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Human eye-head coordination in two dimensions under different sensorimotor conditions

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Abstract The coordination between eye and head movements during a rapid orienting gaze shift has been investigated mainly when subjects made horizontal movements towards visual targets with the eyes starting at the centre of the orbit. Under these conditions, it is difficult to identify the signals driving the two motor systems, because their initial motor errors are identical and equal to the coordinates of the sensory stimulus (i.e. retinal error). In this paper, we investigate head-free gaze saccades of human subjects towards visual as well as auditory stimuli presented in the two-dimensional frontal plane, under both aligned and unaligned initial fixation conditions. Although the basic patterns for eye and head movements were qualitatively comparable for both stimulus modalities, systematic differences were also obtained under aligned conditions, suggesting a task-dependent movement strategy. Auditory-evoked gaze shifts were endowed with smaller eye-head latency differences, consistently larger head movements and smaller concomitant ocular saccades than visually triggered movements. By testing gaze control for eccentric initial eye positions, we found that the head displacement vector was best related to the initial head motor-error (target-re-head), rather than to the initial gaze error (target-re-eye), regardless of target modality. These findings suggest an independent control of the eye and head motor systems by commands in different frames of reference. However, we also observed a systematic influence of the oculomotor response on the properties of the evoked head movements, indicating a subtle coupling between the two systems. The results are discussed in view of current eye-head coordination models.

Key words Saccadic system · Auditory system · Visual system · Eye-head movements · Gaze control models · Human

Introduction

In this paper, human gaze saccades (gaze=eye-in-space=eye-in-head+head-in-space) are investigated in two dimensions (2-D), in order to obtain more insight into the signals controlling the eye and head motor systems. To that end, we have studied the influence of stimulus modality (visual compared with auditory) on the resulting eye-head movement strategies. In addition, eye-head coordination was investigated under conditions in which eye and head were not initially aligned.

Sensorimotor transformations

In 2-D, the sensorimotor transformations for the eye and head motor systems, associated with stimuli of different modalities, are highly non-trivial. In order to illustrate these problems, the different coordinate systems that play an important role in gaze control to auditory and visual stimuli have been schematically depicted in Fig. 1.

For example, since in humans the ears are fixed with respect to the head, the position of an auditory target is initially encoded in a craniocentric frame of reference (**Th**). For that reason, the auditory spatial information does not necessarily correspond to the desired eye displacement vector (**Te**). When generating an accurate eye movement towards an acoustic stimulus, the oculomotor system must therefore take the initial position of the eyes in the orbit into account (**Te=Th-E**). Behavioural (human: Frens and Van Opstal 1994; monkey: Whittington et al. 1981) as well as neurophysiological data (monkey: Jay and Sparks 1984, 1987; cat: Hartline et al. 1995; Peck et al. 1995) have shown that the oculomotor system indeed incorporates this required craniocentric to oculo-centric transformation.

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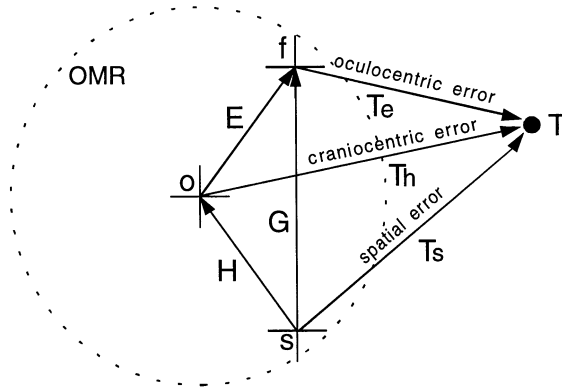


Fig. 1 Relevant reference frames for eye-head coordination. Schematic outline of the relations between the spatial, craniocentric and oculocentric frames of reference for eye and head movements that are of interest in this study. From the scheme, the following vectorial transformations are obtained: $\mathbf{G}=\mathbf{E}+\mathbf{H}$, $\mathbf{Th}=\mathbf{E}+\mathbf{Te}$; and $\mathbf{Ts}=\mathbf{H}+\mathbf{Th}=\mathbf{H}+\mathbf{E}+\mathbf{Te}$. Note that in this specific example eye and head are unaligned, since o and f do not coincide. (s Centre of spatial, or body, frame, o centre of the oculomotor range, OMR , f , fixation point, fovea, G eye-in-space, E eye-in-head, H head-in-space, T target position, Ts target-in-space, Te target-re-eye or gaze motor-error, Th target-re-head or head motor-error)

If eye and head are both controlled by the same oculocentric motor command (\mathbf{Te}), as put forward by a number of gaze control models, this remapping of craniocentric into oculocentric coordinates would, in principal, be sufficient for accurate orienting gaze movements in a multimodal environment.

Conversely, if the head motor system is to be controlled by an independent head motor-error command (\mathbf{Th}), as suggested by recent data, such craniocentric-oculocentric transformation would be inappropriate for the head motor system in the case of auditory targets. Moreover, when orienting towards visual stimuli, the oculocentric retinal error signal (\mathbf{Te}) does not necessarily equal the desired head displacement vector (\mathbf{Th}). Consequently, the retinal error signal needs to be remapped into the appropriate craniocentric head motor command by taking the initial eye position into account ($\mathbf{Th}=\mathbf{Te}+\mathbf{E}$). This means that the head motor system may be subjected to similar sensorimotor transformations as the oculomotor system.

The problem of coordinate remapping has been mainly investigated under head-fixed conditions and little is known about eye-head movements during visually evoked and auditory-evoked orienting behaviour when the two motor systems are initially unaligned. To our knowledge, only Whittington and colleagues (1981) have compared visually evoked and auditory-evoked gaze shifts under head-free conditions in the monkey, but for aligned conditions and horizontal movements only.

Eye-head coordination studies

The nature of combined eye-head movements has been studied extensively in human (Barnes 1979; Gresty

1974; Guitton and Volle 1987; Lauritis and Robinson 1986; Pélisson et al. 1988; Zangemeister and Stark 1982a,b), cat (Blakemore and Donaghy 1980; Fuller et al. 1983; Guitton et al. 1984, 1990) and monkey (Bizzi et al. 1971, 1972; Morasso et al. 1973; Tomlinson and Bahra 1986a,b Whittington et al. 1981). Initially, Bizzi and colleagues (1971, 1972) proposed that head-free gaze saccades are, like head-fixed gaze saccades, programmed as an ocular saccade, independent of the occurrence and size of a concomitant head movement. According to this so-called *oculocentric hypothesis*, the vestibulo-ocular reflex (VOR) would cancel any contribution of the head to the gaze shift by causing the eyes to counter-rotate by the same amount.

However, several experiments have shown that the action of the VOR is actually suppressed during gaze saccades (human: Lauritis and Robinson 1986; Pélisson et al. 1988; Lefèvre et al. 1992; monkey: Tomlinson 1990; Tomlinson and Bahra 1986b). These and other observations (reviewed by Roucoux 1992) have led to the conclusion that in humans and monkeys the oculocentric hypothesis is strictly valid only for gaze shifts smaller than $\sim 10^\circ$.

It is well accepted in the oculomotor literature that, when the head is fixed, eye movements are guided by local feedback of either current eye position (Robinson 1975) or eye displacement (e.g. Jürgens et al. 1981). As an alternative for the oculocentric hypothesis, the conceptual oculomotor model was extended to gaze control in the head-free condition (Guitton and Volle 1987; Lauritis and Robinson 1986). According to this *gaze feedback hypothesis*, an internally created, instantaneous gaze motor-error is used to drive the oculomotor system. In this way, the accuracy of gaze saccades can be maintained, regardless of head movements, even if the VOR is suppressed during the movement.

Note that the concept of gaze feedback by itself does not specify the head motor command. However, it was proposed, on the basis of gaze control studies in the cat, that both the oculomotor system and the head motor system are controlled by the same internally created gaze motor-error signal (Galiana and Guitton 1992; Guitton et al. 1990). Several behavioural and neurophysiological studies provide support for this so-called *common gaze model* (reviewed by Guitton 1992).

Recently, however, this common drive theory has been questioned on the basis of behavioural data obtained from both human and monkey studies. For example, in humans, the direction and spatial trajectories of eye and head movements can be substantially different when very large ($>70^\circ$) gaze movements are made (Glenn and Vilis 1992; Tweed et al. 1995). Moreover, in humans as well as in nonhuman primates, the latencies of eye and head movements are not as tightly coupled as in the cat (monkey: Phillips et al. 1995; human: Tweed et al. 1995). And finally, whereas in cat several aspects of eye and head metrics and kinematics appear to be strongly correlated (Guitton et al. 1984, 1990), they are so to a much lesser extent in monkeys (Phillips et al. 1995).

Based on these data, it was thus argued that the two motor systems are rather controlled by independent driving circuits, each having their own feedback mechanism. According to these *independent gaze models*, the eye and head motor system are driven by a gaze and head motor-error signal, respectively.

Such an independent control could in principle explain the poorly correlated eye and head movement onsets. On the other hand, since human subjects are able to execute gaze shifts with and without head movements at will, there is an apparent need to incorporate at least independent *initiation* mechanisms for the eye and head movement in any human gaze control model. Indeed, Ron and Berthoz (1991) have applied the notion of independent eye-head gating in order to explain dissociated eye and head movements within the boundaries of the gaze feedback hypothesis.

Head movement strategies

In most studies concerning eye-head coordination, attention was focused on the control of eye movements and the role of the VOR during gaze shifts within and beyond the oculomotor range (OMR). In those studies, horizontal gaze shifts were typically elicited with the eyes starting near the centre of the orbit. However, as was pointed out by Volle and Guitton (1993), this does not permit a clear identification of the input signal to the head motor system, since under these conditions the initial motor errors for eye and head are identical. In their one-dimensional study with human subjects, Volle and Guitton (1993) showed that, when eyes and head are not initially aligned, the head movement amplitude is better related to the initial head motor-error (**Th**) than to the initial gaze error (**Te**). Conversely, Delreux et al. (1991) reported that the amplitude of head movements in a sequence of successive eye-head movements was better related to gaze motor error than to head motor error.

Clearly, the question of whether the head motor system is driven by a target-re-head- or a target-re-eye-related command, is difficult to answer on the basis of movements in one dimension. However, this problem can be addressed more readily in 2-D. For example, if both eye and head are driven by a common gaze-error command, it is predicted that the head movement will not be directed towards the stimulus when the initial positions are unaligned (Fig.1). This follows from the fact that (in 2-D) the oculocentric gaze-error command (**Te**) and the head motor error (**Th**) may be different, both in amplitude and in direction. Alternatively, if guided by a craniocentric head motor-error command, head movements are expected to be goal-directed, regardless of the initial eye position.

A preliminary account of the experimental findings has been given in Goossens et al. (1995).

Materials and methods

Experimental setup

All experiments were performed in a completely dark, sound-attenuated room (3×3×3 m). Acoustic reflections of sound frequencies above 500 Hz were strongly reduced by covering walls, ceiling and floor, as well as large objects, with black, sound-absorbing foam. The background noise level was about 30 dB sound pressure level (SPL).

Subjects

Seven healthy human subjects (one woman and six men) between 21 and 38 years old participated in the experiments. Subjects were without any known uncorrected visual, auditory or motor disorders, except for J.O., who is amblyopic in his right eye. Subjects B.B., V.C. and P.H. were naive with regard to the purpose of this investigation. During the experiments, subjects were comfortably seated in a chair that provided good back support. Viewing was always binocular.

Auditory stimuli

Auditory stimuli (600 ms duration, 5 ms rise and fall time) consisted of band-pass-filtered (150 Hz–20 kHz, Krohn-Hite 3343) white noise, generated by a PC-80486 equipped with a digital-analog (D/A) converter (Data Translation DT2821). Such broad-band noise stimuli are known to be well-localizable in 2-D (see Frens and Van Opstal 1995). All sound stimuli were amplified (Luxman 58A) to about 65 dB SPL at the position of the subject's head and delivered through a speaker (Philips AD44725, radius 43 mm) that was mounted on a two-joint robot arm. This robot arm, equipped with stepping motors (type VRDM5; Berger Lahr), which were also controlled by the PC-80486, could rapidly position the speaker anywhere on the surface of a virtual sphere (radius 0.90 m) centred at the subject's head. The speaker's frequency response was not corrected for, since deviations from a flat spectrum were within 10 dB.

Visual stimuli

Visual targets (LEDs, 0.2° diameter as viewed by the subject, intensity 0.15 cd·m⁻²) were mounted on an acoustically transparent wire frame shaped as a half-sphere just proximal to the working range of the robot. The distance between the LEDs and the subject was 0.85 m.

Measurements

Rotations of both the right eye and the head (relative to space) were measured by means of the search-coil technique (Collewijn et al. 1975). The head coil was mounted on top of a light-weight helmet (150 g) worn by the subject. Two sets of large coils (3×3 m), attached along the edges of the room, generated the oscillating horizontal (40 kHz) and vertical (30 kHz) magnetic fields. These fields were homogeneous (deviations less than 10%) within a cube of 1×1×1 m centred at the position of the subject's head and were not affected by the movement of both the robot arm and the speaker. In this way, the orientation of the eye and head could be measured without significant effects of eye and head-coil translations and without interference of the recording apparatus with the acoustic stimuli. The spatial resolution of this method for both eye and head orientation measurements was better than 0.5° over the entire recording range (±45°). Throughout this paper, the term "position" will be used in the sense of orientation.

Timing of the stimulus events and data acquisition were controlled by a PC-80386, equipped with a data-acquisition board

(Metabyte DAS16) and a digital I/O card (Data Translation 2817). This computer communicated through its parallel port with the PC-80486 that controlled the auditory stimuli. Both eye and head position signals were amplified, filtered (low-pass 150 Hz) and sampled at 500 Hz/channel. Sampling started 400 ms prior to the presentation of the peripheral stimulus and continued for 2 s.

Calibration procedure

Eye coil

Subjects were asked to keep their head in a comfortable, straight-ahead position, hereafter called the neutral position, and to fixate a series of LEDs. While fixating an LED, the subject pressed a button, which triggered the recording of the eye-coil signals (500 ms duration). Fixation spots ($n=73$) were presented at spherical polar coordinates $R \in [0, 5, 9, 14, 20, 27, 35]^\circ$ and $\varphi \in [0, 30, 60, \dots, 330]^\circ$, where $\varphi=0^\circ$ corresponds to a rightward position and $\varphi=90^\circ$ is upward. R is the eccentricity of the target relative to the central fixation spot.

Head coil

Calibration of a 2-D head-coil in vivo is not a straight-forward procedure. First, subjects are unable to hold their head in a pre-defined position without artificial means. Second, there is no a priori knowledge regarding the geometric configuration of the axes of rotation of the head. In order to circumvent these problems, we employed a method in which static head positions can be measured by using calibrated eye-coil signals.

A light-weight aluminium pointer (length 40 cm) with a small fixation spot at its far end was mounted on the subject's helmet. When subjects keep fixating this head-fixed point, the eye position relative to the head, \mathbf{E} , remains fixed. Under this condition, the eye position in space, \mathbf{G} (measured with the eye coil), reflects the head position in space, \mathbf{H} , apart from a constant offset, \mathbf{G}_0 , which equals the eye position relative to the head ($\mathbf{G}_0=\mathbf{E}$). To measure \mathbf{G}_0 (typically less than 10° in both dimensions), subjects were asked to assume the neutral head position and fixate the head-mounted fixation point. In this specific condition, $\mathbf{H}=\mathbf{0}$ so that $\mathbf{G}_0=\mathbf{E}=\mathbf{G}$. The neutral head position, which we regard as a behaviourally relevant reference position, was reproducible within about 2° ($n=4$).

After recording the eye offset, the series of fixation spots was presented once more and subjects were asked to roughly direct the head-mounted pointer towards each subsequent LED while *fixating the head-mounted fixation point*. In this way we obtained a series of static head position recordings.

Data calibration

Eye-coil signals were calibrated off-line on the basis of the fixation data obtained in the eye-coil calibration experiment. The azimuth (A) and elevation (E) of the target position relative to the eye are related to the spherical polar angles (R , φ) by:

$$\begin{aligned} A &= \arcsin(\sin R \cdot \cos \varphi) \\ E &= \arcsin(\sin R \cdot \sin \varphi) \end{aligned} \quad (1)$$

Both the (A, E) and the (R, φ) coordinate systems have their origin at the centre LED, such that (0,0) corresponds to the straight-ahead fixation direction. In this way the azimuth and elevation of target positions could be directly matched to the horizontal and vertical eye-coil signals.

Two neural networks, one for each position component, were trained to fit the raw fixation data to the target locations, using a back-propagation algorithm based on the gradient descent method of Levenberg-Marquardt (Matlab; Mathworks). Each of the networks consisted of two input units (representing the raw horizontal and vertical signal), four hidden units and one output unit (rep-

resenting either the horizontal or vertical position signal). Raw eye-coil signals were subsequently calibrated by applying the resulting feedforward networks. This algorithm could adequately cope with minor cross-talk between horizontal and vertical recording channels. Errors were 4% or less over the entire recording range ($\pm 45^\circ$). The result of this calibration procedure yielded the eye position in space (gaze, \mathbf{G} ; see also Fig. 1).

Head-coil signals were calibrated off-line on the basis of the fixation data obtained in the head-coil calibration experiment. First, static head positions were calculated from eye positions relative to space (recorded with the eye coil) according to:

$$\mathbf{H} = \mathbf{G} - \mathbf{G}_0 \quad (2)$$

where \mathbf{H} represents the position of the head in space, \mathbf{G} the position of the eye in space (and fixed relative to the head) and \mathbf{G}_0 the offset position of the eye in space when the head is in the neutral position. Two other neural networks, similar to the ones used for the eye-coil calibration, were subsequently trained to fit the head-coil data. Raw head-coil signals were calibrated by applying the resulting feedforward networks. The result of this calibration procedure yielded the head position in space (head, \mathbf{H} ; see Fig. 1)

Finally, the position of the eye relative to the head (eye, \mathbf{E} ; see also Fig. 1) was obtained from eye position in space \mathbf{G} and head position in space \mathbf{H} according to:

$$\mathbf{E} = \mathbf{G} - \mathbf{H} \quad (3)$$

Because the axes of rotation of the eye and head do not coincide, the eye is translated when the head is rotated. Thus, when the eye fixates a target, with the head at an eccentric position, the direction of gaze can deviate slightly from the target direction when compared with the straight-ahead condition. Since the resulting deviations are small (up to about 3° for a 35° head eccentricity; see, e.g. Collewijn et al. 1982), and because correction necessitates assumptions regarding the geometry of the axes of rotation in multiple dimensions, we have not attempted to correct for this minor translation effect.

Experimental paradigms

In all experiments, subjects were asked to make orienting responses towards peripheral targets as fast and as accurately as possible. Subjects were asked not to move their body, but no specific instructions were given with regard to the speed and accuracy of the head movements.

Aligned experiments

In the first series of experiments (subjects N.C., M.F., J.G., B.B., P.H. and J.O.), head-free gaze movements towards auditory and visual targets were elicited. Subjects were instructed to align their eyes and head in a natural way with an initial LED at the straight-ahead position. After a random period of 800–1600 ms, this fixation spot extinguished and, simultaneously, a randomly selected peripheral target was presented for 600 ms. Targets were presented at spherical polar coordinates $R \in [2, 5, 9, 14, 20, 27, 35]^\circ$ and $\varphi \in [0, 30, 60, \dots, 330]^\circ$. Thus, 84 visual and 84 auditory stimuli were presented randomly interleaved, yielding a total number of $n=168$ different targets at unpredictable locations.

In between trials, and in complete darkness, the robot made two successive movements, even when the stimulus in the next trial was a visual target. These movements were such that the speaker was first moved to a random position and subsequently to the new peripheral target position. This procedure denied the subject of prior knowledge about target modality and excluded both visual and auditory cues regarding the new stimulus position. All subjects reported the impossibility of identifying the stimulus location purely on the basis of the sounds produced by the robots' stepping motors. In an earlier study, this was tested quantitatively in control experiments with several subjects (Frens and Van Opstal 1995).

Unaligned experiments

Auditory and visually evoked gaze shifts under aligned and unaligned initial fixation conditions were measured in the second series of experiments (subjects M.F., J.G., B.B., P.H. and V.C.). Subjects were asked to first align their eyes and head with an initial head-fixation spot. As soon as the head was aligned ($\pm 4^\circ$ window, checked by the computer), the colour of this LED changed from orange to red. This indicated that the head had to be kept in the current position. Subsequently, the head-fixation spot was extinguished and a green gaze-fixation spot was presented. Subjects were instructed to foveate this new LED by a gaze shift without a head movement. Thus, by refixating on this gaze-fixation spot, the eyes and head were no longer aligned. In the aligned fixation conditions, the colour of the head-fixation spot simply changed from red to green. Then, after a random period of 800–1600 ms, the gaze-fixation spot extinguished and, simultaneously, a randomly selected peripheral target was presented for 600 ms. During the fast orienting response towards this target, subjects were allowed to move eyes and head. Aligned conditions were tested randomly interleaved with unaligned conditions. Auditory and visual stimuli, however, were presented in separate experimental sessions.

Figure 2 illustrates the target configurations used in the unaligned experiments. Head-fixation spots were presented at $R=20^\circ$ and $\varphi \in [30, 120, 210, 300]^\circ$. In this way potential effects of initial head position could be probed (see Results). In unaligned conditions the eyes were about 34° eccentric in the orbit, with the gaze-fixation spots at $R=20^\circ$ and $\varphi \in [60_{300}, 150_{30}, 240_{120}, 330_{210}]^\circ$, where the subscripts refer to the direction φ of the head-fixation spots. For each of these starting conditions, targets were presented at $R=35^\circ$ and $\varphi \in [0, 90, 180, 270]^\circ$ re straight-ahead. This configuration yielded a variety of initial gaze and head motor errors between 20 and 55° in several directions. A dissociation between craniocentric and oculocentric target coordinates, by means of direction, circumvents the problems involved in the interpretation of head-movement amplitude. In total, there were $n=32$ different conditions, each of which was tested three to five times. After a few practice trials prior to the recording session, all subjects performed well in this task. Only on rare occasions did subjects fail to keep their head fixed when refixating the gaze-fixation spot. Whenever this occurred, the trial was rejected.

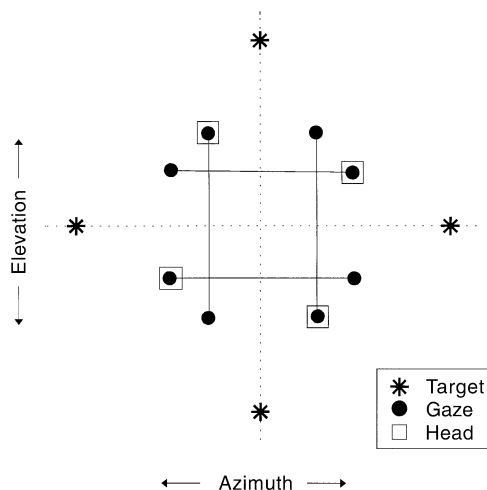


Fig. 2 Target configurations in the unaligned experiments. Initial fixation conditions and target locations applied in the unaligned experiments (drawn to scale, with respect to a spatial coordinate system; see text). Filled dots indicate the gaze-fixation spots ($R=20^\circ$), open squares are head-fixation spots ($R=20^\circ$), and asterisks correspond to auditory or visual target locations ($R=35^\circ$). Corresponding gaze and head-fixation spots used in unaligned fixation conditions are connected by line segments

Data analysis

Saccade detection

Saccades were detected off-line, on the basis of the calibrated signals, by a computer algorithm that applied separate velocity and mean acceleration criteria for saccade onset and offset. Gaze saccades, eye saccades and head saccades were separately detected, using different sets of criteria. Eye saccades were defined as the rapid movements of the eye relative to the head until the estimated onset of the VOR (see, e.g. Fig. 3). In this study, the onset of the VOR was considered to be the instant at which the eye starts counter-rotating in the head or temporarily stabilizes in the orbit (see, however, Lefevre et al. 1992 for a more elaborate, model-based analysis).

All detection markings were visually checked by the experimenter and could be interactively changed, if necessary. This procedure was especially important in the case of head saccades, because the head, being a structure of considerable inertia, could start in a more gradual fashion with sometimes low initial velocities. In all cases, the head-saccadic epochs were therefore judged by the experimenter on the basis of both position and velocity profiles. To gain confidence in the reliability of our detection criteria, a series of head movements ($n=40$) was repeatedly detected, independently, by two experimenters (five times each). This procedure indicated that the uncertainty in head-detection markings, characterized by the mean standard deviation, was restricted to 8 ± 5 ms for head onsets and 17 ± 13 ms for head offsets.

Movement parameters

Several parameters were extracted for each saccade vector (eye, head and gaze saccade): amplitude (R), direction (φ), peak velocity (V_p), mean velocity (V_m), duration (D) and latency re stimulus onset (L). In order to describe spatial and temporal relations between eye and head saccades, additional movement parameters were defined: eye-head latency difference ($\Delta L \equiv L_h - L_e$), relative eye contribution to the total gaze displacement ($C_e \equiv R_e / R_g$) and, similarly, relative head contribution ($C_h \equiv R_h / R_g$). Because C_e and C_h are sensitive to noise for small gaze amplitudes, they were only calculated for $R_g > 5^\circ$. Note that usually $R_e + R_h \neq R_g$, because the eye and head saccades often end at different moments in time (see, e.g. Fig. 3). Thus, in general, $C_e + C_h \neq 1$.

Statistics

Gaze movements with latencies exceeding 400 ms, as well as exceptionally inaccurate movements, were excluded from the analysis. The least-squares criterion was applied to determine the best data-fit in all fit procedures (see Results). The Monte-Carlo bootstrap method was used to estimate the confidence limits of the fit parameters (see, e.g. Press et al. 1992). In this method, one repeatedly performs the regression (e.g. 100 times) on randomly drawn samples (with replacement) of the original data set. The standard deviations are subsequently computed from the resulting set of parameters. In this way, estimates of standard deviations may be obtained without a priori assumptions regarding the underlying probability distributions of the data.

Results

Aligned fixation conditions

In this section we will focus on eye-head coordination during auditory-evoked and visually evoked movements within the oculomotor range which were recorded in the aligned experiments (see Materials and methods). The

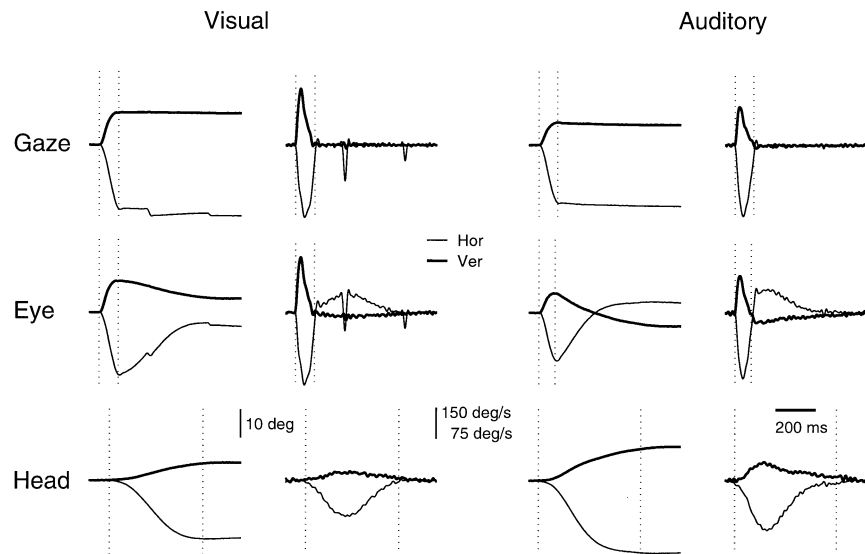


Fig. 3 Saccadic responses. Typical examples of a visually evoked (*left-hand traces*) and an auditory-evoked (*right-hand traces*) oblique gaze shift towards a target at $(R, \phi)=(27,150)^\circ$. Both eye and head were initially aligned with the straight-ahead fixation spot. These plots also illustrate the applied saccade detection criteria. The position (*1st and 3rd column*) and velocity (*2nd and 4th column*) traces are aligned with stimulus onset. Horizontal movement components (*thin traces*) are leftwards and vertical movement components (*bold traces*) are upwards. Saccade onsets and offsets are identified by *dotted lines*. Note the different scale for head velocities. Note also that the head movement of the auditory gaze saccade is larger and starts earlier re eye movement onset than in the visual gaze saccade

aim of these experiments was to determine in what sense the coordination between eye and head depends on target modality.

Response patterns

Figure 3 shows typical examples of a visually evoked and an auditory-evoked coordinated eye-head movement towards the same target location, $(R, \phi)=(27,150)^\circ$. The dotted lines in each subplot indicate the onsets and offsets of the primary saccadic movement epochs (see also Materials and methods). In response to the visual stimulus, gaze is initially displaced by a saccadic eye movement only. After a delay of about 50 ms, a saccadic head movement starts contributing to the movement as well. At the end of the gaze movement, the eye velocity drops and the eye starts to counter-rotate in the orbit at a velocity equal to that of the current head movement, due to the action of the VOR. The onset of the counter-rotation phase was usually quite abrupt, but frequently not synchronized for the horizontal and vertical eye movement components (as in this case).

The pattern of eye-head movements during auditory-evoked and visually evoked gaze saccades was comparable. As illustrated in the right-hand panels of Fig. 3, au-

ditory gaze shifts were also accomplished with a large primary step during which both the eye and head move simultaneously and continuously towards the target. However, the movements displayed in Fig. 3 also illustrate some systematic differences that were found between auditory-evoked and visually evoked responses. First, one may notice that, in the auditory movement, the head onset is less delayed with respect to the eye onset so that the head contributes already to the initial gaze displacement. Second, the amplitude of the auditory head movement is larger than the visual head movement.

Secondary gaze shifts, usually small ones, were frequently observed (e.g. Fig. 3, left-hand columns). These corrective movements consisted of an ocular saccade that was often made while the primary head movement was still continuing for a substantial period of time, after the primary gaze saccade had ended. Occasionally, we observed a slight reacceleration of the ongoing head movement in association with these secondary ocular saccades (not shown). This reacceleration was best observed in auditory-evoked responses, possibly because secondary eye movements, although less frequently present in this condition, tend to be slightly larger. We have not analysed these features in quantitative detail.

In Figure 4, 2-D saccade trajectories of visually evoked (left-hand panel) and auditory-evoked (right-hand panel) primary gaze movements are plotted for a number of different target locations (T). Note that the auditory gaze saccades end quite close to the targets. Comparing auditory and visual head saccades, it can be observed once more that the auditory head saccades tend to be larger, although the gaze saccades in these particular examples are larger too. Furthermore, notice the systematic undershoot of the visual gaze saccades, whereas the auditory gaze shifts are neither systematically hypometric nor hypermetric. Also note that the directions of eye and head saccades are very similar for all target directions.

In summary, the basic pattern of eye-head coordination during auditory-evoked and visually evoked move-

Fig. 4 Saccade trajectories. Two-dimensional saccade trajectories of visually evoked (*left*) and auditory-evoked (*right*) saccades. *Solid, dashed and bold lines* represent the primary gaze, eye and head saccade, respectively. Target locations (*T*) were equal for auditory and visual movements

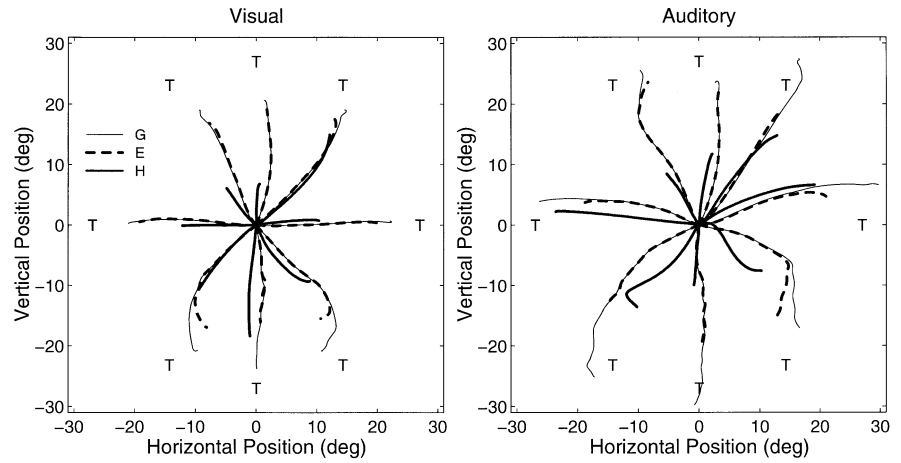
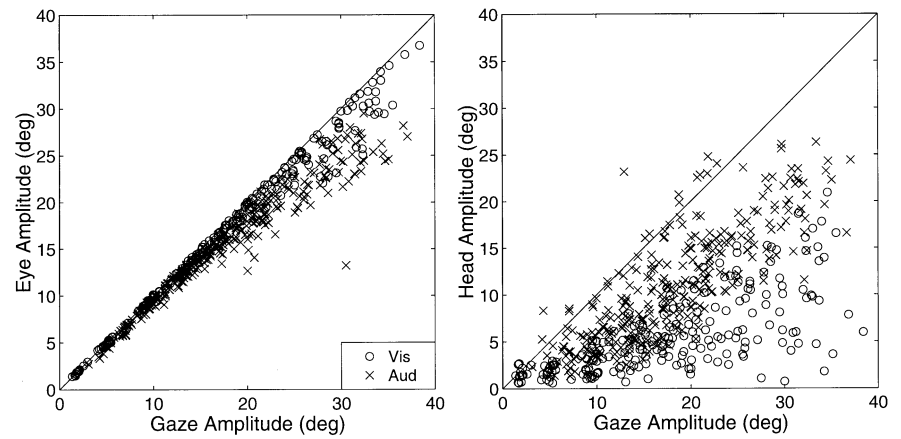


Fig. 5 Eye and head saccade amplitude. *Left* Eye-saccade amplitude as a function of gaze-amplitude for visual (*circles*) and auditory (*crosses*) movements. Note that the eye movements are systematically larger in visual movements (gain: $\alpha_v=0.91\pm 0.01$ vs $\alpha_a=0.75\pm 0.02$; mean \pm SD). *Right* Head-movement amplitude as a function of gaze saccade amplitude for visual and auditory movements. Note that the head saccades are systematically larger in auditory movements (gain: $\alpha_v=0.32\pm 0.03$ vs $\alpha_a=0.66\pm 0.03$). Data from subject N.C., pooled for three experiments and all target locations. See also Table 1



ments is qualitatively comparable, but certain systematic differences do exist. These differences will be quantified below.

Modality dependence

Differences in eye-head contributions. In Fig. 5, the amplitude of both visually evoked (circles) and auditory-evoked (crosses) eye (left-hand panel) and head (right-hand panel) primary saccades are plotted as a function of gaze amplitude. As can be readily observed, there was a distinct difference between the amplitude of visual and auditory head movements. The amplitude gain (slope of the linear regression line) was higher for the auditory-evoked head saccades (see also Table 1). By contrast, the gain for auditory-evoked eye saccades was lower than for visually evoked eye saccades (see also Table 1). Note that this is not trivial, since the saccade-like portion of the eye movement without including the VOR compensatory phase is plotted (see Materials and methods). Also note that there is a substantial amount of variability in the head movements for both stimulus modalities (see also Discussion). For small gaze shifts ($R<15^\circ$) the amplitude of the eye saccade is almost identical to the gaze amplitude, indicating that the gaze shift is predominantly

carried by an eye movement. Nevertheless, head movements were nearly always made, even for these small gaze shifts, as can be observed in Fig. 5, right hand panel.

One may notice in Table 1 that the amplitude gain of head saccades can vary substantially from one subject to another. In particular subject B.B. made large head movements (gain more than 0.70), whereas subject P.H. made relatively small head movements (gain less than 0.20). As is illustrated by the three data sets obtained from subject N.C., the amplitude of head movements can also vary from one experiment to another. In all experiments, however, the amplitude gain was larger ($P<0.001$) for auditory head movements with respect to the visual head movements, except for subject J.G.

Timing differences. Figure 6 (top panels, subject N.C., pooled experiments) shows the relation between the latency of eye and head saccades for visual- (left-hand panel) and auditory-evoked (right-hand panel) movements. It is interesting to see that the latencies of eye and head saccades are less correlated in visually elicited movements than in auditory-evoked responses. Also notice that the slope of the linear regression line for auditory saccades is closer to 1, whereas the slope for visual saccades is much smaller. A slope of 1 would indicate

Table 1 Amplitude gain of eye and head saccades in auditory- and visually evoked primary gaze movements (data pooled for target direction). The listed gains (mean \pm SD) were obtained from a linear regression between the component's amplitude and the gaze amplitude (see Fig. 5). Note, that the gain is always higher ($P<0.001$) for visual eye saccades, as compared to the auditory eye movements. By contrast, the gain for visual head saccades is lower ($P<0.001$, with the exception of subject J.G.) than for auditory head movements. The bottom row shows the mean (\pm SD) gains

Subjects	Eye		Head	
	Visual	Auditory	Visual	Auditory
N.C.	0.95 \pm 0.01	0.83 \pm 0.02	0.18 \pm 0.03	0.62 \pm 0.03
N.C.	0.93 \pm 0.01	0.67 \pm 0.03	0.41 \pm 0.05	0.79 \pm 0.05
N.C.	0.89 \pm 0.02	0.73 \pm 0.01	0.42 \pm 0.04	0.61 \pm 0.04
M.F.	0.83 \pm 0.02	0.63 \pm 0.03	0.46 \pm 0.04	0.60 \pm 0.04
J.G.	0.89 \pm 0.02	0.65 \pm 0.04	0.57 \pm 0.09	0.53 \pm 0.05
B.B.	0.88 \pm 0.02	0.80 \pm 0.03	0.73 \pm 0.05	0.76 \pm 0.06
P.H.	0.92 \pm 0.01	0.81 \pm 0.03	0.14 \pm 0.03	0.19 \pm 0.04
J.O.	0.83 \pm 0.03	0.42 \pm 0.04	0.53 \pm 0.04	0.63 \pm 0.04
mean	0.89 \pm 0.05	0.69 \pm 0.13	0.43 \pm 0.20	0.59 \pm 0.18

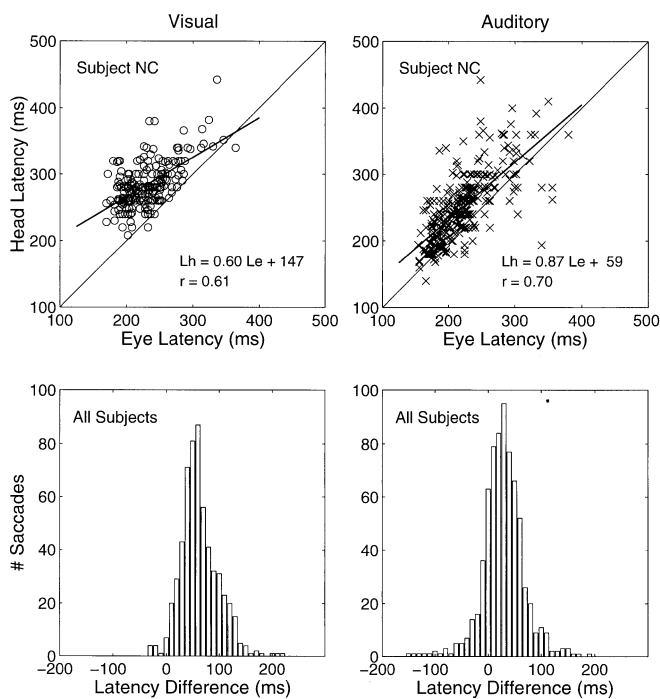


Fig. 6 Eye and head latency. *Top* Head latency against eye latency for visual- (*left*) and auditory-evoked (*right*) movements. Data from subject N.C., pooled for three experiments and all target locations. Note that the correlation coefficient (r) is significantly lower for visual responses ($r_v=0.61$ vs $r_a=0.70$) and that the slope of the regression line is closer to 1 in auditory responses ($\alpha_v=0.60\pm0.06$ vs $\alpha_a=0.87\pm0.07$, mean \pm SD). *Bottom* Histograms of eye-head latency difference (ΔL , positive when the head lags the eye) for visual (*left*) and auditory-evoked (*right*) movements. Data pooled for all subjects and target locations. Note that the head movement tends to come earlier with respect to the eye-saccade onset in auditory-evoked gaze shifts ($\Delta L_v=63 \pm 36$ vs $\Delta L_a=28\pm39$, mean \pm SD) and that the head leads the eye ($\Delta L<0$) much more frequently ($n=119$) than in visually evoked movements ($n=11$). Binwidth 10 ms. See also Table 2

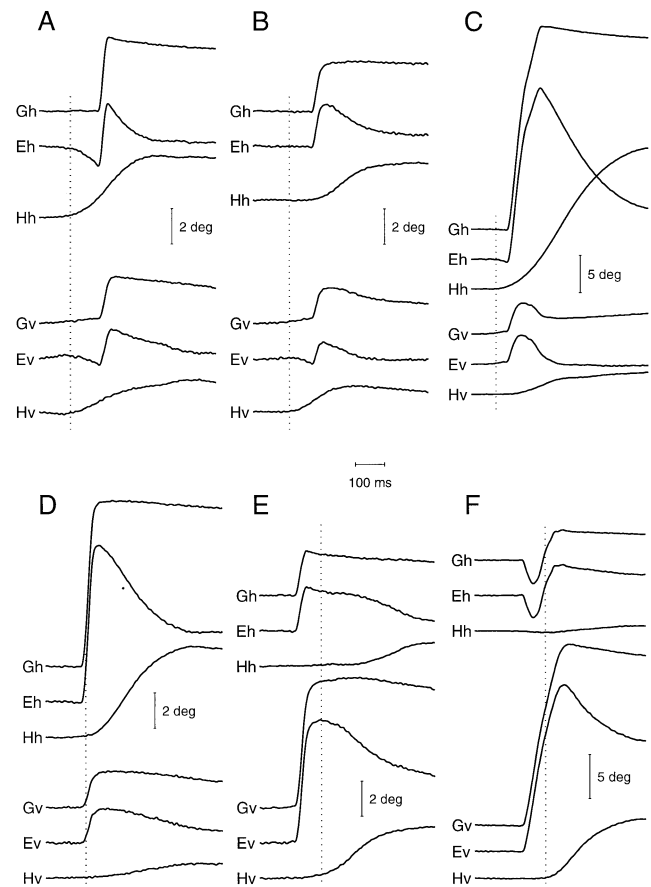


Fig. 7A–F Auditory-evoked responses. Six examples of auditory-evoked gaze shifts with eye-head latency differences spanning the observed range (subject N.C.). Note that even though the head may start slowly, the onset of head motion (*dotted lines*) can be estimated with reasonable accuracy. **A–C** Head onset leads the eye onset. Such long head-lead times were never observed in visually evoked responses. Notice that the eye counter-rotates in the head, prior to the onset of the gaze saccade, indicating an active VOR. **D–F** Head onset is synchronized (**D**) or lags (**E**, **F**) the eye onset. The observation that the head may substantially lead (even for small movements, as in **A** and **B**) as well as lag the eye suggests different saccade initiation mechanisms. For clarity, the sign of the horizontal and/or vertical movement components has been reversed in some of the responses and the traces have been vertically shifted relative to each other. Time scale is identical in all panels

that the head saccade starts at a fixed delay relative to the eye saccade. From Table 2 it can be derived that these timing effects were present in all subjects, except for subject P.H. In this subject the slope was larger for visual movements.

The bottom panels of Fig. 6 show histograms of the eye-head latency difference ($\Delta L=L_h-L_e$, positive when the head lags the eye) during visual- (left-hand panel) and auditory-evoked (right-hand panel) movements (pooled for all subjects). These histograms clearly demonstrate that auditory head saccades tend to come earlier relative to the onset of the eye movement than visual head saccades. Note that in a substantial number of gaze shifts the head leads the eye ($\Delta L<0$). Although much more frequently observed in auditory movements

Table 2 Latency data of visual- and auditory-evoked responses. The first two columns list the latency relative to stimulus onset of eye (L_e) and head (L_h) saccades. The third and fourth column list the slope of the regression lines and correlation coefficient (r) between onset of the eye and head saccade. The last two columns list the eye-head latency difference (ΔL) and the number of responses (n). The bottom row shows the values which were obtained by pooling the data from all experiments. Values are represented as

Ss	Visual						Auditory					
	L_e (ms)	L_h (ms)	Slope	r	ΔL (ms)	n	L_e (ms)	L_h (ms)	Slope	r	ΔL (ms)	n
N.C.	235±38	298±38	0.71±0.10	0.73	54±28	161	234±43	270±46	0.72±0.09	0.67	36±36	155
N.C.	217±42	274±29	0.31±0.12	0.27	56±33	81	217±42	241±48	0.88±0.25	0.64	28±37	82
N.C.	230±30	279±29	0.46±0.07	0.50	50±30	82	204±38	219±45	0.86±0.16	0.69	18±33	84
M.F.	186±39	238±28	0.37±0.10	0.47	57±33	82	192±54	249±69	0.97±0.14	0.77	59±44	77
J.G.	171±28	250±38	0.38±0.13	0.28	79±41	82	195±62	216±50	0.59±0.10	0.73	23±40	78
B.B.	224±39	306±35	0.40±0.08	0.49	80±39	82	244±44	276±51	0.94±0.12	0.74	37±35	80
P.H.	230±36	280±32	0.58±0.11	0.65	53±29	82	155±36	184±28	0.45±0.16	0.54	30±29	80
J.O.	197±19	277±31	0.19±0.21	0.12	77±34	81	213±56	210±51	0.72±0.09	0.80	-4±34	80
mean	212±40	275±37	0.57±0.04	0.59	63±36	734	207±51	236±57	0.82±0.04	0.74	28±39	716

($n=119$), this was occasionally observed in visual movements as well ($n=11$).

Figure 7 shows six examples (Fig. 7A–F; subject N.C.) of auditory-evoked saccades with different eye-head latency differences over a range of amplitudes. The top row (Fig. 7A–C) shows movements in which the head onset (identified by the dotted lines) clearly precedes the eye onset. Note that in these cases the eye initially counter-rotates in the orbit at a velocity equal to that of the head movement. This is indicative for an active VOR, because the fixation spot was no longer present. Examples such as these were not seen in visually evoked responses (see also Fig. 6). Figure 7D–F shows movements where the head onset is synchronized (Fig. 7D) or delayed (Fig. 7E,F) with respect to the eye onset. Such behaviour was most frequently observed, both in auditory-elicited and visually elicited movements (see also Fig. 6).

Table 2 lists latency data for each subject, as well as the pooled results for all subjects. The difference between the eye-head latency difference in the two conditions, on average about 20–30 ms, is quite substantial, since the durations of the recorded gaze saccades were in the range of 50–200 ms (quantitative data in Fig. 8). From the eye and head latency data presented in Table 2, but also from Fig. 6 (top panels), one may infer that the shift in eye-head latency difference is mainly due to shorter head latencies ($P<0.0001$) rather than to longer eye latencies. In all our subjects, the shift in latency difference was highly significant ($P<0.0001$) except for subject M.F., who displayed no significant shift (see Table 2). An extremely large shift in eye-head latency difference (on average 81 ms) was observed for subject J.O.

The frequently observed delay between head onset and eye onset has often been attributed to the fact that the head is a structure of considerable inertia. However, the observation that the head may also lead substantially (even for small movements such as those shown in Fig. 7A,B) suggests different, perhaps modality-depen-

means±SD. Note that in most subjects the slope and correlation coefficient is higher for auditory-evoked gaze movements. Generally, the slope differs from 1, indicating that there is no fixed delay between eye and head onsets. Also notice that the eye-head latency difference is higher ($P<0.0001$, with the exception of subject M.F.) for visual movements, which is mainly due to longer head latencies ($P<0.0001$)

dent, saccade initiation mechanisms for eye and head. Alternatively, one could argue that the observed difference in the timing of eye and head movements may be attributed to a burst signal driving the head with a different gain for the two stimulus conditions. If true, one would expect different kinematic properties of the head movements during auditory and visual conditions.

Kinematics

In Figure 8, the main sequence relations for gaze, eye and head saccades are depicted for visually evoked (circles) and auditory-evoked (crosses) movements (one representative experiment, subject N.C.). These plots illustrate that there were only minor differences in the saccade kinematics under visual and auditory conditions. In auditory-evoked responses, the eye as well as the gaze saccades are slightly slower. Saccade duration is only occasionally longer for auditory-evoked movements. In this particular experiment, the differences were statistically significant ($P<0.01$), but this was not consistent for all experiments.

The main sequence relations for auditory and visual head movements showed no systematic differences. However, they clearly differed from the main sequence relations of the eye (and gaze) saccade. For instance, the amplitude peak-velocity function for eye and gaze movements was well described by an exponential function, whereas a linear fit was more appropriate for the head movements (see also, e.g. Guitton and Volle 1987). Also note that there is a substantial amount of variability in the amplitude duration relationship, indicating that the head movements are less stereotyped, both in auditory-evoked and visually evoked gaze shifts. With respect to horizontal and vertical head-movement components during oblique saccades, we observed that the onsets and offsets of horizontal and vertical components were often synchronized (see qualitative examples in Fig. 3).

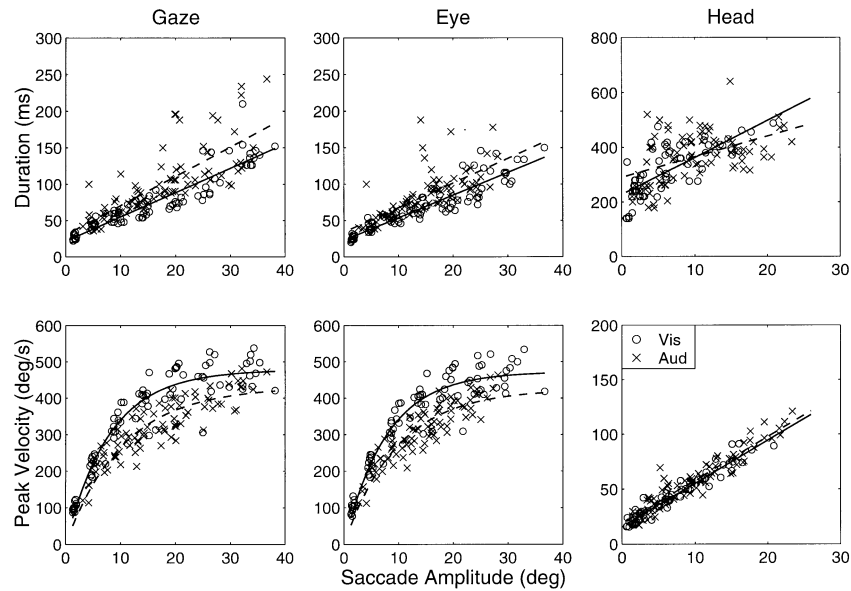


Fig. 8 Saccade kinematics. Duration and peak velocity as a function of amplitude for gaze (*left*), eye (*centre*), and head (*right*) saccades during visual- (*circles, solid fit lines*) and auditory-evoked (*crosses, dashed fit lines*) movements. Notice the differences in scale. Also note that both eye and gaze saccades are only slightly slower under auditory conditions (in complete darkness). However, differences in the kinematics of head movements, which could potentially underlie changes in eye-head timing (see Fig. 6), were not observed. Data from subject N.C. (one experiment), pooled for all movement directions. Fit results:

$$\begin{aligned}
 \text{Gaze: } & \begin{cases} D_v = 3.3R_g + 22 \\ D_a = 4.0R_g + 30 \end{cases} & \begin{cases} V_v = 478(1 - e^{-R_g/8.1}) \\ V_a = 431(1 - e^{-R_g/10.0}) \end{cases} \\
 \text{Eye: } & \begin{cases} D_v = 3.1R_e + 23 \\ D_a = 3.4R_e + 23 \end{cases} & \begin{cases} V_v = 473(1 - e^{-R_e/7.8}) \\ V_a = 425(1 - e^{-R_e/9.8}) \end{cases} \\
 \text{Head: } & \begin{cases} D_v = 13.0R_h + 228 \\ D_a = 7.5R_h + 290 \end{cases} & \begin{cases} V_v = 3.9R_h + 16 \\ V_a = 4.0R_h + 19 \end{cases}
 \end{aligned}$$

Eye-head coupling

In summary, the data described so far suggest a modulation of the eye-head coordination strategy for auditory-evoked and visually evoked responses. Auditory-evoked gaze saccades tended to be endowed with larger head saccades, as well as smaller eye saccades, and the head movement onsets for auditory gaze saccades had shorter latencies than those for visual gaze saccades. Although these findings hint at the possibility of independent, task-related control strategies for eyes and head, they do not yet rule out the hypothesis of a common gaze controller (see Introduction). For example, it is conceivable that only the initiation of eye and head movements is controlled separately for both systems. If guided by a common gaze error signal, it is then expected that the metrics of eye and head will remain coupled, despite uncorrelated differences in initiation. Therefore, in order to investigate further whether eye and head share a common control mechanism, we studied the relative contribution of the eye and head saccades as a function of eye-head latency difference (see Materials and methods for definitions). In

Figure 9, the relative contributions of the eye (Fig. 9A) and head (Fig. 9B) saccades are plotted as a function of the eye-head latency difference for both auditory (crosses) and visual (circles) movements (data pooled for all target positions). As can be observed, the relative contribution of both eye and head saccades is related to the eye-head latency difference. With increasing latency difference the relative contribution of the eye increases as the eye starts earlier with respect to the head. By contrast, the relative contribution of the head decreases with increasing latency difference. Note that the influence of the eye-head latency difference is substantially stronger for the relative contribution of the head (Fig. 9B) than for the eye (Fig. 9A). It was verified that these influences did not emerge from differences in target eccentricity (no correlation between R_t and ΔL , $r = -0.07$, $P > 0.1$).

We observed that the negative correlation between the relative head contribution and eye-head latency difference was consistent throughout all experiments. For most subjects ($n=4$) this correlation was statistically significant ($P < 0.005$, correlation r between -0.26 and -0.64) except for subjects J.G. ($r = -0.06$) and M.F. ($r = -0.08$). Similarly, the positive correlations between the relative eye contribution and eye-head latency difference were statistically significant ($P < 0.0001$, r between 0.39 and 0.64) for all six subjects. In this analysis the auditory and visual data sets were pooled. This seems justified, since the influence of eye-head latency difference is comparable for both conditions, as may be observed in Fig. 9.

Unaligned fixation conditions

So far, we have described the results of experiments in which the eyes and head were always initially aligned. Although there were clear differences between the auditory-evoked and visually evoked movements, a more detailed analysis of the response patterns suggests that

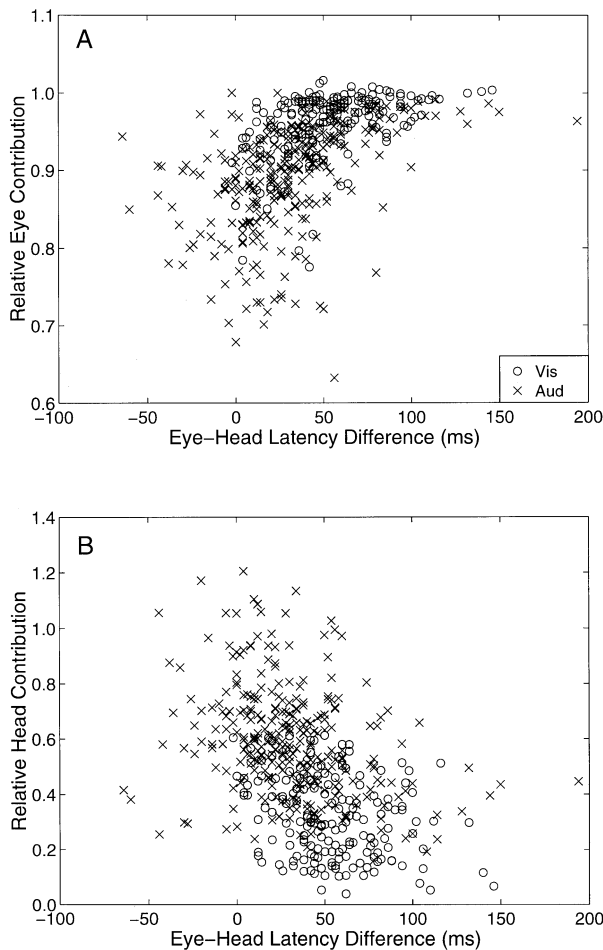


Fig. 9 Eye-head coupling. Relative contributions of the eye (C_e) (A) and head (C_h) (B) as a function of the eye-head latency difference (ΔL). Visual and auditory data are represented by *circles* and *crosses*, respectively. Notice the difference in scale. Pooled data from three experiments with subject N.C. It appears that C_h decreases as a function of ΔL (linear regression, slope $\alpha_h = -2.7 \pm 0.3 \text{ s}^{-1}$, mean \pm SD; pooled auditory and visual data), whereas C_e increases with ΔL ($\alpha_e = 1.0 \pm 0.1 \text{ s}^{-1}$). Note that the influence is similar for auditory and visual conditions

these differences may perhaps not be attributed to an independent control of the eye and head motor systems (see Fig. 9). As explained earlier (see Introduction), it is difficult to assess the driving signals for eye and head motor systems when they are initially aligned, since under these conditions the motor errors for eye and head are identical. In this section we will describe the results of the unaligned experiments (see Materials and methods).

Response patterns

When the eye and head motor systems are driven by the same command, the directions of eye and head saccades should be similar. Under aligned initial conditions this is indeed the case (see Fig. 4). The small differences in movement directions could, at least in principle, be due to differences in the motor plants.

However, when the eyes and head are not initially aligned, single-step gaze shifts can be elicited, during which the eye and head are simultaneously moving in clearly different directions. This is illustrated by Fig. 10, which shows a number of comparable visually evoked (top panels) and auditory-evoked (bottom panels) responses. The left-hand panels in Fig. 10 show the 2-D trajectories of eye, head and gaze movements. One may notice that, apart from different movement directions, neither the initial gaze nor the head movement is aimed straight at the target, but instead follows substantially curved trajectories. Nevertheless, the overall gaze and head movements appear to be goal-directed.

The right-hand panels in Fig. 10 show the horizontal and vertical eye-, head- and gaze-displacement components as a function of time. The vertical displacement signals clearly show that the onset of the head movement preceded the downward-directed eye rotation by about 100 ms. In between head onset and downward eye rotation, the eye is moving in an oblique upward direction, as may be verified from the spatial trajectories, while the direction of head motion is predominantly vertical. Since the upward motion component of the eye cannot be attributed to the VOR (head moves upward too), this indicates that the eye and head are indeed simultaneously moving in different directions during the saccadic response phase of the eye. This was the case in the large majority (more than 80%) of responses for all subjects.

One may also observe in Fig. 10 that the horizontal head velocity, although opposite to the horizontal eye velocity, remains low for the duration of the gaze saccade, as if this head movement component is temporarily suppressed. This behaviour was typical for all movements in which either horizontal or vertical eye and head movement components were oppositely directed.

Although subjects had the subjective impression that their responses were variable, the actual response patterns turned out to be surprisingly reproducible. In this respect, it is also important to compare the auditory-evoked and visually evoked responses. One may notice that these responses are quite similar, despite the fact that under visual conditions the sensory signal for target location (i.e. retinal error) corresponds to the gaze motor error, whereas under auditory conditions this code is related to the head motor error (see Introduction).

Head displacement vectors

Figure 11 shows the head displacement components of visually evoked gaze shifts as a function of horizontal and vertical head motor error (target-re-head, *left*) and gaze motor error (target-re-eye, *centre*). Aligned (*circles*) and unaligned (*crosses*) fixation conditions have been plotted together. It can be readily observed that the head displacement components are highly correlated with the head motor-error components. By contrast, the correlation with gaze motor error is low. Some caution is called for with regard to the interpretation of these plots, be-

Fig. 10 Unaligned eye-head movements. Superimposed examples of visually evoked (*top*) and auditory-evoked (*bottom*) movements, in which the eyes and head were not initially aligned. Data from subject J.G. The *left-hand panels* show the trajectories of eye (*thin trace*), head (*bold trace*) and gaze movements (*dashed trace*). Initial positions of eye, head, and gaze saccades are identified by *Eo*, *Ho* and *Go*, respectively. The *right-hand panels* show the horizontal and vertical displacement components as a function of time. Note that both auditory-evoked and visually evoked responses consist of single-step gaze shifts in which the eye and head move simultaneously in different directions. Also note that the overall gaze and head movements are both goal-directed, although initially neither gaze, nor head movements are aimed straight at the target (*T*)

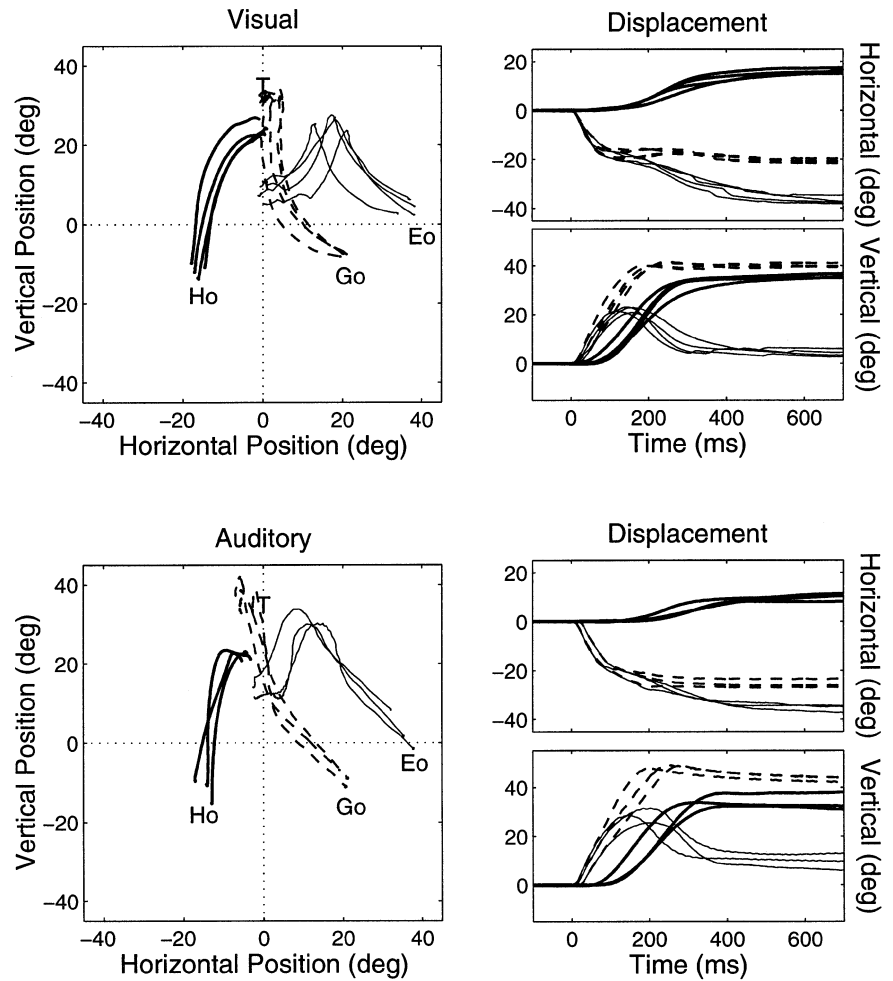
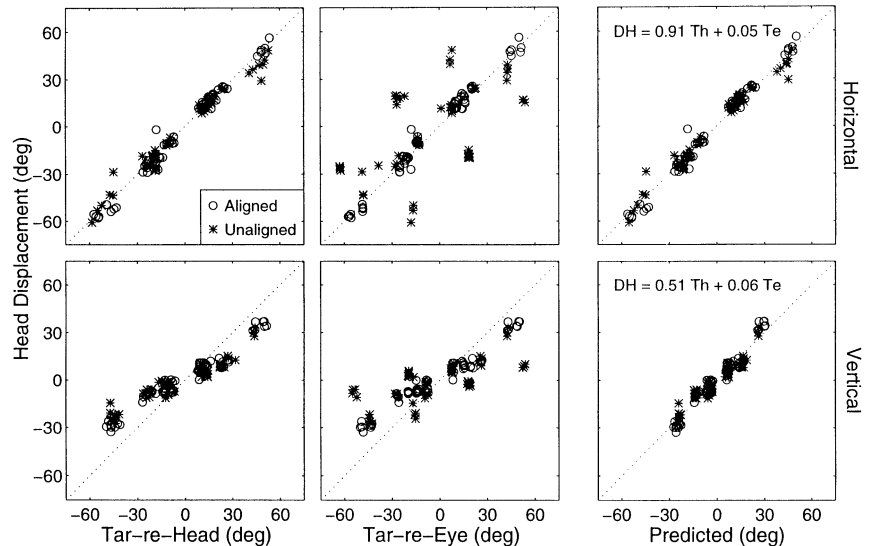


Fig. 11 Head displacement. Horizontal and vertical head-displacement components as a function of horizontal and vertical initial head motor-error (target-re-head, *left*) and gaze motor-error (target-re-eye, *centre*). The panels on the *right* show the results of the multiple linear regression analysis described in the results (Eq. 4). Data from subject B.B., visual responses only. Note that head displacement components are well related to head motor-error (coefficients $a=0.91$ and $d=0.51$) but hardly to gaze motor-error (coefficients $b=0.05$ and $e=0.06$). Also note that with respect to head motor-error, the horizontal gain ($a=0.91$) is substantially larger than the vertical gain ($d=0.51$). See also Table 3



cause the head and gaze motor error components were not entirely uncorrelated (due to the spatial target configurations, see Fig. 2). In order to quantify to what extent the head displacement (ΔH) is related to the initial head motor error (\mathbf{Th}) and the initial gaze motor error (\mathbf{Te}),

we performed a multiple linear regression analysis on the horizontal and vertical displacement components:

$$\begin{aligned} \Delta H_x &= a \cdot Th_x + b \cdot Te_x + c \\ \Delta H_y &= d \cdot Th_y + e \cdot Te_y + f \end{aligned} \quad (4)$$

Table 3 Horizontal and vertical head displacement components as a function of both initial head (**Th**) and gaze motor-error (**Tg**). The listed values are the coefficients a , b , d and e (mean \pm SD) obtained in the multiple regression analysis of Eq. 4. The offsets c and f are not tabulated, since they were always close to zero. The correlation (r) between data and model is listed in each third column. n is

	Subjects	Horizontal			Vertical			
		a	b	r	d	e	r	
Visual	J.G.	0.75 \pm 0.02	0.08 \pm 0.02**	0.98	0.47 \pm 0.03	0.17 \pm 0.03**	0.96	119
	B.B.	0.91 \pm 0.03	0.05 \pm 0.02*	0.98	0.51 \pm 0.03	0.06 \pm 0.03*	0.96	115
	P.H.	0.49 \pm 0.04	0.02 \pm 0.05	0.91	0.27 \pm 0.02	0.00 \pm 0.03	0.85	83
	V.C.	0.56 \pm 0.02	0.01 \pm 0.02	0.96	0.35 \pm 0.02	0.02 \pm 0.02	0.94	116
	M.F.	0.65 \pm 0.04	0.07 \pm 0.05	0.95	0.43 \pm 0.04	0.12 \pm 0.04**	0.95	80
Auditory	J.G.	0.83 \pm 0.02	0.02 \pm 0.02	0.99	0.66 \pm 0.02	0.09 \pm 0.02**	0.98	104
	B.B.	0.92 \pm 0.02	-0.04 \pm 0.02*	0.99	0.53 \pm 0.04	0.06 \pm 0.04	0.94	122
	P.H.	0.56 \pm 0.03	0.00 \pm 0.03	0.96	0.41 \pm 0.03	0.00 \pm 0.03	0.94	124

where the subscripts x and y refer to horizontal and vertical components, respectively. The results of this analysis are illustrated in the right-hand panels of Fig. 11, where the actual horizontal and vertical head displacement is plotted as a function of the corresponding head displacement components predicted by the model fit (Eq. 4). One may observe that there is a good correlation between data and model. In addition, the gains with respect to gaze motor error (b and e in Eq. 4) are small, when compared with the head motor error gains (a and d in Eq. 4). This indicates that head movements are almost completely guided by a command related to head motor error, rather than by gaze motor error.

Table 3 summarizes the results of all experiments. Note that the influence of gaze motor error is insignificant, except for a few cases. In subject J.G., there is a detectable influence of vertical gaze motor error, both for auditory and visual stimuli. It is also of interest to note that the horizontal head motor error gain (a) is systematically larger than the vertical gain (d). In agreement with the results of the aligned experiments, both head motor error gains (a and d) are larger for auditory-evoked movements, when compared with visual saccades.

Movement end-points in space

From Fig. 10 it may be inferred that, also under head-free conditions, the gaze control system takes changes in initial eye position into account when generating an auditory-evoked gaze saccade. This finding is further substantiated in the left-hand panels of Fig. 12. These plots show the final gaze positions (defined as gaze at the end of the head movement) after visually evoked and auditory-evoked gaze shifts for eight different initial fixation conditions, towards the four different target locations (see Materials and methods, and Fig. 2). Observe that, regardless of the initial fixation condition, auditory-evoked gaze shifts remain accurate, although they are endowed with slightly more scatter than visually evoked gaze shifts.

the number of saccades (pooled aligned and unaligned conditions). Note that for all subjects the head displacement depends predominantly on the initial head motor-error (coefficients a and d , $P < 0.0001$) and is hardly related to the initial gaze motor-error (coefficients b and e). Only in a few cases is there some influence of initial gaze motor-error (** $P < 0.001$ and * $P < 0.05$)

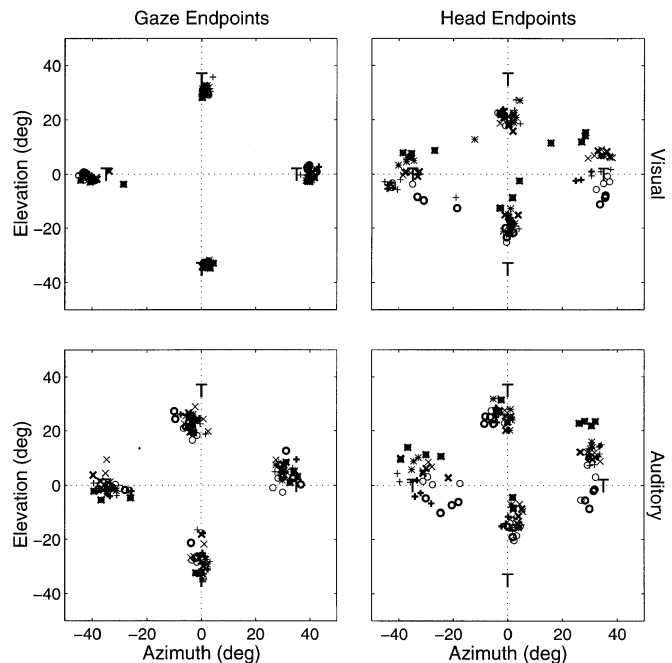


Fig. 12 Final gaze and head positions. Final positions of gaze (*left*) and head (*right*) movements towards four different target locations (T). Auditory and visual responses are depicted in the *top* and *bottom* panels, respectively. Each symbol type indicates a different initial head position, *bold symbols* correspond to unaligned fixation conditions, *thin symbols* to aligned fixations (see also Fig. 2). Note, in the *left-hand panels*, that auditory gaze saccades in the dark remain accurate, regardless of the starting positions of eye and head. Also notice the clustering of the head endpoint data in the *right-hand panels* according to initial head position, indicating that head movements are not directed towards a fixed point in space. Data from subject B.B.

According to the results presented in Figs. 10–12, head movements are goal-directed, regardless of target modality. Note that, in the case of visual stimuli, this property requires that the gaze control system must take eye position into account, since the oculocentric target representation (retinal error) has to be transformed into the appropriate craniocentric head motor error command

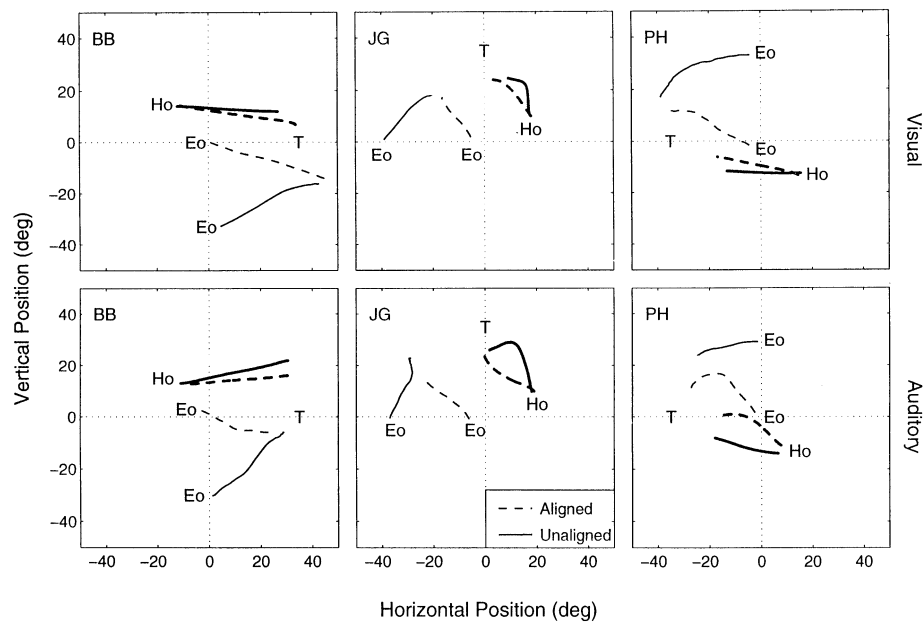


Fig. 13 Oculomotor influence on head trajectories. Comparison between the two-dimensional trajectories of head movements under aligned (*dashed traces*) and unaligned (*solid traces*) fixation conditions. Each panel displays the trajectories of two head saccades (*bold traces*), starting at the same position, as well as the trajectories of the corresponding eye saccades (*thin traces*), which start either at the centre of the orbit or eccentrically. Initial positions of the eye and head are identified by *Eo* and *Ho*, respectively. *T* represents the target location. The *top panels* show data obtained from three subjects under visual conditions and the *bottom panels* show comparable movements for each subject under auditory conditions. Note that when the eye starts eccentrically in the orbit, the (initial) head-movement direction deviates from the direction under aligned fixation conditions. This deviation is typically in the direction of the concomitant eye saccade

(see Introduction). Although the results of Fig. 11 and Table 3 suggest that the head movement is indeed encoded as a (Cartesian) fraction of the initial head motor error (head displacement code), some caution is called for with regard to this interpretation. In principle, the head movement vector could also be specified with respect to the target in space (head end-position code; see Fig. 1).

If head movements are encoded as desired end-points in space, they should end at the same location relative to the target, regardless of initial head position. As is shown in the right-hand panels of Fig. 12, however, this was not the case. Notice that the data are systematically clustered according to initial head position, both for the auditory and visual conditions. This indicates that head movements are rather encoded as a head displacement command.

Head movement trajectories

Despite the fact that the overall head displacement turns out to be poorly related to the gaze motor error (see Fig. 11 and Table 3), we did observe a systematic influence of the initial eye fixation conditions on the head

movement trajectories. This feature is illustrated in Fig. 13 for a number of representative examples obtained from three different subjects, under both auditory and visual conditions. Each of these plots shows the trajectories of two head and corresponding eye saccades towards the same target location in space (*T*), but from different initial eye positions (*Eo*). One may observe that the (initial) head movement direction in the unaligned conditions deviates in a systematic way from the movement direction in the aligned conditions. The effect appears to be in the direction of the concomitant eye displacement vector. This was observed both under auditory and visual conditions, which excludes a sensory-related phenomenon.

Discussion

The purpose of this study was twofold. The first objective was to quantify the differences and similarities of eye-head coordination strategies for gaze saccades towards auditory and visual stimuli. The second objective was to test the predictions of current gaze control models (see Introduction) in 2-D under different sensorimotor conditions.

Modality-dependent coordination

As a result of differences in head movement strategy, the pattern of eye-head coordination was systematically different for visual- and auditory-evoked orienting responses. Mainly due to an overall reduction of head latency in auditory-evoked movements, the eye-head latency differences were shorter in auditory-evoked responses. In addition, the contribution of the eye saccade to the gaze displacement was systematically reduced, whereas the contribution of the head was increased. Note, that the

modality-dependent differences in eye-head coordination strategy are present in a statistical sense, since both response types are endowed with a substantial amount of variability, causing a large degree of overlap.

In this respect, our data are in good agreement with earlier reports in the literature, from which the picture emerges that the relative contributions of eye and head movements are quite variable, both within and across subjects. Moreover, the degree of eye-head coupling may depend on the task, as well as on experimental conditions (e.g. Barnes 1979; review in Fuller 1992; Guitton and Volle 1987; Zangemeister and Stark 1982a,b). These and our findings are consistent with the notion that humans (and non-human primates) have a large oculomotor range ($\pm 45^\circ$), providing a substantial amount of flexibility in response strategies when compared with, e.g. cats ($\pm 20^\circ$).

As noted in the Introduction, however, these apparent differences in movement strategy are not necessarily incompatible with the common drive hypothesis. Also our observation that the relative contributions of the eye and head saccades to the total gaze shift are systematically related to the eye-head latency difference is compatible with the common gaze model. The observed relation, however, was endowed with a substantial amount of noise, suggesting that other factors may also contribute. Indeed, when taking additional movement parameters (mean velocities and amplitudes of eye and head) into account in a multiple linear regression analysis, significantly better predictions for both the eye and head contributions were obtained for all subjects (data not shown). Although these findings indicate a certain degree of eye-head coupling, our unaligned experiments, however, clearly show that the common gaze hypothesis is not tenable.

Different eye and head motor commands

According to the common drive hypothesis, the eye and head are both controlled by the same oculocentric gaze-error command (Galiana and Guitton 1992; Guitton et al. 1990). Thus, both motor systems are expected to move in similar directions throughout the gaze saccade. In the aligned experiments this was indeed observed (Fig. 4). However, the results of the unaligned experiments show that eye and head can also move in quite different directions (Figs. 10, 13), a finding that is incompatible with the common drive hypothesis.

In addition, the data presented in Fig. 12 suggest that the end-points of head movements are not specified in a space- or body-fixed frame of reference. Instead, head movements were best characterized as displacement vectors in a craniocentric frame of reference, regardless of target modality (Fig. 11).

These findings therefore corroborate the results of Volle and Guitton (1993), who tested horizontal gaze shifts in unaligned fixation conditions, but disagree with the findings of Delreux et al. (1991), who let their subjects make sequences of successive eye-head move-

ments. As was briefly mentioned above, the kinematic properties of eye and head movements are both factors that contribute to their relative contributions in the gaze shift. It would therefore be of interest to know whether and how the kinematics of head movements associated with "natural" gaze shifts (Delreux et al. 1991) are different from those associated with "fast" gaze shifts (this study, Volle and Guitton 1993), since, apparently, different head-movement strategies may be involved.

Glenn and Vilis (1992) reported, for very large oblique gaze saccades ($R > 70^\circ$), that the head moves predominantly horizontal and the eye in a more vertical direction. In the aligned experiments, gaze shifts were elicited to targets within the oculomotor range. We noted that the directions of the eye and head movements were very similar (Fig. 4), even though the gains for the horizontal head movement components were found to be slightly higher than the gains for vertical head movements (analysis not shown). The segregation between horizontal and vertical head movement components was more apparent in the unaligned experiments, in which a larger range of amplitudes was employed ($20^\circ < R < 55^\circ$). In these experiments, we obtained consistently different gains with respect to horizontal and vertical head motor-error components (Fig. 11). This difference may relate to the fact that the maximum range for head movement is about 80° horizontal and 50° vertical.

Similar to the findings reported by Tweed et al. (1995), we also observed movements in which the initial motion of neither eyes nor head was directed towards the target. However, the initial deviations of the eye movements were not always in the vertical direction, as reported by Tweed et al. (1995). Instead, deviations in the horizontal direction were observed as well (Fig. 10), depending on the target configuration. It is conceivable that this discrepancy relates to motor constraints imposed by the mechanical properties of the eye and head motor systems, which the gaze control system has to take into account. However, in the Tweed study, it is difficult to distinguish between motor constraints and volitional control strategies, because their subjects made gaze movements upon verbal instructions to known target locations. Using such a paradigm, it is not clear to what extent the movements are guided by a remembered target position, the sensory stimulus, or both.

Despite the fact that the head movement vectors were best described within a Cartesian, craniocentric frame of reference with different gains for horizontal and vertical components (Fig. 11), we did observe clear and consistent influences of the oculomotor system on the head movement trajectories (Fig. 13). In head-restrained humans (Andre-Deshays et al. 1988), monkeys (Lestienne et al. 1984) and cat (Vidal et al. 1982), the tonic level of electromyographic (EMG) activity in dorsal neck muscles has been reported to depend systematically on the position of the eye in the orbit. These EMG data suggest that the head motor system is also influenced by a signal emanating from the oculomotor system. Such an innervation could explain why the (initial) movement

direction of the head typically deviates in the direction of the concomitant eye movement (Fig. 13), but it does not explain why head movements are goal-directed in unaligned fixation conditions. Apparently, the head motor system compensates for the initial direction error, since we frequently obtained substantially curved head movement trajectories that were goal-directed (e.g. Fig. 13, subject J.G.). We consider this finding as an additional indication that the head motor system is, at least partly, controlled by an independent feedback loop.

Neurophysiology

Behavioural (head-free: this study; head-fixed: Frens and Van Opstal 1994; Whittington et al. 1981) as well as neurophysiological data from monkey (Jay and Sparks 1984, 1987) and cat (Hartline et al. 1995; Peck et al. 1995) have shown that the saccadic system incorporates the craniocentric to oculocentric transformation that is required to generate accurate eye movements towards auditory targets in darkness (see Introduction). This process has been shown to be almost complete at the level of the deep layers of the superior colliculus (SC).

Note, however, that our behavioural data indicate that, apparently, the coordinate transformation from an oculocentric visual code into a craniocentric head motor command can be made too. This finding is difficult to interpret in terms of current neurophysiological hypotheses, because so far no evidence for a head-centered target representation feeding into the eye-head premotor system has been reported. Instead, the motor SC has been implicated in the coordination of eye-head movements by sending a common oculocentric gaze-displacement command to both the eye and head motor systems. Indeed, it has been demonstrated that electrical stimulation in the SC of head-free cats (e.g. Roucoux et al. 1980) and monkeys (Cowie and Robinson 1994; Segraves and Goldberg 1992; Freedman et al. 1996) yields coordinated eye-head movements.

In agreement with the hypothesis that the SC encodes a desired gaze displacement, Paré et al. (1994) recently found that stimulation of the cat SC elicits fixed vector gaze shifts when the head is unrestrained, provided that appropriate stimulus parameters are used. When the head is restrained, however, stimulation at caudal sites yields eye movements towards a fixed region in the orbit (see also Roucoux et al. 1980). This region was located near, but not at, the physical limits of the oculomotor range. Similar results have been recently reported for monkeys (Freedman et al. 1996). These neurophysiological data are consistent with behavioural data from the cat (Guitton et al. 1990) and humans (Guitton and Volle 1987) which indicate that the actual command sent to the oculomotor system is neurally limited, rather than that the eye movement is mechanically constrained.

Therefore, Guitton et al. (1990) proposed that the saccadic system limits the dynamic gaze motor-error signal

prior to driving the eye premotor circuits. Alternatively, Phillips et al. (1995) suggested that the oculomotor system is independently driven by a saturated static gaze displacement command. Either way, since the eye may start at different positions in the orbit, the limitation of an oculocentric gaze displacement command does not, in general, prevent the eye from running against the boundaries of the oculomotor range, unless the limits are appropriately adjusted by taking eye position into account as well. Note, that the question of how appropriate limitations have to be set for the eye premotor system is not trivial in 2-D.

A relatively simple solution to this problem would be the assumption that the oculomotor system is controlled by a saturated target-re-head signal. This idea was originally proposed by Volle and Guitton (1987), but abandoned in later studies, because of the lack of evidence for a craniocentric target representation. Whether indeed eye movements are controlled by a target in the head representation or a desired eye displacement signal, is still a matter of debate (see Van Opstal et al. 1995). However, our experiments strongly support the possibility that the head motor system is guided by a head motor-error signal, suggesting that the gaze control system may have access to a craniocentric target representation.

Gaze control model

To put our data in a coherent theoretical framework, Fig. 14 proposes a simple 2-D gaze control model. We adopted the basic outline of the conceptual gaze control schema presented by Guitton and Volle (1987), but introduced a number of changes to accommodate our new findings. For a detailed description of the model the reader is referred to the legend of Fig. 14. Several features of the model are particularly noteworthy.

In the scheme of Guitton and Volle (1987), gaze shifts are specified as a desired gaze position in space (\mathbf{T}_s ; see Fig. 1) and gaze accuracy is maintained by feedback of actual gaze position. By contrast, our schema proposes that a collicular desired *displacement* signal, $\Delta\mathbf{G}_d$, drives the gaze control system, and that the eye and head motor systems share a common gaze displacement feedback signal $\Delta\mathbf{g}$.

To accommodate our finding that head movements are encoded in a craniocentric reference frame, regardless of target modality, we adopted the proposal of Guitton and Volle (1987), that the oculocentric gaze-error signal, \mathbf{m}_g , is converted into a head motor-error signal, \mathbf{m}_h , by adding an efference copy of current eye position, \mathbf{e} . Note, that the gaze and head motor-errors (\mathbf{m}_g and \mathbf{m}_h) are initially identical to the oculocentric and craniocentric target coordinates (\mathbf{T}_e and \mathbf{T}_h ; see Fig. 1), respectively.

Whereas the head-neck system is directly controlled by the dynamic head motor-error, \mathbf{m}_h , this signal is first limited (Sat) before it is fed into the oculomotor system as a desired eye position signal in the orbit, \mathbf{e}_d (see also Guitton and Volle 1987). This prevents the eye from run-

It is important to realize, that in this way the eye and head motor systems are equipped with functionally independent feedback loops that control their own trajectory and kinematics in different frames of reference.

Another important feature of the model is that the initiation of eye and head movements is controlled by separate gating mechanisms. This provides an explanation for the poor time-lock between the eye and head movement onsets and for the observed differences between visual and auditory gaze saccades. A similar modification has been proposed by Ron and Berthoz (1991) to explain dissociated eye and head movements (see Introduction). We speculate that the independent trigger mechanisms may be implemented by different subpopulations of omnipause neurons (Pe and Ph).

Finally, note that the head-saccade generator (**PGh**) also receives a collateral input, (\dot{e}_s), from the oculomotor system. This pathway constitutes a neural coupling between eye and head that accounts for the observed influence of the oculomotor system on the head-neck motor system. As far as we know, little data exist on the nature of this eye-head coupling pathway. In line with an earlier proposal of Galiana and Guitton (1992), we assume that this collateral originates from the output of the oculomotor burst generator (**PGe**).

Preliminary computer simulations with the model indicate that, for unaligned initial conditions, the eye and head movements are both goal-directed, and are in different directions. The eye-head coupling induces curved head trajectories that are qualitatively similar to the ones observed in our data. An example of a simulation with our model is given in the top panels of Fig. 15, for initial fixation conditions similar to those shown in Fig. 10.

The bottom panels of Fig. 15 show the relative eye and head contributions to the gaze saccade as a function of the eye-head latency difference. In our model, the change in head contributions is due to the neural eye-head coupling (\dot{e}_s), which exerts a stronger influence on the head movement at short onset differences. The change in eye contributions is due a combination of two effects that depend on the ongoing head movement: (1) modulation of the eye movement through the action of the VOR; and (2) gaze displacement, being the sum of eye and head movement, is the controlled variable, not eye displacement.

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