

Human Eye-Head Gaze Shifts in a Distractor Task. I. Truncated Gaze Shifts

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Corneil, Brian D., Christine A. Hing, Dorothy V. Bautista, and Douglas P. Munoz. Human eye-head gaze shifts in a distractor task. I. Truncated gaze shifts. *J. Neurophysiol.* 82: 1390–1405, 1999. This study examines two current ideas regarding the control of eye-head gaze shifts. The first idea stems from recent studies involving electrical stimulation in the primate superior colliculus that suggest that a residual feedback of gaze displacement persists for ~100 ms after completion of a gaze shift. In light of this hypothesis, we examined the accuracy of gaze shifts generated very soon after the end of a preceding gaze shift. Human subjects were presented with a visual or auditory target along with an accompanying stimulus of the other modality. The accompanying stimulus appeared either at the same place as the target or at the diametrically opposite position, in which case it was termed a distractor. Subjects often made an *incorrect gaze shift* (IGS) in the direction of the distractor, followed by a *recorrect gaze shift* (RGS) in the direction of the target. We found that RGSs were accurately driven to the target, even when they followed IGSs by <5 ms, regardless of the size of the IGS. The second idea is that a gaze shift cannot be cancelled in midflight. The end point of IGSs frequently fell short of the distractor. The dynamics of these movements, and of the head movement components during the IGSs in particular, suggests that these hypometric IGSs were planned for a much larger excursion but were truncated and superceded by the reversing RGSs. These results emphasize that the gaze shifting system can change the desired goal of a gaze shift in midflight and that the superceding movement is accurate regardless of the metrics or timing of the preceding movement.

INTRODUCTION

Gaze shifts are composed of rapid, coordinated movements of both the eyes (eye-re-head) and head (head-re-space) that serve to reorient the visual axis in space (eye-re-space). Models of the gaze shifting system generally have been constructed to deal with one movement at a time (in citing literature in this paper, we refer to *gaze shifts* or *saccades* depending on whether subjects were or were not able to move their head, respectively). This bias has led to a common assumption that the gaze shifting system is “ballistic,” in the sense that a movement, once initiated, must be driven to completion (see Becker 1989 for a thorough review of this issue). Recently there has been a renewed interest in the performance of the oculomotor system in situations employing multiple stimuli of one or more modalities (Corneil and Munoz 1996; Driver and Spence 1998; Findlay 1997; Frens et al. 1995; Fuller 1996; Goldring et al. 1996; Groh and Sparks 1996; Hughes et al.

1994; Munoz and Corneil 1995; Schall and Bichot 1998; Walker et al. 1995, 1997; Yao and Peck 1997; Zambambieri et al. 1997). In the current and companion (Corneil and Munoz 1999) papers, subjects perform in a multimodal target-distractor experiment (described in the following text). In this experiment, subjects sometimes generate a movement sequence in which the first gaze shift is in the direction of the distractor, followed by a second gaze shift to the target. The two goals in the current paper are to examine the accuracy of the second gaze shift in light of recent results from perisaccadic and postsaccadic stimulation experiments in the primate superior colliculus (SC) (Kustov and Robinson 1995; Nichols and Sparks 1995; Schlag et al. 1998); and to examine the dynamics of the first gaze shift to determine whether this movement was reversed in midflight. We show that the performance of the gaze shifting system in this task illustrates previously unrecognized capabilities and leads to a more comprehensive understanding of the neural control of orienting movements.

Early models of saccadic control postulated that saccades were driven via the comparison of the desired and current eye position within the head (Robinson 1975). A shortcoming of this model was that oculomotor signals within the brain stem do not encode the position of the target relative to the head but instead encode the desired change in eye position (see Moschovakis et al. 1996 for review). Subsequent models (Jürgens et al. 1981; Scudder 1988) therefore suggested that saccades were driven by the comparison of desired and current displacement in eye position. These latter models necessitated the existence of a *displacement integrator* to provide the feedback of current eye displacement. This displacement integrator must be reset to zero before any subsequent saccade, otherwise the residual current displacement feedback could disrupt the accuracy of the next saccade. Recent experiments using electrical microstimulation in the primate SC to evoke a saccade either during or shortly after a naturally generated saccade (Kustov and Robinson 1995; Nichols and Sparks 1995; Schlag et al. 1998) provided evidence for a gradually resetting displacement integrator with a reset time constant of ~45 ms. The metrics of the evoked saccade varied as a function of the amplitude of the natural saccade and either the intersaccadic interval (Nichols and Sparks 1995) or the interval from the onset of the natural saccade to the onset of stimulation (Kustov and Robinson 1995; Schlag et al. 1998).

The majority of naturally generated saccades are separated by enough time that any purported residual command from the displacement integrator would have long since decayed to zero before the onset of the subsequent saccade. However, there are

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a few experimental protocols employing multiple stimuli capable of eliciting closely spaced saccades. In the double-step paradigm, a visual target initially is flashed at one location, and subsequently jumped to a second, final location (Hallett and Lightstone 1976a,b; Wheelless et al. 1966; see Becker 1989 for review). Depending on subject instructions and the timing of target steps, subjects may generate a double-saccade response consisting of a saccade directed to the initial target location and a second saccade to the final target location. In a few rare occasions, it has been reported that the second saccade can follow almost immediately after the end of the first saccade (Aslin and Shea 1987; Becker and Jürgens 1979; Lévy-Schoen and Blanc-Garin 1974; Ottes et al. 1984). Goossens and van Opstal (1997) used the double-step paradigm to test the predictions of a gradually resetting displacement integrator and showed that, contrary to the results obtained in SC stimulation experiments, the second saccade of a double-saccade response was accurate, even when it followed the initial saccade by between 30 and 50 ms. However, Goossens and van Opstal (1997) did not observe many intersaccadic intervals <30 ms, when any residual displacement feedback would maximally affect the metrics of the second saccade. Therefore although their results were inconsistent with a reset constant of 45 ms, their results still could be explained by a gradual reset of the displacement integrator, albeit with a faster time constant.

“Target-distractor” experiments, in which a subject is instructed to look only to one of two different stimuli, also can be used to elicit closely spaced saccades or gaze shifts. Reaction times in such experiments are typically longer than reaction times in double target experiments requiring only a simple detection process (Findlay 1982; Ottes et al. 1985). A neglected aspect of target-distractor experiments is a detailed analysis of movements made to the distractor instead of the target. Such *incorrect gaze shifts* (IGSs), as opposed to the *correct gaze shifts* (CGSs) that go directly to the target, have been reported in only a few previous target-distractor experiments (Corneil and Munoz 1996; Munoz and Corneil 1995; Ottes et al. 1985, 1987; Viviani and Swensson 1982), perhaps because other studies examined only movements to closely spaced visual distractors or to predictable target locations (Walker et al. 1995, 1997; Weber and Fischer 1994). The movement pattern of an IGS and the subsequent *reorrect gaze shift* (RGS) that drives the gaze to the target are basically identical to the double-saccade responses in double-step experiments (Ottes et al. 1985; Viviani and Swensson 1982). We have noted that the inter-gaze shift interval between the end of the IGS and the start of the RGS is quite commonly <20 ms (Fig. 3 of the current paper, see also Fig. 2B of Munoz and Corneil 1995 and Fig. 3 of Corneil and Munoz 1996). One goal of the current paper is to reevaluate the validity of the gradually resetting displacement integrator using a target-distractor paradigm that frequently elicits very short inter-gaze shift intervals.

Another feature we have noted from target-distractor experiments is that the IGS commonly ends short of the location of the distractor (Corneil and Munoz 1996; Munoz and Corneil 1995; Ottes et al. 1985; Viviani and Swensson 1982). The second goal of this paper is to understand the neural mechanisms underlying such hypometric IGSs. On one hand, it is possible that the hypometria results from an averaging of the movements to the distractor and target, as envisioned by

Becker and Jürgens (1979) for double-step responses or because the first saccade is part of a preplanned sequence. Alternatively, it is possible that the hypometria results from a truncation of the IGS due to a midflight change in the internal representation of target position (Minken et al. 1993; van Gisbergen et al. 1981). Note that the essential question is whether hypometric IGSs are completed movements or are interrupted in midflight. If the latter scenario is true, then the first response is not ballistic. To distinguish whether hypometric IGSs are completed or not, we examine their dynamics. If hypometric IGSs are completed movements, then their dynamics should resemble the dynamics of normal, amplitude-matched gaze shifts. If hypometric IGSs are interrupted in midflight, then their early dynamics should be typical of larger gaze shifts driven to the distractor or at least be very different compared with the dynamics of normal, amplitude-matched gaze shifts.

In the current experiments, subjects are free to move their heads. The advantages of allowing the subjects to move their heads are twofold. First, we can examine separately the dynamics of the eye and head components during IGSs. The eyes and head are very different mechanical structures, and the dynamics of the head in particular may reveal more about the initial motor command, given that the head initially accelerates faster for larger head movements (Zangemeister et al. 1981). Second, because the head is unrestrained, we can examine movements of larger amplitude and longer duration than those studied in previous experiments. Longer duration gaze shifts presumably have longer intervals over which they can be interrupted.

In our task, a visual or auditory target is presented along with an auditory or visual accompanying stimulus respectively, either at the same location (*enhancer condition*—Fig. 1A) or at opposite locations (*distractor condition*—Fig. 1B). We have noted before that the number of IGSs generated in the distractor condition depends on the state of visual fixation (Munoz and Corneil 1995) and on the asynchrony between the presentation of the target and accompanying stimulus (Corneil and Munoz 1996). The benefit of using multimodal stimuli is that the processes responsible for the movement patterns we observe are not operative only for visuomotor processing but rather are fundamental processes of the gaze shifting system,

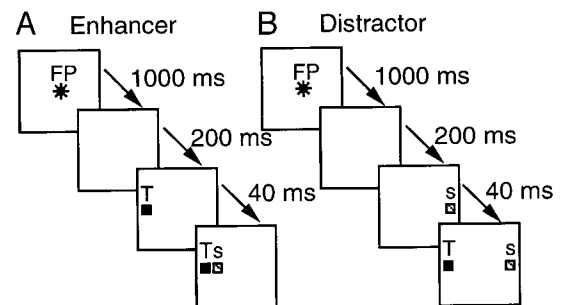


FIG. 1. A and B: schematic representation of the multimodal experiments. Overlying panels show the temporal sequence of the presented stimuli. In all trials, a central fixation point (FP) appeared for 1,000 ms and then disappeared for 200 ms before any peripheral stimuli were presented. In the enhancer condition (A), the target (T) and accompanying stimulus (s) were presented on the horizontal meridian at the same spatial location. In the distractor condition (B), the target and accompanying stimulus were presented on opposite sides of the vertical meridian. Asynchronies were introduced between the presentation of the stimuli. For example in A, the target was presented 40 ms before the accompanying stimulus, whereas the converse was true in B.

regardless of the stimulus modality to which the movements are directed.

Some of the results detailed here have been presented earlier in abstract form (Corneil and Munoz 1994, 1995; Corneil et al. 1997a,b).

METHODS

Experimental setup

All paradigms were reviewed and approved by the Queen's University Human Research Ethics Board. Three male subjects (ages 23, 26, and 37) and one female subject (age 23) were informed of the general nature of the study and consented to participate before the experiments were initiated. These subjects tended to have a large head movement contribution during gaze shifts to targets within the oculomotor range, and as such met criteria for *head-movers* (Fuller 1992; Goldring et al. 1996). We specifically selected head-movers to examine the dynamics of the gaze, eyes, and head during gaze shifts. One subject (*dm*, an author of this paper) was knowledgeable about the specific goals of the experiment, and another subject (*md*) was knowledgeable about the general goals of the experiment. The remaining subjects, *ks* and *jb*, were naive about the goals of the study. All subjects generated qualitatively similar patterns of eye, head, and gaze movements.

Subjects were seated upright in a straight-back chair in the center of a light-tight, sound-attenuated room and faced a translucent visual screen 86 cm away that spanned $\pm 35^\circ$ of the central visual field. The screen was illuminated diffusely (~ 1.0 cd/m²) between trials to prevent dark adaptation. The experiments were performed in darkness except for the presence of red light-emitting diodes (LEDs) and silence except for noise bursts emitted from small speakers. The background lights were extinguished 250 ms before a red LED, referred to as the fixation point (FP—0.3 cd/m²; CIE chromaticity coordinates: $x = 0.78$, $y = 0.21$), was back-projected onto the center of the screen signaling the start of a trial. The FP was illuminated for 1,000 ms and then was extinguished for 200 ms before the presentation of the peripheral stimuli. During this 200-ms "gap" period, the subjects were in complete darkness. We used this gap task to increase the number of IGSs that were generated in the distractor condition (Munoz and Corneil 1995). Once presented, the peripheral stimuli remained on for the remainder of the trial. The peripheral stimuli consisted of a visual stimulus from a red LED (4.7 cd/m²; CIE international chromaticity coordinates: $x = 0.73$, $y = 0.26$) and/or a broadband auditory stimulus from a speaker (74 dB at 4 kHz). The intensities of the peripheral visual and auditory stimuli were taken from preliminary experiments, which found that gaze shift reaction latencies were reduced to a minimum for visual stimuli >0.7 cd/m² and for auditory stimuli >70 dB (Corneil and Munoz 1996). The LEDs and speakers were mounted into small boxes, which were placed to the left and right at varying eccentricities along the horizontal meridian (described in the following text). Subjects were free to adopt any combination of eye and head movements they desired to perform the gaze shift and were not given any feedback about the eye-head strategy they employed or about the accuracy of their gaze shifts.

Experimental paradigms

Subjects were required to perform a series of seven experiments consisting of one control experiment and six multimodal experiments. The purpose of the control experiment was to obtain gaze shifts to visual or auditory stimuli presented alone over a range of eccentricities along the horizontal meridian for comparison with gaze shifts generated in the multimodal experiments. In the control experiment, one of the visual or the auditory stimuli was presented to the left or right. No additional stimuli were presented. The subjects were instructed to look to the presented stimulus as quickly as possible. Within each block of trials, the modality of the target (visual or auditory) and the direction of the target (left or right) were varied

randomly trial by trial so that all variations were presented an equal number of times. In different blocks of trials, the stimulus boxes were positioned to the left and right at ~ 5 , 15, 30, 45, and 60° eccentricity relative to the central FP. Subjects completed a block of 60 trials for each stimulus position. We did not obtain control data from subject *md* at 5° because the scleral search coil broke at the end of the preceding block (see *Data collection and analysis*).

In the remaining six multimodal experiments, the peripheral stimuli consisted of both visual and auditory stimuli. Within each experiment, one stimulus was the designated target, and subjects were instructed to look to the target as quickly as possible. They were not given any specific instructions on how to behave with regard to the accompanying stimulus, although they were informed that it would be presented in each trial. The modalities of the target and accompanying stimulus were always different across blocks of trials. Three of the multimodal experiments employed a visual target with an accompanying auditory stimulus, and the other three experiments employed an auditory target with an accompanying visual stimulus. The experiments were run with the peripheral stimuli at each of ~ 20 , 40, and 60° along the horizontal meridian for a total of six multimodal experiments (i.e., visual or auditory target, at each of 20, 40, and 60°). The peripheral stimuli were presented randomly in one of two conditions. In the *enhancer* condition (Fig. 1A), the target and accompanying stimulus were presented at the same point in space. In the *distractor* condition (Fig. 1B), the target and accompanying stimulus were presented on opposite sides of the vertical meridian. A set of four asynchronies were introduced between the presentation of the target and accompanying stimulus in both enhancer and distractor conditions. The target was presented either 40 ms (Fig. 1A) or 20 ms before the accompanying stimulus, or the accompanying stimulus was presented either 20 or 40 ms (Fig. 1B) before the target. These asynchronies were used to reduce the predictability of the presentation of the peripheral stimuli relative to the disappearance of the central FP. In an earlier study, we found that the yield of IGSs in the distractor condition was increased when the accompanying stimulus was presented before the target (Corneil and Munoz 1996).

All variations within the multimodal experiments (left or right; enhancer or distractor; 4 temporal asynchronies) were interleaved randomly within a block of 160 trials by a 486 computer that controlled the experiment at a rate of 1,000 Hz, and all variations were presented an equal number of times within a single block of trials. Subjects completed two blocks of trials for each experiment. Different experiments were run on different days, although subjects usually completed both multimodal experiments at a given eccentricity on the same day. The selection as to which modality would serve as the target for the first multimodal experiment was varied for different days.

Data collection and analysis

Subjects were positioned in the center of a cube, which set up rapidly oscillating horizontal and vertical magnetic fields (60 and 90 kHz, respectively; phase-angle system from CNC Engineering). Horizontal gaze (eye position in space) and head (head position in space) movements were recorded via the magnetic search coil technique (Robinson 1963) from search coils secured on the eye and head respectively. For measurement of gaze position, a search coil embedded in a contact lens annulus (Skalar Instruments) was placed onto the left or right cornea. To reduce the irritation caused by the search coil, one to two drops of 0.5% proparacaine hydrochloride was administered for topical anesthesia before insertion of the coil. The search coil remained on the eye for a period of ~ 30 min, and subsequent drops of the anesthetic were administered as required. This 30-min period was the amount of time it took to calibrate the gaze signal and run both blocks in one multimodal experiment or all blocks of the unimodal control experiment. Calibration of the gaze coil was achieved by having the subject look to visual stimuli on the tangent screen of known eccentricities while keeping the head still. Occasionally,

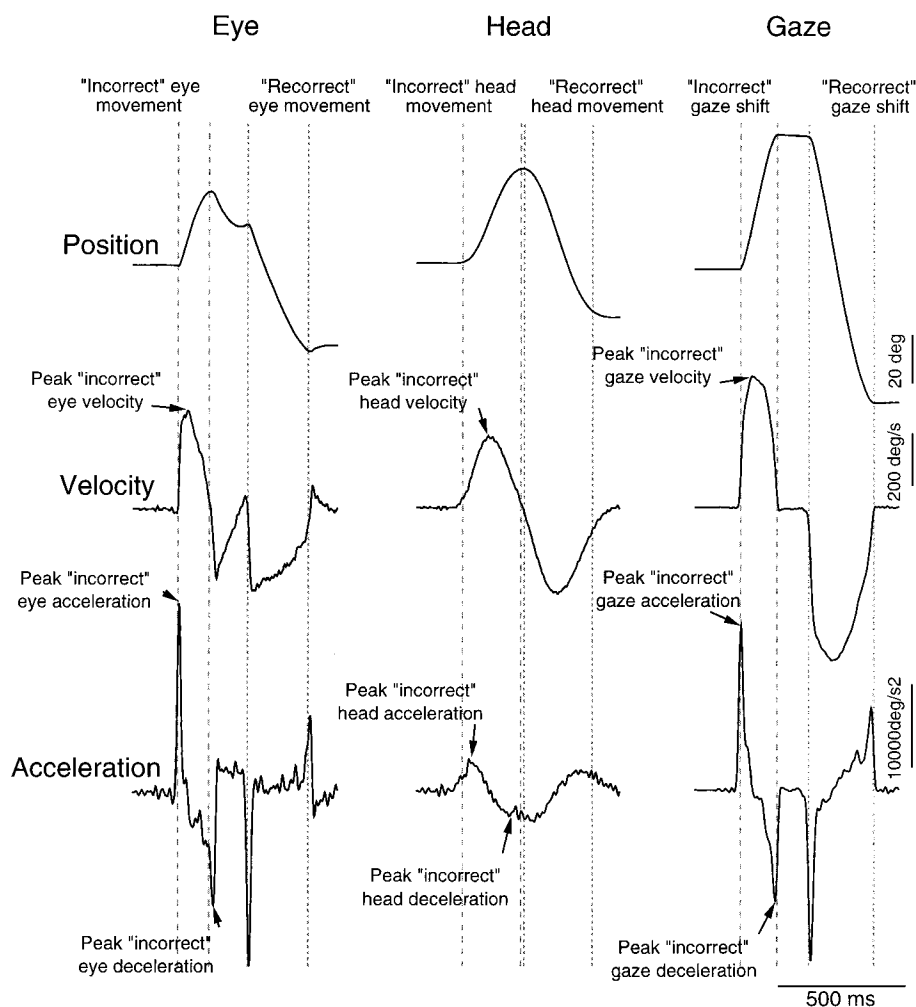


FIG. 2. Position, velocity, and acceleration traces of the movements of the eye (eye-re-head), head (head-re-space), and gaze (eye-re-space) during a representative incorrect gaze shift (IGS), illustrating the movement parameters that were marked for each IGS. Upward deflections in the traces represent rightward movements, and downward deflections represent leftward movements. The movements were divided into 2 portions, an "incorrect" portion in which the movement was directed to the distractor, and a "reconfirm" portion during which the movement was directed to the target. - - -, delineation of the incorrect portion of the movements; ···, delineation of the reconfirm portion of the movements. For each IGS and reconfirm gaze shift (RGS), the start, end, peak velocity, peak acceleration and deceleration of the incorrect and reconfirm portions of the eye, head, and gaze shift were measured, as well as the durations of the acceleration and deceleration periods.

the wire loops within the scleral search coil would break either during the placement or removal of the search coil or during an experiment (as was the case for subject *md* during the control experiments). Depending on how the subject felt and if the search coil had been on the eye for <30 min, a different search coil replaced the broken one, and the experiment was continued. After 30 min, the search coil was removed from the subject's eye, rinsed with hydrogen peroxide and sterile water, and subsequently was placed on the other eye. A second experiment then was run. For measurements of horizontal head position, a search coil was taped securely on the subject's forehead in the frontal plane. The head coil was calibrated as follows. Before the experimental session, an experimenter wore the head coil and a helmet on which a laser was mounted securely. The experimenter then sat in the experimental chair and aligned the laser spot on targets of known eccentricities. At the completion of the day's session, both of the subject's eyes were checked for corneal abrasions. Subject *ks* developed a corneal abrasion and was unable to complete the entire series of experiments using the scleral search coils. For the multimodal experiments at 20°, eye and head movements for subject *ks* were recorded with DC electrooculography and a head potentiometer, respectively, as described previously (Cornel and Munoz 1996; Goldring et al. 1996).

Horizontal gaze and head positions were digitized at 500 Hz. Digitized data were stored on hard-disk, and subsequent analysis was performed off-line on a graphics package designed for the analysis of oculomotor data on a Sun Sparc 2 workstation. Horizontal eye position (eye position in the head) was reconstructed off-line by subtracting the calibrated head signal from the gaze signal. Velocity and

acceleration traces were derived from the eye, head, and gaze position signals by a low-pass finite impulse response filter (Usui and Amidror 1982), with the -3dB cutoff set at 45.9 Hz. The onset of the gaze shift was determined when the gaze velocity exceeded 30°/s. The onset of the eye and head movements during gaze shifts were determined when the corresponding velocities exceeded 30 and 15°/s, respectively. Marks were inserted on each trial by a data analyst on the start, finish, and peak velocity and acceleration of the gaze, head, and eye movement. The durations of the acceleration period for the gaze, eye, or head movement were determined as the time from movement onset to peak velocity, and the duration of the deceleration period was determined as the time from peak velocity to the end of the movement. Examples of the marks inserted on a single trial are shown in Fig. 2. All trials were inspected visually by a second data analyst to check for errors and to ensure consistency. Gaze shifts were classified as anticipatory and were excluded from the analysis if they were initiated <80 ms after the first presented stimulus (Cornel and Munoz 1996). This anticipatory cutoff was derived from a previous set of experiments in our laboratory in which subjects were instructed to anticipate the appearance of a visual or auditory stimulus at 20°. Movements that were initiated <80 ms after target appearance were correct ~50% of the time, whereas movements initiated >80 ms after target appearance were correct ~95% of the time. Gaze shifts with reaction times >500 ms after the onset of the second presented stimulus were excluded due to lack of subject alertness. In total, <1% of gaze shifts were rejected with these two criteria.

RESULTS

In this paper, we describe the metrics and dynamics of gaze shifts generated by subjects in the distractor condition. We refer to the accompanying stimulus presented opposite the target as the “distractor,” although the distractor and enhancer conditions were interleaved randomly within each experiment so the accompanying stimulus is technically not a distractor in the enhancer condition. For brevity, we refer to experiments using a visual target and an auditory distractor as *VisT/audD* experiments, and the converse as *AudT/visD* experiments. If the location of the stimuli is relevant, the terminology *AudT60°R/visD60°L* is used to denote trials wherein an auditory target was presented 60° right and a visual distractor was presented 60° left.

Classes of gaze shifts in the distractor condition

Gaze shifts generated by subjects in the distractor condition were divided into one of two classes depending on the direction of the initial gaze shift with respect to the location of the target. Figure 3A shows traces of gaze shifts generated by *subject md* in *VisT60°L/audD60°R* trials. The subject performed the task correctly and generated CGSs by shifting gaze directly to the target (Fig. 3A, —). He also generated IGSs by shifting gaze initially in the direction of the distractor (Fig. 3A, - - -). IGSs were followed very shortly by RGSs, which brought the subject’s gaze to the target. The shorter reaction times of IGSs compared with CGSs, and the increased number of IGSs generated when the distractor was presented before the target have been described in detail (Corneil and Munoz 1996). These relationships were observed in the present study for all multimodal experiments at all stimulus eccentricities and were not studied in further detail.

The percentages of IGSs generated by each subject in the distractor conditions of the different multimodal experiments are shown in Table 1. The results are pooled across direction for all subjects (no difference in number of IGSs generated to the right or left, paired *t*-test, $P = 0.60$). On average, subjects generated IGSs in 20–30% of all distractor trials (minimum 9%, maximum 63%) in both types of multimodal experiments. In total, we recorded 499 IGSs in *VisT/audD* experiments and 390 IGSs in *AudT/visD* experiments.

Timing and metrics of IGSs and RGSs

Examples of IGSs and subsequent RGSs generated by *subject md* are shown aligned on target onset in Fig. 3B. A cursory examination of this figure reveals considerable variations in the reaction times and amplitude of the IGSs. Furthermore the subsequent RGS brought gaze to approximately the same location.

To begin to examine the validity of the purported gradually resetting displacement integrator during IGS-RGS sequences, we first establish whether the correlations between various metrics during the IGS-RGS sequences resemble those previously reported in double-step experiments (see Fig. 3C for a graphic depiction of the parameters). We measured the reaction time of the IGS relative to target onset because this time is analogous to the “modification time” concept developed in double-step experiments (Becker and Jürgens 1979; Lisberger et al. 1975). The results are pooled across direction for all further analyses (a series of paired *t*-test for all subjects in all

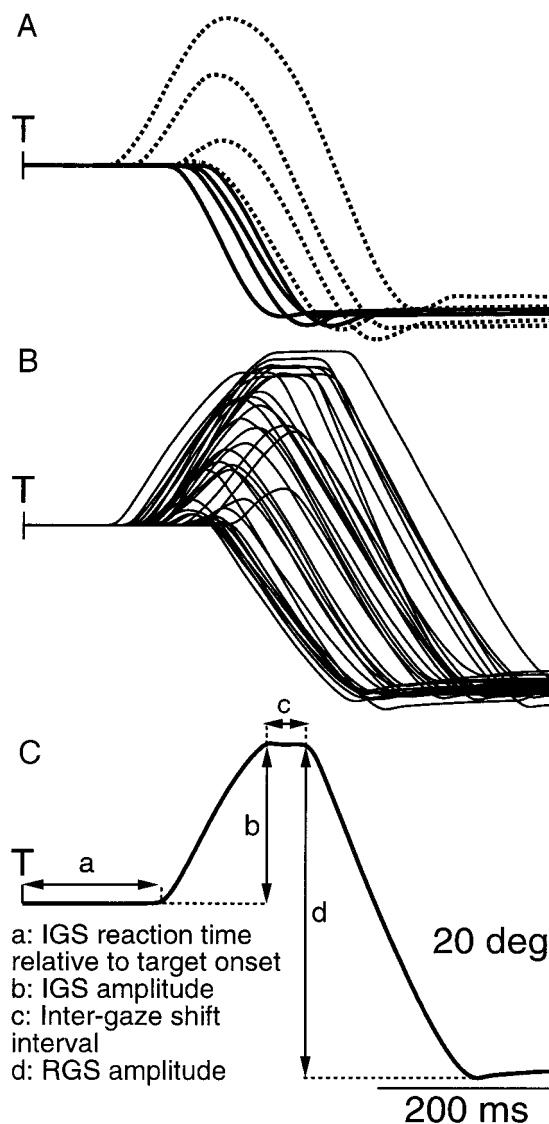


FIG. 3. Metrics of IGSs and RGSs. All traces are aligned on target onset (T). A: gaze traces from *subject md* in *VisT60°L/audD60°R* trials. Correct gaze shifts (CGSs, —) occur when the subject looked directly to the target. - - -, IGS-RGS sequences in which the gaze was initially directed to the distractor before going to the target. IGSs tend to be generated before CGSs. B: all of the IGSs and RGSs generated by *subject md* in the same experiment as A. C: single IGS-RGS sequence displaying the metrics examined in Figs. 4–6.

multimodal experiments compared either the IGS reaction time, IGS amplitude or inter-gaze shift intervals for rightward and leftward directed IGSs; in all cases, $P > 0.40$).

The IGS reaction times, IGS amplitudes, and inter-gaze shift intervals for *subject md* for multimodal experiments at 40° are shown in Fig. 4, A–C, respectively, and a full breakdown of the parameters of the IGSs is shown for all subjects in all multimodal experiments in Table 2. There were some systematic variations in these parameters depending on either the modality of the target and distractor (i.e., in either *VisT/audD* or *AudT/visD* experiments) and on the eccentricity of the stimuli (i.e., at 20, 40, or 60°). A full analysis of these variations departs from the goals of this paper, hence we only briefly summarize the major trends in the data. IGS reaction times tended to be longer in *AudT/visD* experiments and for distractors placed at 60°

TABLE 1. Percentage of IGSs generated in the distractor conditions in VisT/audD and AudT/visD experiments at different amplitudes

Amplitude	Subject				Totals
	<i>dm</i>	<i>ks</i>	<i>jb</i>	<i>md</i>	
VisT/audD experiments					
60°	63	11	22	42	34.5
40°	46	27	22	34	32.3
20°	35	9	21	16	20.3
Totals	48.0	15.7	21.7	30.7	29.0
AudT/visD experiments					
60°	13	13	29	13	22.7
40°	22	13	36	24	23.8
20°	45	32	31	37	36.3
Totals	26.7	19.3	32.0	24.7	20.7

IGS, incorrect gaze shift

[2-factor ANOVA across distractor modality (visual or auditory, $P < 0.0005$) and distractor eccentricity ($P < 0.0005$); and by Newman-Keuls post hoc analyses; a significant interaction effect also was revealed ($P < 0.0005$)].

IGSs varied widely in amplitude (Fig. 4B). They tended to be smaller in VisT/AudD experiments and when distractors were less eccentric [2-factor ANOVA across distractor modality ($P < 0.0005$) and eccentricity ($P < 0.0005$), and by Newman-Keuls post hoc analyses; a significant interaction effect across factors was also revealed ($P < 0.0005$)]. We distinguished between *hypometric IGSs* and *completed IGSs*, depending on how close the IGS brought gaze to the location of the distractor. The cutoff between hypometric and completed IGSs was computed by subtracting two SD from the average of the distribution of CGS end points in the converse experiment when the distractor served as the target. IGSs that fell short of this cutoff were termed hypometric IGSs; the rest were termed completed IGSs. This cutoff for *subject md* is marked in Fig. 4B (---). Percentages of hypometric IGSs are listed for all subjects in Table 2. Significantly more hypometric IGSs were generated in VisT/audD experiments than in AudT/visD experiments (paired *t*-test, $P < 0.05$). The distinction between hypometric and completed IGSs is relevant in the section examining IGS dynamics.

The inter-gaze shift interval between the end of the IGS and start of the RGS was highly variable, ranging from <5 to >300 ms (Fig. 4C, Table 2). This inter-gaze shift interval tended to be shorter in VisT/audD experiments and with more eccentric distractors [2-factor ANOVA across distractor modality ($P < 0.0001$) and eccentricity ($P < 0.0001$), with Newman-Keuls post hoc analysis; a significant interaction effect between factors was observed ($P < 0.0001$)].

IGS amplitude (Fig. 5A) and inter-gaze shift interval (Fig. 5C) tended to be smaller and shorter for longer IGS reaction times (also see Fig. 3B). These trends were consistent for all subjects in all multimodal experiments (24 combinations in all: 4 subjects; 20, 40, or 60°; VisT/audD or AudT/visD experiments; Fig. 5, B and D). The observed correlations were stronger and more likely to reach significance in VisT/audD experiments, possibly due to the greater number of IGSs. These results are analogous to the amplitude-transfer functions de-

scribed by Becker and Jürgens (1979), suggesting that a similar mechanism underlies double-saccade responses in double-step experiments and IGS-RGS sequences.

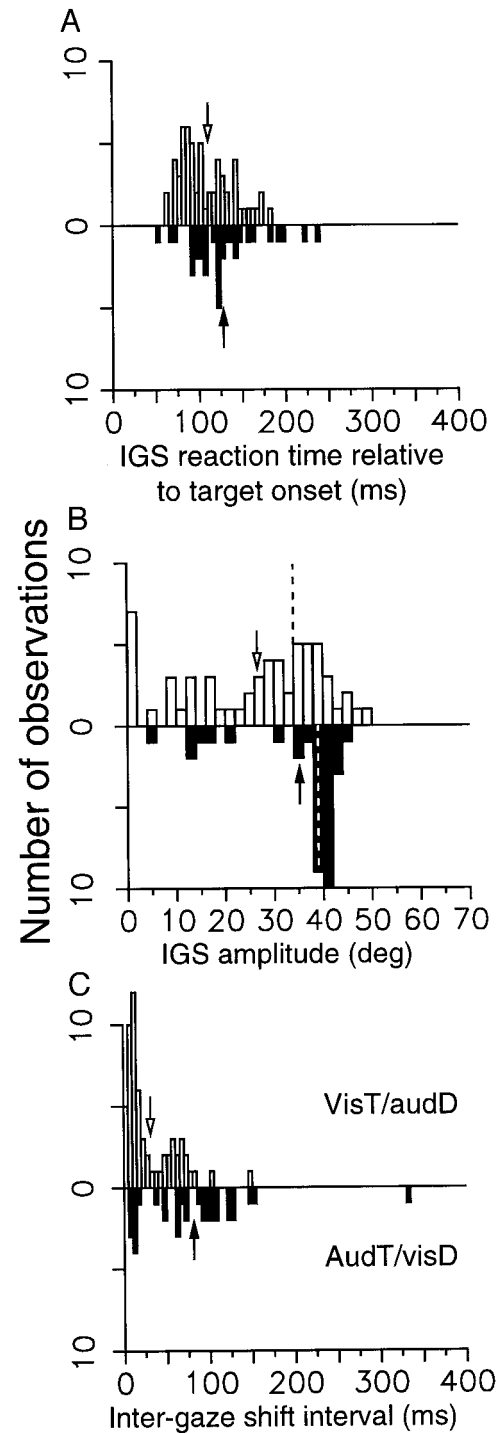


FIG. 4. Frequency histograms for IGS metrics for *subject md* from multimodal experiments at 40°, showing the IGS reaction times relative to target onset (A), IGS amplitudes (B), and the inter-gaze shift intervals between the end of the IGS and the start of the RGS (C). □, data from VisT/audD experiments. ■ data from AudT/visD experiments. ↓ and ↑, mean measure from VisT/audD and AudT/visD experiments respectively. IGS reaction times relative to target onset (A) can be <80 ms because the movement was driven by the distractor, which may be presented before the target depending on the asynchrony. ---, cutoff amplitudes separating hypometric and completed IGSs (see text for details).

TABLE 2. Quantification for all subjects of the IGS reaction times, IGS amplitudes, and inter-gaze shift intervals

Subject Measure	VisT/audD Amplitude			AudT/visD Amplitude		
	60°	40°	20°	60°	40°	20°
<i>dm</i>						
<i>n</i>	98	66	37	21	33	55
RT, ms	128 ± 33	136 ± 32	140 ± 36	183 ± 54	167 ± 55	147 ± 43
Amp, °	36.3 ± 15.0	32.6 ± 12.9	18.1 ± 5.7	47.1 ± 12.2	34.5 ± 12.5	19.7 ± 5.2
Percent Hypo.	72	52	58	20	71	13
IGI, ms	24 ± 31	31 ± 39	54 ± 51	178 ± 122	136 ± 99	135 ± 115
<i>ks</i>						
<i>n</i>	16	36	13	19	19	49
RT, ms	175 ± 35	154 ± 31	233 ± 85	243 ± 58	207 ± 69	208 ± 57
Amp, °	32.3 ± 29.4	22.8 ± 13.0	11.8 ± 6.5	54.1 ± 8.9	34.1 ± 9.1	16.8 ± 6.5
Percent Hypo.	80	78	62	50	50	38
IGI, ms	39 ± 38	47 ± 57	246 ± 66	161 ± 166	135 ± 92	200 ± 119
<i>jb</i>						
<i>n</i>	35	34	32	41	46	32
RT, ms	159 ± 26	129 ± 29	98 ± 38	239 ± 43	141 ± 43	150 ± 46
Amp, °	16.4 ± 10.8	11.3 ± 8.5	10.3 ± 6.0	43.9 ± 13.7	25.3 ± 10.0	16.7 ± 4.1
Percent Hypo.	100	94	64	60	96	69
IGI, ms	24 ± 22	36 ± 42	52 ± 31	132 ± 140	110 ± 81	187 ± 155
<i>md</i>						
<i>n</i>	65	47	20	20	33	22
RT, ms	133 ± 27	114 ± 31	110 ± 33	162 ± 21	128 ± 42	104 ± 48
Amp, °	32.2 ± 21.3	25.3 ± 14.2	14.4 ± 8.6	47.6 ± 13.4	35.0 ± 10.6	19.8 ± 5.0
Percent Hypo.	75	66	45	90	54	35
IGI, ms	23 ± 23	28 ± 31	66 ± 45	94 ± 95	80 ± 63	97 ± 55

Data is given as means ± SD. The percentages of hypometric IGSs are also given (Percent Hypo.). RT, reaction time; Amp, amplitude; IGI, inter-gaze shift interval.

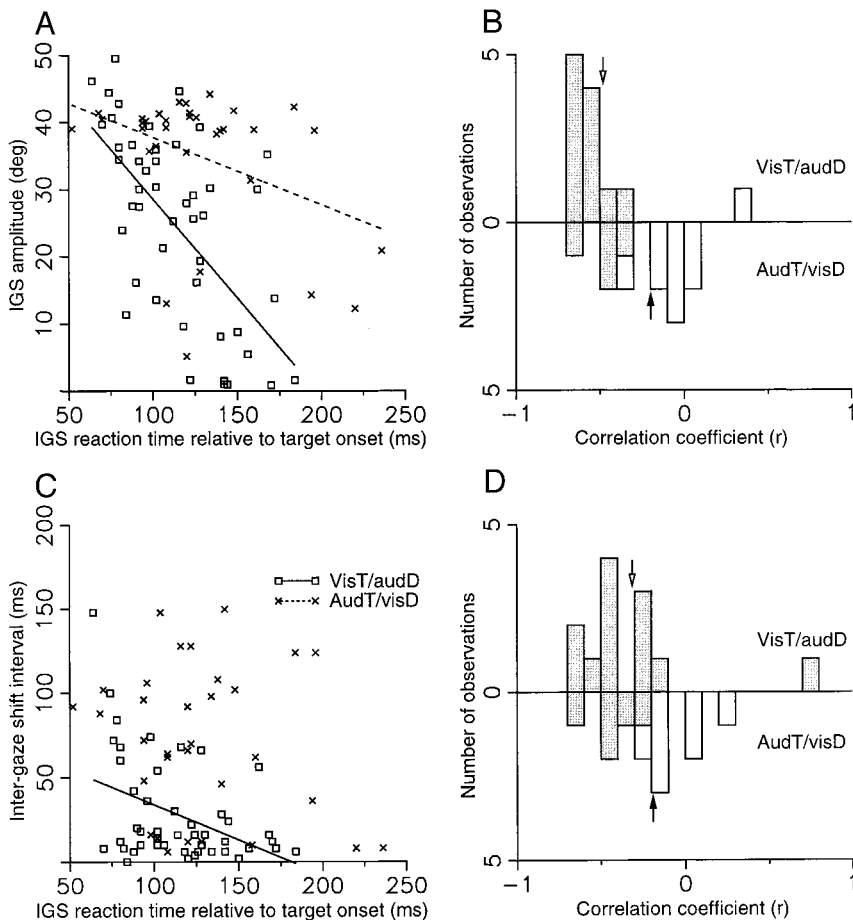


FIG. 5. A and C: plot of IGS amplitude vs. IGS reaction time relative to target onset (A) and inter-gaze shift interval vs. IGS reaction time relative to target onset (C) for subject *md* for experiments at 40°. Each point in A and C represents data from a single IGS. □ and —, observations and regression lines respectively from the VisT/audD experiment. × and - - -, observations and regression lines, respectively, from the AudT/visD experiment. Regression lines are shown for significant correlations. B and D: correlation coefficient distributions from all subjects in all multimodal experiments for the relationship between IGS amplitude vs. IGS target-aligned reaction time (B) and for the relationship between inter-gaze shift interval vs. IGS target-aligned reaction time (D). Data from VisT/audD experiments are shown above the line, data from AudT/visD experiments below the line. ▣, statistically significant correlations ($P < 0.05$). ↓ and ↑, mean correlation coefficient for the histograms from VisT/audD and AudT/visD experiments, respectively. For — in A, $r = -0.65$, slope = -0.30 , y intercept = 58.2. For - - - in A, $r = -0.40$, slope = -0.10 , y intercept = 47.8. For — in C, $r = -0.42$, slope = -0.41 , y intercept = 75. Regression for the AudT/visD relationship in C was not significant.

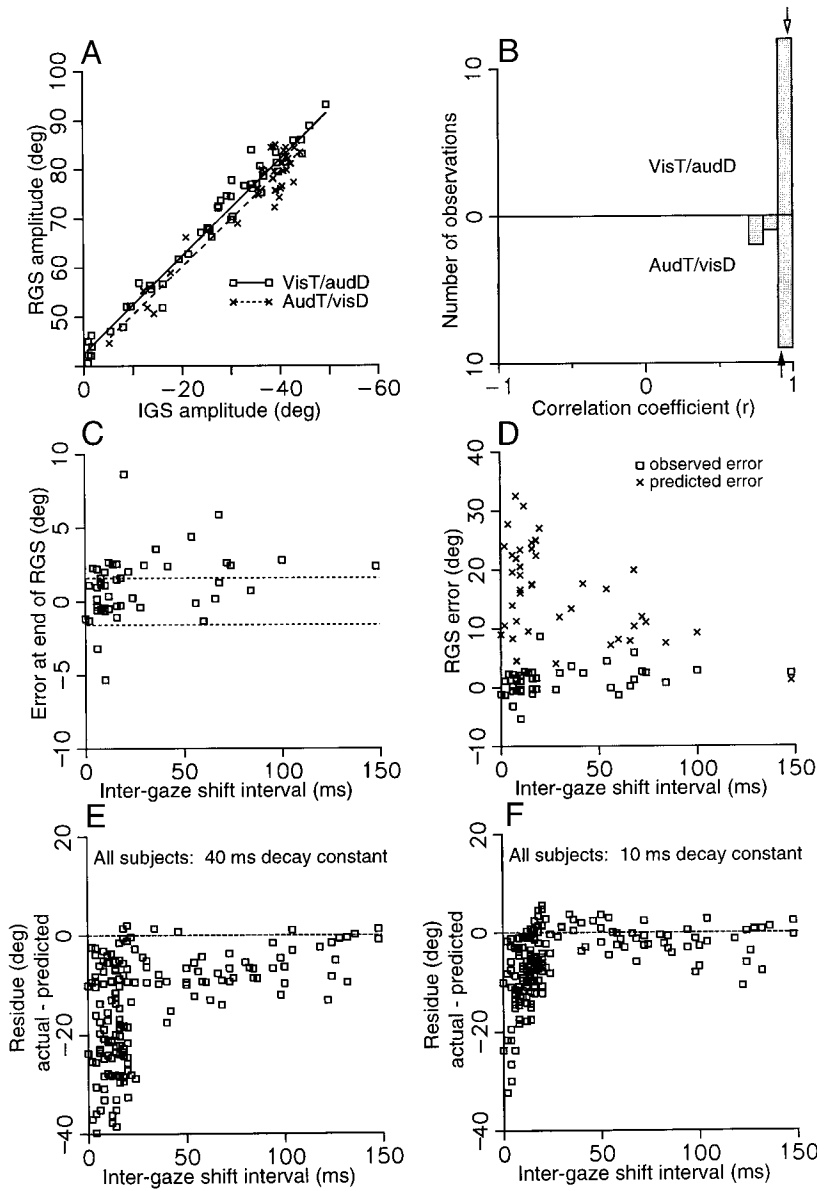


FIG. 6. A: plot of RGS amplitude vs. IGS amplitude for *subject md* at 40°. Same format as in Fig. 5A. For —, $r = 0.98$, slope = 0.99, y intercept = 42.6. For ---, $r = 0.95$, slope = 0.97, y intercept = 40.9. B: correlation coefficient distributions from all subjects in all multimodal experiments for the relationship between RGS amplitude vs. IGS amplitude. Same format as Fig. 5B. C: error at the end of an RGS as a function of the inter-gaze shift interval, generated by *subject md* in VisT/audD experiments at 40°. Each point represents data from a single RGS. Error is the difference between the RGS end point and the mean of the distribution of end points following CGSs in the distractor condition. ---, 1 SD of the distribution of CGS end points centered around 0. An error >0 implies that the RGS was hypermetric compared with the average CGS. D: observed (\square) and predicted (\times) RGS error as a function of the inter-gaze shift interval. Predicted errors were calculated for each RGS based on the amplitude of the IGS and the inter-gaze shift interval based on Eq. 1 ($\tau = 40$ ms, see text for further details). E and F: residue (observed error – predicted error) as a function of inter-gaze shift interval, determined for individual RGSs from all subjects in either VisT/audD experiments at 40° with $\tau = 40$ ms (E) or $\tau = 10$ ms (F). ---, expected residue if the predicted error matched the observed error. Negative values imply that the predicted RGS endpoint was hypermetric compared with the observed RGS endpoint. Movements examined in C–F were limited to those movements in which the IGS amplitude exceeded 5° and the inter-gaze shift interval was <150 ms (see text for rationale).

The amplitude of RGSs scaled well for the amplitude of the preceding IGSs for all subjects (Fig. 6, A and B), even for inter-gaze shift intervals approaching zero. The error at the end of the RGS was obtained by subtracting the RGS end point from the mean end point of all CGSs generated in the distractor condition in the same experiment (CGSs from the enhancer condition were not used as they may have been influenced by the accompanying stimulus). The remaining error at the end of the RGSs did not differ significantly from the error distribution at the end of CGSs (data pooled across all subjects and multimodal experiments, t -test, $P = 0.41$). More importantly, the error at the end of an RGS did not vary as a function of the inter-gaze shift interval (Fig. 6C). Systematic overshoots of the RGSs would have been predicted if the purported displacement integrator gradually resets during the inter-gaze shift interval. The logic for this is as follows. Consider the case in which target and distractor are placed at 40° to the right and left respectively. Following a 10° IGS to the left, the gaze shifting system needs to move 50° to the right to get on target. Assum-

ing that the gaze shifting system encodes this 50° rightward RGS, as opposed to the original 40° gaze shift to the target or to some intermediary location which compensates for any residual decay, then the predicted amount of error at the end of an RGS due to residual feedback within the displacement integrator is given by the equation

$$E_{\text{RGS}} = -A_{\text{IGS}} * e^{(-\text{IGI}/\tau)} \quad (1)$$

where E_{RGS} = predicted error at the end of the RGS; A_{IGS} = amplitude of the IGS (negative for leftward IGSs); IGI = inter-gaze shift interval (ms); and τ = value of decay constant (ms).

The plausibility of the above assumption is considered further in the discussion. We initially set the value of the decay constant at 40 ms, which is at the low end of values determined from SC stimulation experiments (Kustov and Robinson 1995; Nichols and Sparks 1995; Schlag et al. 1998) and results in a faster decay of the resettable integrator. Using Eq. 1, we determined the predicted error for each

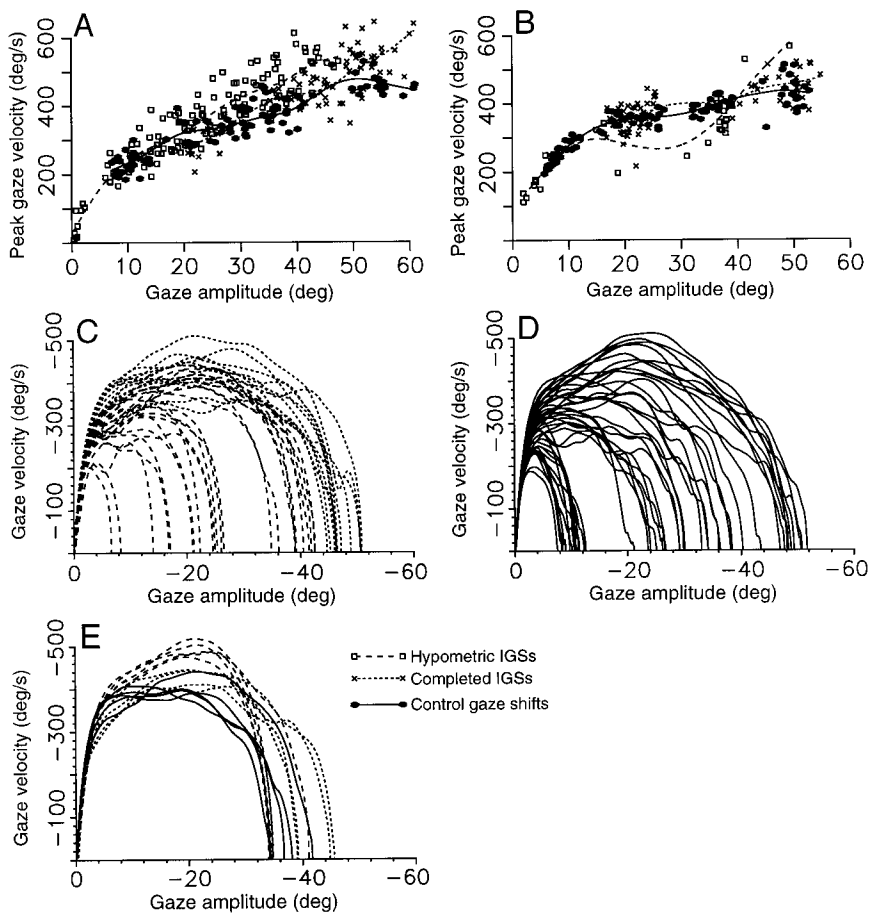


FIG. 7. Dynamics of gaze shifts for *subject dm*. *A* and *B*: main sequence plots relating the amplitude to velocity for movements directed toward auditory stimuli (*A*) or visual stimuli (*B*). Each main sequence relationship plots the observations and fitted curve for individual gaze shifts during control gaze shifts (filled circles and solid lines), hypometric IGSs (open squares and long, dashed lines), and completed IGSs (crosses and short, dashed lines). Main sequence relationships have been fitted with a cubic spline (deBoor 1978). *C–E*: phase-plane plots of velocity vs. amplitude for gaze shifts generated by *subject dm* to auditory stimuli located to the left. Each line represents the phase-plane plot for an individual gaze shift. Long dashed lines denote the phase-plane plots for hypometric IGSs. Short dashed lines denote the phase-plane plots for completed IGSs. Solid lines denote the phase-plane plots for control gaze shifts. *C*: all IGSs generated from VisT40°R/audD40°L trials. *D*: All control gaze shifts to auditory stimuli located to the left. *E*: comparison of the phase-plane plots for gaze shifts between 35 and 45° in amplitude. Hypometric IGSs tended to decelerate faster than amplitude-matched completed IGSs or control gaze shifts.

RGS based on the amplitude of the preceding IGS and the inter-gaze shift interval and compared this predicted RGS error to the observed RGS error as a function of the inter-gaze shift interval (Fig. 6D). We limited our error predictions to those RGSs that followed an IGS $>5^\circ$ and were preceded by an inter-gaze shift interval of <150 ms, as the predicted errors in cases beyond these limits would be negligible. As shown in Fig. 6D, there is a large difference between the observed and predicted RGS errors, particularly for inter-gaze shift intervals <50 ms. The appreciable scatter in the predicted RGS error for similar inter-gaze shift intervals occurs because of the variability in the amplitude of the preceding IGS. We computed the residue as the difference between the actual and predicted RGS errors and plotted this residue as a function of inter-gaze shift interval for all subjects in VisT/audD experiments at 40° in Fig. 6E for $\tau = 40$ ms. As shown by the large residues <0 , the observed RGS error clearly departed from the predicted RGS error (Fig. 6E). We repeated these calculations with $\tau = 10$ ms to test whether the observed RGS accuracy could be explained by a faster decay constant (Fig. 6F). There remained a very large discrepancy between the predicted and observed RGS errors, particularly for inter-gaze shift intervals <30 ms. These behavioral results confirm the conclusions of Goossens and van Opstal (1997) by demonstrating the insufficiency of a gradual decay with $\tau = 40$ ms in accounting for RGS accuracy and extend on their results by demonstrating that a decay with $\tau = 10$ ms is also insufficient to account for the accuracy of RGSs.

Dynamics of IGSs

The second goal of this paper was to resolve whether hypometric IGSs that ended short of the location of the distractor were driven to completion. A key part of the following analyses centers on the comparison of “amplitude-matched” movements. Consider the case when the stimuli were located at 40° and the subject first generated a 10° IGS toward the distractor, followed by a 50° RGS in the opposite direction. If the 10° IGS is driven to completion, then its dynamics should be comparable with the dynamics of other, normal 10° gaze shifts. However, if the 10° IGS is initially planned for an excursion of 40° and superseded by the RGS in midflight, then the early dynamics of the 10° IGS should either be similar to 40° gaze shifts, or atypical of normal 10° gaze shifts. Furthermore if the RGS actively supersedes the ongoing IGS, it is possible that amplitude-matched hypometric IGSs and completed IGSs would differ in their decelerations because the hypometric IGSs would be actively reversed by the RGSs, whereas completed IGSs would be stopped in a normal fashion.

The main sequence relationship relates the amplitude and peak velocity of a gaze shift (Bahill et al. 1975). If the peak velocities during hypometric IGSs are greater than the peak velocities attained during amplitude-matched completed IGSs or control gaze shifts, then the main sequence relationships for hypometric IGSs should lie above the relationships for the other types of movements. Figure 7, *A* and *B*, shows scatter plots of peak gaze velocity as a function of gaze amplitude for *subject dm* during hypometric IGSs, completed IGSs, or con-

control gaze shifts to either auditory (Fig. 7A) or visual (Fig. 7B) stimuli. The gaze main sequence relationships for this subject and for the other three subjects were not consistently different for the three types of gaze shifts.

Main sequence relationships do not provide a complete description of the gaze shift dynamics because they do not provide any quantitative description of either the acceleration or deceleration phases (van Opstal and van Gisbergen 1987). To more thoroughly examine the dynamics of these movements, we constructed phase-plane plots that relate the position and velocity at every point in time during a gaze shift. Phase-plane plots for *subject dm* are shown in Fig. 7, C-E, for leftward gaze shifts directed to auditory stimuli. Figure 7C plots the phase-plane relationships for all leftward hypometric (long dashed lines) and completed (short dashed lines) IGSs generated in VisT40°L/audD40°R trials. The phase-plane trajectories of gaze shifts >25° could be divided roughly into three parts: an initial acceleration portion speeding gaze near to its peak velocity, a middle plateau portion in which the velocity of the gaze shifts is relatively constant between 300 and 500°/s, and a final deceleration portion near the end of the movement.

The phase-plane profiles of the IGSs (Fig. 7C) can be contrasted with those for control gaze shifts (Fig. 7D) generated by the same subject to auditory targets located at different leftward eccentricities. Notice that the initial accelerations of these control gaze shifts resemble the accelerations of both hypometric and completed IGSs. However, control IGSs tended to have a more gradual deceleration than hypometric IGSs [compare the decelerations of movements ~20° for hypometric IGSs (Fig. 7C) and control gaze shifts (Fig. 7D)].

Amplitude-matched movements of ~40° are contrasted directly in Fig. 7E for control gaze shifts (solid lines), hypometric IGSs (long dashed lines), and completed IGSs (short dashed lines). The control gaze shifts and the completed IGSs were both driven to auditory stimuli located at 40°, whereas the hypometric IGSs were generated when an auditory distractor was located at 60°. Qualitatively, these three types of movements have similar acceleration trajectories. Although the hypometric IGSs reached higher peak velocities in the examples shown, the more important feature is that hypometric IGSs tended to decelerate more abruptly than either control gaze shifts or completed IGSs.

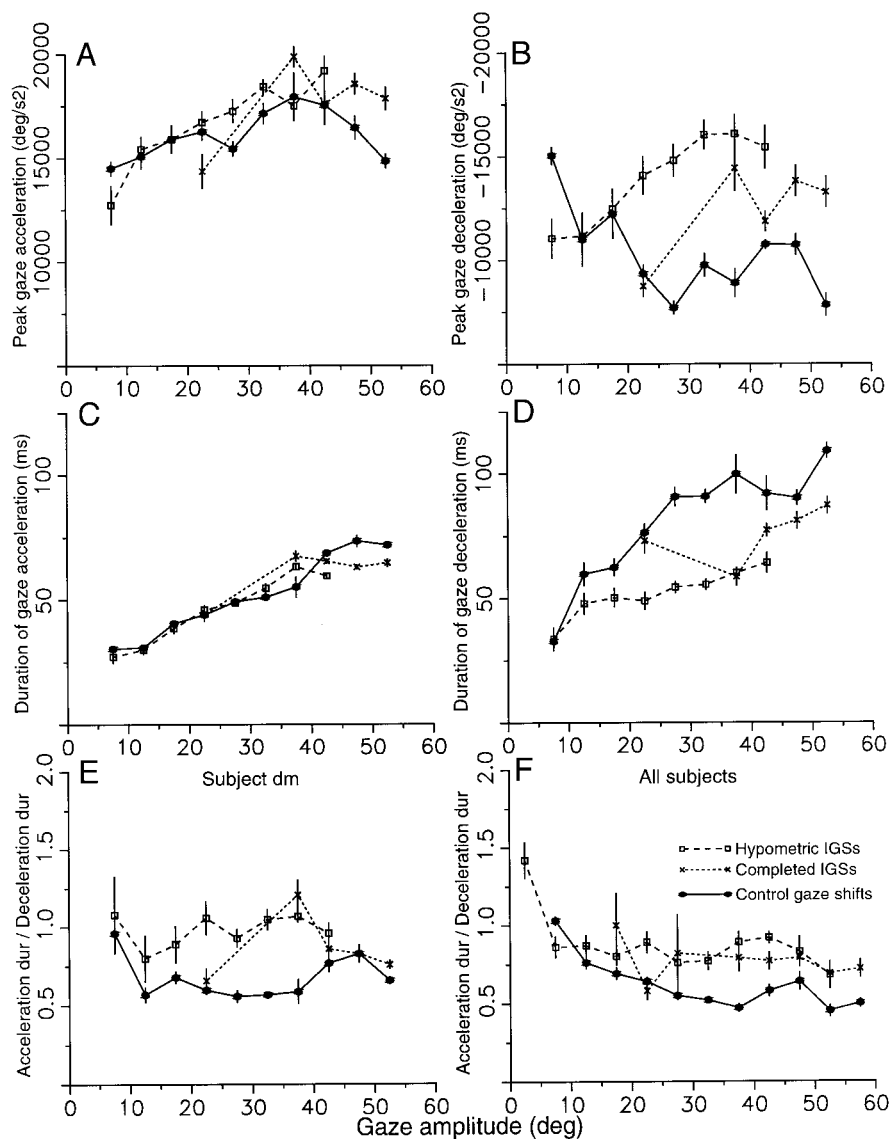


FIG. 8. Plot of the peak gaze acceleration (A), peak gaze deceleration (B), duration of gaze acceleration (C), duration of gaze deceleration (D), and ratio of the durations of the acceleration and deceleration (E) for gaze shifts to auditory stimuli for *subject dm*. Acceleration duration/deceleration duration ratios are shown collapsed across all subjects in F. Each point and associated vertical line represents the mean and standard error for ≥ 5 gaze shifts pooled in 5° amplitude bins. Solid lines and filled circles denote the observations from control gaze shifts. Long dashed lines and empty squares denote observations from hypometric IGSs. Short dashed lines and crosses denote observations from completed IGSs. Hypometric IGSs tended to have larger peak decelerations (B), shorter deceleration durations (D), and larger ratios (E and F) than amplitude-matched completed IGSs and control gaze shifts.

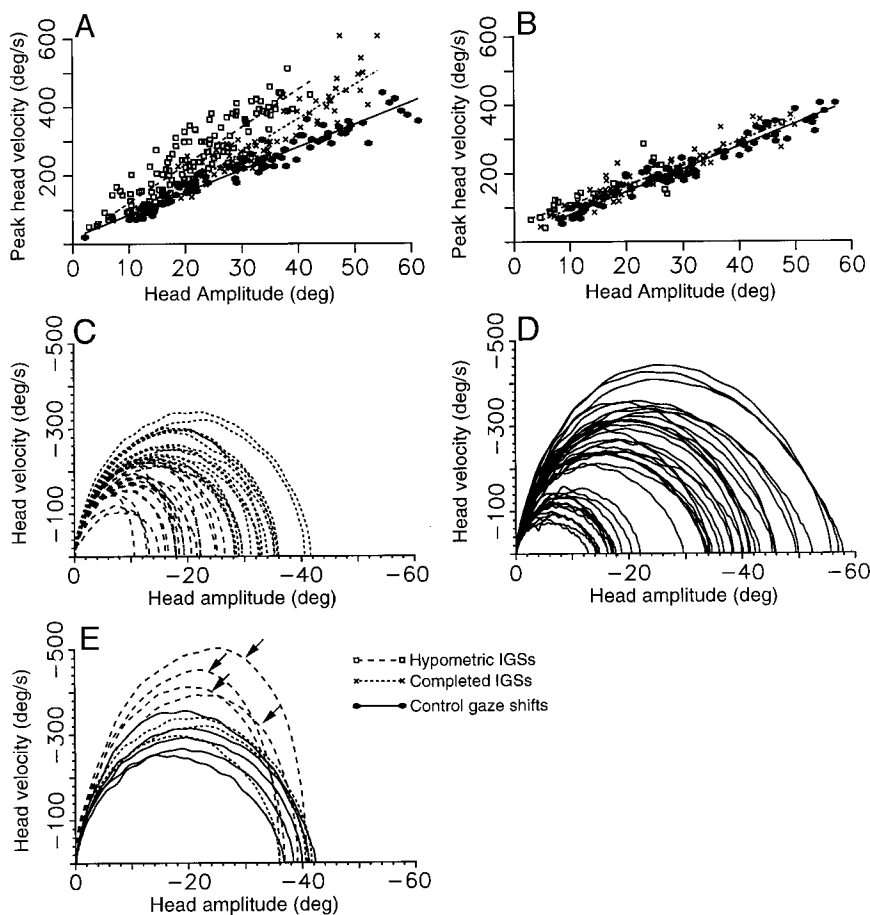


FIG. 9. Dynamics of head movement component during gaze shifts for *subject dm*. Same format as in Fig. 7. *A* and *B*: main sequence plots of head movement component during gaze shifts toward auditory stimuli (*A*) or visual stimuli (*B*). Head main sequence relationships have been fitted with linear regression lines. *C–E*: phase-plane plots of velocity vs. amplitude for the head component during gaze shifts generated by *subject dm* to auditory stimuli located to the left. *C*: head movements during IGSs generated from VisT40°R/audD40°L trials. *D*: head movements during all control gaze shifts to auditory stimuli located to the left. *E*: Comparison of the phase-plane plots for head movements between 35° and 40° in amplitude. Arrows in *E* show the onset of sharp decelerations for the head movement during hypometric IGSs.

To quantify these observations, we measured a number of movement parameters to describe the dynamics of either the acceleration phase lasting from gaze shift initiation to peak velocity or the deceleration phase lasting from peak velocity until the gaze shift end. For each gaze shift, we measured the peak acceleration and deceleration, the duration of the acceleration and deceleration phases, and the ratio of the acceleration duration to the deceleration duration. The acceleration/deceleration duration ratio is one method of extracting information about the “skew,” or shape, of the velocity-time profile of the movements (van Opstal and van Gisbergen 1987) and allows us to collapse results across subjects. The peak acceleration (Fig. 8A) and the duration of the acceleration phase (Fig. 8C) for each of the three types of gaze shifts were similar for amplitude-matched movements. However, the peak deceleration tended to be much higher for hypometric IGSs as compared with either amplitude-matched control gaze shifts and completed IGSs (Fig. 8B), and the duration of the deceleration phase was correspondingly shorter (Fig. 8D). The deceleration dynamics of completed IGSs also tended to be more rapid compared with control gaze shifts. The values of the acceleration/deceleration duration ratio derived from hypometric IGSs were significantly higher than the ratios from either completed IGSs or control gaze shifts for *subject dm* (Fig. 8E) and for all subjects [Fig. 8F; 2-factor ANOVA across distractor modality ($P < 0.0001$) and movement type (hypometric IGSs, completed IGSs or control gaze shifts; $P < 0.0001$); Newman-Keuls post hoc analysis]. The large differences in the deceleration dynamics of hypometric IGSs compared with

amplitude-matched completed IGSs suggests that hypometric IGSs are stopped by a different mechanism compared with either completed IGSs or control gaze shifts. These observations are consistent with the notion that hypometric IGSs initially were planned for a larger excursion but were truncated in midflight by the reversing RGSs.

Dynamics of eye and head movements during IGSs

We also studied the dynamics of the underlying component movements of the eyes and head during IGSs. The head, being a viscoinertial structure, must accelerate more rapidly for larger head movements (Zangemeister et al. 1981). Thus the initial dynamics of the head movement component should be particularly illustrative of the amplitude of the initially desired head movement. Indeed, the dynamics of the head movement during hypometric IGSs strongly suggested that the head movement began on a trajectory typical of a much larger movement but was abruptly reversed by the head movement during the RGS. The main sequence relationships for the head movement component during aurally guided gaze shifts for *subject dm* (Fig. 9A) show that for head movements of similar amplitudes, the peak head velocity was greater during hypometric IGSs than during either completed IGSs or control gaze shifts. This pattern was observed frequently in other subjects for both visually and aurally guided gaze shifts, although it was not observed for *subject dm* during visually guided gaze shifts (Fig. 9B). Phase-plane relationships for head movement components during control gaze shifts and completed IGSs tend to

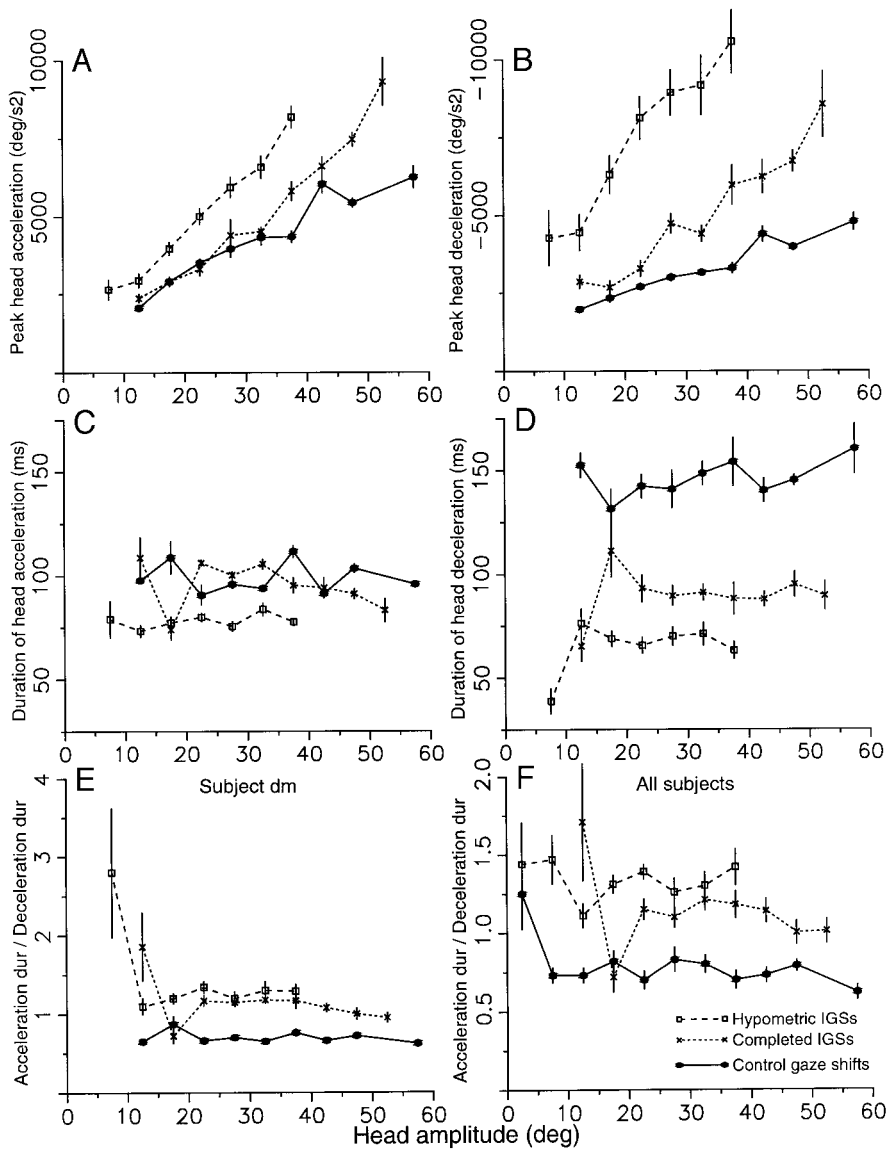


FIG. 10. Plot of the peak head acceleration (A), peak head deceleration (B), duration of head acceleration (C), duration of head deceleration (D), and ratio of the durations of the acceleration and deceleration (E) for head movements during aurally guided gaze shifts for *subject dm*. Acceleration duration/deceleration duration ratio is shown pooled for all subjects in F. Same format as in Fig. 8.

be quite parabolic (Fig. 9, C and D). Peak head velocity and acceleration increased for larger head movements (Fig. 9D) and did not saturate at larger movement amplitudes. The phase-plane traces for head movements during hypometric IGSs depart quite markedly from this parabolic shape and adopt a much more skewed appearance (Fig. 9E, arrows). This skewed appearance resulted mainly from an abrupt deceleration phase (Fig. 10, B and D), although the head also accelerated faster during hypometric IGSs (Figs. 9E and 10, A and C). The shorter deceleration phases resulted in duration ratios that were significantly greater for head movements during hypometric IGSs compared with head movements during either completed IGSs or control gaze shifts [Fig. 10E for *subject dm*, Fig. 10F for all subjects; 2-factor ANOVA across distractor modality ($P < 0.0001$) and movement type ($P < 0.0001$); Newman-Keuls post hoc analysis].

In contrast to the head movement component, the eye movement component did not systematically differ during the different types of gaze shifts. Main sequence relationships for the eye movement (Fig. 11, A and B) showed that the only notable differences between types of gaze shifts were that some subjects

tended to generate much larger eye movements during control gaze shifts than they did during the multimodal experiments (i.e., see Fig. 11A), implying a greater contribution of the head during gaze shifts in multimodal experiments. The phase-plane plots for the eye movement component during IGSs are compared with those from control gaze shifts in Fig. 11, C–E, for *subject jb*. These phase-plane plots tended to be much more parabolic than the phase-plane plots for gaze shifts and displayed prolonged deceleration phases only for movements $>20^\circ$ (Fig. 11, C and D). There were no systematic differences in the phase-plane plots for the eye movement component during control gaze shifts, hypometric IGSs and completed IGSs for eye movements around 15° (Fig. 11E). Quantitatively, the acceleration and deceleration phases of the eye movement component during gaze shifts were fairly similar during hypometric IGSs, completed IGSs, and control gaze shifts (Fig. 12, A–D), although there was a tendency for the peak eye deceleration to be higher and the duration of the eye deceleration to be lower during hypometric IGSs than during complete IGSs or control gaze shifts when the eye movement exceeded 30° (Fig. 12, B and D). The acceleration/deceleration duration ratios (Fig. 12E for *subject jb*, Fig. 12F for all subjects)

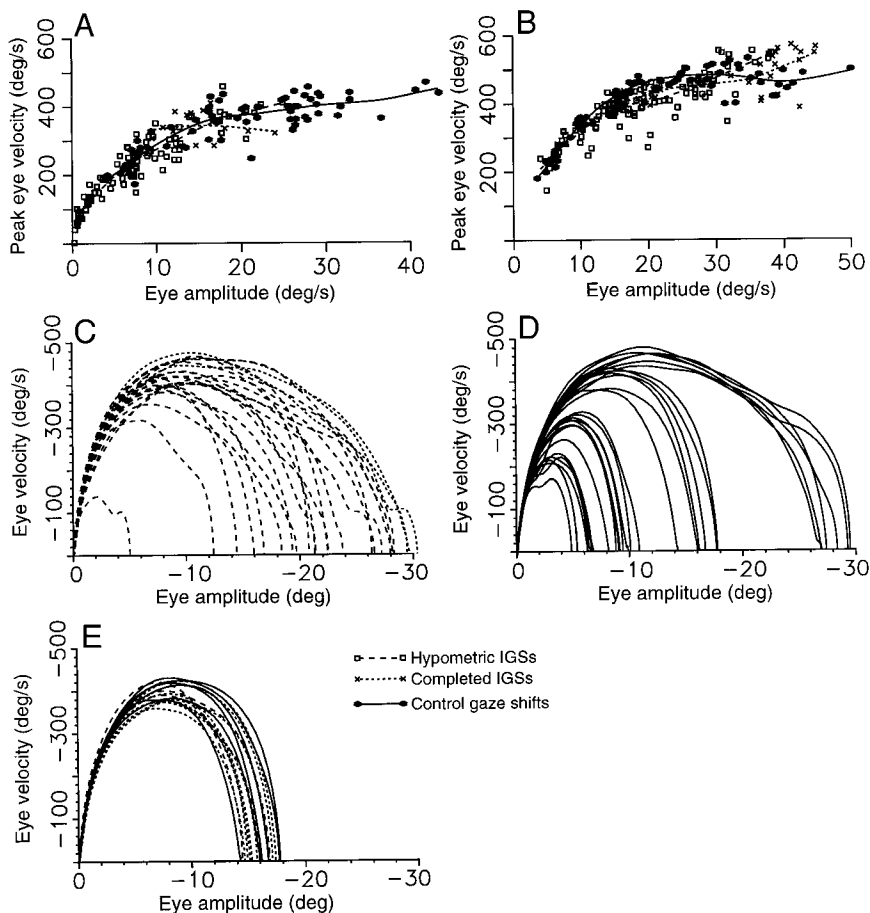


FIG. 11. Dynamics of eye movement component during gaze shifts for *subject jb*. Same format as in Fig. 7. *A* and *B*: main sequence plots of eye movement component during gaze shifts toward auditory stimuli (*A*) or visual stimuli (*B*). *C–E*: phase-plane plots of velocity versus amplitude for the eye movement component during gaze shifts generated to visual stimuli located to the left. *C*: eye movements during IGSSs generated in AudT40°R/visD40°L trials. *D*: eye movements during control gaze shifts to visual stimuli located to the left. *E*: comparison of the phase-plane plots for eye movements between 15 and 20° in amplitude.

did not reliably discriminate the eye movement during hypometric IGSSs from the eye movement during completed IGSSs or control gaze shift [2-factor ANOVA across distractor modality ($P < 0.0001$) and movement type ($P < 0.0001$)]. Post hoc analysis (Newman-Keuls) revealed that the ratios were not significantly different during hypometric IGSSs and control gaze shifts.

DISCUSSION

The results presented in this paper demonstrate that reversing gaze shifts generated in a multimodal target-distractor experiment are accurate regardless of the amplitude of the initial, erroneous gaze shift and of the inter-gaze shift interval. These results complement and extend on the behavioral results of Goossens and van Opstal (1997) in double-step experiments by demonstrating accuracy even when the subsequent gaze shift essentially supercedes and reverses an on-going gaze shift in midflight. These results impose new constraints on models of gaze control, which now must be capable of generating such movement sequences.

We employed some experimental manipulations to increase the number of IGSSs available for study. First, we introduced a 200-ms gap between the disappearance of the central fixation point and the presentation of the peripheral stimuli. This manipulation has been shown to reduce reaction times and increase the incidence of IGSSs compared with when the fixation point remained illuminated (Munoz and Corneil 1995). Second, we introduced asynchronies between the presentation of the target and distractor to decrease the predictability of stimuli appearance relative to fixation point

offset. We have shown that the incidence of IGSSs displays a straightforward dependency on the introduced asynchrony; more IGSSs are generated the sooner the distractor is presented relative to the target (Corneil and Munoz 1996). Third, we allowed subjects to move their heads, which enabled us to study movements out to 60° eccentricity. Larger amplitude gaze shifts last longer (Guitton and Volle 1987), which increases the possibility of gaze shifts being truncated in midflight.

Feedback of gaze position and/or displacement

The accuracy of the RGSs in our behavioral task would not have been predicted if the purported resettable displacement integrator was endowed with a gradual reset with a time constant in the order of 40 ms. Rather, the models developed from postsaccadic stimulation within the superior colliculus (SC) (Kustov and Robinson 1995; Nichols and Sparks 1995; Schlag et al. 1998) would have predicted the RGS to grossly overshoot the target (Fig. 6, *C–E*). The notable accuracy of the many RGSs that followed inter-gaze shift intervals of <30 ms also runs counter to the predictions of a faster decaying resettable integrator (i.e., $\tau = 10$ ms), which could not be addressed by the results obtained by Goossens and Van Opstal (1997) (Fig. 6*F*). Our results are not also consistent with an alternative proposal of an instantaneous reset of the displacement integrator linked to the end of a saccade (Moschovakis 1994), given that hypometric IGSSs are essentially truncated in midflight and hence never reached completion.

How then can the discrepancy between the results from behav-

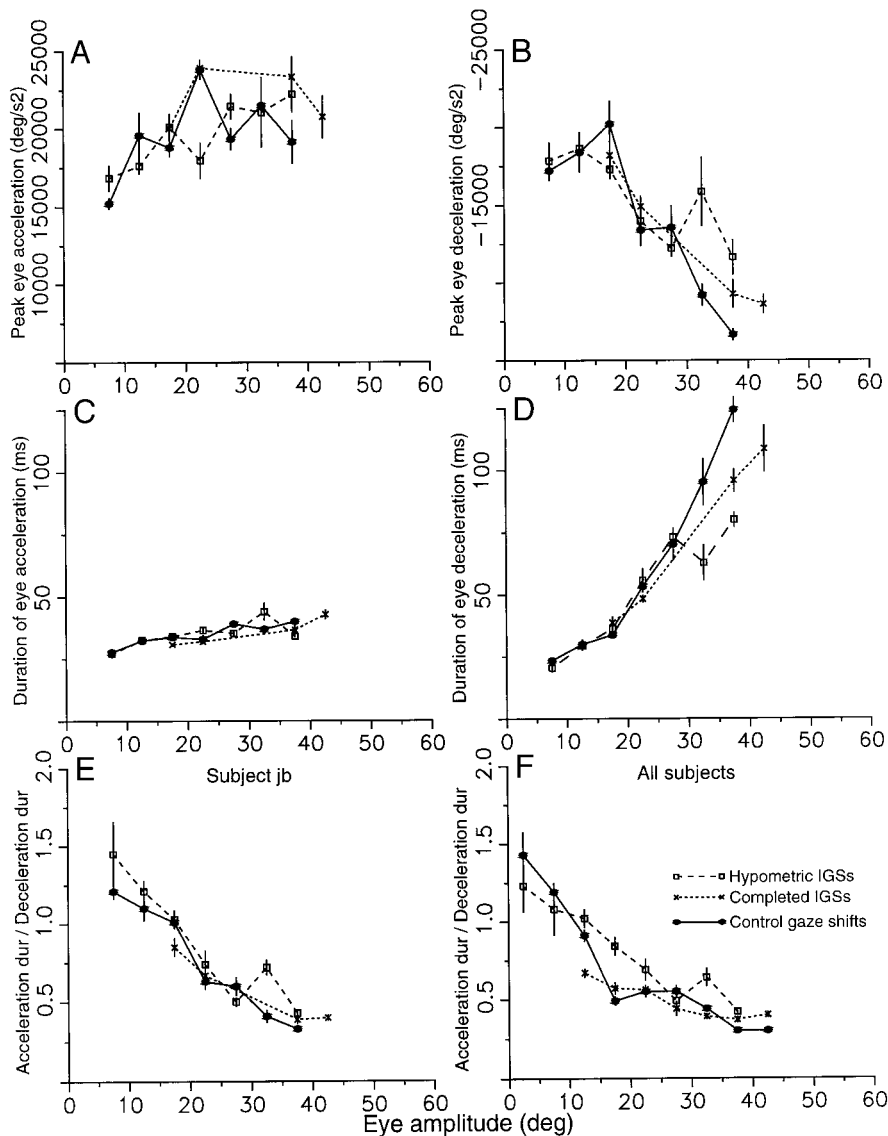


FIG. 12. Plot of the peak eye acceleration (A), peak eye deceleration (B), duration of eye acceleration (C), duration of eye deceleration (D), and ratio of the durations of the acceleration and deceleration (E) for eye movements during visually guided gaze shifts for *subject jb*. Acceleration/deceleration duration ratio is shown pooled for all subjects in F. Same format as in Fig. 8.

ioral experiments and stimulation experiments be accounted for? One unlikely possibility noted by Goossens and van Opstal (1997) was that the natural, accurate second saccade they observed was preprogrammed and accommodated for the properties of a gradually resetting displacement integrator. If this was true, the noted changes in the evoked vector from postsaccadic SC stimulation experiments occurred because the second saccade, imposed by the experimenters, was not able to accommodate for the residual displacement feedback. We consider this scheme unlikely to explain the IGS-RGS sequences because such preprogramming would be computationally very difficult given that neither the amplitude of the IGS nor the inter-gaze shift interval, which together determine the amount of compensation required, would be known beforehand for any accommodating mechanisms. Furthermore recent data recorded from the SC in monkeys performing the double-step task shows no evidence for any dynamic remapping of the SC motor command that would have to underlie such compensation (Goossens 1998). The SC appears to encode faithfully the vector of the impending saccade by always recruiting the same cells at the same SC locus for the same movement, regardless of the time elapsed since the end of the preceding

saccade. Thus it is reasonable for us to assume that the population of SC cells active for an RGS is the same population of SC cells normally active for gaze shifts with the same metrics.

Alternatively, the discrepancy between the accuracy of closely spaced movements generated naturally or electrically could occur simply because electrical stimulation does not activate the SC or other components of the gaze shifting system in a natural manner. Given the behavioral results presented here and in Goossens and Van Opstal (1997), the validity and existence of a gradually resetting displacement integrator in the gaze shifting system must be questioned.

Clearly, some feedback of current eye position or displacement must be available at the time of the RGS generation to account for the amplitude of the preceding IGS. Our data cannot distinguish whether such feedback is operating within a positional or displacement framework. However, if the neural correlate of the displacement integrator does exist, our data shows that it must somehow be instantaneously reset to zero, perhaps by the truncating RGS command, instead of an end of saccade command.

Metrics and dynamics of hypometric IGSs

Many similarities exist between the parameters of the initial response in the double-saccade or IGS-RGS movement patterns. Results from double-step experiments first described “amplitude-transfer” functions, in which the amplitude (Becker and Jürgens 1979) or direction (Aslin and Shea 1987) of the first saccade of a double-saccade response varied as a function of the modification interval (the time from the 2nd target step until the initiation of the 1st saccade). The inter-saccadic interval also was found to vary as a function of the modification interval, tending to decrease for longer modification intervals. Similar quantitative observations have been made in the current report (Fig. 5) and for errors generated in cueing experiments, in which a cue presented before a target draws attention, sometimes incorrectly, to the impending target location (Cavegn 1996). Errors very similar to IGSs also are frequently reported in antisaccade trials in which subjects are instructed to generate a saccade to a spatial location diametrically opposite the location of a peripheral visual stimulus (for review, see Everling and Fischer 1998). Such erroneous prosaccades can be of intermediate amplitude, and the time between the erroneous pro-saccade and the subsequent antisaccade can approach zero (Amador et al. 1998). However, such movement sequences are rare (<1%) and therefore have not been studied in a quantitative manner. Still, the notable similarities between the movement patterns generated in different experimental protocols are suggestive of a common neural mechanism.

We have demonstrated that hypometric IGSs are not completed movements generated from averaging or sequencing mechanisms (see INTRODUCTION), but rather are interrupted in midflight. The critical determinant of the hypometria of IGSs [and indeed whether IGSs are generated at all (Corneil and Munoz 1996)] is the timing of the motor program encoding the RGS with respect to the motor program encoding the IGS. If the motor program encoding the RGS is signaled almost immediately after the initiation of an IGS, then the IGS will most likely be interrupted in midflight by the RGS and the inter-gaze shift interval will correspondingly be short. Alternatively, if the motor program encoding the RGS is delayed until well after the onset of the IGS, then the IGS will most likely be driven to completion and the RGS will only be generated after a longer inter-gaze shift interval. A potential explanation for the paucity of shortened erroneous prosaccades in antisaccade trials is that the motor program for the antisaccade lags too far behind the stimulus-driven erroneous prosaccade to exert any influence, given the added complexity of determining the metrics of the antisaccade based on the location of the target.

To our knowledge, our study is the first attempt to quantify the dynamics of the gaze, eye, and head during the first, erroneous response. The dynamics of deceleration of the gaze and head during hypometric IGSs clearly depart from appropriate trajectories for amplitude-matched movements (Figs. 7, C-E, 8, 9, C-E, and 10) and were consistent with the premise of the head being programmed for a much larger excursion than it achieved (Figs. 9 and 10). This latter point emphasizes why it was important for the subjects in the current experiment to be allowed to move their heads. The acceleration profile of the head is much more illustrative of the initial motor command than movements of either the eye or gaze, given that the

early part of any gaze shift is driven predominantly by an eye movement. The dynamics of the acceleration phase remain fairly constant for eye or gaze movements $>10^\circ$ (Bahill et al. 1981; Fricker and Sanders 1975), whereas the head accelerates more rapidly for progressively larger movements (Fig. 10A for head movements during control gaze shifts) (see also Zangemeister et al. 1981). Assuming that the eyes and head are driven by a common signal at some point (note that if this common signal is within a feedback loop or not is irrelevant), it is clear that the IGS motor command encoded a gaze shift to the distractor. It will be of interest to determine whether a similar analysis of the dynamics of the initial response in double-step, cueing, or antisaccade experiments is consistent with the preceding explanation.

One obvious limitation of our study is that the support provided for a neural mechanism in which one motor program can truncate another in midflight may apply only for stimuli placed in opposite hemifields. It remains possible that an averaging scenario envisioned by Becker and Jürgens (1979), or a type of sequential planning, may apply for stimuli within the same hemifield or placed closer together. We note the conclusions reached by Minken and colleagues (1993) who studied the three-dimensional trajectories of eye saccades in a double-step experiment to targets within the same hemifield. They showed that the torsional trajectory of curved saccades modified in midflight were not consistent with an averaging process but rather were consistent with a midflight change in the goal of the gaze shifting system. However, some of the results observed by these authors were also indicative of an averaging response, so the phenomena of averaging and midflight changes may not be mutually exclusive.

We conclude that the oculomotor system is capable of changing its goal in midflight and that the accuracy of subsequent gaze shifts is achieved regardless of the amplitude of preceding truncated gaze shift or of the inter-gaze shift interval. The discrepancy between our behavioral results and those predicted from electrical stimulation experiments emphasizes the need for caution in interpreting results from electrical stimulation. IGSs are overt manifestations of a distraction process. In the companion paper (Corneil and Munoz 1999), we show that the distractor also can induce early movements of the head before the initiation of a gaze shift.

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