion is exclusively generated by the movement of the head relative to body. We found that even in a typical laboratory setting where a monkey is seated in a standard primate chair, body motion contributes significantly to gaze shifts >40° in amplitude and that the predictable relationships between eye and head movements that had been described in prior investigations (Freedman and Sparks 1997, 2000; Goossens and Van Opstal 1997) can be extended to eye-head-body coordination during gaze shifts. Moreover, our results show that predictable relationships, which govern the coordination of the eye, head, and body movements, are influenced by factors such as initial eye

and head position, and body posture. These findings emphasize that body movement is part of a coordinated series of motor events that determine how we orient gaze, and thus provide new insight into the nature of the motor commands that are normally produced during gaze shifts.

## METHODS

### Animal preparation and experimental setup

Two naïve adult male monkeys (*Macaca mulatta*) were prepared for chronic recording of eye movements. All procedures were approved by the McGill University Animal Care Committee and were in compliance with the guidelines of the Canadian Council on Animal Care. The methods for surgical preparation of the monkeys were similar to those described by Sylvestre and Cullen (1999). Briefly, under general anesthesia and aseptic conditions, scleral search coils were implanted in both eyes of each monkey to monitor gaze position. A stainless-steel bolt was attached to the skull with stainless-steel screws and dental acrylic for restraining the head.

During training and experimental sessions, monkeys were comfortably seated in a stationary chair that was placed in the center of a 1-m<sup>3</sup> magnetic field coil system (CNC Engineering). Experimental sessions were conducted with two different chairs: a standard primate chair and a custom-made primate chair, allowing the monkeys to assume two different but common postures. The standard chair (10 × 10 × 17 in; width × length × height) permitted the monkey to sit perched on its haunches similar to posture adopted while sitting on a tree branch (Fig. 1A, left). In contrast, the custom chair, being larger and shorter (20 × 20 × 9 in), allowed the monkey to adopt a posture comparable to that assumed while sitting on flat earth (Fig. 1A, right). The cervical column was oriented more horizontally in the custom chair such that it was pitched forward ~45°, as compared with 15° in the standard chair. Adult rhesus macaques, while capable of both postures, more

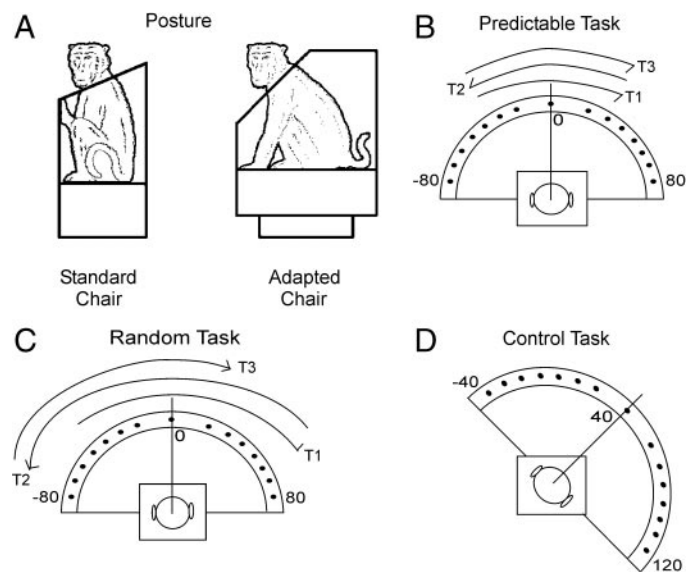


FIG. 1. Behavioral task. *A*: monkeys adopted different body postures in the standard (left) vs. the custom-built adapted (right) chair. *B*: predictable gaze shift task. Subjects fixated an initial target and then a 2nd light-emitting diode (LED) was illuminated on the opposite side of the array at an equal distance from the array midline. The subject then shifted gaze to the new target (T1). This pattern of subsequent targets would alternate between these 2 locations for a total of 8 blocks (i.e., from T2 to T3, etc.). *C*: random gaze shift task. Subjects fixated an initial target and then one of the LEDs on the opposite side of the midline was randomly illuminated (e.g., gaze shifts from T1 to T2, and then to T3). *D*: control array task. Gaze shifts were made as in *C* but with the target set array rotated 40° relative to the body's midline.

commonly adopt the terrestrial posture (Dunbar and Badam 1998), thus our custom chair was designed to encourage animals to adopt this more natural body posture. Each chair was placed in the magnetic field such that the animal's head was centered in the field coils, and the eyes were always at the same distance from the target array. A plastic neck plate confined the monkey to both chairs during the experiment and was angled such that the ability to rotate the neck and shoulders was not compromised.

Gaze, head-in-space, and body-in-space positions were measured using the magnetic search coil technique. Gaze position was measured with the use of scleral coil. The head was positioned in the plane of the horizontal canals irrespective of body posture by means of a specially designed head-holder (Huterer and Cullen 2002) that enabled us to either completely immobilize the animal's head or allowed the monkey to freely rotate its head in the yaw axis. A second search coil was mounted on this head-holder to make measurements of rotational head-in-space position. Monkeys also wore primate jackets (Lomir Biomedical) in which a third search coil was placed at the level of thoracic vertebra 7 ( $T_7$ ) to measure torso position relative to space. Neck muscle activation can produce rotations of the cervical spine (Buford et al. 2002), and these rotations would have confounded our torso rotation measurements. Accordingly  $T_7$  was chosen because it is well below the lowest level of neck muscle insertion ( $T_3$ ) (Szebenyi 1969). Proper placement of the torso coil at  $T_7$  was ensured by using X-rays of both monkeys coupled with spinal palpation, and the coil was calibrated in each posture and a series of control gaze shifts were recorded to confirm that the coil mounted in the jacket provided a reliable measure of torso rotation. Specifically, we simultaneously recorded from the jacket coil as well as from a second coil that was temporarily secured directly to the animals' shaved back (at the level of  $T_7$ ) using a medi-trace adhesive electrode patch from which the metal attachment pin had been removed (Graphics Controls). Velocity and position signals were identical for both coils indicating that the jacket coil relayed an accurate measure of torso rotation relative to space.

Monkeys were trained to fixate small red light-emitting diode (LED) targets, which were located on a semi-circular plane located 55 cm from the eyes, for a juice reward. By convention,  $0^\circ$  was situated directly in front of the monkey when the animal was facing forward. To generate large gaze shifts, targets were spaced, starting at  $\pm 20^\circ$ , every  $10^\circ$  to a maximum eccentricity of  $80^\circ$  on either side of the animal with a central LED at  $0^\circ$ . Thus the largest shift possible between two targets was  $160^\circ$ .

### Behavioral task

Gaze shifts were generated using two different types of target sequences: highly predictable target sequences and random target sequences. Targets from both types of sequences were presented in the same manner; after the monkey maintained fixation of the initial LED target for 1,000–1,900 ms, it was extinguished, and a second LED was illuminated in the contralateral half of the target array. The monkey would then make a gaze shift to the new target. The fixation time for all subsequent targets were also variable, again between 1,000 and 1,900 ms. In trials where predictable target sequences were used, a target at an eccentric location was initially illuminated followed by the illumination of a second target at an equal angle on the opposite side of the mid-line. The selected targets would alternate between these two locations (e.g., from  $-30$  to  $30^\circ$ ) for a 32-s-long sequence (Fig. 1B), such that the location (but not the timing) of the target sequence was predictable. In trials where random target sequences were used, targets were sequentially illuminated at different locations alternating between both sides of the array mid-line (Fig. 1C). Thus the location of the next target relative to the contralateral half of the target array was not predictable and the gaze shifts were achieved in a manner similar to prior studies by Freedman and Sparks (1997, 2000). Trials using both types of target sequences were run

with monkeys sitting in both the standard and adapted primate chairs. Monkeys were only rewarded for trials in which the initial target was fixated within  $\pm 2.5^\circ$  and which ended with gaze falling within  $5^\circ$  of the new target and the target window was captured within 1,100 ms of target onset, regardless of accompanying head or body movements to avoid biasing the types of voluntary movements performed. The juice reward was delivered when the animal's gaze reached the desired target by means of a tube that moved with the animal's head.

A third target condition was used to establish why each animal systematically adopted a particular body position relative to the center target. This paradigm was designed to allow us to determine if the body position bias could be explained by one or both of two possibilities: that the primate chair constrained body movement to this location or the strategy of the animal was to align the preferred body offset close to the center of the target set. In this target condition, the semicircular LED array was shifted by  $40^\circ$  to the right (Fig. 1D). Our rationale was the following: if the structure of the primate chair systematically constrained a monkey's body position to certain angles, then the body offset should remain the same regardless of the target set center. If, instead, each animal's strategy was to align its body with the center of the target array, then the shift in the target array should result in a corresponding shift (i.e.,  $40^\circ$ ) in the average body position. Alternatively, an incomplete shift would suggest an influence of both factors.

### Data collection and analysis

Rex, a QNX-based, real-time data-acquisition system (Hayes et al. 1982), was used to control target position, monitor performance, and collect data at a sampling rate of 1,000 Hz. Data were then imported into Matlab (The MathWorks, Natick MA) programming environment for analysis. Recorded gaze, head-in-space, and body-in-space position signals were digitally filtered with zero-phase at 125 Hz using a 51<sup>st</sup>-order finite-impulse-response (FIR) filter with a Hamming window. The CNC system coil was linear over a range of  $\pm 55^\circ$  (i.e.,  $110^\circ$  of rotation) and nonlinearities in the signals recorded beyond this range were corrected during off-line analysis. The range of linearity was the same for the head search coil, which was centered in the 1-m<sup>3</sup> coil system as well as for the torso coil in both postures. Eye position was calculated as the difference between the recorded gaze- and head-position signals; head-on-body was calculated as the difference between the recorded head-in-space and body position signals. Gaze, eye-in-head, head-on-body, and body-in-space position signals were digitally differentiated to produce velocity signals.

Only gaze shifts that were initiated 120–250 ms after the onset of the new target were included for analysis. Thus anticipatory gaze shifts (e.g., Fischer and Weber 1993; McPeck and Schiller 1994) were not included in our data set. As noted in the preceding text in the description of our behavioral tasks, the timing of target sequences was never predictable in our study. This feature of the paradigm served to minimize the occurrence of anticipatory gaze shifts, so that even in experiments where the location of the target was predictable, they occurred on only  $\sim 7\%$  of the trials for *monkey B* and  $\sim 5\%$  of the trials for *monkey V*.

For large target displacements, monkeys often generated gaze shifts that were comprised of two steps (a large gaze shift followed by a smaller "corrective" gaze shift) to reach the target (Fig. 2B, arrow). In these cases, only the first step of the gaze shift was considered for analysis. To be included in the data set, a given gaze shift needed to constitute  $\geq 95\%$  of the specified movement for gaze shifts  $\leq 70^\circ$ . For larger target amplitudes, this criterion could not be met because generally the monkeys could not visualize the target and so were required to guess (contralateral random trials) or predict (predictable trials) the target location. In these cases, movements of  $\geq 70^\circ$  were considered for analysis. Monkeys were monitored via a video camera throughout the course of each experiment to exclude from subsequent analysis the rare incidents where the feet moved.

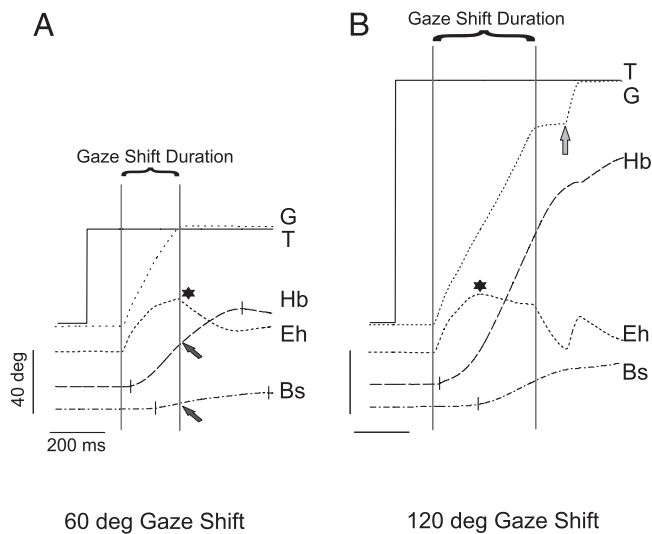


FIG. 2. Example 60° (A) and 120° (B) gaze shifts that were made by *monkey V* in the standard chair and were characterized by marked body movements. *B*: solid gray vertical lines denote gaze shift onset and offset. Black stars represent offset of eye movement contribution to the gaze shift, which is defined as the time when the eye began to move in the direction opposite of intended change in gaze. In both examples, this point corresponded to gaze shift offset. The filled arrows in *A* denote the contributions of head and body movement to the gaze shift, and vertical tick marks denote the onset and offset of each segment's movement. Larger displacements were often achieved by a series of steps; the gray arrow in *B* marks the second step of a multi-step gaze shift. Note, that the 60° gaze shift was made to a visible target, whereas the 120° gaze shift was made to a target that would have been initially outside of the monkey's peripheral vision. *G*, *E<sub>h</sub>*, *H<sub>b</sub>*, *B<sub>s</sub>*, horizontal gaze, eye-in-head, head-on-body, and body-in-space position, respectively. Target position is shown by the solid trace denoted as *T*.

Gaze, eye, and head movement onset and offset were determined using a velocity threshold of 25%/s. Body movement onset and offset were not defined by a velocity threshold. Rather, because body velocities were generally relatively slow, onset was determined with a criterion of velocity exceeding  $\pm 3$  SD of the mean of the noise of the velocity signal in the 90-ms period prior to the gaze shift onset. A comparable analysis of head velocity traces demonstrated that this method similarly estimated onset times that were comparable to those detected by the 25%/s velocity threshold ( $P > 0.1$ ).

The contribution of eye-in-orbit, head-on-body, and body-in-space movements were calculated (interval denoted by the 2 vertical lines in Fig. 2, *A* and *B*) for each gaze shift amplitude. In addition, the total amplitudes of the eye-in-orbit, head-on-body, and body-in-space movements, which were made in association with each gaze shift, were calculated. Toward the end of a gaze shift, the eyes often rolled back toward a medial position in orbit while the head and body continued to move in the direction of the gaze shift. The time at which the eye began moving in the direction opposite to that of the gaze shift was defined as the eye movement offset (Fig. 2, *A* and *B*, black stars), and in turn, total eye amplitude was calculated as the distance traveled by the eye from gaze shift onset until this point. Total head movement amplitude was defined as the amplitude of the head movement that occurred between head movement onset and end [Fig. 2*A*, head displacement (*H<sub>b</sub>*) between the 2 vertical tick marks]. Total body amplitude was similarly defined [Fig. 2*A*, body displacement (*B<sub>s</sub>*) between the 2 vertical tick marks]. Because the head and body continued to move once gaze was stable (Fig. 2*A*, arrows), head and body "amplitudes" were always larger than their respective "contributions" to the gaze shift.

A Student's two-sample *t*-test was used to determine significance between and across different behavioral tasks. For analysis of amplitude-dependent trends, gaze shifts were sorted by amplitude into

separate data sets, each spanning 10° and ranging from 20 to 130°. Over 100 gaze shifts were collected for each amplitude bin for predictable target sequences in both postural conditions. A comparable data set was collected for unpredictable target sequences for gaze shifts  $\leq 110^\circ$ . As noted in the preceding text, the largest gaze shifts were accomplished using a series of multi-step gaze shifts. As a result, single step movements  $> 110^\circ$  were rarely recorded in response to unpredictable target sequences. Nevertheless, we were able to collect some 120° movements for this condition (66 in *monkey B*; 10 in *monkey V*) in the standard posture.

## RESULTS

### Data set and overview

We recorded gaze shifts made by two rhesus monkeys (*monkeys B* and *V*) while they sat with their bodies untethered in either a standard primate chair or a custom-made chair that was designed to allow them to assume a more natural sitting posture (see METHODS). The orienting movements that are considered here include only those for which the positions of the eyes-in-orbit (*E<sub>h</sub>*), head-on-body (*H<sub>b</sub>*) and body-in-space (*B<sub>s</sub>*) were stable prior to the gaze shift. In addition, movements that did not meet our behavioral criteria (see METHODS) were excluded from analysis. In total, the present report is based on the analysis of the 6,667 gaze shifts from *monkey V* and 8,697 gaze shifts from *monkey B* that complied with these requirements.

Figure 2 shows examples of 40° (Fig. 2*A*) and 120° (Fig. 2*B*) eye-head-body gaze shifts made by *monkey V* while seated in a standard primate chair and orienting to targets that appeared at random locations in the contralateral half of the target array (see METHODS). The *two top traces* of each panel show the profiles of target and gaze (= eye-in-space) position; the *bottom traces* show the accompanying displacements of the eye-in-head, head-on-body, and body-in-space. Both example gaze shifts are typical in that they were accompanied by body, as well as eye and head movements. For the larger (120°) gaze shift, the body movement was well underway during the interval where the gaze shift was in progress. In contrast, for the smaller (40°) gaze shift most body movement occurred once the gaze shift had been completed.

During the experimental sessions, the monkey was free to employ any eye-head-body movement strategy it desired to acquire initial fixation of the target and redirect its gaze in space to the new target. In the following text, we describe in more detail the features of the specific strategies which were employed. Initially, we focus on gaze shifts such as those shown in Fig. 2, in which the monkey sat in a standard primate chair and oriented to unpredictable target sequences. We then specifically consider the influence of body posture and target predictability on eye-head-body coordination strategies.

**INITIAL FIXATION STRATEGY.** Theoretically, any number of different combinations of eye, head, and body motions could have been used to acquire initial fixation of targets before gaze shift onset. We found, however, that in both monkeys (Fig. 3, *A* and *B*) most of the gaze redirection was accomplished by rotation of the head (filled squares). For example, to fixate the most eccentric targets (e.g., targets located 80° from center) monkeys made head rotations as large as 60°, such that most of the required gaze redirection was accomplished by rotation of the head on neck. Overall, the amplitude of head rotation was well

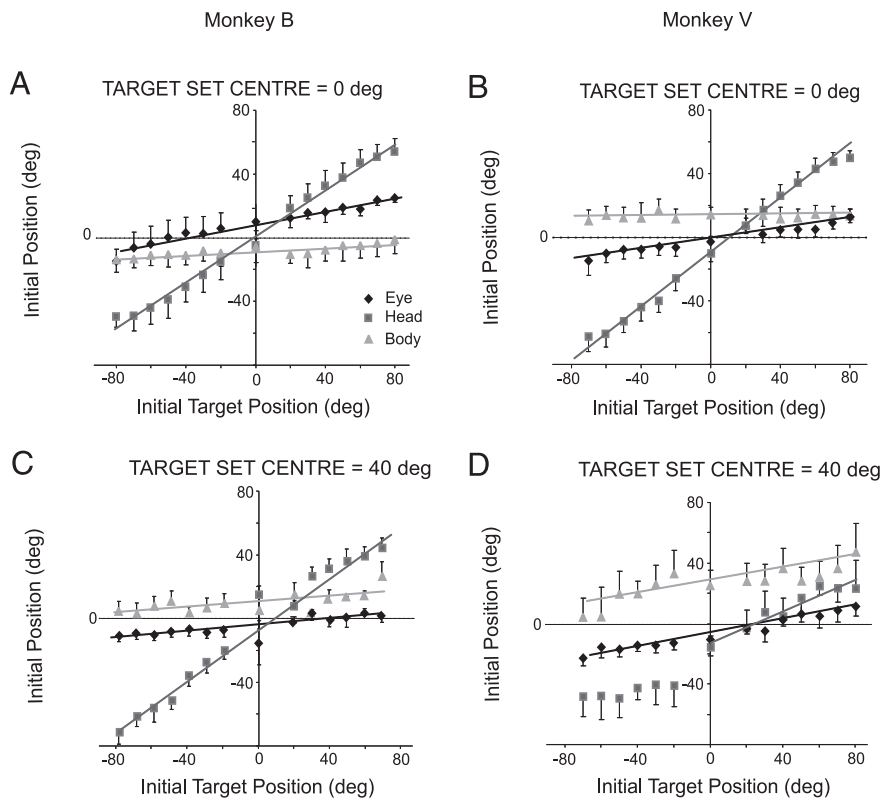


FIG. 3. Initial fixation strategy. Although any number of different combinations of eye, head, and body orientations could have been used to acquire initial fixation of targets, both monkeys used similar strategies. *A* and *B*: average initial eye-in-head (diamonds), head-on-body (squares), and body-in-space positions (triangles) used to acquire initial fixation of targets when the target array was centered relative to the front of the chair. Most of the required rotation was accomplished by rotation of the head-on-body. *C* and *D*: average positions used to acquire initial fixation of targets when the target array was shifted  $40^\circ$  relative to the front of the chair. The animals rotated their bodies such that they were similarly aligned with the center of the shifted array as in *A* and *B*. *A* and *C* and *B* and *D* show results from *monkeys B* and *V*, respectively. In this and subsequent figures, error bars represent SD.

correlated with target eccentricity (*monkey B*:  $R^2 = 0.992$ ; *monkey V*:  $R^2 = 0.994$ ). In contrast, eye position relative to the orbit (diamonds) remained within a relatively restricted range ( $\pm 15^\circ$ ) and tended to deviate only slightly toward the direction of the target with increasing eccentricity (*monkey B*:  $R^2 = 0.96$ ; *monkey V*:  $R^2 = 0.92$ ). For example, *monkey B* rotated its eyes  $15^\circ$  to fixate a target of  $80^\circ$  eccentricity, as compared with only  $5^\circ$  for a target of  $20^\circ$  eccentricity. Mean body position also remained within a limited range of orientations for each monkey. This range was between  $\sim 0$  and  $20^\circ$  for *monkey B* and  $\sim 9$  and  $14^\circ$  for *monkey V*. As was the case for the initial eye and head rotation, initial body rotation increased as a function of target eccentricity (*monkey B*:  $R^2 = 0.75$ ; *monkey V*:  $R^2 = 0.59$ ).

As is evident from Fig. 3, *A* and *B*, the body was initially positioned within a relatively restricted range of orientations (triangles). There are two likely explanations for this observation. On the one hand, it is possible that each monkey's strategy was to align its body near the center of the target array and to deviate it minimally. Alternatively, the design of the chair may have constrained the body to a limited range of positions relative to the chair. To test between these possibilities we carried out an additional experiment in which monkeys made gaze shifts to the same target sequences, when the target array had been rotated by  $40^\circ$  (i.e., the control task presented in Fig. 1*D*, see METHODS). If the animals' body movement was restricted by the chair design, we expected the range of initial body positions (relative to the chair or equivalently space) to be similar between the two sets of gaze shifts (0 and  $40^\circ$  centered arrays). The results of this experiment are illustrated in Fig. 3, *C* and *D*. In this figure, initial target position is measured relative to the center of the shifted target array. Average body position for *monkeys B* and *V* would have been  $-50$  and  $-25^\circ$

respectively, if body position had been restricted by the constraints of the chair. Instead, both animals re-aligned their bodies with the center of the shifted array such that they actually slightly overcompensated for the array's shift; *monkey B*'s average body position was approximately  $+5^\circ$  from the shifted array center (Fig. 3*C*), and *monkey V*'s average body position was  $+25^\circ$  from the new center (Fig. 3*D*). Consequently we conclude that the chair did not impose a specific initial body position but that instead the monkeys employed a strategy in which they rotated their bodies to maintain relatively constant alignment with the center of the target array.

#### Eye-head-body coordination during gaze redirection

Figure 4 shows the trajectories of the gaze, eye, head, and body velocities made during  $40$ ,  $80$ , and  $120^\circ$  gaze shifts while the monkeys sat in a standard primate chair and tracked unpredictable target sequences. Both monkeys used a similar strategy to redirect their gaze, which was characterized by the sequential movement of the eyes, head, and body, respectively. Gaze and eye velocities were initially indistinguishable; their trajectories peaked early at  $\sim 450^\circ/\text{s}$ , then declined to a relatively low velocity of  $\sim 300^\circ/\text{s}$ , and then continued to decrease for the remainder of the gaze shift. The onset of head movement lagged that of eye movement for all gaze shift amplitudes ( $P < 0.05$ ) and did not vary as a function of gaze amplitude ( $P > 0.1$ ). Once initiated, a longer time course was required to reach peak head velocity than peak eye or gaze velocity. Finally, the onset of body movement lagged both eye and head movement for all amplitudes of gaze shifts ( $P < 0.05$ ). Peak velocity was achieved either late in the gaze shift (e.g., see  $120^\circ$  gaze shifts; Fig. 4, *bottom*) or even after the gaze shift (e.g., see  $40^\circ$  gaze shifts; Fig. 4, *top*). Body motion made a

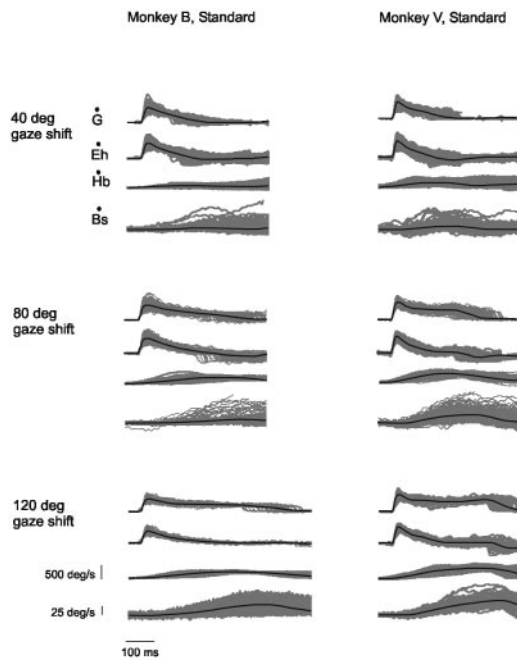


FIG. 4. Gaze shift strategy. Average gaze, eye, head, and body velocity trajectories (dark lines) superimposed on individual trials (light lines) for 40, 80, and 120° amplitude gaze shifts made while monkeys sat in the standard chair and oriented to unpredictable target sequences. Gaze shifts of each amplitude were relatively stereotyped for a given monkey and were characterized by the sequential movement of the eye, head and body (see text).  $G'$ ,  $E_h'$ ,  $H_b'$ , and  $B_s'$ , gaze, eye-in-head, head-on-body and body-in-space velocities, respectively.

significant contribution to redirecting gaze for gaze shift amplitudes  $>40^\circ$  (see Fig. 5, *E* and *F*, below).

**RELATIVE CONTRIBUTIONS OF EYE, HEAD, AND BODY MOVEMENT TO GAZE REDIRECTION.** Figure 5 illustrates the relative contributions and total amplitudes of eye, head, and body movements made during gaze shifts as a function of gaze shift amplitude for both monkeys. The contribution of the eye increased linearly as a function of gaze amplitude for both monkeys for gaze shifts up to  $\sim 60^\circ$  (Fig. 5, *A* and *B*; Table 1). For larger gaze shifts, the eye's contribution then plateaued and/or decreased with increasing gaze amplitude for *monkeys B* and *V*, respectively. Overall, the amplitude of the eye movement's contribution to gaze shifts and the total eye movement made in

TABLE 1. Relationships among amplitude, contribution, and gaze amplitude

Component	Parameter	Equation	VAF
Eye	<i>Monkey B</i> Amplitude	$y = 0.45x + 15.3$	0.96
	<i>Monkey V</i> Amplitude	$y = 0.284x + 15.2$	0.98
Head	<i>Monkey B</i> Amplitude	$y = 60.5\ln(x) - 190.8$	0.94
	<i>Monkey B</i> Contribution	$y = 0.71x - 16.2$	0.99
	<i>Monkey V</i> Amplitude	$y = 53.8\ln(x) - 161.8$	0.95
	<i>Monkey V</i> Contribution	$y = 0.89x - 17.4$	0.99
Body	<i>Monkey B</i> Amplitude	$y = 0.43e^{0.029x} + 0.186$	0.98
	<i>Monkey B</i> Contribution	$y = 0.06e^{0.039x} - 0.067$	0.99
	<i>Monkey V</i> Amplitude	$y = 0.61e^{0.028x} + 0.585$	0.94
	<i>Monkey V</i> Contribution	$y = 0.55e^{0.025x} - 0.914$	0.99

VAF, variance accounted for.

association with gaze shifts were virtually indistinguishable (see Fig. 2). Head movements were found to make a significant contribution to gaze shifts greater than  $\sim 25^\circ$  ( $P < 0.05$ ), and the amount of this contribution was linearly related to gaze shift amplitude over the entire range that was tested (Fig. 5, *C* and *D*, open squares). Similarly, the total head movement amplitude was linearly related to gaze amplitude for gaze shifts  $<90^\circ$  as had been previously reported (see *Eye-head-body coordination is governed by predictable relationships*). We found, however, that this relationship began to plateau for larger amplitude gaze shifts (Fig. 5, *C* and *D*, closed squares). For both monkeys, body movement also made a small, but significant contribution to gaze shifts as small as  $40^\circ$  ( $P < 0.05$ ), and the slope of this relationship increased as a function of gaze amplitude over the range of  $40$ – $120^\circ$  (Fig. 5, *E* and *F*, open triangles). Total amplitude of body movement (Fig. 5, *E* and *F*, closed triangles) showed a similar increase as a function of gaze amplitude over this same range. Comparison of the head and body movement amplitude trends indicated that increases in gaze amplitude beyond  $100^\circ$  were facilitated via recruitment of body movement, as the amplitude of the head movement begins to plateau. Because a monkey's peripheral vision is limited to  $\pm 80^\circ$ , it is important to note that gaze shifts of  $90$ – $120^\circ$  were made to targets that were not visible at gaze shift onset. Nevertheless, the monkeys' prior knowledge of the task ensured that they made gaze shifts that spanned the entire range of possible targets. Notably, there were no marked discontinuities in these kinematics relationships for gaze shifts  $>90^\circ$ . The strategies that were used to make gaze shifts in this amplitude range are further considered below (see Fig. 11).

A well-documented feature of eye-head gaze shifts in humans and rhesus monkeys is that eye position does not exceed approximately  $35^\circ$ , a deviation well short of either species' oculomotor range (i.e.,  $\pm 55^\circ$ ). We found that this observation can be extended to gaze shifts as large as  $120^\circ$ , where the eyes, head, and body move; for both monkeys, the peak eye position saturated at  $\sim 35$ – $37^\circ$  relative to the orbit. In addition, we found that rotations of the head-on-body, like the eye-in-orbit, are constrained by a functional limit during eye-head-body gaze shifts, which lies well within the limits of the physical range. Neck rotations are physically limited by mechanical constraints to between  $\pm 90$  and  $100^\circ$  in humans (Thornton and Jackson 1980), and we verified that comparable limitations exist in rhesus monkeys by passively rotating the head relative to the body. We then compared the amplitude of the head-on-body movement that accompanied gaze shifts of a specific amplitude, when the head began at different positions relative to the body. This analysis was limited to a subset of movements that were made with the eyes centered in the orbit. The results of this analysis are plotted in Fig. 6*A* for the two monkeys. First, as expected, the final position of the head-on-body increased as a function of its initial orientation for a given amplitude gaze shift (i.e., see Fig. 3). Second, and more importantly, final head-on-body position increased toward the ipsi-target side (positive values) as a function of gaze shift amplitude (for a given initial position), until reached a maximal deviation of  $\sim 60^\circ$ , regardless of gaze shift amplitude.

**EYE, HEAD AND BODY VELOCITIES AS A FUNCTION OF GAZE AMPLITUDE.** The results shown in Figs. 5 and 6 establish that body movements make a significant contribution to larger gaze shifts

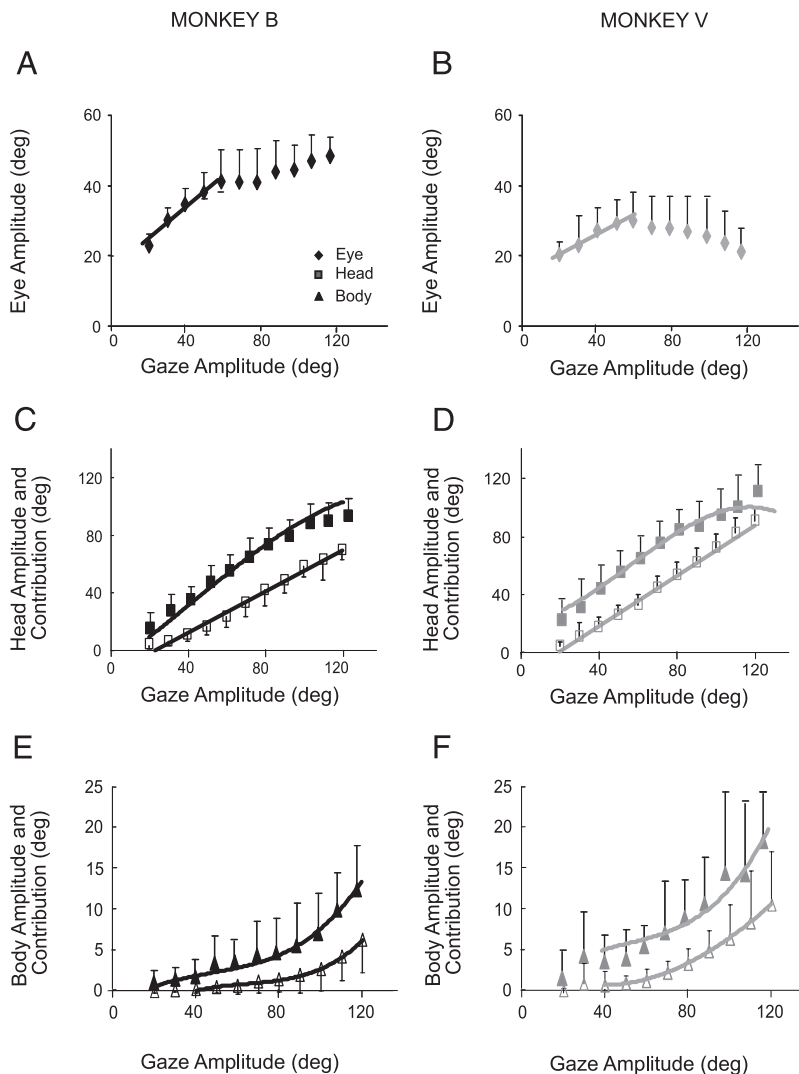


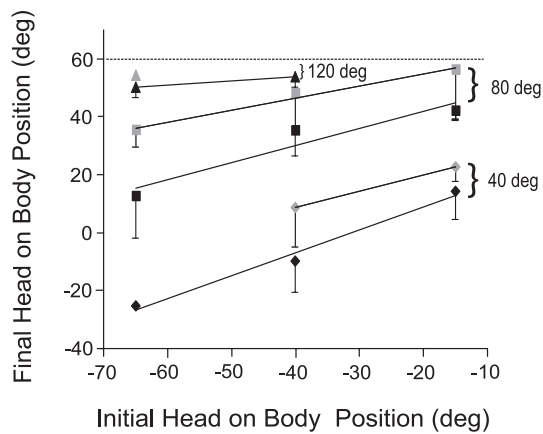
FIG. 5. Total eye movement amplitude (*A* and *B*), total head amplitude and contribution (*C* and *D*), total body amplitude and contribution (*E* and *F*) as a function of gaze amplitude for both animals (contribution, open symbols; amplitude, closed symbols). Gaze shifts  $>25^\circ$  were used to calculate best fit lines for head data and gaze shifts  $>40^\circ$  were used to calculate fits for body data. The functions used to fit each animal's data set are superimposed as —. Equations can be found in Table 1. Logarithmic fits to the relationship between total head and gaze amplitude (*C* and *D*) provided a 7 and 14% increase in variance accounted for (VAF) relative to a linear fit for *monkeys B* and *V*, respectively. Exponential fits to the relationships between body amplitude and contribution, and gaze amplitude (*E* and *F*) provided a 9 and 10% increase in VAF relative to a linear fit for *monkeys B* and *V*, respectively. Note, there was no advantage to using higher-order polynomials for these fits; for example, fitting the same data with a 2nd-order polynomial required the estimation of 3 rather than 2 (Table 1) free parameters while residuals were larger.

and as a result head-on-body rotations typically do not exceed  $\sim 60^\circ$  even for gaze shifts as large as  $120^\circ$ . To further characterize the kinematics of these eye-head-body gaze shifts, relationships between peak movement velocities and amplitudes were quantified over the full range of gaze amplitudes. First, the relationship between peak body velocity and total body amplitude was examined. Peak velocity increased as a linear function of amplitude for the entire range of amplitudes that were tested ( $R^2 = 0.99$  for both *monkeys B* and *V*), indicating that it was well predicted by the amplitude of the body movement. As is shown in Fig. 6*B*, peak body velocity also increased as a function of gaze amplitude. For both monkeys, however, the slope of this relationship increased with increasing amplitude mirroring the rise reported above for total body amplitude and body contribution as a function of gaze amplitude (see Fig. 5, *E* and *F*).

We next quantified the relationships between peak gaze, eye, and head velocities and gaze amplitude. The results of this analysis are plotted in Fig. 7 for both animals. Peak eye velocity (diamonds) did not systematically vary as a function of gaze amplitude ( $P > 0.05$ ) but was relatively fixed at  $\sim 450^\circ/\text{s}$  even for gaze shifts as large as  $120^\circ$ . This plateau was well within the  $300\text{--}550^\circ/\text{s}$  range over which peak eye

velocity plateaus reported previously for gaze shifts  $\leq 90^\circ$  (Freedman and Sparks 1997; Goossens and Van Opstal 1997; Tomlinson and Bahra 1986a,b). The relationship between peak gaze velocity (circles) and gaze amplitude showed similar features. This was not surprising because eye and gaze movements were initially indistinguishable and reached peak velocity near gaze shift onset (see Fig. 4). It is noteworthy that neither eye nor gaze velocity profiles exhibited substantial reaccelerations later in the gaze shift (see DISCUSSION). In contrast, peak head velocity did vary systematically as a function of gaze amplitude. For gaze shifts  $< 90^\circ$ , peak head velocity increased linearly as a function of gaze amplitude (Fig. 7, squares). When the range of gaze shifts was extended to include amplitudes from  $90$  to  $120^\circ$ , peak head velocity began to plateau at velocities of  $\sim 200$  and  $\sim 300^\circ/\text{s}$  for *monkeys B* and *V*, respectively. Taken together, these results indicate that the observed relationships between peak velocities and gaze shift amplitude were analogous to those observed between movement amplitudes and gaze shift amplitude; as peak head velocity began to plateau as a function of gaze amplitude, peak body velocity increased exponentially, suggesting a trade off in the contribution of these two body segments to the overall gaze movement.

### A Head-on-Body Position



### B Body Velocity

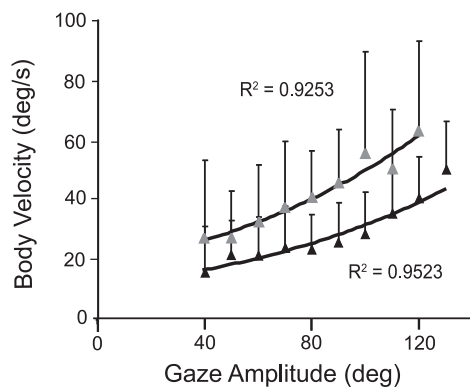


FIG. 6. *A*: final head position is plotted as a function of initial head position for *monkeys B* (black symbols) and *V* (gray symbols). Three initial head-on-body positions were chosen:  $15^\circ (\pm 5^\circ)$ ,  $40^\circ (\pm 5^\circ)$ , and  $65^\circ (\pm 5^\circ)$  and compared for 3 amplitudes of gaze shifts (i.e., 40, 80, and  $120^\circ$ ) in which the head moved in the opposite direction. Mean final head position is plotted  $\pm$  SD.  $R^2$  values for regressions were 0.917 and 0.986 for gaze shifts of  $80^\circ$  for *monkeys B* and *V*, respectively, and 0.984 for  $40^\circ$  amplitude gaze shifts in *monkey B*. Both animals' final head-on-body position never exceeded  $60^\circ$ . Note, as a result of the monkeys' initial fixation strategy, it was impossible to collect  $>10$  gaze shifts in some conditions. *B*: average peak body velocity plotted as a function of gaze shift amplitude. Data are shown for *monkeys B* (black triangles) and *V* (gray triangles). Correlation coefficients are provided. Exponential fits to the relationships between body velocity and gaze amplitude provided a 3 and 6% increase in VAF relative to a linear fit for *monkeys B* and *V*, respectively. Means  $\pm$  SD. Bin width =  $10^\circ$ . The functions used to fit each animal's data set are superimposed as solid lines. Equations are as follows, for *monkeys B* and *V*, respectively:  $y = 3.17e0.0186x + 10.04$  (VAF: 0.956),  $y = 17.91e0.0104x - 0.497$ ; (VAF = 0.941).

#### Effects of initial eye, head, and body position on movement amplitudes

Prior studies of eye-head gaze shifts have shown that the starting position of the eyes relative to the orbits has an important influence on the coordination of eye and head movements during gaze shifts (see INTRODUCTION). To test whether it might similarly be possible to predict the kinematics of large gaze shifts if initial eye-in-orbit and head-on-body positions are known, we first analyzed gaze shifts for which initial eye-in-orbit position was held constant at two different positions [contralateral to target by  $10 \pm 2^\circ$  (contra 10), and  $30 \pm 2^\circ$  (contra 30)]. Initial body position was held constant by

excluding trials for which its initial position did not fall within  $-10^\circ (\pm 5^\circ)$  and  $0^\circ (\pm 5^\circ)$  of target center for *monkeys B* and *V*, respectively (to account for each animal's natural offset to optimize the number of trials meeting restrictions, see Fig. 3). As shown in Fig. 8 (*A* and *B*), the eye's contribution to the gaze shift increased when it began more eccentric relative to the center of the orbit. Table 2 shows the linear relationship between eye, head, and body contributions and gaze amplitude. As orbital eccentricity increased, both head and body contributions decreased for the same amplitude of gaze shift as compared with head and body contributions when the eye was less eccentric. This was confirmed by finding that the  $x$  intercept of the best fit lines defining the relationship of each segment's contribution to gaze amplitude was greater when the eye was more eccentric in the orbit. In addition, slopes for the relationship between head and body contributions and gaze amplitude were generally smaller for the more eccentric eye-in-orbit condition, again consistent with the conclusion that gaze shifts, which were initiated with the eye more eccentric in the orbit, are accompanied by smaller head and body movements.

We next assessed whether the initial position of the head relative to the body influenced the coordination of eye, head, and body movements during gaze shifts. We first predicted that the head, like the eye, should make a larger and faster contribution

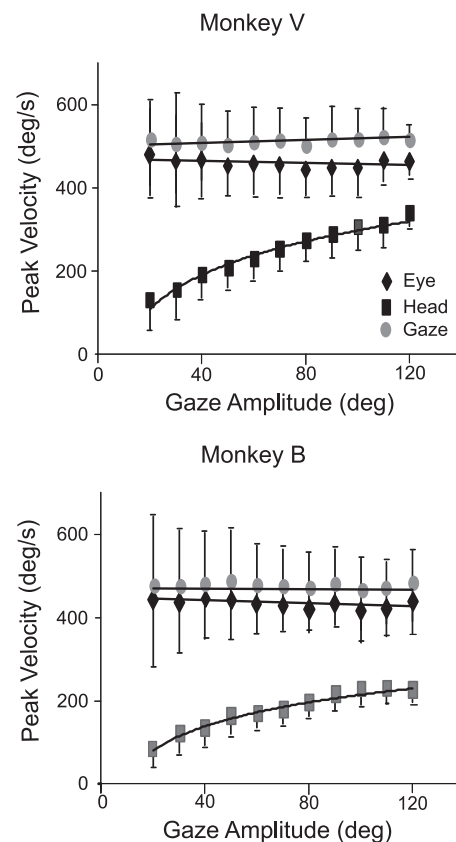


FIG. 7. Average peak gaze (circles), eye (diamonds), and head (squares) velocity plotted as a function of gaze shift amplitude. Peak gaze and eye velocities remained constant across the entire range of gaze amplitudes ( $20$ – $120^\circ$ ). Peak head velocity increased as function of gaze amplitude and then plateaued for gaze amplitudes  $>90^\circ$  at  $\sim 200$  and  $\sim 300^\circ/\text{s}$  for *monkeys B* and *V*, respectively. Logarithmic fits to this relationship provided a 1.3 and 6% increase in VAF relative to a linear fit, for *monkeys B* and *V*, respectively. Means  $\pm$  SD. Bin width =  $10^\circ$ .



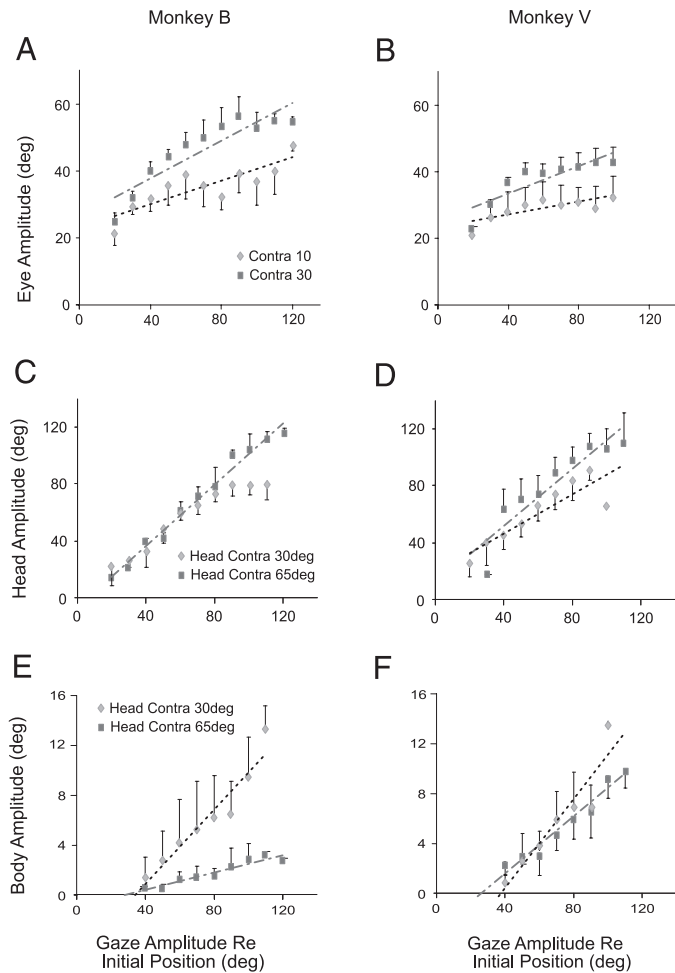


FIG. 8. Effect of initial conditions. *A* and *B*: eye amplitude plotted as a function of gaze amplitude. Movements were made with the eyes starting at 2 different orbital eccentricities,  $10 \pm 2^\circ$  (diamonds) or  $30 \pm 2^\circ$  (squares) contralateral to the target. The lines of best fit are superimposed on the data. *Monkey B*:  $y = 0.17x + 23$ ,  $R^2 = 0.71$  ( $10^\circ$  eccentricity) and  $y = 0.28x + 26$ ,  $R^2 = 0.83$  ( $30^\circ$  eccentricity). *Monkey V*:  $y = 0.1x + 23$ ,  $R^2 = 0.57$  ( $10^\circ$  eccentricity) and  $y = 0.2x + 25$ ,  $R^2 = 0.73$  ( $30^\circ$  eccentricity). A comparison of head amplitude (*C* and *D*) and body amplitude (*E* and *F*) for gaze shifts in which the head started at different initial positions relative to the body, always in the contralateral direction relative to the target. Data are shown for gaze shifts in which the head was initially rotated either  $25\text{--}35^\circ$  (contra 30; diamonds) or  $60\text{--}70^\circ$  (contra 65; squares) relative to the body. All movements were made with the eyes initially centered in the orbit, and initial body position at  $10 \pm 5^\circ$  and  $0 \pm 5^\circ$  relative to target center, for *monkeys B* (*C* and *E*) and *V* (*D* and *F*), respectively. The lines of best fit are superimposed on the data. Head amplitude for  $60\text{--}70^\circ$  rotations:  $y = 1.1x - 7$  for *monkey B* ( $R^2 = 0.98$ );  $y = 1.0x + 11.8$  for *monkey V* ( $R^2 = 0.85$ ), Head amplitude for  $25\text{--}35^\circ$  rotations: regression comparable to that of the  $60\text{--}70^\circ$  data for *monkey B* until relationship saturation at  $\sim 80^\circ$ ;  $0.69x + 19.4$  ( $R^2 = 0.78$ ) for *monkey V*. Body amplitude for  $60\text{--}70^\circ$  rotations:  $y = 0.15x - 5.1$  ( $R^2 = 0.91$ ) for *monkey B*;  $y = 0.18x - 6.7$  ( $R^2 = 0.87$ ) for *monkey V*. Body amplitude for  $25\text{--}35^\circ$  rotations:  $y = 0.03x - 1$  ( $R^2 = 0.91$ ) for *monkey B*;  $y = 0.11x - 3$  ( $R^2 = 0.96$ ) for *monkey V*.

bution during large gaze shifts in which the head began more eccentric to the target. To test this, a comparison was made between gaze shifts for which the head was rotated either  $25\text{--}35^\circ$  (contra 30) or  $60\text{--}70^\circ$  (contra 65) relative to the body midline (head-on-body) at the initiation of the gaze shift. Analysis was limited to gaze shifts for which initial eye position was within  $10^\circ$  of center position and initial body position was  $-10^\circ$  ( $\pm 5^\circ$ ) and  $0^\circ$  ( $\pm 5^\circ$ ) relative to target center,

for *monkeys B* and *V*, respectively. Table 2 shows the linear relationship between eye, head and body contributions and gaze amplitude from this analysis. As shown in Fig. 8, *C* and *D*, large gaze shifts ( $>90^\circ$ ) that were initiated with the head more eccentric relative to body midline were accompanied by larger head movements, as was predicted. Furthermore, for *monkey V*, the head contribution to smaller gaze shifts also depended on its initial deviation relative to the body.

Our second prediction was that, in contrast to head-on-body movement, body-in-space movement would make a smaller contribution during gaze shifts in which the head began more eccentric to the target. This would be a logical strategy for the monkey to adopt, since when the head begins more eccentric to the body, a smaller body movement for a given amplitude gaze shift would allow the head and body to become more closely aligned by gaze shift end. Again a comparison was made between gaze shifts for which the head was rotated either  $\sim 30$  or  $\sim 65^\circ$  relative to the body midline (head-on-body) at the initiation of the gaze shift. Data are plotted for *monkeys B* and *V* in Fig. 8, *E* and *F*, respectively. *Monkey B*'s response matched the prediction such that the body's contribution to the gaze shift decreased when the initial head position was more eccentric relative to body midline. Results in *monkey V* showed a similar but less striking trend.

#### Influence of posture on eye-head-body coupling

We next addressed whether eye-head-body coordination might change as a function of sitting posture. We compared

TABLE 2. Effect of initial conditions on contributions to gaze shifts

Parameter	Initial Eye Position		Initial Head Position	
	Contra 10	Contra 30	Contra 30	Contra 65
<i>Monkey B</i>				
<i>n</i>	354	272	127	48
Eye contribution				
R	0.71	0.83	0.64	0.72
Slope	0.17	0.28	0.07	-0.095
X-int	-135.9	-93.6	-437	484.5
Head contribution				
R	0.89	0.92	0.96	0.96
Slope	0.8	0.71	0.81	0.98
X-int	28.3	36.8	23.1	33.1
Body contribution				
R	0.37	0.78	0.52	0.55
Slope	0.064	0.037	0.077	0.022
X-int	46.2	45	44.8	47.6
<i>Monkey V</i>				
<i>n</i>	971	110	71	60
Eye contribution				
R	0.57	0.73	0.56	0.42
Slope	0.096	0.21	-0.14	-0.12
X-int	-240.6	-118.6	202.9	290.6
Head contribution				
R	0.91	0.94	0.89	0.95
Slope	0.87	0.8	1	1.03
X-int	24.2	34.1	20.3	26.7
Body contribution				
R	0.33	0.59	0.63	0.78
Slope	0.074	0.088	0.095	0.092
X-int	34.5	50.33	44.2	51.2

*n*, number of trials; X-int, *x* intercept; Contra, contralateral.

gaze shifts made in a standard primate chair with those made in a custom chair that was designed to facilitate a more natural sitting posture (see METHODS and Fig. 1A). In the more natural posture, body movements were achieved by the animal rotating its shoulders while its forelimb paws remained on the ground. This behavior was comparable to that observed when the monkey oriented for treats when sitting on the floor of its home cage. To determine whether the monkey's sitting posture altered the coordination of eye-head-body movements, the relationships between the movements of each body segment and gaze amplitude were quantified. First, we compared the amplitudes of eye, head, and body movements that were made in both postures. In Fig. 9, A–C, the amplitude of each movement is plotted as a function of gaze amplitude for *monkey B* (black symbols) and *monkey V* (gray symbols). To

facilitate comparison across the two conditions, the lines of best fit from gaze shifts made in a standard primate chair (solid lines, see Fig. 5) and the data from gaze shifts made in the adapted chair (symbols) are superimposed. Eye movement amplitude was greater in the standard than adapted chair for gaze amplitudes  $>80^\circ$  in *monkey B* (Fig. 9A;  $P < 0.05$ ) and for the entire range of gaze shift amplitudes in *monkey V* ( $P < 0.001$ ). Head-on-body amplitude showed the opposite trend in both monkeys; head movement amplitudes were greater in the adapted chair for all gaze shift amplitudes (Fig. 9B;  $P < 0.001$  and  $P < 0.01$  for *monkeys B* and *V*, respectively). In contrast, the amplitude of body movement was comparable in the two conditions (Fig. 9C;  $P > 0.1$  and  $P > 0.5$  for *monkeys B* and *V*, respectively). Taken together, these results suggest that there is a trade-off in the relative contribution of eye and the head movement to gaze reorientation for these two postures.

The effect of posture on eye-head-body coordination was further quantified by comparing the peak velocities of the eye, head and body in the two conditions. Figure 9, D–F, plots peak velocities as a function of gaze shift amplitude. The effect of posture on peak movement velocities was similar to its effect on movement amplitude. Peak head velocities were significantly larger for both animals in the adapted chair (Fig. 9E;  $P < 0.01$ ,  $P < 10^{-4}$ ). Thus monkeys not only generated more head-on-body movement in the adapted chair (Fig. 9B), but their head movements were faster (Fig. 9E). In contrast, peak body velocities, like body amplitudes, were not altered by differences in posture (Fig. 9F;  $P > 0.1$ ,  $P > 0.1$ ). The only discrepancy between the two animals' behavior was in the effect of posture on peak eye velocity. Peak eye velocities were systematically greater for *monkey B* in the adapted chair (Fig. 9D;  $P < 0.001$ ), whereas for *monkey V*, peak eye velocities in the adapted chair were only marginally slower (i.e., gaze shifts  $<80^\circ$ ;  $P < 0.05$ ) or comparable (i.e., gaze shifts  $\geq 80^\circ$ ;  $P > 0.05$ ) to those generated while sitting in the standard chair.

In summary, although body kinematics were not influenced when the monkey sat in a more natural posture, differences in sitting position did influence the strategy of eye-head coordination that was employed. One possible explanation for this difference is that the monkeys were better balanced in the adapted chair, and as a result were more likely to move their head on their bodies (see DISCUSSION). This increase in head movement further implies that the eye remained more centered in the orbit during gaze shifts in this condition. Indeed, this is what was observed; initial eye position was significantly less eccentric in the adapted chair ( $P < 10^{-6}$  for *monkey B*,  $P < 0.001$  for *monkey V*).

#### Influence of target predictability on eye-head-body coupling

To determine whether target predictability altered eye-head-body coupling during orienting gaze shifts, we compared the kinematics of gaze shifts made to fixate random versus predictable target sequences. Targets were sequentially illuminated at locations alternating between both sides of the array mid-line. For simplicity, we termed these gaze shifts unpredictable but emphasize that they were unpredictable relative to the contralateral half of the target array (see METHODS). Prior studies of eye-head gaze shifts had demonstrated that head movement velocity and initiation is relatively faster for predictable targets (Bizzi et al. 1972; Guitton and Volle 1987;

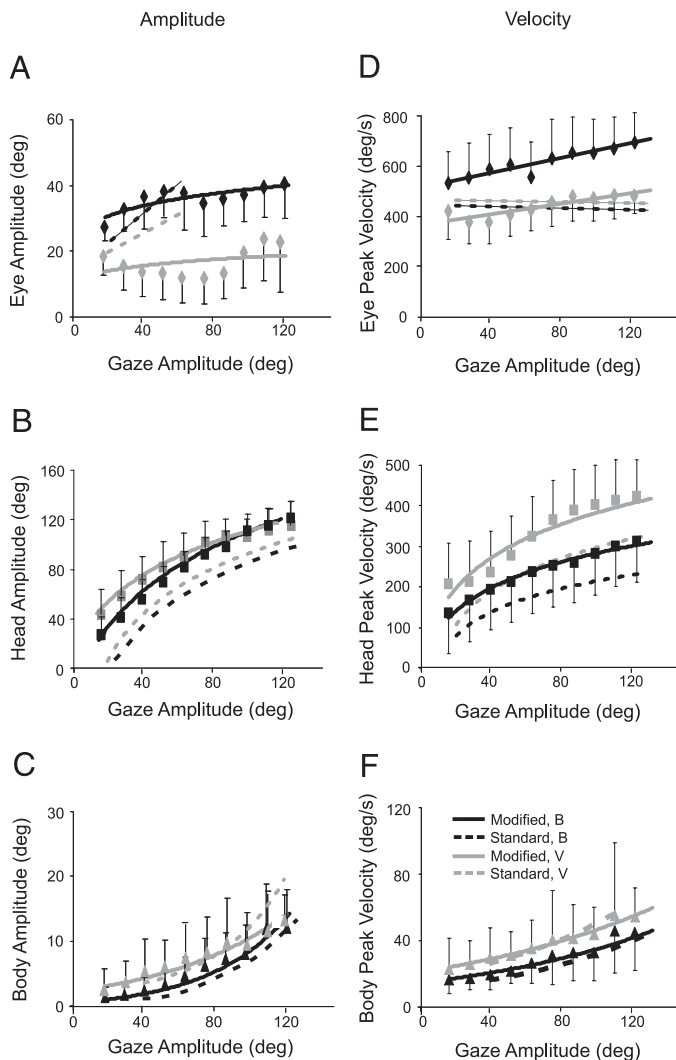


FIG. 9. Effect of posture on eye, head, and body amplitude and velocity during gaze shifts. Horizontal eye, head, and body amplitudes and velocities plotted as a function of gaze shift amplitude for movements made while monkeys were seated in an adapted chair that allowed them to adopt a more natural sitting position. The fits from movements made in a standard primate chair are superimposed as ---. A–C: eye-in-head (A), head-on-body amplitude (B), and body-in-space (C) amplitude and as a function of gaze amplitude. D–F: eye-in-head (D), head-on-body amplitude (E), and body-in-space (F) velocity and as a function of gaze amplitude. *Monkey B* data are represented by black symbols, *monkey V* data by gray symbols. Means  $\pm$  SD. Bin width =  $10^\circ$ .

Moschner and Zangemeister 1993; Phillips et al. 1995; Zangemeister and Stark 1982a,b). By extension, we expected that the initiation and velocity of both head and body movements would be faster for highly predictable target sequences. Gaze shifts elicited by unpredictable target sequences have been described in detail in the preceding text (i.e., Figs. 2–9). Gaze shifts to spatially predictable target sequences were made in which the cued target alternated between two equal and opposite locations on either side of the mid-line. Because the timing of the target presentation was not predictable, the occurrence of anticipatory gaze shifts was minimized (see METHODS). However, monkeys could theoretically make predictive or biasing head and/or body movements without penalty.

The summary curves showing the main findings from our analysis of gaze shifts to random versus predictable target sequences are plotted in Fig. 10. Data are shown for *monkey B*, and comparable results were obtained from *monkey V*. Consistent with prior reports, the latency of head movement onset was significantly shorter when tracking predictable target sequences for gaze shift amplitudes which were smaller than  $90^\circ$  (Fig. 10A;  $P < 0.01$ ). For gaze shift amplitudes  $>90^\circ$ , where the monkey would not have been able to visualize the target (see *Gaze accuracy*), head latency values were comparable for random and predictable trials (*monkey V*,  $P > 0.05$ ; *monkey B*,  $P > 0.05$ ). Interestingly, the initiation of both head and body movements followed gaze shift onset during tracking of predictable as well as unpredictable target sequences. It is likely that anticipatory head/body movements would have been more prominent for predictable target sequences if the timing of target presentations had not been variable (see DISCUSSION).

Total head amplitudes (Fig. 10B) and peak velocity (C) also differed for predictable versus random target sequences (amplitude:  $P < 0.001$ ,  $P < 0.05$ ; velocity:  $P < 0.05$ ,  $P < 0.01$  for *monkeys B* and *V*, respectively), such that head movements were significantly larger and faster when the target sequence was predictable. In contrast, none of body latency, amplitude, or peak velocity was significantly different for either monkey (Fig. 10, A–C, respectively; latency:  $P > 0.5$ ,  $P > 0.5$ ; amplitude:  $P > 0.1$ ,  $P > 0.05$ ; velocity:  $P > 0.05$ ,  $P > 0.5$  for *monkeys B* and *V*, respectively). Thus the changes in the initiation and velocity of head movements observed in our experiments were not mirrored by corresponding changes in body movements.

#### Influence of target predictability on gaze accuracy

The peripheral vision of a rhesus monkey fixating forward has a range of approximately  $\pm 80^\circ$  (Van Essen et al. 1984). In our experiments, monkeys tended to align their heads with the initial target keeping their eyes approximately centered relative to the orbit (see Fig. 3). Accordingly, for target displacements greater than  $\sim 80^\circ$ , the target would have been outside of their field of view. These observations then raise two important questions: first how accurate are gaze shifts that are made to the periphery versus more central targets, and second what strategy do monkeys use to make gaze shifts to targets that cannot be seen?

To address these issues, we plotted gaze amplitude as a function of target displacement in Fig. 11. Data from random target sequence trials (black lines) and predictable sequence trials (gray lines) were superimposed. For both animals, target accuracy during random trials substantially declined for gaze

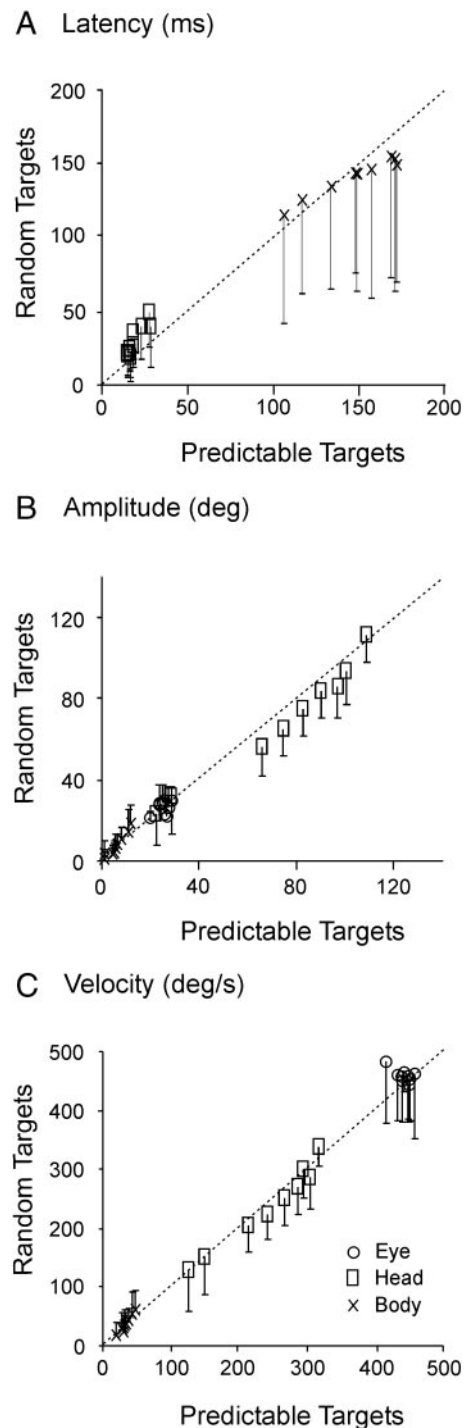


FIG. 10. Summary of the effects of target predictability on gaze shift kinematics. Comparison of the latency relative to gaze shift onset (A), amplitude (B), and peak velocity (C) of eye (circle), head (square), and body (cross) movements made during gaze shifts to unpredictable vs. predictable target sequences. Data are shown for *monkey B*. Head latency was significantly shorter for predictable gaze shifts  $<90^\circ$ . Head amplitudes and velocities were greater for predictable targets than for random targets. Each point represents the mean  $\pm$  SD of a  $10^\circ$  wide gaze amplitude bin. The dotted line represents the unity line.

shifts more than  $\sim 70^\circ$  amplitude such that the gaze shift undershot the target. In addition, the average amplitude of the first gaze shift made to fixate target displacements spanning

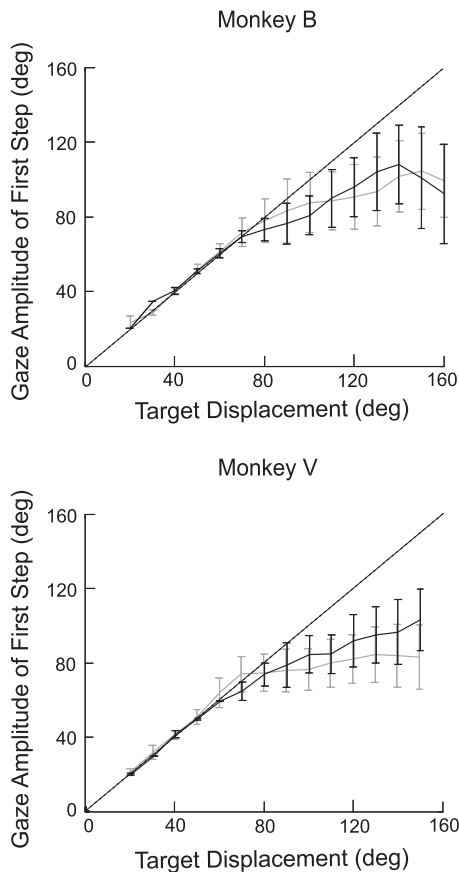


FIG. 11. Gaze accuracy. The gaze amplitude of the first step of a multi-step gaze shift is plotted as a function of target displacement for gaze shifts where the eye was initially centered in orbit ( $\pm 7^\circ$ ). Accurate gaze shifts would lie along the dotted unity line. During both unpredictable (black line) and predictable (gray line) target sequences to large target eccentricities (i.e.,  $>80^\circ$ ), the target would fall outside of the visual field of the animals. Accordingly the accuracy of gaze shifts decreased and the amplitude became more variable. Each point represents the mean  $\pm$  SD of a  $10^\circ$  wide gaze amplitude bin.

$70\text{--}160^\circ$  eccentricities was relatively constant (i.e.,  $\sim 70^\circ$ ) in both animals. Accordingly, gaze shifts  $>70^\circ$  were generally performed by generating additional movements (i.e., multiple step gaze shifts). In predictable trials, the animals' alternated their gaze between the same two targets and as a consequence theoretically knew the location of the next target. Thus we predicted that gaze would be more accurate even for target displacements  $>70^\circ$ . Knowledge of the future target location, however, did not guarantee accurate gaze shifts. This was demonstrated by the fact that *monkey V* took advantage of knowledge of future targets by making less hypometric gaze shifts to increase the size of the initial step from an amplitude of  $70^\circ$  to a plateau at  $\sim 90^\circ$ . In contrast, *monkey B* performed in the same manner regardless of the predictability of the target sequence. Thus while monkeys can take advantage of their knowledge of future target location to plan gaze shifts outside of their visual field, they did not consistently take full advantage of this possibility within the constraints of our experimental design (see METHODS).

## DISCUSSION

The main goal of this study was to establish whether the coordination of eye, head, and body movements is governed by

predictable relationships during gaze shifts. The principal findings were that the body contributes to gaze shifts in a systematic manner, such that it is part of a coordinated series of motor events that determine how we orient between objects of interest; in a typical laboratory setting where a monkey is seated in a standard primate chair, body motion contributes significantly to gaze shifts  $>40^\circ$  in amplitude; the coordination of eye-head-body gaze shifts is influenced by body posture; when monkeys are allowed to adopt a more natural sitting posture, head-on-body movements are faster; movements of the head-on-body are faster and larger for predictable than for random target sequences indicating that the coordination of eye-head-body gaze shifts is influenced by target predictability.

### *Why move the eye, head, and body to reorient gaze?*

Prior studies have shown that head motion accomplishes an increasingly greater percentage of eye-head gaze shifts for target displacements  $>40^\circ$  and as a result the eyes usually remain within  $\sim 35^\circ$  of center position (Bizzi et al. 1971; Barnes 1981; Freedman and Sparks 1997; Guitton and Volle 1987; Roy and Cullen 1998; Tomlinson and Bahra 1986; Zangemeister and Stark 1981, 1982a,b). The results of the present study (Fig. 6) extend this finding by showing that eye position remains within this same range even for gaze shifts as large as  $120^\circ$ . Likewise, we found that monkeys typically did not move their head more than approximately  $\pm 60^\circ$  relative to their bodies during large gaze shifts. Thus the rotation of the eye-in-orbit and head-on-body remains well within the physical limits of ocular (approximately  $\pm 50^\circ$ ) (Lauritis and Robinson 1986; Tomlinson and Bahra 1986) and neck motility ( $\pm 90^\circ$ ) (Thornton and Jackson 1980) during large eye-head-body gaze shifts.

The obvious question that arises from this finding is: if gaze redirection could have been accomplished by the use of the eyes and head alone, why did the monkeys choose to rotate their body at all, particularly because it requires considerable work to overcome the body's large inertial load? We propose that an advantage inherent to using body movement to shift gaze is that it helps to center the eyes in the orbit and the head on the body. Accordingly, the movement of body allowed both the eye and head deviation to remain within comfortable ranges, while facilitating the redirection of gaze toward a target of interest. It is likely that this eye-head-body gaze reorientation strategy possesses the teleological advantage of ensuring when a second object of interest appears in the vicinity of a current target, a subject can more rapidly align its gaze with the new object since a smaller effort will be required to rotate the eyes (as compared with the head) (Peng et al. 1996; Zangemeister et al. 1981), or—if required—to rotate the head-on-body as compared with body-in-space.

### *Eye-head-body coordination is governed by predictable relationships*

The findings of the present study provide several lines of evidence that the contribution of body movement to gaze shifts is part of a coordinated series of motor events. First, we found that the onsets of eye, head, and body movements were sequential and stereotyped. Our findings agree well with those of previous studies of eye-head gaze shifts to unpredictable

targets, for which head movements typically lag eye movements (see Guitton 1992) as well as with studies of whole body turns in humans, for which eye, head, body, and foot movements are recruited in succession (Hollands et al. 2004). Evidence from single-unit recording and stimulation experiments in monkeys have shown that neurons in the intermediate layers of the SC provide an important drive to head and eye premotor pathways to produce eye-head gaze shifts (reviewed in Sparks 1999). The proposal is consistent with the observation that activation of the neck musculature and eye movements are strongly coupled during head-restrained saccades (André-Deshays et al. 1991; Bizzi et al. 1971; Corneil et al. 2002, 2004; Lestienne et al. 1984) and eye-head gaze shifts (Bizzi et al. 1971; Zangemeister and Stark 1982a). Furthermore, the results of more recent experiments have shown that the activation of neck muscles generally occurs before gaze shift onset (i.e., Corneil et al. 2004) and is temporally locked to the appearance of a novel target. This suggests that head movements are controlled by the recruitment of the low-threshold tectoreticulospinal pathway, which is independent of the brain stem saccadic burst generator that controls eye movements (see discussion in Corneil et al. 2004). The differential gating of collicular drive to the premotor pathways for eye and head movements facilitates force development at neck muscles, thereby optimizing the contribution of the relatively higher inertial head to shifting gaze. We propose that the activation of the muscle groups that rotate the body, like those that activate neck muscles, are coupled with the onset of eye movements during large gaze shifts and that this activation, like that of the head, is likely to occur via pathways that are independent of the brain stem saccadic burst generator.

Second, our results extend those of previous studies that have described predictable relationships between eye and head movements (e.g., Freedman and Sparks 1997; Morasso et al. 1973; Phillips et al. 1995; Tomlinson 1990; Tomlinson and Bahra 1986a) to the gaze shifts in which movements of head-in-space are composed of head-on-body and body-in-space rotations. We found that amplitude of head-on-body rotation saturated for gaze shifts  $>90^\circ$  (Fig. 5) and that this was offset by the exponential relationship between gaze amplitude and body movement. We also found that gaze shifts that were initiated with the eye more eccentric in the orbit were accompanied by smaller body as well as head movements (Fig. 8). This latter observation confirms and extends the results of the prior investigations of the influence of orbital eccentricity on eye-head coordination (Freedman and Sparks 1997, 2000; Goossens and Van Opstal 1997) but differs from those of Gandhi and Sparks (2001), who reported that initial head position does not appear to influence eye-head coupling. Taken together, our finding that eye-head-body coordination can be described by predictable relationships lends further support to the proposal that the premotor control of eye, head, and body movements is not only synchronized but is coordinated to redirect gaze in space. Possible mechanisms that could underlie coordination of these multi-segmental movements are considered below (see *Substrates for coordinating eye-head-body gaze shifts*).

### *Influence of posture on the coordination of eye-head-body movements*

We found that although body movement kinematics did not change as a function of sitting posture, total head amplitude was larger and eye amplitude was smaller when monkeys sat in the adapted primate chair. Hence it is likely that more arboreal postures enhance stabilizing systems that would make moving large masses, such as the head and torso, undesirable. On the other hand, terrestrial postures that have greater stability for the lower body could facilitate head movement. Previous work in monkeys has shown that different head postures change the timing and activation of neck muscles for similar amplitude movements (Corneil et al. 2001; Thomson et al. 1994). There are at least two possibilities, which are not mutually exclusive, that could account for the differences in the relative activation of neck muscles in these two conditions: differential suppression of neck reflexes and/or changes in the mechanical properties of the head that necessitate the modification of the pattern of muscle activation to rotate the head in the same direction.

Consistent with the first possibility, it has been proposed that the relative efficacies of the vestibulo-collic reflex (VCR) and/or cervico-collic reflex (CCR) pathways might be influenced by posture (Land 2004; Solomon et al. 2002). The VCR and CCR stabilize unexpected head movements with respect to space or with respect to the trunk (reviewed in Peterson 1988), and there is evidence the signals carried by VCR pathways differ during active versus passive head movements (Boyle et al. 1996; McCrea et al. 1999; Roy and Cullen 2001, 2004). However, given that VCR and CCR gains are minimal in normal rhesus monkeys and humans (reviewed in Cullen and Roy 2004), it is unlikely that the differential modulation of these reflexes as a function of posture would play a primary role in altering the coordination of head and body movements.

A second possible explanation is that the head command that signals the pattern of muscle activation is influenced by the animal's specific posture. In our experiments, monkeys made horizontal head movements with the cervical column oriented vertically in the standard chair and more horizontally in our adapted chair. Previous studies in cats have compared electromyographic patterns of muscle activation during horizontal head rotations, with the cervical column in different orientations (Thomson et al. 1994). Posturally invariant patterns of activation were observed in one set of muscles, whereas a second group of ancillary muscles were activated in a posturally dependent manner. A more recent study in rhesus monkeys has shown that neck movements of similar amplitudes but starting in different postures are also associated with systematic variations in timing and magnitude of neck muscle activation (Corneil et al. 2001). Thus it is likely that in the present study, differential patterns of muscle activation occurred in the ancillary muscles between postures, which resulted in differences in the ensuing movement kinematics. Future studies will be required to determine whether the differential activation of neck proprioceptors helps to shape the motor commands that are issued by these structures as a function of posture.

### *Does target predictability alter the coordination of eye-head-body movements?*

Our results show that the movement of the body, like that of the head, contributes to large gaze shifts in a systematic

manner when monkeys attended to unpredictable target sequences. Previous studies of combined eye-head gaze shifts have shown that head-movement velocity and initiation are influenced by target predictability; they are relatively faster for more predictable target sequences (Bizzi et al. 1972; Guitton and Volle 1987; Moschner and Zangemeister 1993; Phillips et al. 1995; Zangemeister and Stark 1982a,b). In fact, when target timing as well as location is predictable, “early head movements” that begin with much shorter latencies and more strongly time locked with target onset than gaze shift onset are facilitated (Bizzi et al. 1972; Moschner and Zangemeister 1993; Pelisson et al. 2001; Stahl 1999). As a result, head-movement amplitude increases when expected eye-in-orbit eccentricity is large, presumably to minimize the deviation of the eye-in-orbit at gaze shift end (Stahl 1999). In the present study, we addressed whether the velocity and initiation of body as well as head-on-body movement are relatively faster for gaze shifts made to target sequences where the location, but not timing, of the next target was known. We found that head-on-body movements were larger and their onset was faster in predictable trials than in random trials. However, this prediction was not confirmed for body movements (Fig. 10); target predictability did not influence body amplitude, velocity, or latency. This result was possibly a consequence of the random task which the monkeys performed because the random element was constrained to a location within one half of the target array. The monkeys may have adopted a strategy to keep the body relatively stable because they knew the next target would appear contralateral to the current target position. Oommen et al. (2004) have shown that head movements contribute more to gaze shifts when subjects expect to make a second larger gaze shift in the same direction. By extension, we predict that body movements would be larger in a situation where the monkey expects to make a second large gaze shift in the same direction.

It is also important to emphasize that our experimental design effectively minimized the occurrence of both anticipatory gaze shifts (see METHODS) and head/body movements (see Fig. 10) even when the location of the next target was predictable. In our study, the timing of each target presentation was never predictable because the monkeys were required to maintain fixation of the initial target for a variable period before the second target was illuminated to obtain a reward. It is likely that anticipatory head as well as body movements would have been more prominent if target timing as well as location had been predictable. For example, Bizzi et al. (1972) found that monkeys make anticipatory head movements when making large gaze shifts made to targets alternatively presented between two fixed locations at regular intervals.

#### *Context dependence of movement kinematics*

The relative contribution of body movement to a gaze shift varies depending on the goal of the gaze shift. In the present study, the monkey's goal was to align its axis of gaze with the target. In turn, the monkey received a juice reward via a delivery system that moved with its head. Accordingly, there was no requirement for the animal to orient its head or body in any particular manner to gain access to the reward and as a result body movement comprised of a relatively small component of an entire gaze shift. In contrast, in a gaze shift task where subjects made gaze shifts between two work surfaces

(see Land 2004), body displacements of  $>100^\circ$  and velocities  $\sim 120^\circ/\text{s}$  routinely accompanied gaze shifts of  $\sim 130^\circ$ .

A critical difference between the Land study and our experiments is that in Land's study subjects were required to work at the new location once they had completed the gaze shift, whereas in our study, there was no constraint that required the monkeys to align their body with the visual target. Accordingly, because the movement of the body requires the expenditure of a considerable amount of energy, our monkeys adopted a strategy in which body movements were minimized. We predicted that if the goal of the task was to orient to a food target, which the monkeys could then reach and eat, then body movements might become more prominent. In fact, in preliminary experiments, we have observed that gaze shifts are accompanied by significantly larger body movements when food targets are presented on either side of a barrier. Under circumstances when a monkey is required to align its mouth to accept a reward, body movement can reach amplitudes as large as  $50^\circ$  and peak velocities of  $\sim 120^\circ/\text{s}$  during large ( $>70^\circ$ ) gaze shifts.

#### *Substrates for coordinating eye-head-body gaze shifts*

An important implication of the findings presented here is that body movement is part of a coordinated series of motor events that determine how we orient between objects of interest. How our brain produces precise multi-joint movements, such as eye-head-body gaze shifts, remains an important question in motor control. Studies of movement kinetics during locomotion and turning in humans have emphasized the importance of interactions between “top-down” and “bottom-up” mechanisms. During turning movements, the eyes and head lead the trajectory while the body and legs lag (Imai et al. 2001), suggesting a top down hierarchical control scheme (Grasso et al. 1996; Pozzo et al. 1990). Furthermore, movements of each segment are also linked by means of bottom-up mechanisms (reviewed in Mergner and Becker 2003) that utilize sensory inputs (i.e., vestibular, proprioceptive, somatosensory and visual information) and/or motor efference copy signals. It is likely that the coordination of eye, head, and body movements during gaze shifts is achieved by comparable mechanisms.

First, it is likely that these orienting movements are driven, at least in part, by a common drive from a shared upstream controller. As discussed in the preceding text, one likely candidate is the SC, which projects not only to the premotor saccadic pathway but also to the nucleus reticularis gigantocellularis (NRG) (for review, see Isa and Sasaki 2002; Peterson and Richmond 1988). The NRG, in turn, projects to ipsilateral neck motoneurons such that electrical stimulation of the NRG results in the generation of horizontal head movements (Quessy and Freedman 2004). Accordingly, collicular output neurons have direct access to both the saccadic and neck premotor circuitry, thereby providing a physiological substrate by which eye and head movements can be driven in a coordinated fashion during gaze shifts. Moreover, direct stimulation of NRG can evoke movement of the upper torso as well as head movements (Cowie and Robinson 1994). Although further experiments will be required to determine if stimulation of the superior colliculus might evoke body turning movements in a loosely constrained monkey, the finding that stimulation of the

deeper layers of the SC can perturb arm movements (Courjon et al. 2004) provides evidence that activation of the SC can influence the control of body segments below the eyes and head.

Second there are two lines of evidence to support the idea that eye-head-body orienting movements are also linked by means of bottom-up mechanisms. Previous behavioral studies in humans and non-human primates have further demonstrated synchronization between movements of the eyes and feet during locomotion (Hollands and Marple-Hovatt 2001; Hollands et al. 1995; Solomon and Cohen 1992). During whole-body turns, correlations between eye and foot movements can be higher than those between the head and body (Holland et al. 2004). It has been suggested that an efference copy of the motor command to trunk and/or limb movement may support the coordination of such multi-segmental movements and ensure accuracy (Solomon and Cohen 1992). Alternatively, many prevailing theoretical frameworks regard multi-joint coordination as being achieved by means of integrative feedback control. Recent work on coordinated eye-head gaze shifts show that the neurons in the circuitry, which controls saccadic eye movements, are instantaneously updated following experimentally applied head perturbations to preserve global movement accuracy (Sylvestre and Cullen 2006). The short latency of these on-line modulations indicates that head-movement-sensory feedback is available to the brain stem eye premotor circuitry via di- or trisynaptic projections during eye-head gaze shifts. It remains to be determined whether feedback of body movement might be similarly available to the brain stem eye premotor circuitry.

### Conclusions

Taken together, our results show that body movement is a natural part of a coordinated series of motor events that determine how gaze is voluntarily reoriented in space. Although the coordination of eye, head, and body movements during gaze shifts may be achieved by means of a common drive, it is also likely that a parallel cortical drive to the head and body is used to adjust the overall head contribution as a function of different behavioral contexts. For example, tasks in which the goal is to align the body, and not just gaze, with a visual target would have different kinematics requirements and are likely to recruit other pathways. Nevertheless our results in monkeys performing a simple gaze redirection task emphasize the need for caution in the interpretation of data from neurophysiological studies of the control of saccadic eye movements and/or eye-head gaze shifts because single neurons will code motor commands to move the body as well as the head and eyes.

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