

Human Eye-Head Gaze Shifts in a Distractor Task. II. Reduced Threshold for Initiation of Early Head Movements

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Corneil, Brian D. and Douglas P. Munoz. Human eye-head gaze shifts in a distractor task. II. Reduced threshold for initiation of early head movements. *J. Neurophysiol.* 82: 1406–1421, 1999. This study was motivated by the observation of *early head movements* (EHMs) occasionally generated before gaze shifts. Human subjects were presented with a visual or auditory target, along with an accompanying stimulus of the other modality, that either appeared at the same location as the target (enhancer condition) or at the diametrically opposite location (distractor condition). Gaze shifts generated to the target in the distractor condition sometimes were preceded by EHMs directed either to the side of the target (*correct* EHMs) or the side of the distractor (*incorrect* EHMs). During EHMs, the eyes performed compensatory eye movements to keep gaze stable. Incorrect EHMs were usually between 1 and 5° in amplitude and reached peak velocities generally <50°/s. These metrics increased for more eccentric distractors. The dynamics of incorrect EHMs initially followed a trajectory typical of much larger head movements. These results suggest that incorrect EHMs are head movements that initially were planned to orient to the peripheral distractor. Furthermore gaze shifts preceded by incorrect EHMs had longer reaction latencies than gaze shifts not preceded by incorrect EHMs, suggesting that the processes leading to incorrect EHMs also serve to delay gaze-shift initiation. These results demonstrate a form of distraction analogous to the incorrect gaze shifts (IGSs) described in the previous paper and suggest that a motor program encoding a gaze shift to a distractor is capable of initiating either an IGS or an incorrect EHM. A neural program not strong enough to initiate an IGS nevertheless can initiate an incorrect EHM.

different biomechanical properties (Guitton and Volle 1987; Pelisson et al. 1988; Zangemeister and Stark 1981).

One of the predominant features of eye-head coordination during gaze shifts is that different experimental protocols elicit different patterns of eye-head coordination. For example, the timing and contribution of the head are modified readily by target predictability (Bizzi et al. 1972; Moschner and Zangemeister 1993; Zangemeister and Stark 1982a,b), initial head position or velocity (Goossens and van Opstal 1997; Pelisson et al. 1988; Phillips et al. 1995; Tomlinson 1990; Volle and Guitton 1993), target direction and amplitude (Freedman and Sparks 1997b; Gretszy 1974; Pelisson et al. 1988; Tomlinson and Bahra 1986; Uemura et al. 1980), target modality (Fuller 1996; Goldring et al. 1996; Goossens and van Opstal 1997; Whittington et al. 1981), subject instruction and alertness (Fuller 1992a; Zangemeister and Stark 1982a), and various pathological conditions (Dichgans et al. 1973; Kasai and Zee 1978; Zangemeister and Stark 1982a; see Fuller 1992b for review). Models of gaze control have undergone significant evolution to account for the highly labile patterns of eye-head control. One early model of gaze control (Lauritis and Robinson 1986) was constructed by extending the Robinson model of saccadic eye movements (Robinson 1975) by postulating that a gaze motor error drove both the eyes and head. However, a frequent observation in eye-head coordination studies is that subjects sometimes move their head in the direction of the target before the gaze shift begins (see Fuller 1992b for review). Such early head movements (hereafter termed EHMs), which have been reported to lead the gaze shift by up to 300 ms (Zangemeister and Stark 1982b), are compensated for by a vestibuloocular reflex (VOR) eye movement so that gaze position remains stable during the EHM. If the head was driven solely by a distributed drive to the eye and head, then the head movement ought always to lag the eye movement given the different efferent delays in moving the eye and head (Zangemeister and Stark 1981). Thus it was recognized that the head can receive a control signal in advance of the signal related to gaze-shift initiation.

The accompanying paper described the performance of humans in a multimodal distractor condition, wherein a distractor and target were placed on opposite sides of the initial fixation point (Corneil et al. 1999). We differentiated between correct gaze shifts (CGSs) and incorrect gaze shifts (IGSs) based on whether the subject initially looked to the side of the target or distractor, respectively. The metrics and dynamics of IGSs, particularly of those hypometric IGSs reversed in midflight, strongly suggested a direct competition between two parallel

INTRODUCTION

Humans employ gaze shifts to rapidly relocate where they are looking in space. Gaze shifts can be accomplished solely by an eye movement (i.e., a movement of the eyes within the head) or by combining the eye movement with a head movement (i.e., a movement of the head in space). The resultant sum of the eye and head movements is the gaze shift (i.e., a movement of the eye in space). Early studies of human eye-head coordination revealed that the head movement was an integral part of large gaze shifts because the latter portions of large gaze shifts frequently were achieved by a rapid head movement while the eyes remained stationary, or even counterrotated, within the head (Bartz 1966; Gretszy 1974; Guitton and Volle 1987; Lauritis and Robinson 1986). The accuracy of such large gaze shifts emphasizes the high degree of coordination that must exist between the eye and head given their

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motor programs, each encoding a gaze shift to either the target or distractor. In this paper, we examine the same behavioral data for EHMs preceding CGSs in the distractor condition. We show that such EHMs can be generated to either the target or the distractor (termed *correct EHMs* and *incorrect EHMs*, respectively). Furthermore the metrics and dynamics of incorrect EHMs suggest they initially were programmed for a much larger excursion and are very similar to the head movements during hypometric IGSs. These remarkable similarities suggest a common neural origin for the command to move the head during either incorrect EHMs or IGSs and suggest that the salient difference between these two types of movements is whether a gaze threshold is reached.

Some of the results in the present study have been presented earlier in abstract form (Corneil and Munoz 1995; Corneil et al. 1997a,b).

METHODS

The experimental setup, experimental paradigms, and data collection were described in the preceding paper (Corneil et al. 1999). Briefly, four adult subjects were placed in a magnetic coil system, and the movements of their gaze and head were measured via search coils placed on the eye and head, respectively. The subjects performed a series of seven experiments that consisted of one control experiment and six multimodal experiments. In the control experiment, subjects generated gaze shifts to visual or auditory stimuli presented alone either to the right or left. In the multimodal experiments, one of the visual or auditory stimuli was designated the target, while the other served as an accompanying stimulus. The stimuli were either presented at the same point on the horizontal meridian (*enhancer* condition) or on opposite sides of the vertical meridian (*distractor* condi-

tion) (see Fig. 1 of Corneil et al. 1999). Each of the visual or auditory stimuli served as the target when the stimuli were presented at ~ 20 , 40 , or 60° , for a total of six multimodal experiments. *Subject ks* developed a corneal abrasion before completing the entire series of multimodal experiments. The data for this subject from the experiments at 20° were not analyzed in this paper because the data were obtained using techniques with much lower spatial resolution (see the companion paper for more details).

Data analysis

The goal of this paper was to identify and analyze early head movements (EHMs) that occurred before the initiation of a correct gaze shift (CGS). During EHMs, the eyes perform a compensatory VOR that maintains gaze stable on the fixation point at the center of the screen. EHMs were classified as either *correct EHMs* if the EHM was directed to the side of the target or as *incorrect EHMs* if the EHM was directed away from the target (hence, toward the distractor in the distractor condition). Subjects generated EHMs freely and were not given any feedback regarding their performance during any of the experiments.

As in the previous paper, all trials were inspected visually by a data analyst. Figure 1 shows representative position and velocity traces for CGSs that were either: not preceded by an EHM (Fig. 1A), preceded by a correct EHM (Fig. 1B), or preceded by an incorrect EHM (Fig. 1C). CGSs that were preceded by EHMs were distinguished from CGSs without EHMs primarily by the presence of the VOR movement before gaze shift onset (compare the eye and head velocity traces in Fig. 1, B and C, with those in A). Head movements were classified as EHMs if both the head and the accompanying VOR eye movement preceding the onset of the CGS exceeded 0.25° in amplitude and $15^\circ/\text{s}$ in velocity. The onset of the CGSs were determined by the crossing of a gaze velocity threshold of $30^\circ/\text{s}$. We recognize that criteria for identifying EHMs were arbitrary and that some EHMs with low

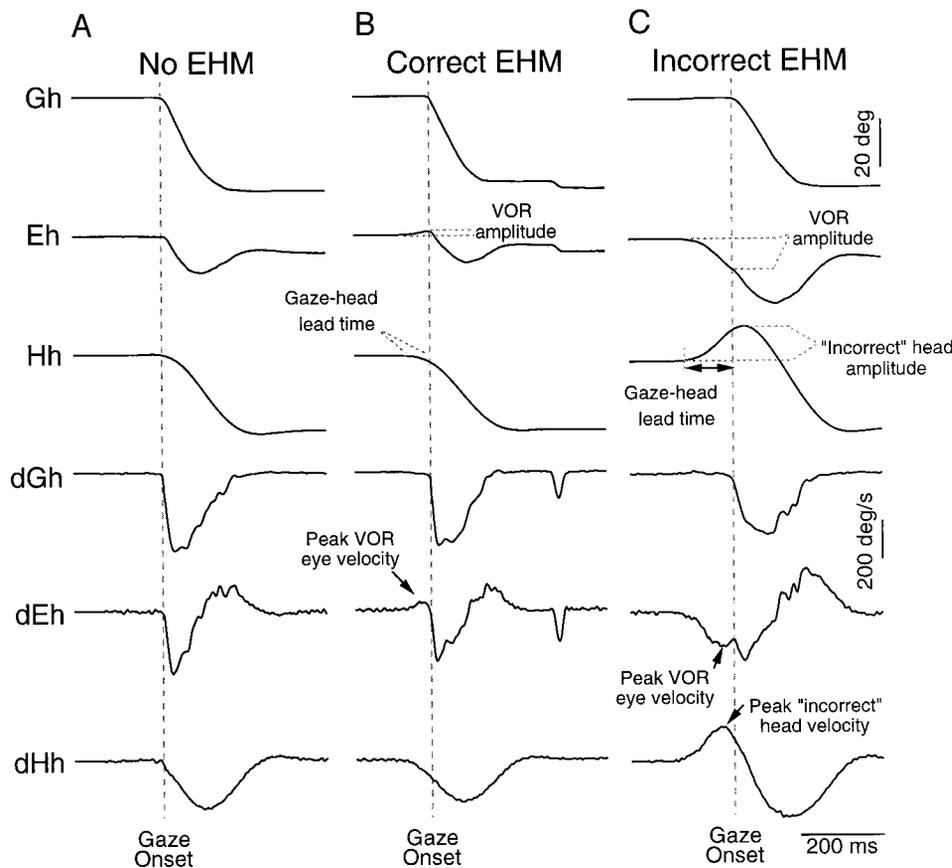


FIG. 1. Position and velocity traces of the eye (eye-re-head, shown by Eh and dEh, respectively), head (head-re-space: Hh and dHh) and gaze (eye-re-space: Gh and dGh) during representative correct gaze shifts (CGSs) illustrating the movement parameters that were analyzed for CGSs with no early head movement (EHM; A), with a correct EHM (B), and with an incorrect EHM (C). In this and all following figures, upward deflections in the traces represent rightward movements, and downward deflections represent leftward movements. Light vertical dashed lines delineate the start of the CGS, and the EHMs in B and C are easily seen as those movements occurring before CGS onset. For correct EHMs (B), the amplitudes, peak velocities and accelerations of the compensatory vestibuloocular (VOR) eye movement were measured. For incorrect EHMs (C), the amplitudes, peak velocities of the incorrect head movement and the compensatory VOR eye movement were measured. We also measure the peak acceleration and deceleration, and acceleration and deceleration durations of incorrect EHMs (not shown).

velocity head movements $<15^\circ/\text{s}$ were not marked. These criteria were at the limit of signal resolution ($\sim 0.1^\circ$). Marks were inserted on identified trials to measure the reaction time, amplitude, and peak velocity of the EHM and the accompanying VOR (Fig. 1). The peak acceleration and deceleration and the duration of the acceleration and deceleration phases of the incorrect EHM also were measured. The acceleration duration was measured from the start of the movement until the peak velocity, and the deceleration duration was measured from peak velocity to the end of the movement. All trials were inspected by a second data analyst to check for errors and to ensure consistency within and between subjects.

RESULTS

We describe EHMs that occasionally were generated before gaze shifts in the enhancer or distractor condition. We focus initially on a qualitative description of EHMs and outline their incidence and directions relative to the target in both the enhancer and distractor conditions. Subsequently we examine the timing, metrics and dynamics of incorrect EHMs in the distractor condition. We adopt the same terminology used in the preceding paper (Corneil et al. 1999) to refer to the different multimodal experiments. *VisT/audD* refers to the experiments using a visual target and an auditory distractor, and *AudT60°R/visD60°L* denotes trials wherein an auditory target was placed 60° to the right and a visual distractor 60° to the left.

Incidence of EHMs

CGSs were divided into three subclasses based on the occurrence and direction of the EHM relative to target location: CGSs not preceded by an EHM (no EHM—Fig. 2A), CGSs preceded by a correct EHM directed to the target (Fig. 2B), and CGSs preceded by an incorrect EHM directed away from the

target and hence toward the distractor (Fig. 2C). Five examples of each subclass are shown in Fig. 2 for *subject ks* from *VisT40°R/audD40°L* trials. The gaze position traces in Fig. 2, A–C, are virtually indistinguishable, demonstrating that the subject performed the task correctly and shifted gaze directly to the target regardless of the preceding EHM. In Fig. 2A, the onset of the head movement is synchronous with or slightly after the onset of the gaze shift. In Fig. 2B, the head begins to move in the direction of the target before the onset of the CGS and gaze is maintained at the fixation point by a compensatory VOR eye movement. The onset of the gaze shift is achieved by an acceleration of the eye and head toward the target. Differences between movements illustrated in Fig. 2, A and B, are apparent in comparing the eye and head position traces and the head velocity traces before gaze onset. In Fig. 2C, the initial movements of the head are directed toward the distractor, and again gaze is maintained by compensatory VOR eye movements. At the time of gaze shift onset, the eyes accelerate in the direction of the target, and the head rapidly switches direction and accelerates toward the target. The examples shown in Fig. 2C demonstrate unequivocally that the head can move initially in one direction even though the ensuing CGS proceeds in the opposite direction.

A condensed breakdown of the incidences of CGSs, further separated into the three subclasses, and IGSSs for the different experiments (*VisT/audD* vs. *AudT/visD*) and experimental condition (enhancer vs. distractor) is shown in Table 1. The results are pooled across stimulus eccentricity and direction. More incorrect EHMs were generated in *VisT/audD* experiments (range 12–28%) than in *AudT/visD* experiments (range 3–8%; paired *t*-test, $P = 0.0003$), although the notable proportion of incorrect EHMs from *AudT/visD* experiments

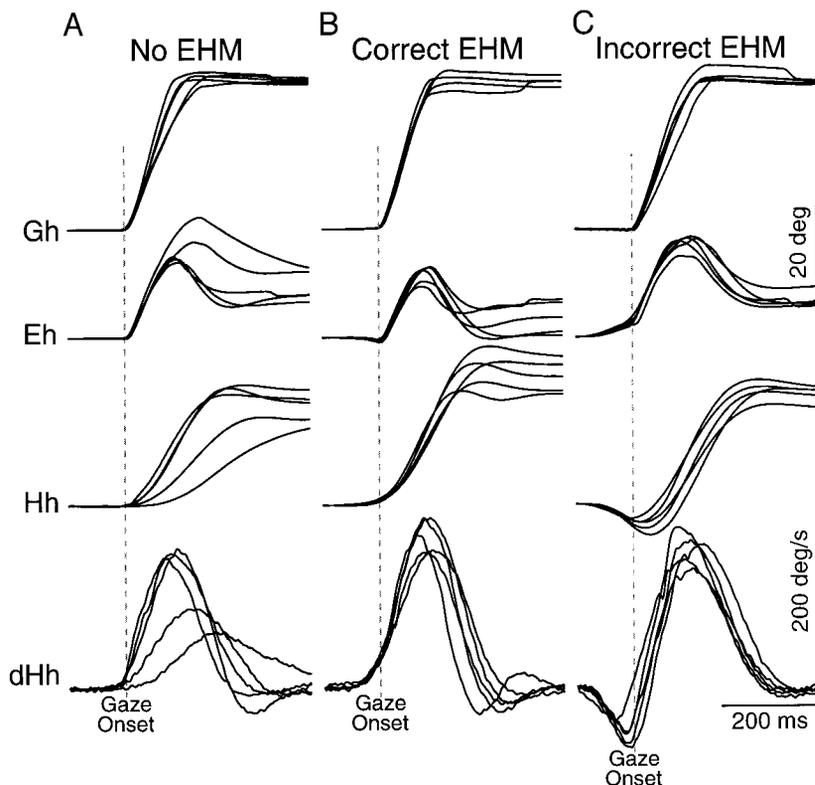


FIG. 2. Gaze (Gh), eye (Eh), and head (Hh) position traces and head velocity (dHh) traces of 5 examples from each of the 3 subclasses of CGSs: those without an EHM (A), those with a correct EHM (B), and those with an incorrect EHM (C). All examples are from *subject ks* from *VisT40°R/audD40°L*. ---, start of the CGS.

TABLE 1. Percentage of correct gaze shifts and incorrect gaze shifts

Subject	Movement Type, %	VisT/audD		AudT/visD	
		Enhancer	Distractor	Enhancer	Distractor
<i>dm</i>	CGS	99	52	100	73
	no EHM	59	24	79	40
	cEHM	34	16	17	25
	iEHM	6	12	4	8
	IGS	1	48	0	27
<i>ks</i>	CGS	100	81	100	87
	no EHM	19	20	36	17
	cEHM	79	33	63	67
	iEHM	2	28	1	3
	IGS	0	19	0	13
<i>jb</i>	CGS	100	78	97	68
	no EHM	72	44	85	55
	cEHM	19	10	7	5
	iEHM	9	24	5	8
	IGS	0	22	3	32
<i>md</i>	CGS	100	69	100	75
	no EHM	98	55	98	67
	cEHM	1	1	1	3
	iEHM	1	13	1	5
	IGS	0	31	0	25
Total	CGS	100	70	99	76
	no EHM	62	36	75	45
	cEHM	33	15	22	25
	iEHM	5	19	2	6
	IGS	0	30	1	24

The correct gaze shifts (CGS) have been broken down into those movements consisting of no early head movement (EHM) (no EHM), correct EHM (cEHM), or incorrect EHM (iEHM). Data for *subject ks* at 20° were not analyzed (see Corneil et al. 1999).

shows that incorrect EHMs were not due to a modality-dependent orienting strategy. All four subjects generated EHMs in both experiments but did so in differing proportions. Although there were exceptions, subjects generated correct EHMs in both the enhancer and distractor conditions and generated more incorrect EHMs in the distractor condition than in the enhancer condition (paired *t*-test, $P < 0.05$). The fact that more incorrect EHMs were generated in the distractor condition than in the enhancer condition demonstrated that EHMs were predominantly stimulus driven. However, EHMs also may be generated voluntarily as demonstrated by the small number of incorrect EHMs generated in the enhancer condition (range 1–9%).

Time of onset of head and gaze movements

We measured the “lead time” as the difference between the initiation times of the eye (or gaze) and head. This value was positive if the gaze shift began before the head movement and negative if the head movement began before the gaze shift (as is the case for EHMs). Figure 3 compares the lead times for those CGSs generated in the distractor condition that were preceded by an incorrect EHM to those CGSs in which the movement of the head was in the correct direction (i.e., CGSs with or without a correct EHM). Data are shown for both AudT/visD (Fig. 3A) and VisT/audD (Fig. 3B) experiments. CGSs consisting of correct EHMs or no EHMs were pooled together because the distributions of their lead times overlapped considerably, suggesting that such movements do not form distinct movement classes. Because of this, we did not

study any characteristics of correct EHMs beyond their incidence. The lead times within each experimental series were pooled across the different stimulus eccentricities for this analysis (1-factor ANOVA of lead time across distractor eccentricity, $P = 0.88$). Incorrect EHMs tended to begin much earlier relative to CGS onset than the head movement during all other CGSs with correct head movements (*t*-test for data collapsed across all subjects, $P < 0.0001$) and also began earlier than those CGSs with negative lead times (*t*-test for data collapsed across all subjects, $P = 0.0001$).

Metrics of incorrect EHMs

To further characterize the underlying neural mechanisms of incorrect EHMs (i.e., are they driven to the *location* of the stimulus, or are they driven simply in the *direction* of the stimulus?) we examined the metrics of the incorrect EHMs. Figure 4A shows traces of 13 incorrect EHMs generated by *subject md* in VisT20°L/audD20°R trials. The lead time, amplitude, duration and peak velocity of all 32 incorrect EHMs generated at 20° by *subject md* are shown collapsed across movement direction in Fig. 4B–E respectively (confirmed by a *t*-test at $P > 0.05$). The incorrect EHMs shown here tended to be $< 5^\circ$ in amplitude, 75°/s in peak velocity and last between 50–150 ms, although some of the larger incorrect EHMs exceeded 10° at peak velocities of over 100°/s. A summary of the incorrect EHM metrics and dynamics for all subjects is shown in Table 2. The results are collapsed across direction for all subjects (confirmed by a *t*-test when > 10 incorrect EHMs were generated in each direction, $P > 0.05$).

Incorrect EHMs were larger and attained higher peak velocities and accelerations when they were driven to auditory distractors and when they were generated to more eccentric stimuli. The effects were assessed using a two-factor ANOVA across distractor modality (visual vs. auditory) and distractor eccentricity (20, 40, or 60°) with Newman-Keuls post hoc analysis on the various parameters of the incorrect EHM (lead time, amplitude, duration, peak velocity, and peak acceleration). Incorrect EHMs generated in VisT/audD experiments were larger in amplitude ($P = 0.022$) and reached a higher peak velocity ($P = 0.015$) than incorrect EHMs generated in AudT/visD experiments. For more eccentric distractors, incorrect EHMs tended to be shorter in duration ($P = 0.001$), yet reach higher peak velocities ($P < 0.05$) and accelerations ($P < 0.0001$). These results demonstrate that incorrect EHMs are driven, at least in part, by the location, and not simply the direction, of the distractor.

The amplitude, duration, and peak velocity of incorrect EHMs were somewhat dependent on the lead time. For the incorrect EHMs shown in Fig. 4, the earlier the incorrect EHM was initiated relative to the CGS, the larger the amplitude (Fig. 5A), longer the duration (Fig. 5C), and larger the peak velocity (Fig. 5E). These relationships were fairly consistent across all subjects in which five or more incorrect EHMs were generated in a single experiment (as was the case in 20 of the 22 multimodal experiments run on the 4 subjects, excluding the data for *ks* at 20°). The correlations between these metrics and the lead time reached significance at the $P < 0.05$ level in 7 of 20 cases for the correlation of amplitude versus lead time (Fig. 5B), 19 of 20 cases for duration versus lead time (Fig. 5D), and 6 of 20 cases for peak velocity versus lead time (Fig. 5F). These dependencies of the incorrect EHM metrics to the lead

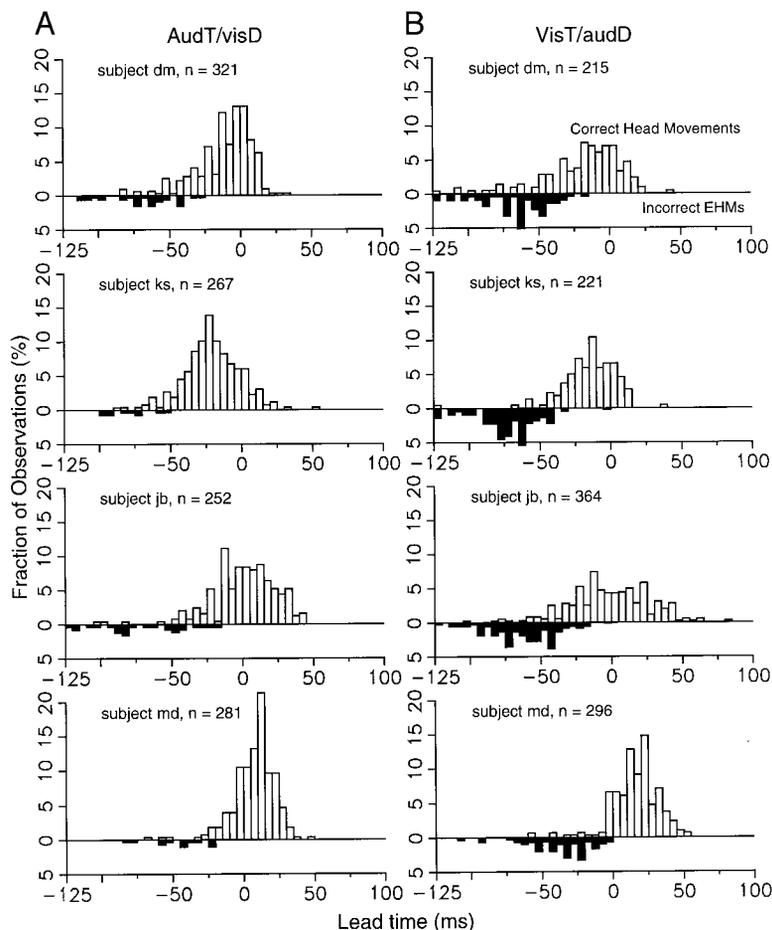


FIG. 3. Frequency histograms for all subjects of the lead time (time of initiation of head movement relative to gaze shift initiation). Negative lead times imply that the head started to move before CGS onset, as was the case for EHM's. All CGS's for each subject, given by the number at the top of each graph, were generated in the distractor conditions, and the data from the different eccentricities have been grouped for AudT/visD experiments (A) and VisT/audD experiments (B). ■, lead times for incorrect EHM's. □, lead times for all CGS's in which the head moved to the target (see text for further explanation as to why CGS's with and without a correct EHM were grouped together). Total number of CGS's in each graph differ because each subject generated different numbers of IGS's not included in this analysis.

time are similar to the dependencies of the metrics of IGS's to the reaction time of the IGS relative to target onset observed in the previous paper (see Corneil et al. 1999).

Dynamics of incorrect EHM's

Close examination of the dynamics of the head during incorrect EHM's can illustrate whether EHM's followed dynamic profiles similar to normal amplitude-matched head movements or profiles typical of much larger head movements (see Corneil et al. 1999 for more detail). Figure 6 illustrates the main sequence relationships for incorrect EHM's and head movements from gaze shifts generated in unimodal control experiments for head movements to auditory (Fig. 6A) and visual (Fig. 6B) stimuli. Virtually all incorrect EHM's attained higher peak velocities when compared with amplitude-matched head movements from control gaze shifts. For all subjects, the slope of the linear regression line through the main sequence data was greater for incorrect EHM's than for control head movements (paired *t*-test contrasting slopes of main sequence relationship for head movements during incorrect EHM's and control gaze shifts, $P < 0.0001$).

EHM's attained higher peak velocities than amplitude-matched head movements during control gaze shifts because incorrect EHM's followed a very different dynamic profile. Various parameters of the acceleration and deceleration of incorrect EHM's are compared with the head movement generated during control gaze shifts in Fig. 7. The phase-plane traces of all incorrect EHM's generated by *subject ks* from VisT40°L/audD40°R trials are

shown in Fig. 7A. The amplitudes of the incorrect EHM's from these examples ranged from <0.5 to almost 20° , and the peak velocities ranged from ~ 20 to $>250^\circ/\text{s}$. The phase-plane traces from incorrect EHM's ranging from ~ 10 to 20° (Fig. 7B, dashed line) are contrasted with amplitude-matched control head movements (Fig. 7B, dark, solid lines) and control head movements between 30 and 40° (Fig. 7B, light, solid lines). The head movement during incorrect EHM's initially accelerated along a dynamic profile similar to 30 – 40° control head movements but suddenly departed from this profile via a sharp deceleration (compare Fig. 7B, dashed with light solid lines). Head movements made during control gaze shifts tended to have similar accelerations and decelerations, resulting in the characteristic parabolic phase-plane trajectories (Fig. 7B, solid line), whereas the unequal acceleration and deceleration dynamics during incorrect EHM's resulted in a skewed phase-plane trajectory (Fig. 7B, dashed lines).

Differences between various parameters of the acceleration and deceleration of the head during incorrect EHM's and control head movements are quantified in Fig. 7, C–G, for *subject ks* and in Fig. 7H for all subjects. Amplitude-matched incorrect EHM's tended to have slightly larger peak accelerations (Fig. 7C) and correspondingly shorter acceleration phase durations (Fig. 7E) than head movements from control gaze shifts. Incorrect EHM's also had much larger peak decelerations (Fig. 7D) and shorter deceleration durations (Fig. 7F). We derived the ratio of the acceleration and deceleration durations to obtain a measure of the skewness of the head velocity-time relationship (van Opstal and van Gisbergen 1987), allowing us to combine the observations of this ratio across

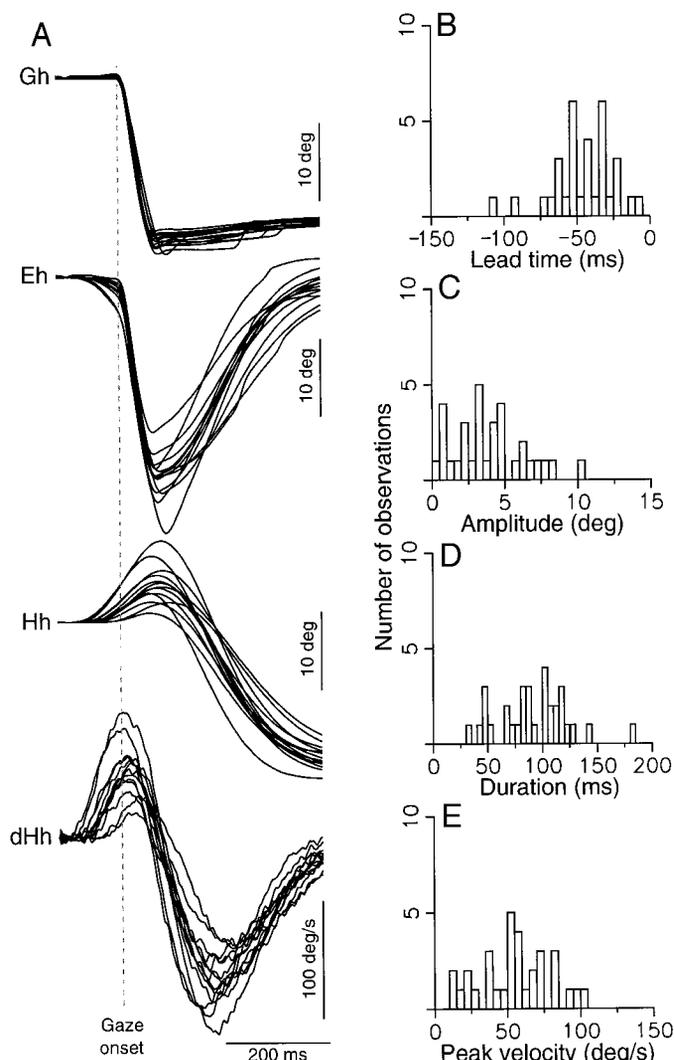


FIG. 4. Metrics of incorrect EHM. A: gaze (Gh), eye (Eh), and head (Hh) position and head velocity (dHh) traces are shown for the 13 incorrect EHM generated by *subject md* in VisT20°L/audD20°R trials. ---, onset of the CGS. B–E: frequency histograms for the 32 incorrect EHM generated in either direction for the lead time (B), amplitude (C), duration (D), and peak velocity (E). Bin widths are 5 ms in B and D, 0.5° in C, and 5°/s in E.

all subjects. These values are shown for *subject ks* in Fig. 7G, and for all subjects in Fig. 7H. This ratio was significantly higher during incorrect EHM than during control head movements (Mann-Whitney rank-sum test, $P < 0.0001$). These results emphasize the differences in the dynamic profiles of incorrect EHM and suggest that the incorrect EHM were planned for a much larger excursion but were reversed rapidly by the ensuing CGS. These results are very similar to the results obtained for the head movements that were generated during hypometric IGSs (see Figs. 10 and 11 of Corneil et al. 1999).

Incorrect EHM preceding IGSs

The emphasis up to this point has been on EHM preceding CGSs. However, EHM also were observed preceding IGSs, although these rare movements were not studied quantitatively. A representative example of such a movement is shown in Fig. 8 for each of the four subjects, from VisT60°R/audD60°L trials, to emphasize that this phenomenon was not limited to

one subject. In each example shown, an incorrect EHM was generated before a hypometric IGS. Incorrect EHM before IGSs were compensated for by VOR movements to maintain gaze on the initial fixation point. During the small incorrect gaze shift, the amplitude of the eye movement component was quite small and the eye velocity was considerably slower than the velocity of the incorrect gaze shift. Thus the IGSs largely were carried by a movement of the head toward the distractor (Fig. 8, A and B in particular).

Comparative reaction latencies of different categories of target-directed gaze shifts

Our final analysis sought to determine whether the reaction latencies of gaze shifts directed to the target differed depending on whether the movement was preceded by an incorrect EHM or an IGS. Both incorrect EHM and IGSs can be thought of as behavioral manifestations of a “distraction,” so it could be predicted that these classes of movements [i.e., either CGSs, which follow incorrect EHM, or RGSs (*reorrect gaze shifts*), which follow IGSs] would have longer reaction times than CGSs not preceded by any overt movement to the distractor. Only data from the distractor condition were used for this analysis. To compare the reaction latencies of these different categories of gaze shifts across the subjects and across each multimodal experiment, it was necessary to normalize the reaction latencies to the mean reaction latencies for CGSs not preceded by incorrect EHM. This procedure derived, for each subject, three relative reaction latency distributions: CGSs not preceded by incorrect EHM (normalized around a value of 1), CGSs preceded by incorrect EHM, and RGSs, which were preceded by IGSs. The normalized reaction latencies then were collapsed across all subjects (Fig. 9). A one-way ANOVA of the reaction latencies across the three movement categories demonstrated that the mean relative reaction latencies of CGSs preceded by incorrect EHM and RGSs tended to be progressively longer than for CGSs not preceded by any incorrect EHM ($P < 0.0001$, post hoc analysis with Newman-Keuls). Thus it took subjects longer to look to the target if this target-directed gaze shift was preceded by some overt measure of distraction. Furthermore it suggests that incorrect EHM and IGSs result from progressively larger distraction processes, seeing that it took longer to generate the target-directed gaze shift after an IGS than after an incorrect EHM. A theoretical model to account for the generation of incorrect EHM is forwarded in the discussion and will detail how it is possible that incorrect EHM and IGSs are derived from the same motor program.

DISCUSSION

We have described the occurrence and properties of small head movements that occasionally lead gaze shifts, and proceed in directions that may or may not match the direction of the ensuing gaze shift. The metrics and dynamics of incorrect EHM are typical of much larger head movements, and the interplay between movement parameters of incorrect EHM and the subsequent CGSs are similar to the interplay between IGSs and subsequent RGSs described in the previous paper (Corneil et al. 1999). These results suggest that incorrect EHM and IGSs are directed by a common motor program

TABLE 2. *Quantification of the movement parameters of incorrect EHMs generated in the distractor condition*

Subject	VisT/audD			AudT/visD		
	60	40	20	60	40	20
<i>dm</i>						
Number	14	22	24	6	15	13
Lead time	55 ± 12	69 ± 28	73 ± 31	58 ± 22	74 ± 27	73 ± 27
Amplitude	3.9 ± 3.0	2.92 ± 3.3	4.3 ± 3.1	2.6 ± 2.3	2.6 ± 2.8	3.34 ± 2.7
Duration	66 ± 20	74 ± 30	97 ± 37	62 ± 23	66 ± 26	87 ± 34
Peak Velocity	79.3 ± 50.9	44.0 ± 35.2	55.4 ± 26.9	50.2 ± 31.8	46.8 ± 36.4	49.5 ± 27.8
Peak Acceleration	1697 ± 848	942 ± 481	1138 ± 434	3191 ± 1522	1025 ± 585	992 ± 411
<i>ks</i>						
Number	47	29	—	3	7	—
Lead time	72 ± 21	73 ± 27	—	88 ± 11	76 ± 18	—
Amplitude	6.3 ± 5.8	4.2 ± 3.4	—	2.8 ± 1.9	1.9 ± 2.5	—
Duration	72 ± 27	80 ± 24	—	76 ± 17	59 ± 26	—
Peak Velocity	112.1 ± 82.5	69.4 ± 43.8	—	57.6 ± 26.8	35.7 ± 32.5	—
Peak Acceleration	2051 ± 1164	1417 ± 723	—	1715 ± 482	907 ± 572	—
<i>jb</i>						
Number	35	44	34	13	10	6
Lead time	81 ± 24	62 ± 26	52 ± 25	89 ± 27	48 ± 22	82 ± 41
Amplitude	3.3 ± 2.4	2.9 ± 2.3	3.0 ± 2.3	3.0 ± 2.4	1.3 ± 1.1	0.9 ± 1.1
Duration	88 ± 27	87 ± 31	111 ± 44	91 ± 27	69 ± 36	109 ± 67
Peak Velocity	49.1 ± 24.3	45.1 ± 25.2	34.7 ± 20.0	47.4 ± 26.7	22.6 ± 11.2	12.2 ± 9.8
Peak Acceleration	2873 ± 922	1021 ± 406	676 ± 318	2902 ± 1015	654 ± 176	334 ± 207
<i>md</i>						
Number	8	19	32	2	5	6
Lead time	20 ± 11	27 ± 20	46 ± 21	51 ± 44	47 ± 9	41 ± 20
Amplitude	1.7 ± 0.9	2.2 ± 1.3	3.6 ± 2.6	0.6 ± 0.2	1.4 ± 1.4	1.1 ± 1.2
Duration	51 ± 15	63 ± 20	87 ± 34	53 ± 24	57 ± 14	63 ± 35
Peak Velocity	45.4 ± 16.8	45.0 ± 19.2	51.1 ± 26.3	20.8 ± 4.2	29.8 ± 25.4	20.8 ± 11.8
Peak Acceleration	1171 ± 313	1159 ± 404	1092 ± 455	744 ± 124	753 ± 428	661 ± 131

Measures of lead times and durations are given in milliseconds, amplitudes in degrees, peak velocities in degrees per second, and peak accelerations in degrees per second squared. Data are given as means ± SD.

orienting to the distractor. This common motor program may result in an incorrect EHM if it is quickly superseded by the motor program encoding the CGS to the target or may result in an IGS if initiated far enough in advance of the target-directed motor program. This discussion first focuses on the implications of the findings to previous studies of eye-head control. Next, we discuss the implications of incorrect EHMs on models of gaze control. We then summarize the various influences a distractor can impart in target-distractor experiments and lastly outline a conceptual neural mechanism to describe the generation of incorrect EHMs and IGSs.

Relations to previous studies on eye-head control

Our results demonstrate that the direction of an EHM can be independent of the direction of the impending gaze shift. The higher proportion of incorrect EHMs in the distractor condition compared with the enhancer condition supports the notion that these movements are predominantly stimulus driven, although they also can be generated voluntarily. Furthermore incorrect EHMs can be driven to either auditory or visual distractors.

EHMs have been noted frequently in previous monkey and human studies (Barnes 1979; Bizzi et al. 1971, 1972; Goossens and van Opstal 1997; Gretszy 1974; Guitton and Volle 1987; Laurutis and Robinson 1986; Morasso et al. 1973; Moschner and Zangemeister 1993; Phillips et al. 1995; Ron et al. 1993; Tweed et al. 1995; Zambarbieri et al. 1997; Zangemeister and Stark 1981, 1982b). It is very common for cats to move their head in the direction of the target in advance of a gaze shift

(Fuller et al. 1983; Guitton et al. 1984, 1990). The presence of a head movement before gaze shifts in humans is a distinguishing feature of the “predictive” mode of gaze shifts identified by Bizzi and colleagues (1972), as well as gaze shift Types IIIb and IV identified by Zangemeister and Stark (1981, 1982b). A thorough review by Fuller (1992b) documented and categorized the many observations of EHMs. However, most if not all of these studies employed a single target. Using the terminology adopted for this paper, all previous EHMs reported in the literature were correct EHMs. The use of the distractor condition in our studies introduced a second possible location to which EHMs could be generated, thereby enabling the uncoupling between the directions of the EHM and the ensuing gaze shift, as well as a parametric analysis of incorrect EHMs.

We emphasize that this “uncoupling” we have observed is different from the uncoupling of the head and gaze reported by Ron and colleagues (Ron and Berthoz 1991; Ron et al. 1993), who observed gaze shifts in a double-step experiment where the gaze and head were aimed to separate target locations *during* the gaze shift. Such uncoupling during a gaze shift has been reported to be extremely difficult to generate voluntarily (Collewijn et al. 1992). Ron and colleagues (1993) interpreted their results as being indicative of a modification of the neural command to foveate the second step in a manner analogous to what was observed by Becker and Jürgens (1979) when the head was unrestrained. They proposed that the dissociation between the goals of the eyes and head was achieved because this modified command was only distributed to the eye, not the head, control system. Essentially, they observed

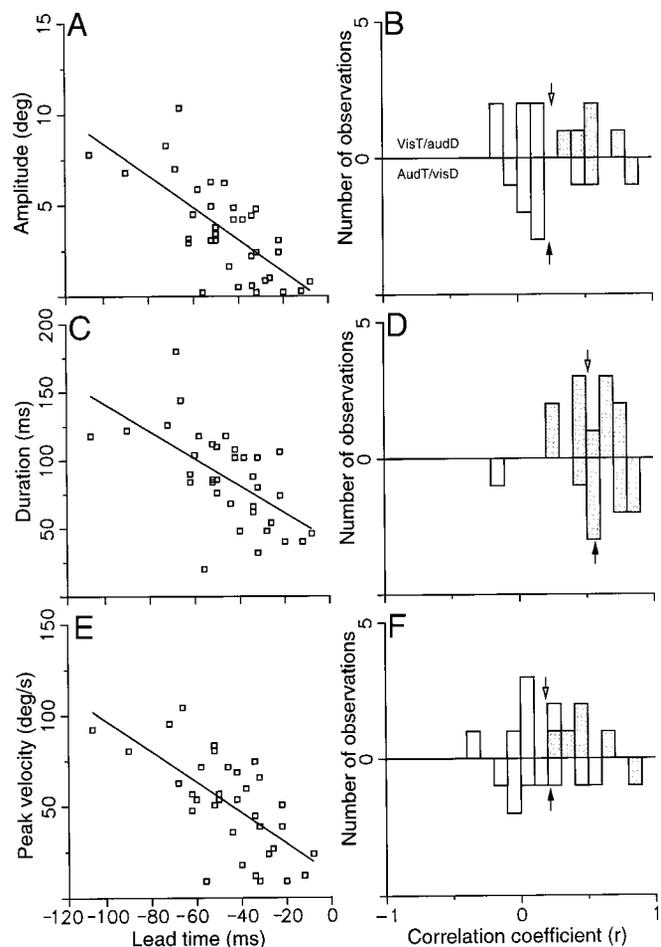


FIG. 5. Plots of the incorrect EHM amplitude (A), duration (C), and peak head velocity (E) vs. the lead time for the data presented in Fig. 4. Each point in A, C, and E represents data from a single incorrect EHM, and regression lines represent significant correlations ($P < 0.05$). B, D, and F: correlation coefficient distributions from all subjects in all multimodal experiments in which >5 incorrect EHMs were generated for the relationship between lead time and incorrect EHM amplitude (B), duration (D), and peak head velocity (F). Histograms above the 0 line show data from VisT/audD experiments; histograms below the line show data from AudT/visD experiments. \square , statistically significant correlations ($P < 0.05$). \downarrow and \uparrow , mean correlation coefficient for the histograms from VisT/audD and AudT/visD experiments, respectively. For the regression line in A, $r = 0.70$, slope = 0.09, y intercept = -0.41 ; in B, $r = 0.60$, slope = 1.00, y intercept = 41.4; in C, $r = 0.66$, slope = 0.84, y intercept = 12.8.

the modification of an ongoing eye-head gaze shift with an eye-only gaze shift.

Goossens and van Opstal (1997) also reported that the directions of the eyes, head, and gaze during gaze shifts can differ if the eyes and head are not aligned at the start of the gaze shift. They concluded that the head movement vectors were described best if driven by a craniocentric signal relating target position relative to the head, but also noted that there were some influences of the oculomotor system on head movement trajectories (see also Volle and Guitton 1993). Our results do not specifically address this type of dissociation, although if the eyes and head were unaligned initially, it would be interesting to see if EHMs would be aimed to the target and if there is any influence of the oculomotor error on the trajectories of the EHM.

Another difference between the EHMs observed in the dis-

tractor condition and those already reported in the literature is the lead time. Incorrect EHMs tended to be generated more in advance of the CGS than correct EHMs, and mean lead times for incorrect EHMs ranged from 20 to 90 ms. Fuller's review of eye-head coordination (Fuller 1992b) categorized mean lead times of ≤ 50 ms for EHMs directed to a target. Incorrect EHMs may have longer lead times than correct EHMs because incorrect EHMs are a behavioral manifestation of a distraction that must be suppressed and overcome before the ensuing CGS can be generated. This requisite suppression takes time, so that the reaction time for a CGS is greater if the CGS is preceded by an incorrect EHM compared with a CGS not preceded by incorrect EHMs (Fig. 9).

The main new finding of this paper is that orienting movements of the head can be generated before gaze shifts in a direction that sometimes differs from the direction of the ensuing gaze shift. To our knowledge, an explicit study of the metrics and dynamics of EHMs with stimuli at differing eccentricities has not been performed, so a potential explanation for correct EHMs previously studied was that they were generated simply in response to the direction of the target. We found that the peak velocities and accelerations of incorrect EHMs were larger when generated in the presence of more eccentric distractors (Table 2, Fig. 7), clearly demonstrating that incorrect EHMs were influenced by the location of the distractor, not simply the direction of the distractor. The metrics of incorrect EHMs also depended on the lead time. Those incorrect EHMs that were initiated earlier relative to the ensuing CGS tended to have larger amplitudes and reach higher peak velocities (Fig. 4). Thus the metrics of an incorrect EHM were determined primarily by how long the incorrect EHM was allowed to progress before being superseded by the ensuing CGS. These observations are analogous to those made in the preceding paper (Corneil et al. 1999) detailing the truncation of an ongoing IGS by the subsequent RGS. Given the comparable metrics and dynamics of incorrect EHMs and IGSs, as well as the reaction latencies of the ensuing gaze shifts to the target, we propose that the head movements during incorrect EHMs and IGSs share a similar neural mechanism. The only difference is whether the motor program encoding the movement to the distractor is potent enough to initiate a gaze shift. In the case of incorrect EHMs, the motor program encoding the movement to the distractor was not strong enough to surpass a gaze threshold but was still potent enough to surpass a head threshold, thereby initiating an incorrect EHM. In the case of IGSs, the motor program encoding the movement to the distractor was potent enough to surpass a gaze threshold and initiate an IGS. One cost of this gaze error was that it took subjects even longer to generate the target directed gaze shift than it did after incorrect EHMs (Fig. 9). Thus we propose that the threshold for the initiation of an orienting head movement is lower than the threshold for the initiation of a gaze shift.

Incorrect EHMs and models of gaze control

Evidence for strong coupling between eye and head movements comes from a number of sources. First, in head unrestrained cats and monkeys, stimulation of the superior colliculus (SC), a structure long thought to be an integral center for the generation of saccadic eye movements, leads to gaze shifts composed of eye and head movements that are

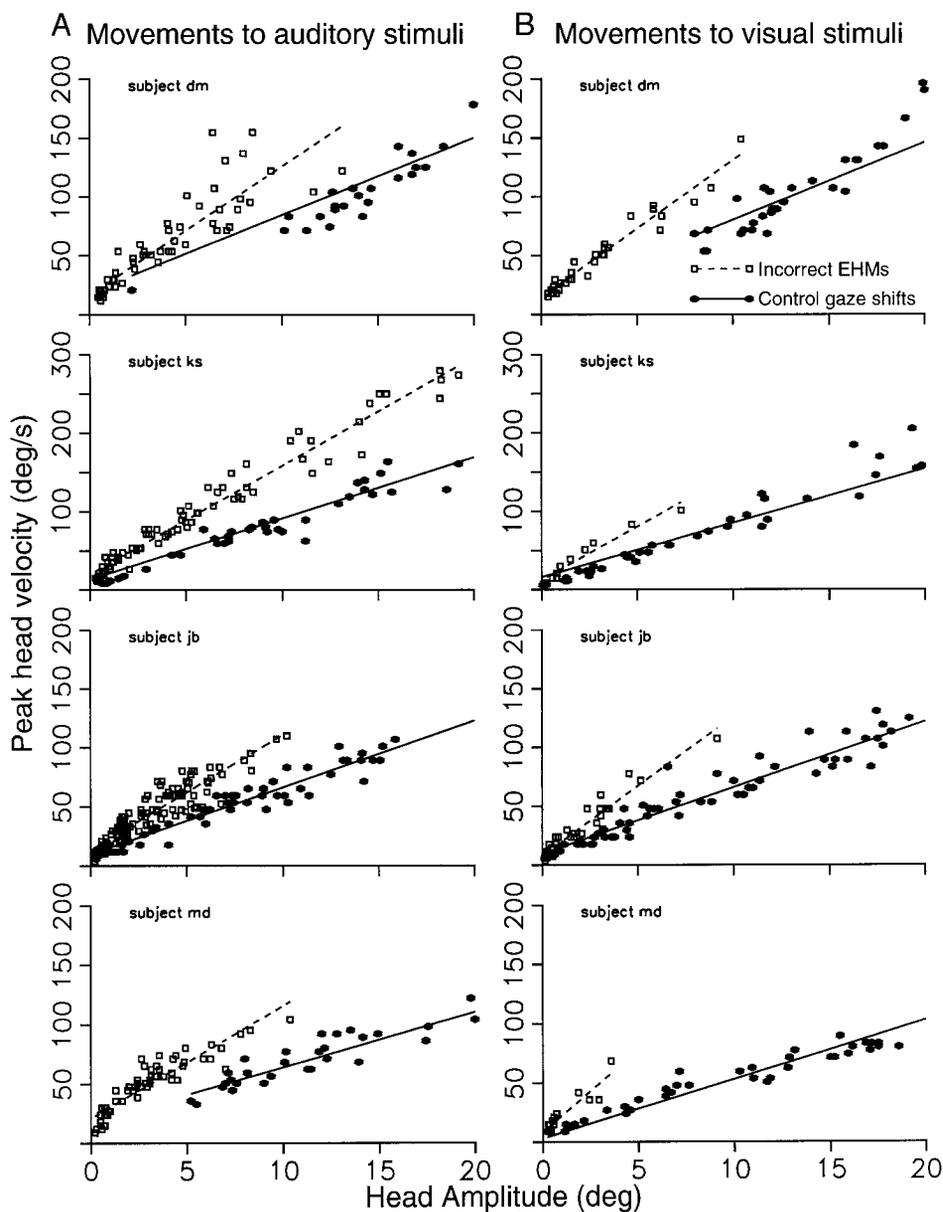


FIG. 6. Main sequence (peak velocity vs. amplitude) plots of the head movement directed to auditory (A) or visual (B) stimuli. Data are shown for all 4 subjects. Each main sequence relationship plots the observations from individual head movements and the fitted linear regression during incorrect EHMs (\square and - -) or control gaze shifts (\bullet and —). For all subjects, the regression line for the incorrect EHMs was significantly steeper than that for control gaze shifts.

very similar to those generated naturally (Freedman et al. 1996; Paré et al. 1994; Roucoux et al. 1980; Segraves and Goldberg 1992). Electrical stimulation in the primate SC also has been shown to induce short latency responses on the electromyographic activity of dorsal neck muscles (Corneil et al. 1998a,b). Second, the activity patterns of cells in the caudal portion of the SC also suggests that the SC encodes a gaze movement, and not the underlying movements of the eyes or head alone (Freedman and Sparks 1997a; Munoz et al. 1991b). Furthermore, the dynamics of movements of the eyes and head in cats during gaze shifts modified in mid-flight strongly implicate a distributed signal to both the eye and head (Guitton et al. 1990).

However, other experimental observations have suggested a high degree of independence between movements of the eyes and head. Cowie and Robinson (1994) noted that electrical stimulation in the SC could elicit movements of either the eyes or head separately (see Freedman et al. 1996 for a discussion of potential reasons for the differences in

the findings of these 2 monkey SC stimulation studies). Furthermore behavioral observations in monkeys (Phillips et al. 1995) and humans (Goosens and van Opstal 1997; Tweed et al. 1995; Zambarbieri et al. 1997) have shown that the timing and metrics of eye and head movements within gaze shifts are much more variable than would be expected if the eyes and head were driven solely by a common drive signal. Our results from the current experiment offer a potential explanation for some of these seemingly contradictory results. We have shown that an orienting head movement can be initiated more or less independently of a gaze shift. It is therefore possible that some of the controversy arises from the head being driven, at least in part, by an orienting signal that is not strictly related to the gaze shift. For example, the previously reported appreciable variability in the lead times and the metrics of head movements that accompanied gaze shifts could result from a varying combination of a gaze-related head command and a correct EHM. Of course, it remains to be determined conclusively if

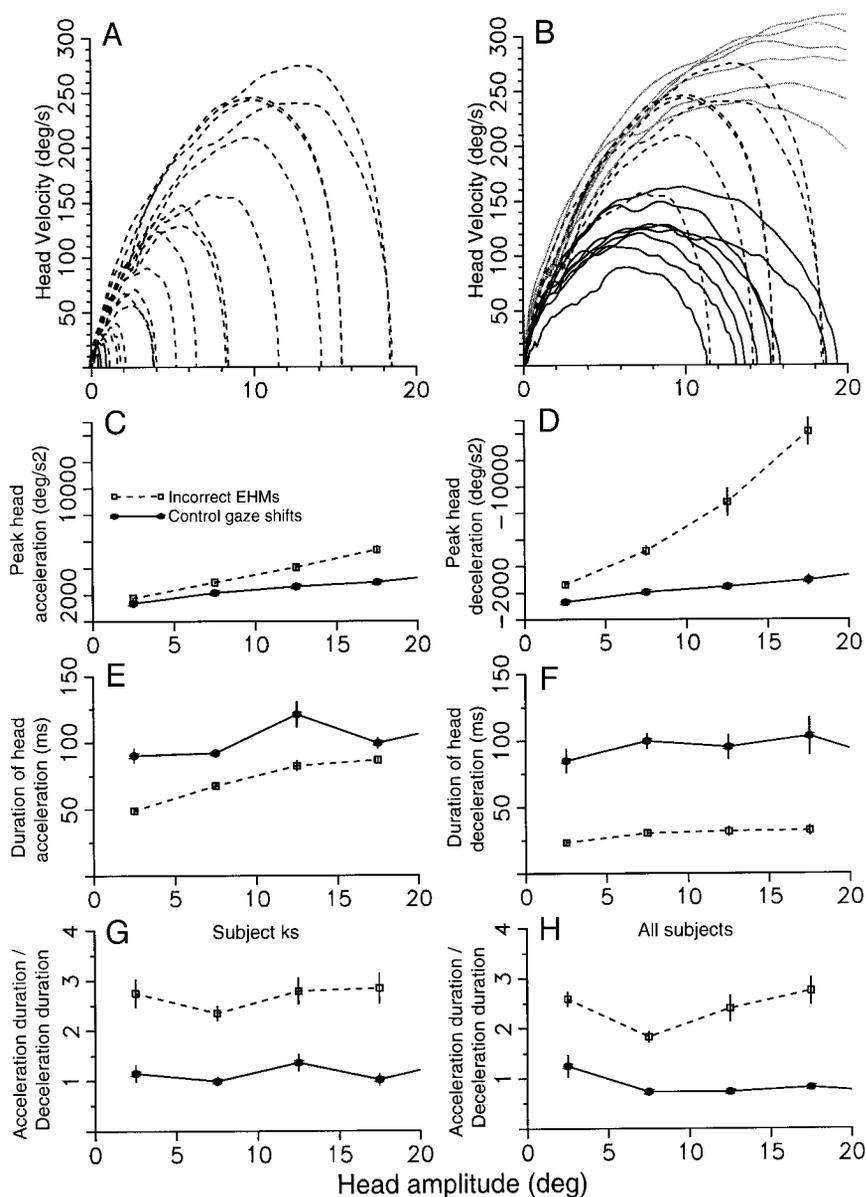


FIG. 7. Data from head movements generated by *subject ks* to auditory stimuli. *A* and *B*: phase-plane plots of head velocity vs. head amplitude. Each line represents a single head movement. *A*: head movements from all incorrect EHMs from VisT40°L/audD40°R trials. *B*: comparison of the phase-plane plots of head movements for head movements between 15 and 20° during incorrect EHMs (dashed lines) and during control gaze shifts (dark, solid lines) and for head movements between 30 and 40° during control gaze shifts (light, solid lines). *C–H*: parameters of the acceleration and deceleration phases of head movements during incorrect EHMs (empty squares and dashed lines) and control gaze shifts (filled circles and solid lines) plotted against head amplitude. Data in *H* are from all subjects. Each point and associated vertical lines represent the means \pm SE from ≥ 5 head movements pooled in 5° amplitude bins. *C*: peak acceleration of the head movement. *D*: peak deceleration of the head movement. *E*: duration of the acceleration phase. *F*: duration of the deceleration phase. *G* and *H*: ratio of the duration of the acceleration phase to the duration of the deceleration phase for *subject ks* (*G*) or for all subjects (*H*) for movements to incorrect EHMs to auditory stimuli.

there is a functionally relevant head-orienting signal linked obligatorily to large gaze shifts. Our results emphasize that an examination of the relative timing of the initiation of movements of the eyes and head is not sufficient to reveal the full nature of orienting drives to the head.

Influences of a distracting stimulus on eye-head coordination

We have found that distractors cannot only impart temporal effects to delay target-directed responses but can also impart spatial influences and induce erroneous responses (either IGSSs or incorrect EHMs). Both of these effects are dependent on the temporal register of the target and distractor (Corneil and Munoz 1996), and on the subject's state of visual fixation at the time of stimulus presentation (IGSSs: Munoz and Corneil 1995; incorrect EHMs: unpublished observations). Such results are consistent with the scheme proposed in the following text, in which certain oculomotor

areas are relatively disinhibited during the gap period in the gap task employed here, thereby leading to higher incidences of both IGSSs and incorrect EHMs. Our results are somewhat in agreement with the results of Walker and colleagues (1997), who stressed that remote distractors act to delay saccade initiation. However, we do not agree with their interpretation that this delay is mediated through an *extended fixation zone* within the SC (the relevant structure of the SC is described in the following text). Rather, we believe these temporal influences are mediated by competitive interactions between the motor programs encoding movements to either the target or the distractor. In the presence of a distractor, the resolution of this competition in favor of the target takes longer. Furthermore by decreasing the predictability of the time of target and distractor presentation, as well as varying the target location, the resolution occasionally may favor the distractor and lead to some overt form of distraction. In support of this hypothesis, it has been

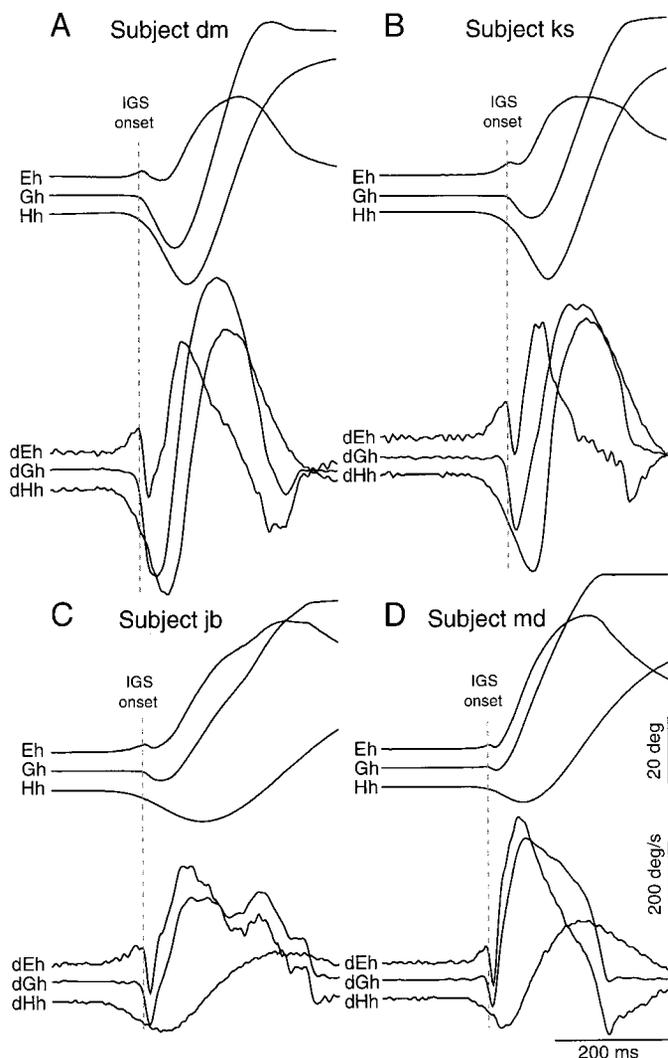


FIG. 8. Position and velocity traces of eye (Eh and dEh), head (Hh and dHh), and gaze (Gh and dGh) during incorrect gaze shifts (IGSs), which were preceded by incorrect EHMs. Data are shown for subjects *dm*, *ks*, *jb*, and *md* in A–D, respectively, from VisT60°R/audD60°L trials. ---, onset of the IGS. Note that the eye movement components of these IGSs were quite small and slow and that the IGSs were carried predominantly by a head movement, particularly for subjects *ks* and *dm*.

noted that remote regions of the SC seem to be linked via potent inhibitory connections (Munoz and Istvan 1998).

Neural model of the generation of incorrect EHMs and IGSs

We now outline a neural mechanism to account for the generation and similarities of IGSs and incorrect EHMs. This simplified scheme is meant only to convey predicted patterns of activity within various oculomotor structures and is based on patterns of activity known at three separate levels of the oculomotor system within the brain stem and spinal cord (see structure of model in Fig. 10A). The top level is the SC, a multilayered structure in the dorsal midbrain known to display saccadic or gaze-related activity before either visually guided (see Sparks and Hartwich-Young 1989 for review) or aurally guided (Jay and Sparks 1987a,b) movements. The middle level encompasses the known brain-stem premotor circuitry within the pons for horizontal movements (see Moschovakis et al.

1996 for review). The bottom layer represents the motor plants for the eyes and head. The three layers are connected by simple top-down projections (Fig. 10A). For the sake of brevity, we have grossly simplified these connections, and we stress that the connections shown in Fig. 10A are not meant to be precisely anatomically correct nor exclusive. The circuitry within and between each level is no doubt far more extensive than shown. In discussing our model, we first will outline the major features of the upper two levels of control based on evidence from neurophysiological experiments and will then outline how the model operates in the distractor condition.

Activity within the SC falls into two broad functional classes. Fixation neurons in the rostral SC are active when the eyes are immobile, and silent during saccades or gaze movements (Munoz and Guitton 1991; Munoz and Wurtz 1993; Peck 1989). In contrast, movement-related cells in the caudal SC are active before aurally or visually guided movements into a restricted region of oculomotor space, which defines the cell’s movement field (Freedman and Sparks 1997a; Jay and Sparks 1987a,b; Mays and Sparks 1980; Munoz and Wurtz 1995; Munoz et al. 1991a; Sparks et al. 1976; Wurtz and Goldberg 1971). Thus the neural signals encoding the location of either visual or auditory stimuli have been transformed onto a common oculocentric reference frame within the SC (Frens and van Opstal 1998; Jay and Sparks 1987a,b; Mays and Sparks 1980). The reciprocal discharge of fixation cells and movement-related cells are thought to result at least in part from intrinsic inhibitory connections between the rostral and caudal regions of the SC (Fig. 10A) (Meredith and Ramoa 1998; Munoz and Istvan 1998). Furthermore caudal regions of one SC are able to inhibit activity in caudal regions of the other SC, presumably by connections through the collicular commissure (Munoz and Istvan 1998).

Movement-related cells in the caudal SC are divided further into two subtypes based on their activity patterns prior to gaze

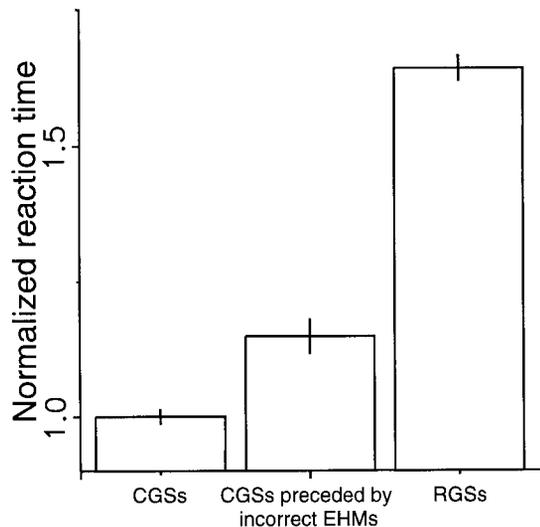


FIG. 9. Bar graph of normalized mean reaction latencies from all subjects for 3 categories of target-directed gaze shifts: CGSs not preceded by incorrect EHMs, CGSs preceded by incorrect EHMs, and RGSs (recorrective gaze shifts), which followed IGSs. Data for each subject were normalized to the mean reaction latency for CGSs not preceded by incorrect EHMs and subsequently pooled across all subjects. Error bars denote SE. Normalized reaction times were significantly different for the different categories of target-directed gaze shifts ($P < 0.0001$).

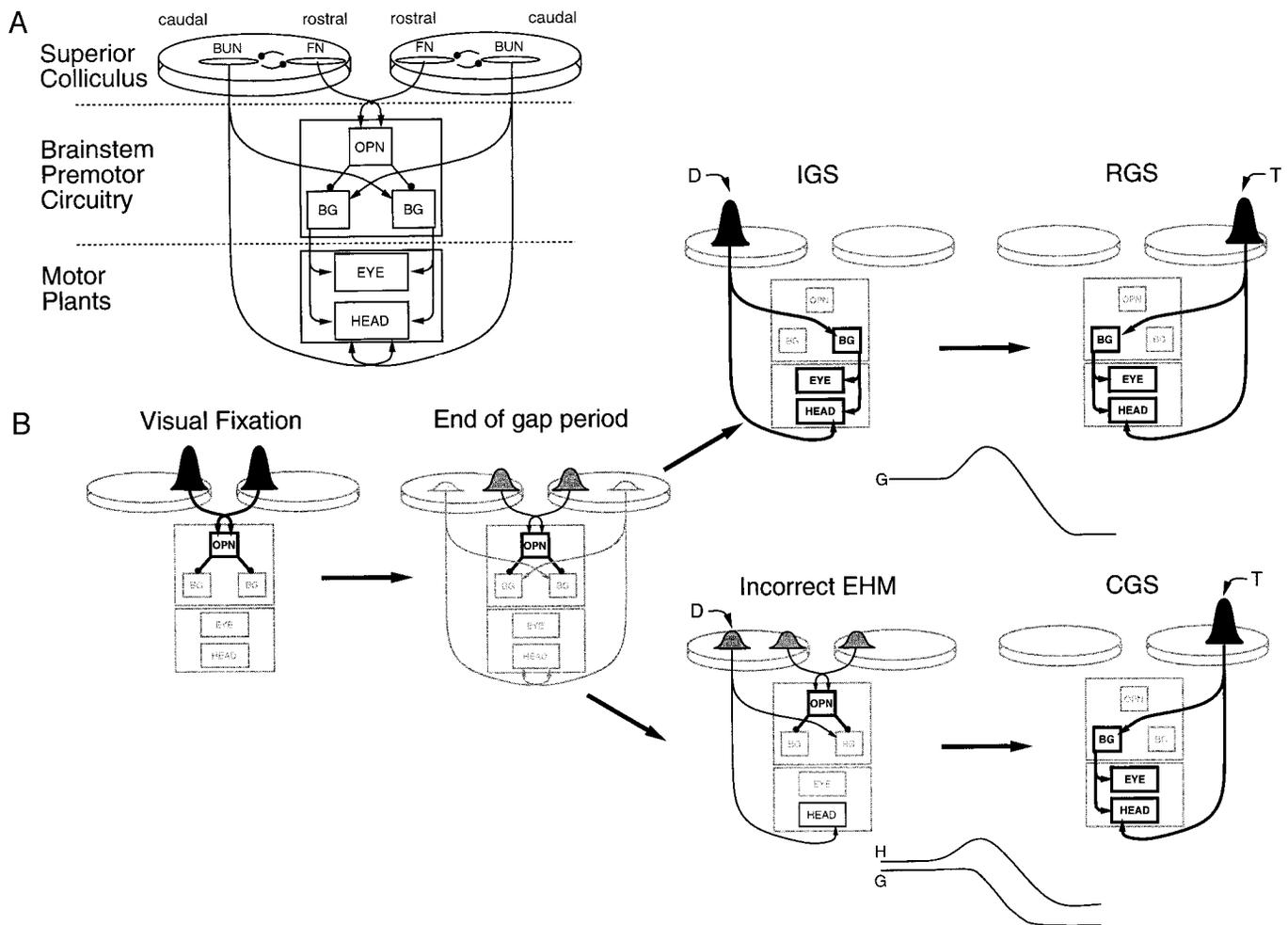


FIG. 10. Simplified depiction of a neural model of oculomotor control proposed to account for the generation of IGSs and incorrect EHM. Collicular burst neurons are not shown. See text for further details. For this model, arrows demonstrate excitatory projections, and lines with circles on the end demonstrate inhibitory connections. *A*: model is based on processes interacting within 3 separate layers in the brain stem and spinal cord. All connections within and between the layers in this simplified model are shown. Buildup neurons (BUNs) and fixation neurons (FNs) within the 2 superior colliculi are mutually inhibitory and project respectively onto either the burst generator (BG) or omnipause neurons (OPNs) located in the brain-stem premotor circuitry. OPNs inhibit the BG. During gaze shifts, the output of the BG is distributed to both eye and head motor plants. BUNs also have a 2nd projection that bypasses the OPNs to drive the head. *B*: state of the model in sequential temporal intervals in a distractor task. Darkness and height of the Gaussians in the SC denote an increased activity level of SC populations. Color and thickness of projection lines also denote the intensity of the activity carried along the projections, with a darker and thicker line implying a more intense signal. Populations or projection lines that are not active are not shown. Activity within this model is shown at 6 different intervals: during visual fixation of the central fixation point, at the end of the gap interval, at the initiation of an IGS, at the initiation of an RGS, at the initiation of an incorrect EHM and at the initiation of a CGS. Traces below the IGS-RGS and incorrect EHM-CGS sequences show the horizontal gaze (*G*) or head (*H*) traces of these movements. Note that the superior colliculus (SC) BUN population encoding the RGS is located further along the rostrocaudal dimension of the SC than the SC BUN population encoding the CGS. *D* and *T* convey the movement signals to either the distractor or target respectively that impinge on caudal regions of the SC.

shifts. Both burst (not shown in Fig. 10) and buildup neurons discharge a high-frequency, phasic burst of activity just before a movement into the cell's movement field (Munoz and Wurtz 1995). However, buildup neurons also show a gradual increase in their activity well in advance of the movement, and recent results have correlated this buildup activity during the gap period to the reaction latency of the ensuing movement (Dorris and Munoz 1998; Dorris et al. 1997). Buildup neurons also tend to be located slightly more ventral than burst neurons (Munoz and Wurtz 1995). Interestingly, using anatomic tracer techniques, May and Porter (1992) showed that there are two separate output channels from the monkey SC. A more dorsal

pathway projects to the medial paramedian pontine reticular formation, and the more ventral pathway projects more laterally to the reticular formation. As outlined in the following text, we speculate that the more ventral pathway may carry a signal that can initiate an orienting head movement.

In the brain-stem premotor circuitry, the omnipause neurons (OPNs) and the neurons of the burst generator (BG) display analogous activity patterns to fixation- and movement-related cells in the SC, respectively (see Moschovakis et al. 1996 for review). The OPNs essentially gate the activity of the BG so that the BG can only discharge when the OPNs have been silenced. In Fig. 10A, we have drawn connections from the

rostral regions of the colliculi to the OPNs and from the caudal regions of the colliculi to the BG. This is a simplification; we recognize that the SC by no means provides the sole drive to these regions (Everling et al. 1998), and there exists a gradient of projections along the rostrocaudal dimension of the SC to the OPNs and BGs (Büttner-Ennever et al. 1997; Gandhi and Keller 1997).

The essence of our model is that buildup neurons can drive the head in one of two ways (Fig. 10A). Both buildup and burst neurons provide a drive to the eyes and head through their projections to the BG (Gandhi and Keller 1997; Istvan et al. 1994; Scudder et al. 1996). Because the BG is gated by the OPNs, these collicular projections can drive the head only during gaze shifts. We also propose that some projections from buildup neurons bypass the OPNs and BGs and access the head motor plant without being gated by the OPNs. Note that we are not proposing a direct projection from the SC to head motoneurons, as the tectospinal pathway in monkeys is very weak if existent (May and Porter 1992). Rather the drive to the head is likely relayed through nuclei within the reticular formation not represented in Fig. 10 (Cowie et al. 1994).

Our specific prediction for the neural drive of EHM is that a portion of the projections from SC buildup neurons bypass this OPN "gate" and access head premotor centers. This bypass signal then could drive incorrect EHM or correct EHM, without evoking gaze shifts, depending on the level and location of buildup activity within the SC. Our supposition is based on the following evidence. First, buildup activity can occur well in advance of a gaze shift (Dorris et al. 1997; Glimcher and Sparks 1992; Munoz and Wurtz 1995), an obvious requirement because EHM lead gaze shifts. Second, anatomic and neurophysiological evidence suggests that the SC is possibly the earliest node within the oculomotor system at which both visual and auditory targeting signals are mapped onto a common oculocentric reference frame (see Stein and Meredith 1993 for review). This is of obvious import given that incorrect EHM can be generated to both visual and auditory distractors. Third, projections from the caudal SC distribute to both eye and head premotor centers, and some of these projections to head centers bypass the purported OPN gate (Cowie et al. 1994; Grantyn and Grantyn 1982; May and Porter 1992). Fourth, it has been shown that OPNs pause for the entire gaze shift in cats and not just for the saccadic eye movement component (Paré and Guitton 1998). Interestingly, Fig. 1 of Paré and Guitton (1998) illustrates what we would classify as an EHM while recording from an OPN and shows that the OPN continued to discharge during the EHM, demonstrating a drive to the head in cats that is not gated by OPNs. There is currently some debate as to whether the premotor circuitry within the primate brain stem encodes the entire gaze shift (Tomlinson and Bance 1992) or just the rapid eye movement component (Phillips et al. 1999; see Paré and Guitton 1998 for review). Fifth, electrical stimulation of the primate SC evokes short-latency facilitatory or inhibitory responses on the EMG activity of dorsal neck muscles (Corneil et al. 1998a,b), presumably through tecto-reticulo-spinal pathways. More importantly, these EMG responses are not obligatorily dependent on the stimulation evoking a gaze shift. Furthermore in many sites within the SC, the threshold for evoking EMG responses on the neck muscles was less than the threshold for evoking saccades or gaze shifts (unpublished observations).

How then would this simplified framework operate to account for the observed behaviors described in the current and preceding (Corneil et al. 1999) papers? During visual fixation, fixation neurons and OPNs are active and effectively suppress any movements (Fig. 10B—visual fixation). However, by the end of the gap period (Fig. 10B—end of gap period) and before the appearance of any stimuli, the SC enters a more disinhibited state, which is characterized by a decrease in the level of fixation neuron activity (Dorris and Munoz 1995; Munoz and Wurtz 1995) and a concomitant increase in the activity of buildup neurons at sites coding the movement to either the target or the distractor (Dorris and Munoz 1998). In spite of the decrease in fixation cell activity, OPNs maintain their inhibitory influence on the BG (Everling et al. 1998). Furthermore the drive from the buildup neurons that bypasses the OPNs is not strong enough to initiate an EHM.

By the time of arrival of the first stimulus, the caudal regions of both SC are in a relatively more disinhibited state compared with during visual fixation. The determinant as to whether an IGS or CGS will be generated is the amount of buildup activity and fixation related activities in the opposing colliculi. If the fixation neuron activity is still relatively high and the buildup activity is relatively low, then it will take subjects longer to generate a gaze shift, hence subjects will more likely generate a CGS. However, if the buildup activity is high and the fixation neuron activity is low, then the subject will have a greater chance of generating a movement to the signal that arrives first. If the target signal arrives first, then the subjects will drive a CGS with a short reaction latency. If the distractor signal arrives first, then subjects will generate either an IGS (Fig. 10B—IGS) or an incorrect EHM (Fig. 10B—incorrect EHM). Again, the level of buildup activity determines whether an IGS or an incorrect EHM will be generated. In the case of an IGS, the distractor signal impinges on an already high level of buildup activity, and the summed activities exceed a certain threshold, thereby initiating the high-frequency burst in overlying burst and buildup cells to drive the BG and silence the OPNs. Once this IGS has been initiated, it can be reversed by an RGS at any time, and the timing of this reversal command determines whether the IGS ends short of the distractor (i.e., is a hypometric IGS) or not, as well as the inter-gaze shift interval (Corneil et al. 1999). The accuracy of the ensuing RGS is ensured by nonvisual compensation, so that the location of buildup and burst neurons encoding the RGS within the SC is progressively located more caudally for larger RGSs (Fig. 10B—RGS). The scaling of the RGS amplitude based on the amplitude of the IGS, and the probable location of the cell population encoding the RGS, was discussed in the previous paper (see discussion of Corneil et al. 1999). Clearly, the reversal of the IGS by the RGS requires some factor or factors not depicted in Fig. 10B, otherwise the inhibition from the contralateral caudal SC would inhibit the motor program for the RGS during an on-going IGS. We speculate that the burst and buildup activities within the SC are affected in midflight by processes originating outside the SC related to target discrimination and selection. A change in the desired goal of the gaze shift would facilitate the development of the motor program to the target and suppress the motor program to the distractor.

However, if the arrival of the distractor signal is not potent enough, or does not develop early enough, to cause the appro-

priate burst and buildup cells to reach the threshold for gaze initiation, then the combination of the distractor signal with the preexisting buildup activity may be strong enough to initiate an incorrect EHM without an IGS via the projection bypassing the OPNs (Fig. 10B—incorrect EHM). As the gaze threshold was not attained, the OPNs remain activated, preventing the increased activity in the SC created by the presentation of the distractor from driving the BG. After a certain delay and after the target has been correctly identified, the incorrect EHM is quickly reversed by the subsequent CGS to the target (Fig. 10B—CGS).

This architecture provides plausible explanations for many of our experimental results. First, the similarities in the metrics of incorrect EHMs and IGSs occur because the extents of both of these movements are determined by how long it took for the ensuing target-directed gaze shift to be generated, regardless of whether the extant movement to the distractor was a movement of gaze (accomplished by both eye and head movements) or by a movement of the head alone. The neural correlate of the modification interval initially conceived by Becker and Jürgens (1979) is the time from the onset of the movement to the distractor until the initiation of the target-related SC motor program. Second, the dependency of metrics and dynamics of incorrect EHMs on the distractor eccentricity is explained by the activation of progressively more caudal populations of buildup neurons for more eccentric distractors, thereby encoding progressively stronger head movements. Third, the similarities between the metrics and dynamics of the head movement during either incorrect EHMs or hypometric IGSs occur because both types of movements initially are encoded for a large excursion. Fourth, the increased activity of the distractor-related buildup neuron population during IGSs compared with incorrect EHMs are more difficult to overcome by the motor program encoding the target-directed gaze shift, thereby explaining why target-directed gaze shifts have progressively longer latencies when preceded by incorrect EHMs or IGSs (Fig. 9).

Portions of this model are readily testable. First, this model predicts that the motor program encoding the RGS should move progressively more caudal during an on-going IGS and that the location of the RGS motor program should encode the metrics of the RGS, regardless of the inter-gaze shift interval. Evidence for such remapping recently has been shown to occur during double-step experiments in the primate SC (Goossens 1998). Second, EHMs should be correlated with the presence of buildup activity in the caudal regions of the SC contralateral to the EHM movement direction. Third, there should be a gradient in the activity of the population of buildup neurons encoding a gaze shift to a distractor, being highest before IGSs, slightly lower before incorrect EHMs, and lowest or non-existent before CGSs not preceded by incorrect EHMs. Fourth, low levels of sustained stimulation current in the caudal SC that are insufficient to evoke gaze shifts should be capable of driving movements of the head that resemble EHMs.

Conclusions

Our results suggest separate thresholds for the initiation of gaze shifts and orienting head movements and emphasize that a simple examination of eye and head onset times is not a sufficient approach to fully understand eye-head coordination

during gaze shifts. Future studies will require more complicated experimental protocols, such as employing multiple stimuli to tease apart different facets of orienting commands, and more sophisticated experimental techniques, such as combining extracellular recording and stimulation of neural centers with the recording of electromyographic neck muscle activity in behaving animals, to further understand the decomposition of orienting signals into the final movement commands for the eye and head.

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