

RESEARCH ARTICLE

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Combined eye-head gaze shifts to visual and auditory targets in humans

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Abstract We studied the characteristics of combined eye-head gaze shifts in human subjects to determine whether they used similar strategies when looking at visual (V), auditory (A), and combined (V+A) targets located at several target eccentricities along the horizontal meridian. Subjects displayed considerable variability in the combinations of eye and head movement used to orient to the targets, ranging from those who always aligned their head close to the target, to those who relied predominantly on eye movements and only moved their head when the target was located beyond the limits of ocular motility. For a given subject, there was almost no variability in the amount of eye and head movement in the three target conditions (V, A, V+A). The time to initiate a gaze shift was influenced by stimulus modality and eccentricity. Auditory targets produced the longest latencies when located centrally (less than 20° eccentricity), whereas visual targets evoked the longest latencies when located peripherally (greater than 40° eccentricity). Combined targets (V+A) elicited the shortest latency reaction times at all eccentricities. The peak velocity of gaze shifts was also affected by target modality. At eccentricities between 10 and 30°, peak gaze velocity was greater for movements to visual targets than for movements to auditory targets. Movements to the combined target were of comparable speed with movements to visual targets. Despite the modality-specific differences in reaction latency and peak gaze velocity, the consistency of combinations of eye and head movement within subjects suggests that visual and auditory signals are remapped into a common reference frame for controlling orienting gaze shifts. A likely candidate is the deeper layers of the superior colliculus, because visual and auditory signals converge directly onto the neurons projecting to the eye and head premotor centers.

Key words Eye movement · Head movement · Visual orienting · Auditory orienting · Multisensory integration · Human

Introduction

Humans usually rely on the coordinated motion of the eyes and head to look from one point of interest to another (Gresty 1974; Barnes 1979; Zangemeister and Stark 1982b; Guitton and Volle 1987; Fuller 1992; Land 1992). In this paper, the visual or gaze axis is defined as the sum of the eye relative to the head plus the head relative to space. Combined eye-head movements are essential for gaze shifts to targets located beyond the oculomotor range (± 50 – 55° eccentricity in human subjects; Guitton and Volle 1987) and are often used to fixate targets of smaller eccentricities. Human subjects adopt various strategies of eye-head coordination when looking to eccentric visual targets (Zangemeister and Stark 1982b; Guitton and Volle 1987; Fuller 1992). Some subjects always move their head, while others only move their head when targets are located beyond the oculomotor range. Fuller (1992) separated subjects into what he referred to as *head-movers* and *non-movers*. He suggested that the clustering of head-movers or non-movers may reflect the choice of reference coordinate systems. Head-movers may rely on extrinsic spatial or earth-fixed coordinates, thus trying to align the head close to a target, keeping the eyes centered in the orbit. Non-movers may instead choose intrinsic or head/body oriented coordinates, not moving the head unless required. If this hypothesis is correct then subjects defined as non-movers may switch to become head-movers when targets are located beyond the oculomotor range. Whether human subjects adopt similar strategies when looking at auditory targets is unknown.

Eye and head movements are usually coupled together in human gaze shifts (Gresty 1974; Barnes 1979; Zangemeister and Stark 1982b; Guitton and Volle 1987; Fuller 1992; Land 1992), so it has been proposed that a

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common drive signal acts upon both the eye and head motor systems. Other experiments have challenged the idea of common drive to the eye and head motor systems by providing a paradigm in which eye and head motion can become uncoupled (Ron and Berthoz 1991; Ron et al. 1993). The above studies investigating the coordination of eye and head movements in humans have relied on using visual stimuli as targets, whereas most studies that have investigated how humans orient the visual axis to auditory or combined auditory and visual stimuli have been conducted predominantly with the head immobilized (Zahn et al. 1978; Zambarbieri et al. 1982; Lueck et al. 1990; Hughes et al. 1994; Frens and Van Opstal 1995; Frens et al. 1995).

Several differences in the processing of auditory and visual information may influence gaze-orienting strategies. First, there are considerable differences in the visual and auditory afferent latencies to the central nervous system. Second, the initial reference frames used to localize visual and auditory stimuli are different. Visual stimuli are initially localized using retinotopic coordinates, while auditory stimuli are localized in head-centered or craniotopic coordinates.

To date, it remains unclear whether human subjects use similar combinations of eye and head movement when looking at visual, auditory, or combined (auditory+visual) stimuli. Furthermore, it is not known how the speed and reaction latency of gaze shifts to targets of different modalities may be influenced by target location. The goal of this study was to characterize eye-head gaze shifts generated by human subjects looking at visual, auditory, and combined targets located at various eccentricities (5–60°) along the horizontal meridian, to determine whether target modality influences the degree of coupling of eye and head movements, as well as the reaction time and speed of the orienting movements. Some aspects of these data have been presented in abstract form (Dorris et al. 1993, 1994).

Materials and methods

All protocols were reviewed and approved by the Queen's University Human Research Ethics Board. Thirteen healthy subjects (nine men, four women), ranging from 21–35 years of age, participated in the experiments. This subject pool was composed of the five authors and eight other naive subjects. All subjects were informed of the general nature of the study and consented to participate before experiments were initiated. The different strategies of eye-head coordination that we describe (see Results) were equally distributed among the authors and the naive subjects. Eleven subjects normally wore corrective eye glasses for mild myopic vision, but did not require them for these experiments as the visual targets were sufficiently intense. Subjects had no known ocular, acoustic, neurological, vestibular, or cervical pathological symptoms.

Eye and head movement recordings

Horizontal eye movements were recorded with d.c. electro-oculography (EOG). Ag-AgCl skin electrodes were placed on the outer canthus between each eye and the temple. Another reference electrode was placed just above the eyebrows in the center of the fore-

head. The signal was amplified and filtered with a d.c. preamplifier (Grass P18). In order to minimize EOG drift, subjects wore the electrodes for approximately 15 min before recording and calibration began. Head movements were recorded with a low-torque precision potentiometer connected via a universal joint to the rotational axis of a hockey helmet. This helmet assembly was mounted to a steel rod that was firmly attached to the ceiling. All subjects reported no discomfort or difficulty in moving their head in the apparatus. The head position signal was calibrated to known angles of rotation. To match the gain of the head signal with the eye signal, subjects were instructed to fixate upon a stationary visual target and rotate their head from side to side. The gain of the eye signal was adjusted to be equal and opposite to the head signal. This calibration was repeated throughout each experiment.

Experimental paradigm

Subjects were seated upright in a straight-backed armchair in the center of a light-tight, sound-attenuated room. A visual screen was located 86 cm in front of the subject. A small light-emitting diode (LED 2 cd/m²) was back-projected onto the center of the screen to serve as a fixation point (FP) to center the subject's gaze axis before each trial. The experiments were performed in silence and darkness except for the presence of target stimuli that consisted of either: (1) a visual stimulus (LED, 5 cd/m²); (2) an auditory stimulus (66-dB broad noise burst emitted from a small speaker); or (3) a combined auditory/visual stimulus. The LED was mounted upon the speaker so that the two stimuli were located at the same position in space. Each trial started with the appearance of the FP. After 1000 ms, the FP was turned off and there was a 200-ms gap of no stimuli before an eccentric target (T) was presented for 1000 ms to either the left or right of the FP. Subjects were instructed to look from the FP to the T. No reference was given to them regarding the combination of eye and head movement to be used. At the end of the trial, the T was turned off and a diffuse light (1.0 cd/m²) was projected across the visual screen for the 300- to 1000-ms intertrial interval to prevent subjects from dark-adapting to the testing room. The background lights were extinguished when the FP came on, signifying the start of each trial.

The two small boxes that emitted the target stimuli were positioned 85 cm away from the subject, at several eccentricities (5°, 10°, 20°, 30°, 40°, and 60° along the horizontal meridian) relative to the FP. Seven subjects were tested at these eccentricities, and an additional six subjects were tested with targets located at only 20°, 40°, and 60° eccentricity. In each block of trials, two target positions were possible, one on each side of the FP. The targets were always separated by at least 50° (e.g., 5° right and 60° left; 40° right and 10° left; 20° right and 30° left; etc.). Although the two target eccentricities remained constant within each block of trials, target direction and modality were randomized. Subject responses remained constant within a block of trials, suggesting that increased expectation of target location did not influence characteristics of gaze shifts that we quantified. Subjects typically performed three to six blocks of 90 trials in each block, with short breaks between blocks to maintain alertness. Each session lasted approximately 1 h. Most subjects were tested on more than one day.

Data acquisition and analysis

A 486 computer, running a real-time data acquisition software package (Hays et al. 1982), controlled the experimental parameters (e.g., FP and T appearance/disappearance) and stored the data on hard disk. Signals from both eyes and head were low-pass filtered (50 Hz; Intronic) and digitized at 500 Hz. The eye and head movement traces were monitored on-line. Off-line data analysis was performed on a Sun Sparc 2 workstation. Gaze position (eye re space) was constructed off-line by adding the calibrated eye (eye re head) and head (head re space) position traces together. Velocity traces were derived from the position traces by applying a

finite impulse response (FIR) filter. The onset, termination, and peak velocity of eye, head, and gaze movements were determined, based on position and velocity criteria. The onset of eye and gaze movements was determined when the corresponding velocity exceeded $30^\circ/\text{s}$. The onset of the head movement was determined when the velocity exceeded $15^\circ/\text{s}$. Movement characteristics such as latency to onset, amplitude, velocity, and duration of movements were computed. Movements with reaction latencies of less than 80 ms were classified as anticipatory and excluded from computation of mean reaction times. Gaze shifts with reaction times greater than 500 ms were also excluded owing to presumed lack of attention by the subject.

Results

Gaze strategies

Figure 1 shows the relative contributions of the horizontal eye (Eh) and head (Hh) toward the gaze shifts (Gh) for two subjects that looked at visual targets 20° , 40° , and 60° to the right and left of the FP. One subject (Fig. 1A) relied predominantly on eye movements, fixating upon the eccentric targets by moving the eyes to extreme orbital positions. Head movements only occurred with gaze shifts to targets located at 60° . Another subject (Fig. 1B) always used a combination of eye and head movements to fixate targets and ended the movements with the eyes closer to the center of the orbit and the head almost aligned with the target.

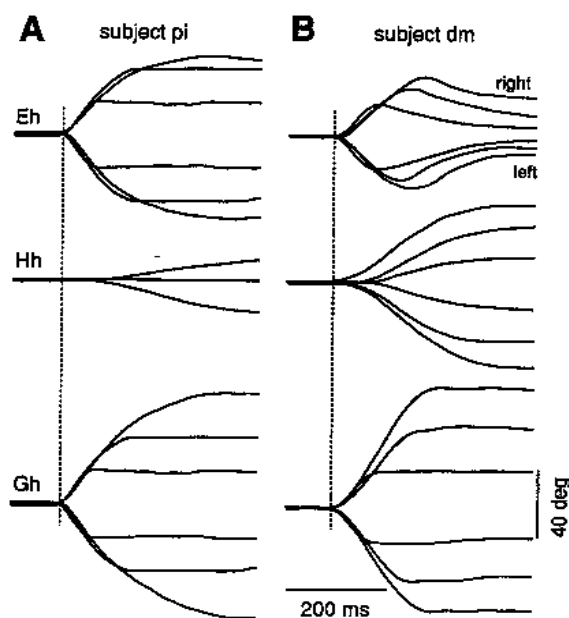


Fig. 1A, B Contrasting strategies of eye and head movement for two subjects orienting to visual targets at 20° , 40° , and 60° to the right and left of the central fixation point. The relative contributions of horizontal eye (Eh) and head (Hh) toward total gaze shift (Gh) are aligned on gaze movement onset. Upward and downward deflections in traces represent rightward and leftward movements, respectively. **A** This subject made no head movements for gaze shifts to targets located at eccentricities of up to and including 40° . **B** This subject used a combination of eye and head movements for gaze shifts to all eccentricities studied

The two different strategies of eye and head movement shown in Fig. 1 are contrasted quantitatively in Fig. 2, in which the mean maximum amplitude of the head (Fig. 2A) and eye (Fig. 2B) movement is plotted against target eccentricity. The plots reveal considerable differences in the amount of head rotation used by the two subjects (Fig. 2A). Subject P.I. only made a head movement to the 60° target, while subject D.M. moved the head to targets at virtually all eccentricities tested (5° – 60°), always aligning the head close to the target. The differences in the maximal magnitude of eye rotation between the two subjects was somewhat smaller (Fig. 2B). Although both subjects had similar maximum deviations in eye rotation, the subject that tended to align the head with the target (D.M.) relied on the vestibulo-

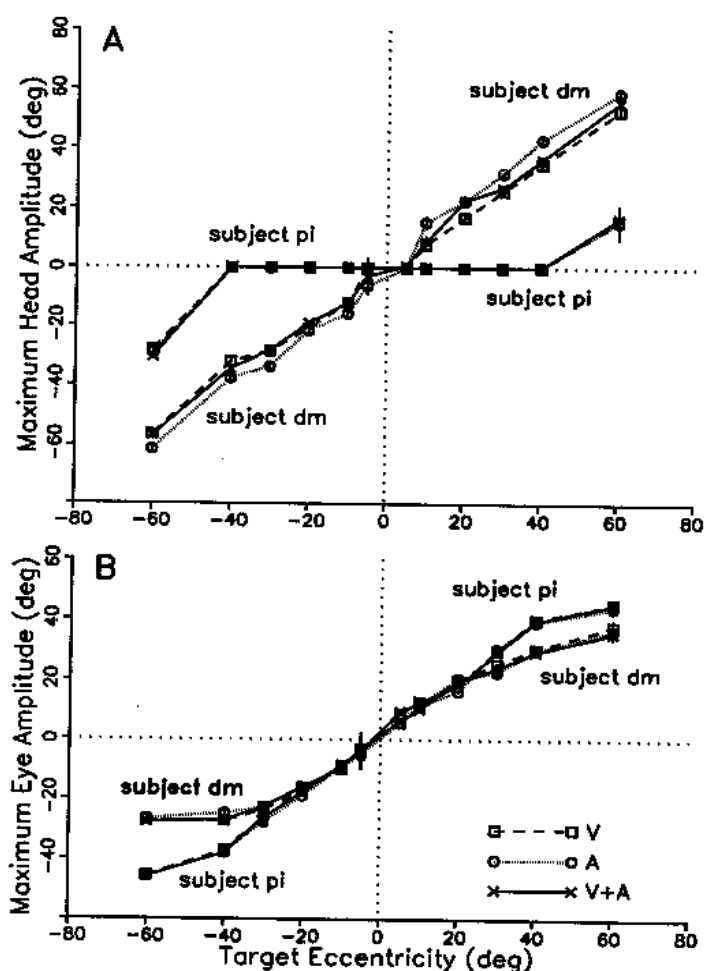


Fig. 2A, B Quantification of the strategies of eye and head movements utilized by the two subjects shown in Fig. 1. Maximum head amplitude (A) and maximum eye amplitude (B) are plotted against target eccentricity. Vertical bars denote SEM. Each data point was computed from 12 to 15 individual trials. Data are shown for movements to targets in the three different conditions: visual (empty squares, dashed line), auditory (empty circles, dotted line), and combined visual and auditory (crosses, solid line) targets. The strategies of the individual subjects remained consistent regardless of the type of target stimulus. In this and all subsequent figures, positive eccentricities denote rightward movements and negative eccentricities denote leftward movements

ocular reflex to counterrotate the eyes once gaze was on target (see Fig. 1B), while subject (P.L.) tended to keep the eyes in an eccentric position (Fig. 1A).

The individual strategies of eye-head coordination used by each subject were conserved for each of the different target modalities tested: visual (V), auditory (A), and combined (V+A). Figure 2 shows that the curves obtained with these different modalities superimpose almost perfectly. For virtually all subjects, there was no statistical difference (t -test, $P > 0.05$) in the amount of head or eye movement for the different modalities at any of the target eccentricities tested. Only 1 subject out of the 13 tested varied his strategy between the visual and auditory tasks, using slightly greater head rotation for eccentric auditory targets (greater than 30°). Thus, despite the different reference frames initially used to localize visual and auditory stimuli, and the diversity in strategies adopted by different subjects, there was remarkably little intrasubject variability.

The 13 subjects used in this study employed varying combinations of eye and head movement to foveate eccentric targets. Figure 3A plots the gain (maximum head amplitude/target eccentricity) against target direction and eccentricity for 13 subjects looking at visual targets, illustrating the between-subject variability in the amount of head movement accompanying gaze shifts to targets at different eccentricities. Subjects ranged from those who aligned their head on target (i.e., gain ~ 1) to those who only moved their heads for large target offsets (greater than 40°) and, even then, only moved their heads slightly. Note that for target eccentricities of 20° , when head movement was not essential to look at the target, the subjects tended to fall into two separate groups: those that did not move the head (gain less than 0.1; $n=5$; solid lines in Fig. 3A), and those that did move the head (gain greater than 0.5; $n=8$; dashed lines in Fig. 3A). The considerable difference in the gain between these two groups at this eccentricity suggests that, rather than a continuum in gaze strategies, subjects tended to adopt one of two separate strategies. As target eccentricity increased, head motion became essential and there was a tendency toward a continuum of gain across our sample of subjects.

Because subjects tended to adopt one of two strategies when looking to targets at 20° eccentricity, we explored whether the non-head movers (i.e., gain less than 0.1 for 20° targets) gradually increased the gain when looking at targets having greater eccentricities or whether they suddenly shifted from zero gain to high gain. Figure 3B, C shows, for two non-head movers, the gain for individual gaze shifts to targets located at 20° , 30° , 40° , and 60° eccentricity. For both subjects, there was a gradual increase in gain as target eccentricity increased. The gain was zero for almost all movements to the 20° target, and ranged from about 0.4 to 0.6 for most movements to the 60° target. The distribution of gains for individual movements to the 40° targets ranged from 0.2 to 0.5 and failed to reveal a bimodal distribution of low and high values on different trials. These data suggest that, when

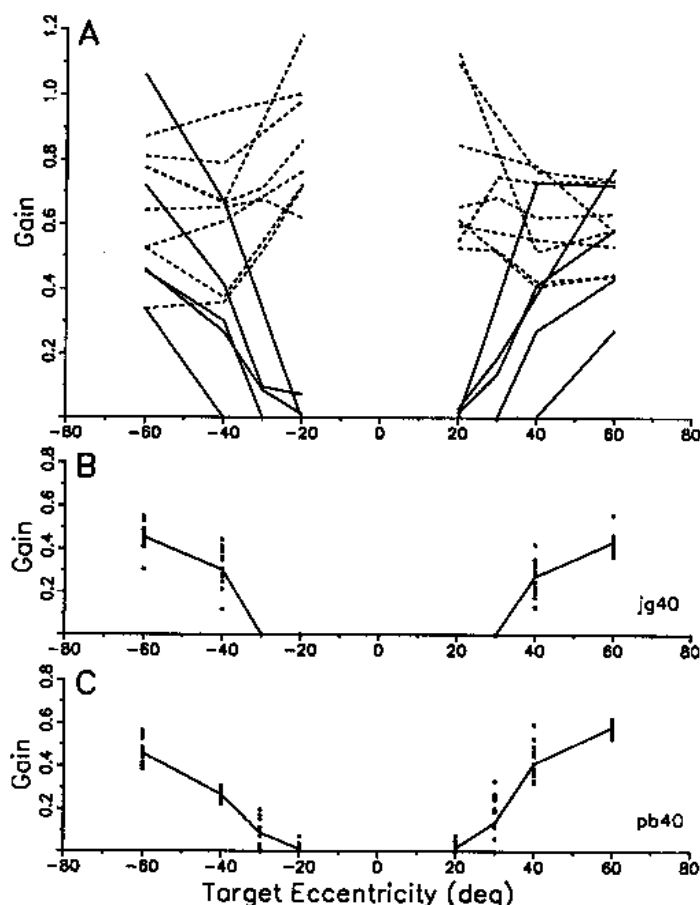


Fig. 3A–C Relationship between the total amount of head movement and target eccentricity (20 – 60°) for all 13 subjects tested in the visual target condition. **A** Gain (head amplitude/target eccentricity) is plotted against target eccentricity. Subjects ranged from those that aligned their head with the target (gain 1) to those who relied predominantly on eye movements (gain 0). The *solid lines* represent subjects having almost no gain for movements to targets at 20° eccentricity, while the *dashed lines* represent subjects having high gain at 20° . **B**, **C** Gain versus target eccentricity for two subjects having zero gain at 20° eccentricity. Each point represents data from an individual trial. Note the gradual increase in gain as target eccentricity increased

subjects began to recruit head motion into a gaze shift, the gain gradually increased for increasing eccentricities, rather than suddenly shifting from low to high gain.

Multisensory interactions

Reaction time

Target location and modality had a pronounced effect on the reaction latencies of all subjects. Figure 4 plots the mean gaze latency versus target eccentricity for the three target conditions (V, A, V+A). The results from two different subjects are shown, illustrating the consistent trends among all subjects. These trends in gaze reaction latencies were the same for both the left and the right direction. For each modality, the curves had a similar shape; there was an increase in latency for central tar-

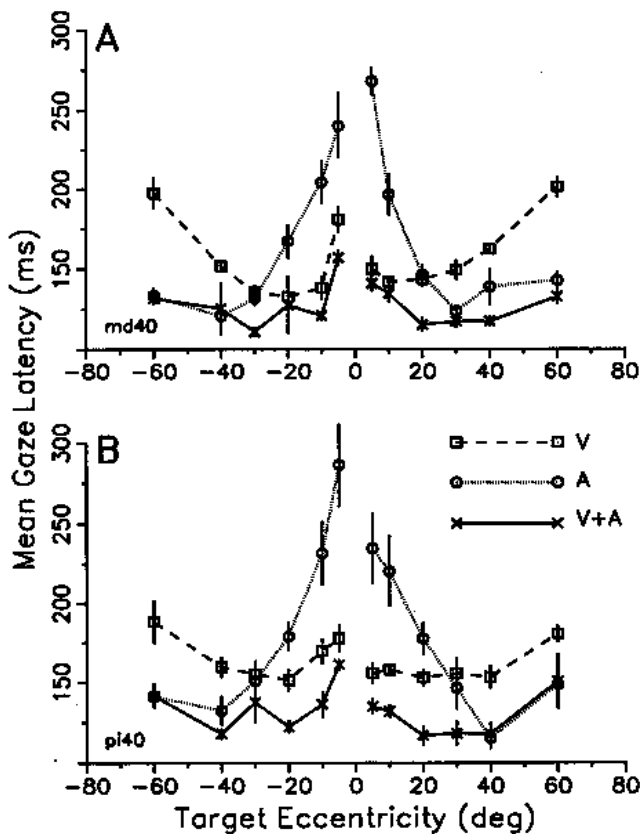


Fig. 4 Mean gaze latency (\pm SE) versus target eccentricity for two subjects in each of the three target conditions: visual (empty squares, dashed line), auditory (empty circles, dotted line), and combined visual+auditory (crosses, solid line). Each data point was computed from 12–15 individual trials. The auditory stimulus alone (A) elicited the longest reaction latencies for central targets ($<20^\circ$), while the visual stimulus alone (V) elicited the longest latencies for targets in the far periphery ($\geq 40^\circ$). The combined target (V+A) produced the shortest latencies

gets, followed by a valley for more peripheral targets, and then an increase in latency for the most eccentric targets. However, the curves had several characteristics that were modality-dependent. Presentation of the auditory target alone produced the longest latencies for small target eccentricities (less than 20°), while the presentation of the visual target alone produced longer latencies at larger eccentricities ($\geq 40^\circ$).

The difference in reaction latency between the visual and auditory target conditions is exposed in Fig. 5A, where the latency difference (auditory reaction latency minus visual reaction latency) is plotted against target eccentricity for the seven subjects tested at 12 different target locations. Subjects consistently had longer latencies for movements to auditory targets close to the center and shorter latencies to auditory targets located beyond 30° eccentricity. Most subjects (at least five of seven) had significantly shorter reaction latencies for movements to the visual target at 5° and 10° eccentricity and significantly shorter reaction latencies for movements to the auditory target at 40° and 60° eccentricities (t -test, $P < 0.05$). The thick dashed line represents the mean of

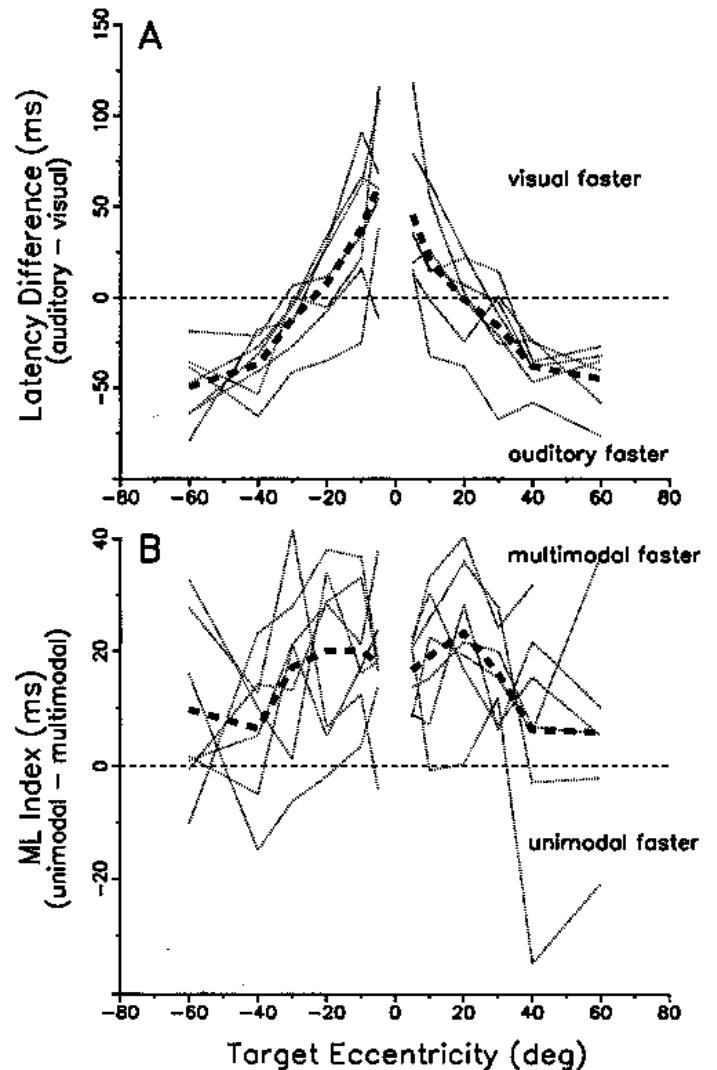


Fig. 5 A Latency difference (auditory reaction time minus visual reaction time) is plotted against target eccentricity for the seven subjects tested at 12 different target locations. A positive difference implies that visual reaction times were faster than auditory times, while a negative value implies the converse. The thick dashed line represents the mean latency difference of the seven subjects. B Multisensory latency (ML) index is plotted against target eccentricity for the same seven subjects as in A. The ML index is the shortest unimodal reaction latency minus the reaction latency in the combined (visual+auditory) target condition. A positive index implies that subject reaction time was faster in the multimodal condition than in either unimodal condition alone. The thick dashed line represents the mean ML index of the seven subjects

the seven subjects and reveals a consistent transition at around 20° eccentricity. A Friedman repeated-measures ANOVA on ranks determined that there were differences in median values between target locations ($P < 0.0001$). There were, however, no significant differences between directions of movements for the same eccentricity, except for 10° and 20° (Student-Newman-Keuls test, $P < 0.05$).

The combined target condition (V+A) almost always produced the shortest reaction latency, regardless of eccentricity (e.g., see Fig. 4). The latency of gaze shifts to

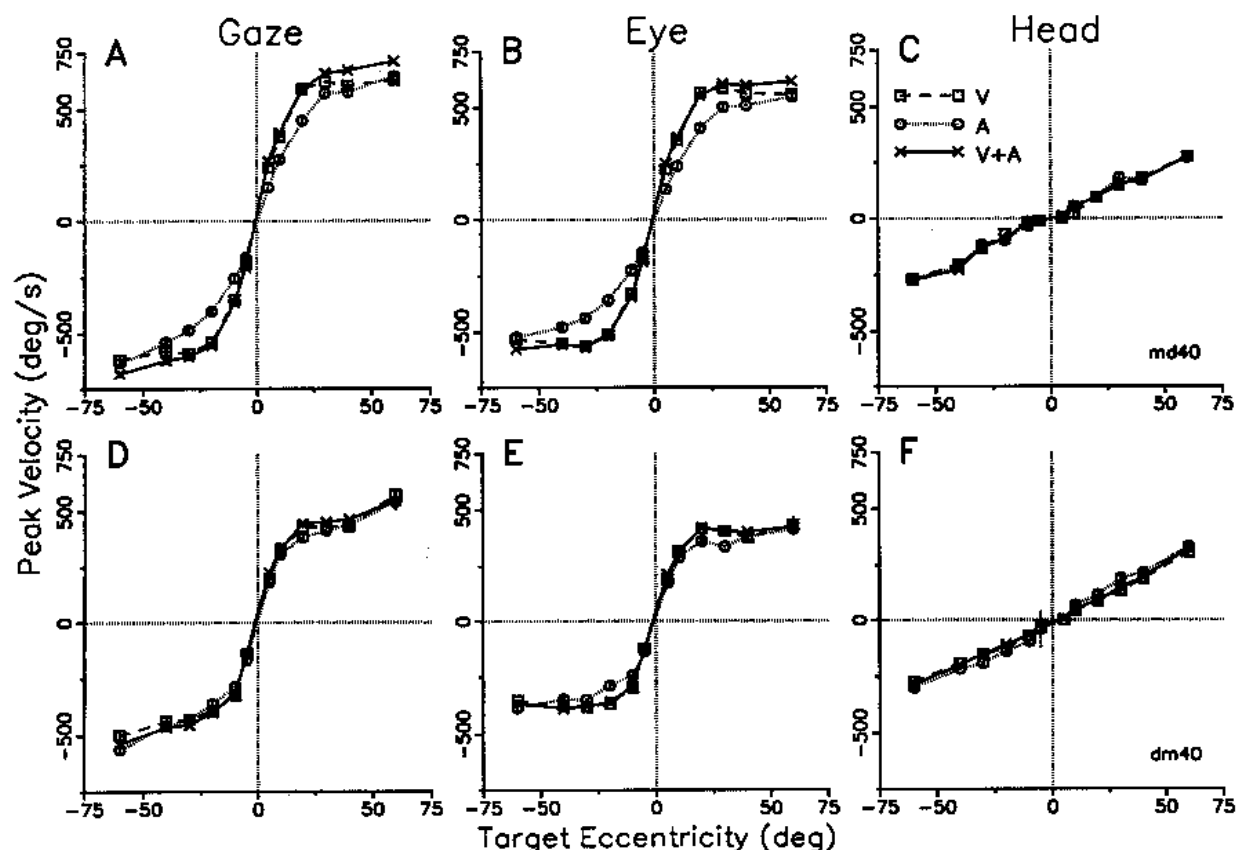


Fig. 6 Peak gaze (A, D), eye (B, E), and head (C, F) velocity plotted against target eccentricity for two subjects. Note that peak gaze and eye velocity was reduced for movements to the auditory target at eccentricities between 10 and 30°. The error bars refer to SEM. In most cases the bar length is less than the symbol size. Each data point was computed from 12–15 individual trials. Data are shown for movements to targets in the visual (empty squares, dashed line), auditory (empty circles, dotted line), and combined visual+auditory (crosses, solid line) conditions

Beyond this eccentricity, the multisensory effect was diminished. A one-way repeated-measures ANOVA determined that there were differences in mean values of the ML index between target locations ($P < 0.0001$). There were, however, no differences between directions of movement for targets at the same eccentricity (Student-Newman-Keuls test, $P > 0.05$).

the combined target were often, but not always, significantly less than the single modality producing the shortest latency. To compare quantitatively the amount of multimodal interaction for all subjects at all target eccentricities tested, we computed a *multimodal latency (ML) index*, where:

$$\text{ML index} = \text{shortest unimodal latency} - \text{multimodal latency} \quad (1)$$

A positive index implies that subject reaction time was shorter in the combined target condition than in both unimodal conditions. Figure 5B shows the ML indices for the seven subjects tested at 12 different target locations. Almost all subjects had a positive ML index at most target eccentricities. The ML index was greatest at 10° and 20° eccentricity and for four subjects this difference between the multimodal and shortest unimodal reaction latency was significant (t -test, $P < 0.05$). The thick dashed line in Fig. 5B represents the mean ML index for the seven subjects and shows that, in the combined condition, reaction times were typically reduced by about 20 ms at target eccentricities of up to and including 30°.

Peak velocity

The speed of the gaze shift was also influenced by target modality and eccentricity. In Fig. 6, peak gaze, eye, and head velocity are plotted against target eccentricity for two subjects. The peak velocity of the gaze, eye, and head increased for movements to targets at greater eccentricities. For targets located beyond 20–30° there was a saturation in peak gaze and eye velocity. No such saturation was observed in peak head velocity for movements to targets at eccentricities up to and including 60°.

At a given eccentricity, peak gaze velocity sometimes varied in the different target modality conditions. Figure 7A shows the differences between peak gaze velocity for movements to visual and auditory targets at the various eccentricities tested for seven subjects and highlights some consistent trends in the data. Most notably, peak gaze velocity in the visual target condition was consistently faster than in the auditory target condition for movements to targets between 10 and 30° eccentricity. This difference was significant for all subjects at 20° ec-

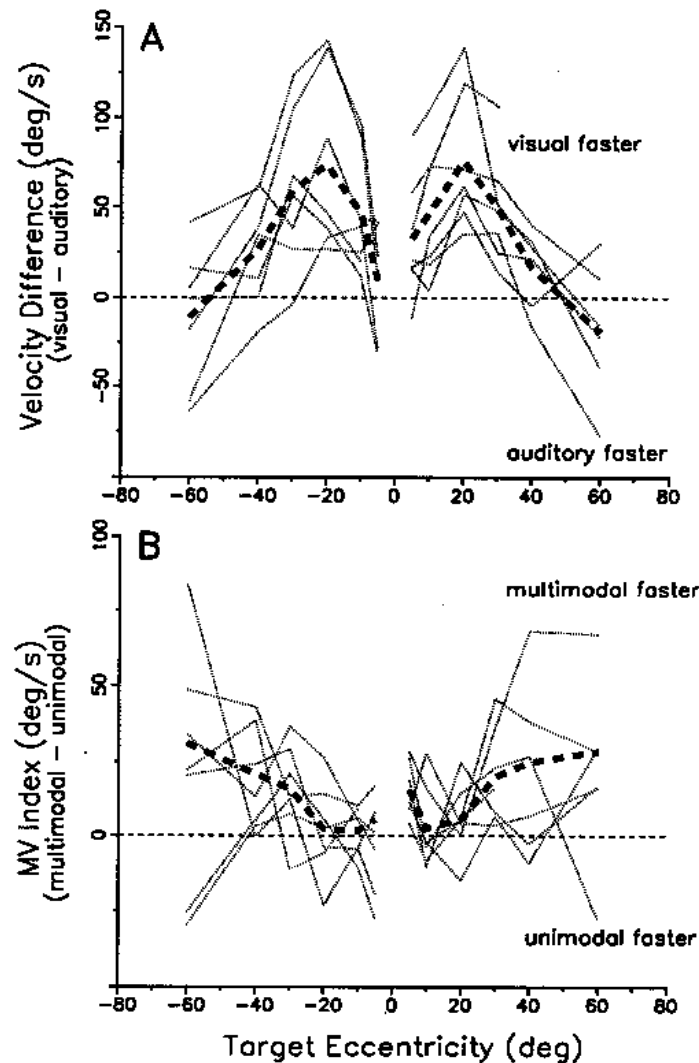


Fig. 7 **A** Velocity difference (peak gaze velocity in the visual target condition minus peak gaze velocity in the auditory target condition) is plotted against target eccentricity for the seven subjects tested at 12 different target locations. A positive difference implies that visually guided gaze shifts had greater velocity than aurally guided gaze shifts, while a negative value implies the converse. The thick dashed line represents the mean of the seven subjects. **B** Multisensory velocity (MV) index is plotted against target eccentricity for the same seven subjects. The MV index is the peak gaze velocity in the combined (visual+auditory) target condition minus the fastest unimodal peak gaze velocity. A positive index implies that the peak gaze velocity was faster in the combined condition than in the fastest unimodal condition. The thick dashed line represents the mean MV index for the seven subjects

centricity and at least five of seven subjects at 10° and 30° eccentricity (t -test, $P < 0.05$). This difference in peak gaze velocity between the auditory and visual target conditions was not apparent for movements to targets at greater or lesser eccentricities. The thick dashed line once again represents the mean of the seven subjects. A one-way repeated-measures ANOVA determined that there were differences in the mean values between target locations ($P < 0.0001$). There were, however, no differences between directions of movement for targets at the same eccentricity (Student-Newman-Keuls test, $P > 0.05$).

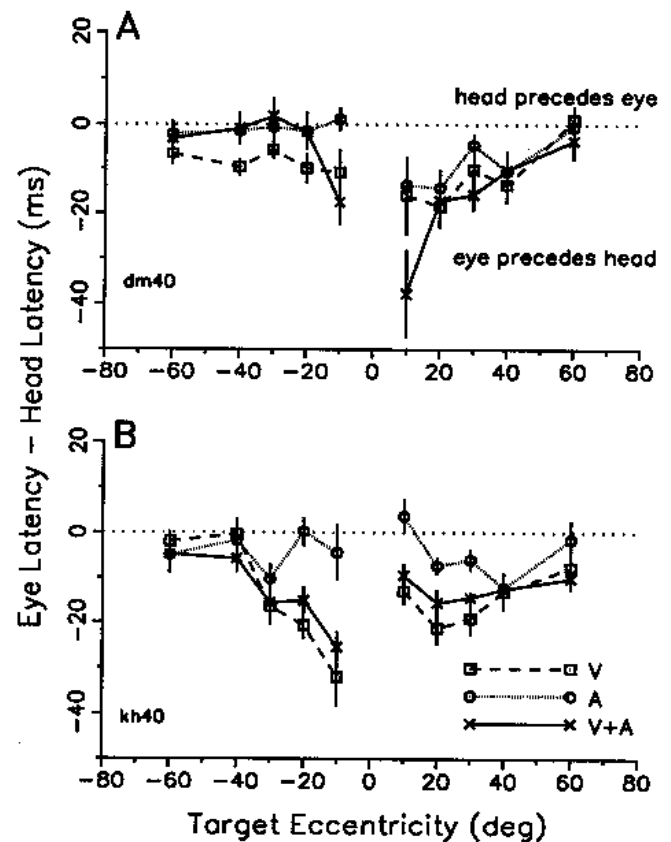


Fig. 8A, B Effect of the timing between eye and head movements (eye latency-head latency) plotted as a function of target eccentricity for all three target conditions (visual, auditory, and combined) for two subjects. Both subjects tended to have eye movements preceding head movements (negative values on ordinate) which was accentuated at smaller target eccentricities when the head movement often began at the end of the saccade. Error bars correspond to SEM. Note that eye movement onset preceded head movement onset for gaze shifts to the visual target more so than gaze shifts to the auditory target

From the data presented in Fig. 6A, D, it is apparent that, in the combined target condition, peak gaze velocities were comparable with the fastest unimodal condition but not faster. To quantitatively determine the influence of the combined target on peak gaze velocity, we computed a *multimodal velocity (MV) index*, where:

$$\text{MV index} = \frac{\text{multimodal peak velocity} - \text{fastest unimodal peak velocity}}{\text{fastest unimodal peak velocity}} \quad (2)$$

A positive index implies that the peak gaze velocity was faster in the combined condition than in both unimodal conditions. Figure 7B summarizes the MV indices for the seven subjects tested at 12 different target eccentricities. The multimodal effect was essentially negligible for all subjects at all eccentricities tested (t -test, $P > 0.05$). However, there was a trend toward a larger MV index for large target eccentricities in both directions. Thus, although the combination of visual and auditory targets led to shorter reaction times, it did not lead to any significant modification in the dynamics of the gaze shifts. The thick dashed line represents the mean MV index. A one-

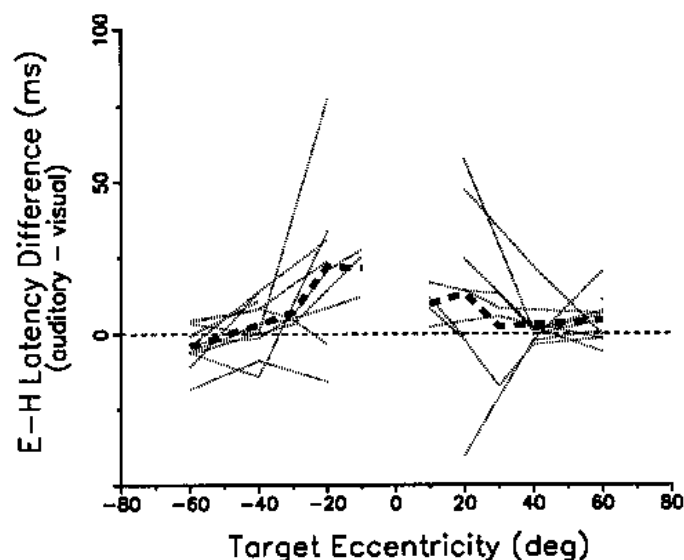


Fig. 9 Summary of the eye-re-head latency difference between the auditory and visual target conditions for 11 subjects. The difference in the latency of the eye relative to the head (*E-H latency*) in the auditory target condition minus the *E-H latency* in the visual target condition is plotted against target eccentricity. The thick dashed line represents the mean of the 11 subjects

way repeated-measures ANOVA also determined that there were no differences in mean values between target locations ($P > 0.05$).

Eye-head coupling

The individual traces illustrated in Fig. 1 show that subjects tended to initiate eye movement shortly before head movement. We investigated the relative timing between the onset of head and eye motion after target presentation under the different target conditions for all subjects. Figure 8 shows the effect of target eccentricity and modality on the timing of eye and head movements for two subjects that moved the head during gaze shifts to all targets of 10° or more eccentricity. Both subjects tended to have eye movement onset precede head movement onset (negative values on ordinate), and this was accentuated at small target eccentricities when the head movement frequently began near the end of the eye saccade. Note also that the eyes tended to lead the head most often when subjects looked at the visual targets and least often when subjects looked at the auditory targets. The combined target condition (V+A) tended to produce intermediate responses.

The difference in the relative timing between onset of head and eye motion in the auditory and visual target conditions is summarized for 11 subjects in Fig. 9, where we plot the difference in the latency of the eye relative to the head (*E-re-H latency*) in the auditory target condition minus *E-re-H latency* in the visual target condition. A positive value implied more time between eye and head onset in the visual target condition. The thick dashed line represents the mean of the 11 subjects. For small target

eccentricities (less than 30°), eye movement onset tended to precede head movement onset more in the visual target condition than in the auditory target condition, and this difference between the visual and auditory target conditions was not evident for larger target eccentricities ($\geq 30^\circ$). However, a one-way repeated-measures ANOVA determined that there were no differences in mean values between any target locations ($P > 0.05$).

Discussion

Gaze strategies

We have shown that human subjects employ idiosyncratic combinations of eye and head rotation to fixate upon eccentric targets presented along the horizontal meridian. Humans have an oculomotor range of ± 50 – 55° (Guitton and Volle 1987) so that head movement was essential only to fixate targets beyond these limits. When targets were presented within the oculomotor range, any contribution of head movement to the gaze shift was possible. Some subjects always moved their head to align with the target (e.g., Fig. 1B), while others relied exclusively on eye movement (e.g., Fig. 1A). These alternative strategies were seen among both the informed and naive subjects in our study and we conclude that this had no bearing on our main findings. When targets were located well within the oculomotor range (e.g., 20° eccentricity), we found that subjects could be separated into two groups that used alternative strategies with little evidence for a continuum. Fuller (1992) also found that subjects could be separated into head-movers and non-movers and further suggested that it reflected the choice of reference coordinate systems (extrinsic versus intrinsic coordinates, respectively). Although subjects can consciously shift from one strategy to the other, there may be a bias toward either end of the continuum in natural behavior as subjects rely on either extrinsic or intrinsic reference frames. When we looked at the behavior of individual non-movers, we found that they gradually increased their reliance upon head motion in a graded fashion for targets at increasing eccentricity (Fig. 3B, C). They did not shift suddenly from one end of the continuum to the other, as if switching from one coordinate system to another.

A new finding in this study is that we found very little within-subject variability in the strategy of eye-head motion adopted by individual subjects in the three different target conditions utilized: visual, auditory, and combined (see Fig. 2). Each subject relied upon the same combination of eye and head movements to achieve fixation of targets at a given eccentricity. This is perhaps somewhat surprising, because visual and auditory stimuli are initially localized in different frames of reference (visual stimuli: retinotopic; auditory stimuli: craniotopic). Although our results support the hypothesis that, during the planning and execution of these movements, visual and auditory signals are remapped into a common reference system, some caution is warranted. A more direct test of

this hypothesis would be to manipulate initial eye and head positions and determine whether the resultant eye-head synergies remained constant for different target modalities. To date, such manipulations have been done for visually guided gaze shifts only (Volle and Guitton 1993).

Eye and head movements are usually coupled together in human gaze shifts (Gresty 1974; Barnes 1979; Zangemeister and Stark 1982a, b; Guitton and Volle 1987; Fuller 1992; Land 1992). We also found tight coupling between eye and head movements during gaze shifts to visual and auditory targets. Gaze shifts almost always began with the initiation of the eye saccade, followed by the onset of head movement (see Figs. 1, 8). Electromyographic recordings from neck muscles, however, reveal synchronous activation of extraocular and neck muscles (Zangemeister and Stark 1982a). The delay between the onset of movement of the eyes and the head was attributed to the biomechanical lag in overcoming the inertia of the head. The lagging of the head may also depend on the twitch characteristics of muscles in the extraocular versus skeletal muscle; twitch contraction time is faster in the extraocular muscles (Barmack et al. 1971) as compared to other skeletal muscles (Botterman et al. 1986). In addition, the presence of more connective tissue in skeletal, as compared to extraocular muscle, may further lengthen twitch contraction times in neck muscles.

Dissociation between eye and head movements can occur when subjects follow a visual stimulus that is flashed at one location and then jumps to a second location immediately prior to movement onset (Ron and Berthoz 1991; Ron et al. 1993). Ron and coworkers (1993) found that, in response to two sequential targets, the initial head motion was usually toward the first flash offset, whereas the concomitant eye saccade was to the second flash. They suggest that, during this dissociation, either each system behaves individually, in ways opposite to its usual mode of operation during cooperative actions, or the initial command to one system is modified, so that the eyes and head aim at different offsets. This independence of the saccadic and head control systems suggests that there is more than one type of command in the brain controlling eye and head movements. Thus, the eye and head premotor centers may receive convergent commands of different origins, which may account for some of the diverse behaviors seen in human subjects.

Neurophysiological studies in animals have begun to investigate the underlying neural circuitry that could account for the coupling between eye and head movements during orienting gaze shifts. Electrical stimulation of the deeper layers of the cat superior colliculus elicits tightly coordinated eye-head movements that are very similar to natural eye-head orienting movements (Roucoux et al. 1980; Paré et al. 1994). Stimulation of the deeper layers of the monkey superior colliculus also elicits combined eye-head movements, but the degree of coupling appears somewhat reduced (Segraves and Goldberg 1992; Cowie and Robinson 1994). In addition, single-cell recording

studies in cat have revealed correlations between the discharge of tecto-reticulo-spinal neurons (projecting to the eye and head premotor neurons in the reticular formation of the brainstem) and characteristics of eye and head orienting movements (Grantyn and Berthoz 1985; Munoz et al. 1991; Olivier et al. 1993). Because these collicular output neurons also respond to visual and auditory stimuli (Meredith and Stein 1986; Guitton and Munoz 1991), they may play a critical role in coordinating eye and head movements to visual and auditory targets. Experiments in awake behaving monkeys have determined that visual (Mays and Sparks 1980) and auditory (Jay and Sparks 1987) signals required to localize a target with a saccadic eye movement are remapped from their initial frames of reference into the motor error coordinates of the deeper layers of the superior colliculus (i.e., the amplitude and direction of eye rotation required to foveate the target). This represents at least one structure where visual and auditory signals relevant to orientation of the gaze axis share a common reference system. If the superior colliculus is involved in coordinating aspects of the orienting gaze shifts in humans, this common reference frame may account for the consistent gaze strategies employed by subjects in our study when orienting to visual and auditory targets.

Multisensory interactions

We found that both target modality and eccentricity influenced gaze reaction latencies (see Figs. 4, 5). Kalesnykas and Hallett (1994) provided a thorough description of the latency-eccentricity function of human subjects looking to visual targets 0.25–66°. However, they used subjects whose heads were immobilized during the experiments. They described a bowl-like latency-eccentricity function, with increased latencies for targets at eccentricities of less than 0.75° and greater than 12°. The longer latency saccades for large target eccentricities were presumed to be due, at least in part, to decreases in visual acuity in the periphery of the retina. We have extended the results of Kalesnykas and Hallett (1994) to the head-unrestrained condition. We found a similarly shaped latency-eccentricity function for gaze shifts to visual targets, except we did not test target eccentricities of less than 5° owing to limitations in the EOG recording technique.

We found that the shape of the latency-eccentricity function was somewhat different for movements to auditory targets, in which the longest reaction times were obtained for targets of less than 20° eccentricity (see Fig. 4). The auditory afferent pathway has a shorter latency than the visual pathway. For example, the afferent delay for transmission of visual information to the deeper layers of the cat superior colliculus is about 50 ms (Syka et al. 1979; Peck et al. 1980; Meredith et al. 1987; Guitton and Munoz 1991), whereas the delay for auditory information is only about 10 ms (Wise and Irvine 1983; Middlebrooks and Knudsen 1984; Hirsch et al.

1985). If similar mechanisms are present in humans, then the auditory stimuli should elicit gaze shifts at shorter reaction latencies. This difference in afferent processing between visual and auditory stimuli can account for the faster reaction times to auditory targets in the far periphery that we observed (e.g., $\geq 40^\circ$; see Fig. 5A), but it cannot account for the slower reaction times when auditory targets were located at up to and including 20° eccentricity. The increase in reaction latency for auditory saccades at up to and including 20° eccentricity was also found by others studying saccadic reaction times in head-fixed human subjects (Zahn et al. 1978; Zambarbieri et al. 1982; Frens and Van Opstal 1995) and might be due to minimal interaural timing and intensity differences at the level of the subject's ears when the auditory targets were located near the midline. This ambiguity could lead to increased reaction latencies. In our study, when auditory targets were placed at eccentricities greater than 20° , they were presumably easier to localize, resulting in faster reaction times.

The combination of visual and auditory targets at the same spatial locus elicited the shortest reaction latencies in our experiments (see Fig. 5B). Despite the reduction in latency, there was no significant increase in the speed of movements to the multimodal targets (Fig. 7B). Other studies have also found that reaction times for saccadic eye movements to multimodal targets are faster than to auditory or visual targets alone (Engelken et al. 1989; Hughes et al. 1994; Frens et al. 1995). The above experiments, however, were all done with the head fixed. Our results extend these findings to the head-unrestrained condition. Stein and coworkers (1989) have shown that subthreshold auditory and visual stimuli are able to elicit orientations from awake behaving cats only when the stimuli are presented simultaneously at the same spatial locus. However, using this apparatus they were unable to assess the degree of coupling between the eyes and head, the reaction time, or the speed of the movements.

We observed that, at eccentricities between 10 and 30° , gaze shifts to auditory targets had lower peak velocities than movements to visual targets (Fig. 7A). Similar observations have been made for saccades elicited in the head-fixed condition (Zahn et al. 1978; Zambarbieri et al. 1982). For targets located beyond 30° eccentricity, we found the peak velocity of gaze shifts to the visual and auditory targets to be similar. This increase in velocity for gaze shifts to the auditory target, relative to gaze shifts to the visual target, may be due to facilitated localization of the auditory target at these greater eccentricities. Alternatively, because peak gaze velocity saturated for gaze shifts to targets located beyond 30° eccentricity (see Fig. 6A, D), any difference between the visual and auditory target conditions was muted.

The superior colliculus is a prime candidate for the locus of the multisensory interactions that could influence gaze latency. Cells in the deeper collicular layers of the cat receive convergent visual and auditory inputs (Meredith and Stein 1986; Peck 1987; Guitton and Munoz 1991). The visual and auditory receptive fields of

these multisensory neurons often overlap so that an auditory or visual stimulus from a specific region in space can activate the same group of collicular output neurons to trigger a coordinated eye-head orienting movement to align the visual axis with the stimulus. When visual and auditory stimuli are presented at the same spatial locus, there can be a marked enhancement in the sensory responses of these collicular multisensory neurons in anesthetized, paralyzed cats (Meredith and Stein 1986). This increased responsiveness, if also present in human subjects, could reduce the time to threshold for triggering a movement, leading to a reduction in the reaction latency.

Because there was no significant impact of the multisensory target on gaze velocity in our experiments (see Fig. 7B), we conclude that, although the convergence of auditory and visual signals in the superior colliculus reduces the time to threshold for movement initiation, it does not modify the resulting velocity. Either this multisensory convergence does not increase the intensity of the movement-related activity in the colliculus or, if it does, then local or downstream neural elements may already be in a saturated state when the visual signal is presented and any additional input to this element (i.e., auditory input) cannot drive the movement any faster. In our experiments, the intensity of the visual and auditory stimuli were well above threshold. Perhaps combining visual and auditory stimuli at threshold intensities would lead to changes in the velocity of gaze shifts to the combined target.

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