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Head movement propensity

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Summary. In studies of human eye-head coordinated saccadic gaze shifts, different laboratories have found greatly different magnitudes of head movements for a given amplitude of gaze shift (head movement gain). The present study was conducted to examine why, and to quantify volitional head movements. Fixation/target lights were located at 20° and 40° on either side of a central light. There were two tasks or modes. In the non-aligned mode, gaze fixation (first light) was followed by a gaze step to the target (second light) accurately and quickly. In the head-aligned mode, the head was aligned within 3° of the first fixation light (i.e., initial starting position) before the step sequence began. In both non-aligned and head-aligned modes, subject instructions pertaining to the second target light concerned only gaze; there was no requisite head position. The head movement propensity of nine subjects was ranked according to the mean gain (head/target amplitude) of two 40° jumps (0–40° and −20 to +20°) in the *non-aligned* mode. This ranking method clearly identified extreme head-movers and non-movers. The moderate movers were further characterized by three additional criteria, derived by comparing the gains in different jumps, which varied in starting position and amplitude. First, when the two 40° jumps were compared, typically the gain of non-movers was less in the symmetric jump (−20 to +20°) with the gain of the head-movers was greater in the symmetric jump. Second, in the *head-aligned* mode the gain of non-movers progressively increased when the starting position was progressively moved eccentrically, whereas the gain of head-movers increased only slightly, if at all. Third, when the gains of two symmetric (40° and 80°) jumps were compared, the head-movers consistently had opposite trends from non-movers. These three comparative criteria and the initial criterion together define head movement propensity. To explain the above observations, three effects are proposed. First, a "midline-attraction" effect causes resistance to movement away from the midline in non-movers and an increase in movement amplitude if the jump starts eccentrically. Second, a "resetting" effect occurs when the eccentricity of the jump is varied; the stopping position is reset closer to the target. Third, an "awareness/arousal" effect increases the gain in the head-aligned mode due to the intrinsic nature of the alignment procedure. Minor physical movement impediments were added to the recording apparatus; these impediments essentially had no effect on head movement gain, and only slightly altered peak head velocity of large movements. Thus, nonphysical variations in eliciting gaze shifts likely determine gain in different laboratories; gain is reliable if measured on a relative scale among similarly tested subjects. Individuals have an innate behavioral propensity to move their head; this may in part reflect the individual's method of constructing stable coordinate systems relating internal to external reference frames, with head-movers initially choosing extrinsic spatial or earth-fixed coordinates and non-movers choosing intrinsic coordinates.

Key words: Head saccadic gain – Head saccades – Gaze – Eye–head coordination – Human

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Introduction

When individuals examine their visual environment with eye–head coordinated saccades, the line of sight, or gaze, is defined by the angle of the visual axis relative to a spatially constant (or earth-fixed) surround. The gaze angle in this case is computed by adding the position of the head in space and the angle of the eye in the head. The latter ocular angle is expressed in orbital coordinates, with the primary position defined as 0° (the horizontal primary position is obtained when a point at infinity, located on the sagittal cranial plane, is fixated; see Jampel and Shi 1992). Recruitment of human horizontal head movements is generally mandatory when the gaze shift demands an ocular orbital eccentricity exceeding 40°. If the gaze saccade can be executed by an eye movement within this ±40° orbital "window", the amplitude of head movement is discretionary, and the extent to which the head is recruited is termed head movement propensity.

The discretionary recruitment of the head in shifting the visual axis is analogous to the movements of the fingers during writing: there is a small window within which the pen can be moved solely by the fingers; beyond that range, the wrist, elbow, or shoulder must be recruited. However, some individuals incorporate wrist movements well before the window is reached, while others move the wrist hardly at all, translating the forearm with elbow and shoulder movements when the limit of finger movement is reached. If finger movements are severely limited, the wrist, and even the elbow, may be recruited for less accurate and efficient translation of the fingers.

Thus within a certain window these two precisely controlled parts, the eyes and the fingers, have a range of movement freedom: their movements can be autonomous, or augmented, or even supplanted, by coordinated movement of the platform upon which they are carried. As with an immobilized wrist, an immobilized head-neck does not prevent execution of many gaze shifts necessary to modern livelihood, such as reading or driving a vehicle, due to the independence and wide range of eye movements. Thus, in normal free-ranging humans there is a wide range of discretion in head recruitment for a given gaze shift, just as there is a normal wide range of wrist movements which may be incorporated in writing.

There is little agreement in the literature on the extent to which individuals recruit head movements in gaze shifts. In some studies (reviewed in Fuller 1992a), head movements are recruited only after ocular orbital eccentricity exceeds 30–40°, while in others the head is recruited for all sizes of gaze shifts, down to 5° or 10°. As stated above, a useful characterization of head movements can be based on a threshold of about 40° of ocular orbital eccentricity for long (more than 1–2 s) fixation periods. (Guitton and Volle, in 1987, found the physical oculomotor range to extend to 50° or 55°, but most subjects find prolonged maintenance of eccentricities beyond 40° unpleasant.) Thus, subthreshold and suprathreshold gaze shifts are relative to a 40° ocular orbital eccentricity. For example, if the eyes are initially at 35° right, a 10° amplitude right (ipsiversive) gaze shift will be suprathreshold, whereas a 70° amplitude left shift will be subthreshold or discretionary.

In a recent study, following the precedent of Afanador and Aitsebaomo (1982), Bard et al. (1992) segregated subjects based on how much they recruited the head in subthreshold gaze shifts. When latencies of head movements were measured for different eccentricities, head-movers and non-movers gave different results, suggesting a significant difference in elementary motor control between the two groups. Therefore it would be useful to have a means of characterizing head movement propensity, both within and beyond the threshold of discretion.

In the present study there were two goals: (1) to define a test paradigm for head movement propensity and to examine how and why head movements are affected by different experimental variables; (2) to address and explain the discrepancies in the literature on discretionary head movements in subthreshold and suprathreshold gaze shifts.

Materials and methods

Subjects

Nine young adults, aged 22–35 years (mean 26 years ± 4 SD) were recruited from among dental students (eight) and postdoctoral fellows (one). All subjects were given a description of the experiment and they signed informed consent forms. They were not paid and none had participated in laboratory experiments before. Nearly all sessions were conducted between 0900 and 1300 hours, with three conducted between 1400 and 1800 hours.

Six subjects were emmetropic, and three were myopic and were their corrective lenses (one with contactlenses, two with spectacles) during the session. The four men averaged 82 kg (72–88) in weight, 178 cm (175–178) in height. The five women averaged 52 kg (44–54) in weight, 160 cm (150–170) in height. All but one subject were preferred or predominantly right handed.

Head holder

Subjects were fitted with a custom-made helmet consisting of two molded acrylic sheets (1–1/2 in. wide × 1/4 in. thick) mated to form a cross. The cross lay on top of the head oriented anteroposteriorly (sagittal member) and laterally (coronal member). The sagittal member was adjustable to fit snugly against the forehead and occiput, and the coronal member straddled the parietotemporal areas to just above the ears. An adjustable headband was attached to each of the four ends of the cross.

The head holder was mainly stabilized by a bite plate; the plate was connected to the coronal member of the cross as follows. Two aluminum rods (1/4 in. diameter) extended from the bottom of the coronal member on each side to the maxillary area and were adjustable in the pitch axis. A third aluminum horizontal rod (3/16 in. diameter) connected the two side rods. The horizontal rod was connected to a mold of the maxillary teeth (occlusal bite plate).

The occlusal bite plate was formed by molding an arc of semicured dental acrylic (methyl methacrylate) to a cast of the subject's teeth or to the teeth themselves. The arc completely enclosed the maxillary teeth back to the second molars. After it was cured, the arc was melded by more acrylic to two small machine screws and then to a 2-in. sleeve, which snugly (0.002 in. tolerance) fit the 3/16-in. horizontal rod. Sliding the horizontal rod through the sleeve thus connected the maxillary teeth to the coronal member of the cross. The completed occlusal bite plate allowed the subjects to swallow, talk, etc. normally and without discomfort. No mandibular force was required to keep it in place. In some exceptional sessions (three subjects, one or two sessions each; see Results, Fig. 7, and Table 1) the horizontal rod had only a bite bar.

When the head holder was in place, a 5 × 1/4 in. dummy rod was placed in a receptacle (a boss with a 1/4 hole and set screw) at the top of the cross. The subject sat in front of an earth-horizontal grid, and, with their head attitude in the Frankfort plane (an earth-horizontal line between the infraorbital ridge and the bony external auditory meatus), the pitch axis of the holder was adjusted until the dummy rod was parallel to the earth-vertical. The receptacle was independently adjustable in the sagittal plane (anterior–posterior, A–P) and was moved until it was plumb with the mastoid process. With the subject maintaining the Frankfort plane, they were asked to move their head 40–60° left and right; eccentric rotation was easily visible against the background grid. The receptacle was adjusted until the dummy rod rotated without translation.

Silver–silver chloride cup electrodes were applied to the skin just lateral to the lateral canthus for electro-oculographic recording of horizontal eye movements. Substantial direct current (DC) stability was realized by vigorously rubbing the conductive gel into the skin immediately before applying the gel-filled cup electrode. The oculogram was coupled to battery-operated FET buffers, the output of which was amplified by DC amplifiers.

Experimental apparatus

The subjects were led into a semidarkened room (2.2 cd/m^2) and seated in a secretarial typing chair mounted on a rotatable platform. The chair was adjusted in height, the back inclined or reclined to suit the subject, and the chair was translated fore–aft to align the dummy rod with the axis of rotation. The head holder was mated to a series of connecting devices that finally mated to a rotary potentiometer (pot), the rotation of which was concentric with the rotation of the entire platform upon which the subject was seated. The head could be rigidly fixed in all axes or freed to move in essentially all planes and axes as described below.

The head holder receptacle was mated by a 1/4-in. stud to a 1 × 4-in.-long aluminum rod. The other end of the rod was coupled to a universal joint, which itself was connected to one or two translatory bellows. Each bellow (part no. T1–10; Pic, Middlebury, Conn., USA) was 3/4 × 1–1/2 in. long, allowing horizontal and vertical translation. The bellows were coupled to a bearing housing and the horizontal pot. The distance between the head holder and the bearings was 24 cm, which by virtue of the universal joint and bellows, allowed translation of the head in the horizontal plane within an 8-cm radius from the center of rotation with negligible horizontal and vertical forces, which were absorbed by the bellows.

Head movements were recorded in degrees (deg) about the vertical axis with a linearity within 0.8% between 0 and ±40° and less than 0.1° hysteresis. A similar pot recorded platform angular rotation. Translation of the head fore–aft (A–P), and side–side (medial–lateral, M–L) was recorded by linear pots coupled just above the head holder by a bearing at the axis of rotation; an 8-cm Delrin rod (1/8 in) coupled the bearing sleeve to a ball-and-socket joint and to the linear pot. This coupling insured that pitch (affecting the A–P translation, APT) and roll (affecting the M–L translation, MLT) movements were minimally hindered and that there was minimal cross-talk between the angular and linear measurements, which had a slight (0.2 mm) hysteresis due to the ball-and-socket joint. Pitch and roll movements were crudely measured by gauges mounted on the head holder.

The subjects were not in an enclosed environment, and the investigator stood silently behind them during sessions. Any changes in posture were noted; if, during the course of the session (usually within the first 30 min), there was consistently more than 3 cm APT, the back of the chair was adjusted a few deg to realign the axis of rotation. Prolonged MLT was corrected simply by moving the subject's back in the chair. In procedures requiring large (more than 40°) head-on-trunk eccentricities, most subjects did not move their shoulders; if they did, they were instructed after the trial-block (see below) to make the movement only with the head, and data from that trial-block were discarded.

The subjects faced a perimeter arc located 114 cm from the axis of rotation and extending 40° to either side of the midline. Nine lights (6-min arc, 5.0-mcd intensity) extending from −40 to +40° were spaced every 10° on the arc.

Definitions

The subject was instructed to look carefully and accurately at a *fixation* light, which after a variable interval (0.6–2.2 s) was extinguished; simultaneously a *target* light was illuminated, at which the subject was instructed to look directly, as quickly and accurately as possible until the light was extinguished (1.4–1.7 s). The single trial of the fixation to target sequence constituted a *jump* or a *step*. A random sequence of 20 jumps constituted a *block* of trials or a block of jumps. A block was conducted in a variety of *modes*, with the head fixed or free; only the latter will be considered here. In any day, a *session* consisted of 20–25 blocks in a variety of modes. Sessions were separated by at least 2 days and lasted 1.5 h (not including preparation time).

In this communication, only 4 of the 20 jumps are of main concern and are shown in Fig. 1C. These *primary jumps* are named for the starting or fixation points: a, 0°; b, 20°; c, 40°. In this report only rightward jumps are considered, and thus the b and c fixation points were at −20° and −40°, as shown in Fig. 1. Every block contained these 4 primary jumps; an additional 11 secondary, or extra, jumps will be considered only briefly. The remaining 5 tertiary jumps will not be considered; they were leftward jumps.

Head movement paradigms. Only two modes are relevant here: first, the *non-aligned* mode had no constraints other than directing the gaze to the fixation and target points quickly and accurately. Second, in the *head-aligned* mode the head was aimed at the fixation light within a ±1.5° window before the jump sequence was begun. In the alignment procedure the fixation light was first dimly illuminated and the subject instructed to move their head toward the light until a tone (from a speaker directly overhead) sounded continuously. The tone was activated when the head movement signal was within the electronically defined window centered on either of the three (0°, 20°, and 40°) fixation points. After the tone had sounded for 2 s, both the tone and the dimmed fixation light were turned off, and 1–1.5 s later the same, but brighter, fixation light came on, signaling the subject that the jump sequence had begun. If the head moved out of the window, the dim light came on again and stayed on until the tone again sounded continuously. However, once the bright light came on, the subject's instructions were not altered from the non-aligned mode, and any mention of head movement associated with the jump sequence was assiduously avoided.

A single session typically included two to three non-aligned and two to three head-aligned blocks. Thus, the data base, in either mode, was three to five sessions for a total of 6–15 data points per subject per jump.

Data analysis

Two measurements are of concern here. Head movement amplitude, or neck angular deviation (NAD), was rounded to 1° for each jump (NAD resolution was 6 min arc) and measured off-line from tape-recorded signals (frequency response of the NAD channel was 100 Hz), interfaced to a modular computer, and reproduced on a pen recorder. Samples of 1.3 s following the jump were adequate for analysis in most subjects and were sampled at a rate of 1 KHz. The NAD signal was differentiated electronically (analog) and the peak velocity rounded to 2°/s. These two signals are shown in Fig. 1A, which illustrates three 40° jumps.

Figure 1B shows four examples of head movement profiles. The first example was seen in 90–100% of all head movements, depending on the subject. In five subjects, 3–10% of the jumps were accompanied by overshoot of the NAD signal (second example). The peak of the overshoot was recorded as the amplitude of the head movement, not the smaller final resting position which shortly followed. In two of these subjects and in one other, the third example was seen in 2–4% of movements: there was an early slowing of the head just after peak velocity had been reached, resulting in an undershoot, followed by a slow slide to the final resting position ["glissade", a term borrowed from oculomotor literature (Bahill et al. 1975)]. Finally, the fourth example shown in Fig. 1B is a combination of under- and overshoot. This was even more rare, occurring in two subjects in fewer than 1% of the movements.

Horizontal eye movement will be only superficially considered. The oculogram gain was adjusted during a variety of voluntary and imposed head movements (see e.g., Fuller 1981 and Fig. 8A, below). In a free head capable of translation and pitch, calibration of the oculogram (without qualification) can be accurate to only a few deg arc. It is well known (Viirre et al. 1986) that *any* angular measurement (by search coils, potentiometers, etc.) must take into account

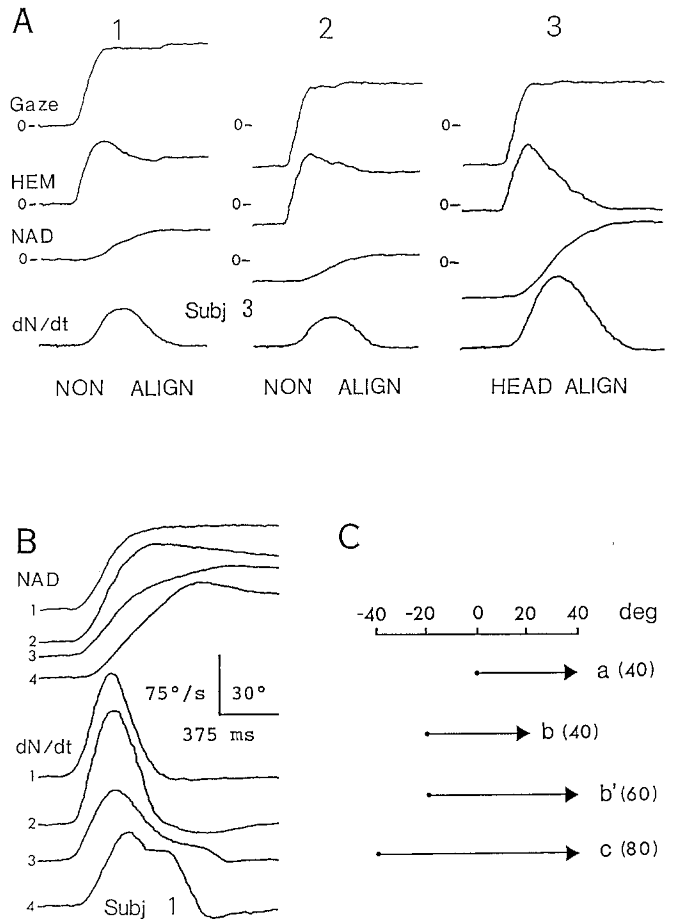

Fig. 1A–C. Execution of target steps. **A** Horizontal eye movements (*HEM*) and head movements (neck angular deviation, *NAD*) were elicited by steps between fixation and target lights located at 0° and +40° (*A1*) or between −20 and +20° (*A2, 3*). The sum of HEM and NAD *(Gaze)* and the first derivative of NAD (head velocity, *dN/dt*) are also shown for each target presentation. Panels *A1* and *A2* are in the non-aligned mode, and *A3* is in the head-aligned mode, in which the subject matched the NAD signal with the fixation point within 3°. All three panels are from subject 3. **B** Four traces of head movements (*NAD*) and head velocity (*dN/dt*) for 40° target steps from subject 1 showing different types of velocity profiles: (*1*) the most common shift, (*2*) overshoot, (*3*) undershoot or "glissade", (*4*) combination of (*2*) and (*3*). Calibration in **B** is for all traces, which begin 50 ms after the fixation to target light jump. *Right* movements are positive and represented by *upward deflections.* **C** Schematic of the four jumps; fixation or starting point at *beginning of arrows,* and target or stopping point at *end of arrows.* At *top* are spatial locations of lights in degrees, while amplitude (in degrees) of each jump is indicated next to the jump designation (*a, b, b', c*)

MLT for the absolute amplitude of gaze shift (and head movement) and APT for the relative amplitude of the shift.

Results

The first part of this section concerns ranking the subjects and provides several indices of head movement performance. The second part concerns how some of these indices reflect normal and experimental variations or alterations in head movement.

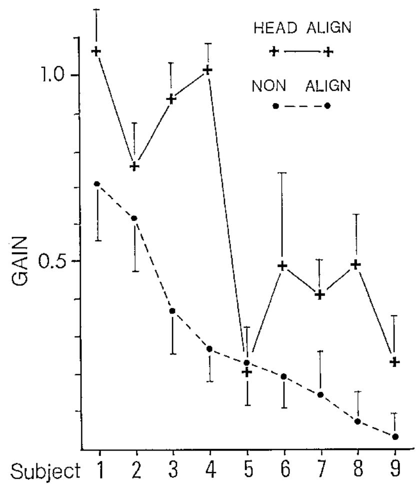

Fig. 2. Subject ranking by head novement amplitude. Lower curve *(broken line)* is the mean gain (head movement amplitude/target amplitude) for two 40° target steps (shown in Fig. 1) for subjects 1–9 *(horizontal axis)*; there was no requirement for alignment (i.e., all non-aligned) of the head. Upper curve *(solid line)* is provided for comparison and is the average gain for the same two steps, but with the head aligned with the fixation point before the step. *Vertical lines* are 1 SD

Head movement characteristics and indices

The subjects were ranked according to head movement amplitude in the non-aligned mode, as shown in Fig. 2 (broken line). They are classified as extreme (1,2) or moderate (3,4) head-movers, or as moderate (5,6,7) or extreme (8,9) non-movers. The non-aligned mode was chosen because it is the more common test mode in the literature. Of the four primary jumps, the two 40° jumps (a and b) represent the most common means of target presentation – originating from the midline or symmetrically crossing the midline. Since this subtle difference yields very different results (see below), the mean of the two jumps expressed as gain (movement amplitude/jump amplitude) was used to rank each subject. This ranking will be used throughout.

While it is clear that the ranking (Fig. 2, non-aligned) distinguishes extremes (1 versus 9), the transition between the rest of the subjects is gradual. Consideration of another criterion – the averaged gain of the same two jumps in the head-aligned mode – aided in the distinction between head-movers and non-movers. With this additional criterion, there is a clear division (Fig. 2, solid lines) between subjects 4 and 5 (Subj 4 and 5), and thus between head-movers and non-movers; note, however, the exact order differs (i.e., subjects would be in a different order if the head-aligned gains were used). In this introductory example it can be seen that any ranking criterion must be supplemented by other criteria (more of which will be described below) and that in any supplementary criterion exceptions are to be expected.

Head movement patterns. In Fig. 3 the gains of each subject are shown in both modes (head-aligned and non-aligned). Only one extreme head-mover (Subj 2) shows closely related patterns in the two modes. In other sub-

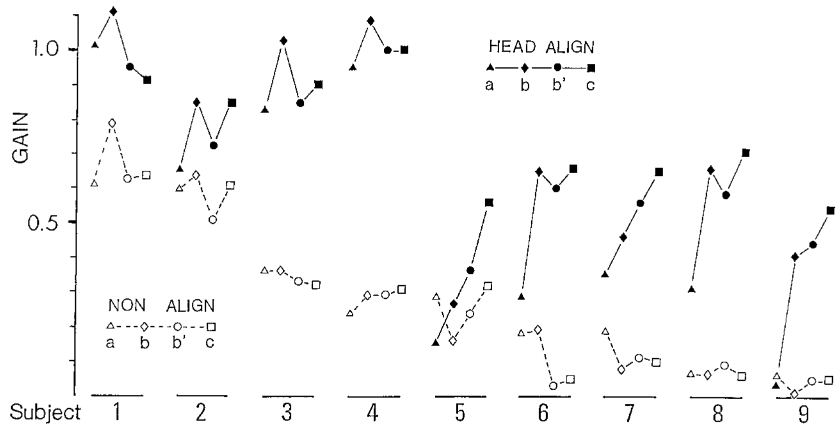

Fig. 3. Comparison of head movement amplitudes. Gain of head movements in each of the four primary target steps for the head-aligned and non-aligned paradigms. Each point is the average of 3–5 sessions (2–3 blocks/session) per subject; subject number is indicated on the *horizontal axis,* as in Fig. 2. The separate primary jumps (and symbols) are: *a (triangles),* from 0 to 40°; *b (diamonds),* from 20 to 20°; *b' (circles),* from 20 to 40° (60° step); *c (squares),* from 40 to 40°. *Filled symbols* connected by *solid lines* denote the head-aligned mode, and *open symbols* connected by *broken lines* denote the non-aligned mode

jects the patterns are dissimilar; for example, in Subj 3 and 4 the head-aligned gains are much higher than the non-aligned, whereas in Subj 5 the two modes are nearly superimposed. Nevertheless, three generalities describe the pertinent patterns. An extended statistical treatment can be found in the Appendix.

First, the gains of the a and b jumps will be considered (in Fig. 2 the means of the two were shown). Comparing the two jumps in just the head-aligned mode (Fig. 3, filled triangles and diamonds), in all nine subjects the b gain is larger than the a gain. Note three of four head-movers actually moved their head beyond the b jump target (gain more than 1.0). The pooled means of all nine subjects were 0.51 for a and 0.73 for b. However, in the non-aligned mode (open symbols), the patterns are different in the two groups: in three of four head-movers, the pattern is the same as before (b is larger), whereas in three of five non-movers, the b gain is smaller than a (and in one of four and two of five, respectively, the gains are essentially the same). Thus in the head-aligned mode, by originating the jump off the midline (b), the gain was always larger than the jump originating from the midline (a) of the same amplitude. Conversely, the non-aligned mode differentiated the majority of the non-movers from head-movers by opposite patterns.

The second generality concerns the three jumps ending at 40°: the a jump starts at 0°, while the b' jump starts eccentrically at 20° and the c jump starts at 40° (see Fig. 1C). Comparing the progressive increase (following the order of a, b', c) in gain of these three jumps in the head-aligned mode reflects the extent to which subjects resist moving their heads off the midline (a), and the fidelity with which they return to it (b', c). Thus, if the gain is over 0.33 for the b' jump and over 0.50 for the c jump (indicating that the head crosses the midline), but is very small for the a jump, the steep progression of gain represents the subject's attraction to the midline. In all non-movers the b' and c gains were over 0.33 and 0.50, respectively; comparing it with the a gain, especially in Subj 6, 8, and 9, the dramatic increase in gain is clear and distinct from the more modest changes in the head-movers. This pattern of progressive increase in gain with eccentric starting positions will be reexamined at the end of this section (see Fig. 5).

The third generality: in the centric–eccentric (a) jump, the head-aligned mode produces larger head movements than in the non-aligned mode in seven of the nine subjects (Subj 5 and 9 are the exceptions). The similarity of results in both groups suggests an effect different from the preceding two generalities.

Normalized velocity. As shown earlier (Fig. 2), the subjects were divided into head-movers and non-movers based on gain. However, diametrically opposite results were obtained when the velocity of head movement was used to rank the subjects.

It is generally agreed (Barnes 1979; Gresty 1974; Guitton and Volle 1987; Zangemeister and Stark 1981; present results, see Fig. 7) that head movement peak velocity is related to amplitude. Therefore, a more meaningful measurement of peak velocity ought to take into account the accompanying amplitude. This is done in Fig. 4: the normalized velocity is the ratio or quotient of peak velocity/amplitude (degrees per second per degree).

In Fig. 4, the order of subjects (abscissa) is essentially random; ranking by any of the four measurements plotted (Fig. 4) bears no resemblance to ranking by gain. Therefore, normalized velocity has no relation to head movement propensity.

Having dispensed with the utility of normalized velocity as a ranking criterion, there are two observations that will be useful later. First, seven of nine subjects have a slightly faster normalized velocity in the non-aligned mode. Second, the two exceptions, Subj 5 and 9, were also exceptional in the abovementioned third generality concerning gain, in which the a jump (40°) was compared in the two modes.

A final observation nicely relates the different velocities to an individual characteristic: while the subjects are listed in order of normalized velocity (abscissa, Fig. 4), they are actually segregated by gender – the first four are men, and the last five are women. As reference to the Materials and methods section (Subjects) will reveal, the men were considerably more robust than the women – hardly a surprising anthropometric observation.

Individual jumps. Changing the focus from subjects to targets and combining the forgoing considerations of

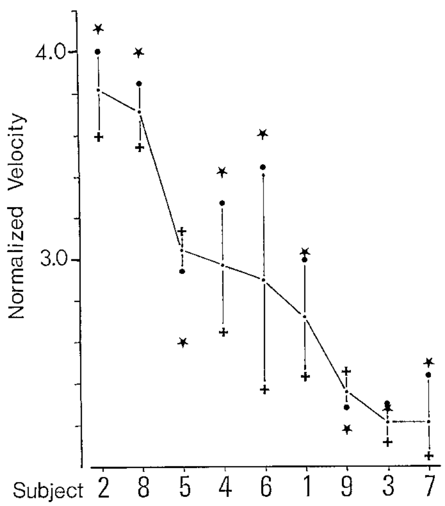

Fig. 4. Relationship of rank to normalized velocity. Subject rank order, assigned in Fig. 2 on the basis of head movement gain, is rearranged on the *abscissa* according to the normalized velocity (peak head velocity/amplitude) on the *ordinate*. Separate averages of head-aligned *(crosses)* and non-aligned *(large dots)* blocks are connected to the combined means *(small dots)* by *vertical lines*. Average of a and b non-aligned movements – used in the original ranking (Fig. 2) – is shown by *stars*. The first four subjects (2, 8, 5, and 4) were men and the remaining five were women. Unlike the measurements of gain, in which the head-movers (1–4) and non-movers (5–9) were always separated, in the normalized velocity the two groups were intermixed. Ordinate units are degrees per second per degree

amplitude and velocity, Fig. 5 shows the mean of all data for each of the four primary targets. In the head-aligned mode the centric–eccentric (a) jump had the lowest gain (Fig. 5A); there was relatively little difference between the other three jumps, or between any of the jumps in the non-aligned mode. Rearranging the order of the head-aligned jumps and plotting each subject separately clearly distinguishes head-movers from non-movers (this pattern was partially described earlier in the second generality regarding gains).

In Fig. 5A (A2), the horizontal axis shows the a, b', and c jumps (amplitudes of 40°, 60°, and 80°, respectively) which start from a progressively more eccentric position, but end at the same point (40° on the side opposite). It also shows the c, b pattern, two symmetric jumps differing in amplitude (80° versus 40°). The first pattern (a, b', c) shows a steep progression of gains in all non-movers as the starting position is moved eccentrically, whereas this pattern is much attenuated in head-movers (easily seen in the averaged large symbols for each group). (It is noted that the steep progression is magnified in non-movers in this analysis; this will be covered in a later publication, in preparation, on auditory responses.) The second pattern (c, b) shows opposite trends in head-movers and non-movers. Data for both patterns are consistent with the first and second generalities covered earlier (see Head movement patterns and Fig. 3): movement of the head eccentrically increases the gain in non-movers and distinguishes them from head-movers (Fig. 5A (A2)). Finally, note that the transition between movers (Subj 4) and non-movers (Subj 5) is marked and clear in this presentation. Thus, as stated on several occasions, more than one criterion is required to characterize head movement propensity.

The non-aligned normalized velocity was slightly faster than the head-aligned mode in seven of nine subjects; Fig. 5B reflects this tendency, but as the large SD suggests, the trend is not consistent. However, the differences between the two modes is accentuated if the two exceptional subjects are removed (Subj 5 and 9, Fig. 4) and if only symmetrical jumps (b and c) are compared, eliminating midline effects. In this case the pooled mean head-aligned velocity is 2.51°/s per deg and for non-aligned velocity is 3.18°/s per deg, a 24% difference, or nearly 2 SDs.

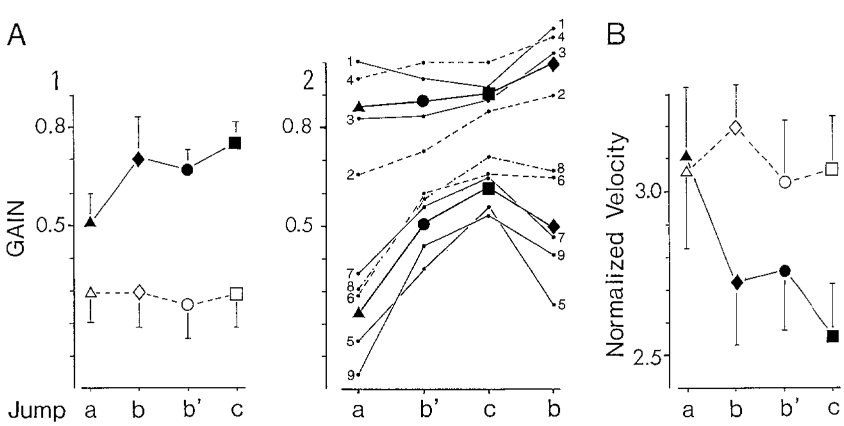

Fig. 5A, B. Head movement amplitude and velocity for each target step. **A** Gain of head movement for all subjects. *A1*, mean gain in each of the four primary jumps, *a*, *b*, *b'*, and *c* (see Fig. 1C). Head aligned *(filled symbols)* and non-aligned *(open symbols)* as in Fig. 3. *A2*, mean gain (head-aligned only) of head-movers *(1–4)* and non-movers *(5–9)*; jumps are rearranged to show progressive increase in gain in non-movers as fixation point was moved eccentrically (*a*, *b'*, *c*), and to show differing patterns between the head-movers and non-movers for the large and small symmetric jumps (*c* and *b*). Standard *large symbols* represent average gains, while each individual subject's data are represented by *dots* connected by *thin solid or broken lines*. **B** Normalized head velocity (peak head velocity/amplitude) shown for the same four primary steps for all subjects. Symbols are as in *A1*. *Vertical lines*, 1.0 SD (**A**), 0.5 SD (**B**)

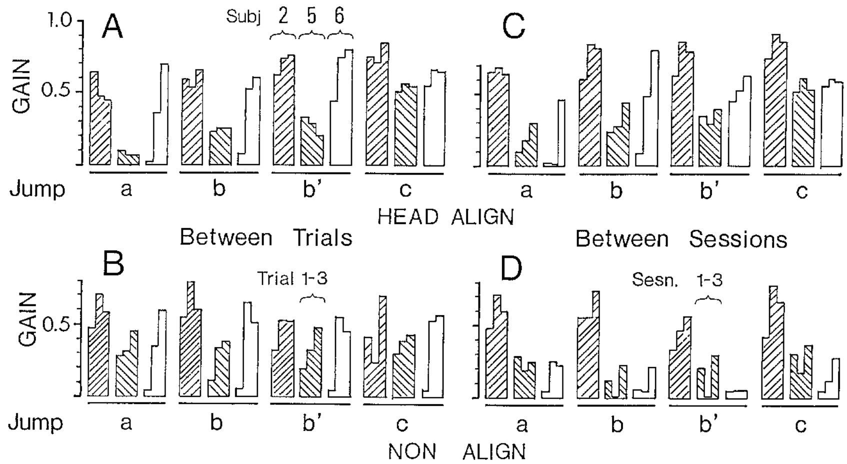

Fig. 6A–D. Gain changes with experience. Each *narrow bar* represents a single movement. Data from two representative subjects *(Subj 2, 5; crosshatched bars)* and one exceptional subject *(6; clear bars)*. Gains are shown for each jump *(a, b, b', c)* from the first, second, and third trial block *(Trial 1–3)* in the first session (**A, B**), or for the same jumps from the first trial block of three successive sessions (*Sesn. 1–3;* **C, D**). Gains for each subject are shown in the head-aligned (**A, C**) and non-aligned (**B, D**) modes

Alterations of head movement

The remainder of this section concerns the alteration of head movements by physical impediments. Since these impediments lasted a full session, it is necessary to demonstrate that head movement gain does not change across sessions due to experience from repeated exposures. Thus, the effect of repeated exposures will be addressed first; next, the effects of intentionally introduced physical impediments to head movement will be presented.

Dependence of gain on experience. In six of the subjects all sessions were identical. Figure 6 shows the data of two subjects (Subj 2 and 5) representative of five subjects; it also shows a single unrepresentative subject (Subj 6) who changed gain with experience. Data from these three subjects will be compared and contrasted.

Each of the single movement gains in Fig. 6 is from an identical period in each of the subjects' experience: the same movement/jump of the first three blocks of the first session is shown in Fig. 6A, B. For changes between sessions, only the first trial (i.e., from the first block) of each session is considered (Fig. 6C, D).

In only one panel was there a suggestion in all six subjects of an increase in gain with experience: in Fig. 6B (non-aligned mode gains compared within the same session) there was typically an increase in gain from the first to second block and, occasionally, a further increase in the third block. Thus, in the non-aligned mode there may be a "warm-up" required; the changes between the second and third trial were less consistent.

There was no such warm-up evidenced in the head-aligned mode (Fig. 6A) in any of the five subjects, even if the first block was the very first head-free event of the session. However, Subj 6 showed a dramatic increase in some jumps.

Gain changes between sessions in the head-aligned mode (Fig. 6C) weakly suggested an effect of experience, again with Subj 6 showing the largest changes. Experience did not affect gain in the non-aligned mode between sessions (Fig. 6D), even in Subj 6. When a similar analysis of normalized velocity was undertaken (in the same four comparisons), there was also no evidence of a consistent effect of experience.

Restrictions to head movement. Having now advanced the notion that there is little consistent change between sessions in all but one subject, the issue of movement restriction is addressed. Three subjects (3, 7, and 8) were tested with different physical arrangements of the apparatus; the data from Subj 3 is presented in detail and is representative. In Fig. 7 the four primary jumps (shown with different symbols) from four consecutive sessions are supplemented by 11 extra (x) jumps. The x jumps are: 10°, 20°, and 30°a, b and c jumps, respectively, one 40° c jump, and one 60° c jump. In the first session (Sesn 1) a bite bar was used (see Materials and methods, Head holder), and the amount of translation possible was reduced to one half of normal by removing one of the two bellows.

The results of movement encumbrances are clear (Fig. 7, Sesn 1): all movements beyond 30° are slowed, and movements between 20 and 30° show a progressive slowing. The four largest movements represent a mean of 66° and are a mean of 41°/s below (slower than) control values (Sesn 3 and 4), or 0.62°/s per deg below 2.14°/s per deg (slope of the reference lines in Fig. 7).

In Sesn 2 (Fig. 7) the bite plate and translatory freedom were standard. The result is clear for movements between 30 and 60°, all of which are scattered around the reference line. However, the two largest movements (70° amplitude, filled squares) are still 20°/s below the reference line. In Sesns 3–4 the chair position was optimal, while in Sesns 1–2 the chair was 2.5 cm behind this position. With the chair in the optimal position the largest movements (filled squares) are closer to the reference line in Sesns 3, 4 than in Sesn 2. It is suggested that the two large jumps in Sesn 2 were affected by the very minor maladjustment in the subject's preferred position (similar results were seen in Subj 7 and 8). As reference to the individual primary jumps in Fig. 7 will confirm, there was no consistent effect on amplitude, and therefore gain, in any of the sessions.

Table 1 lists data from a similar treatment of Subj 8. The same data base was used: 4 primary jumps and 11

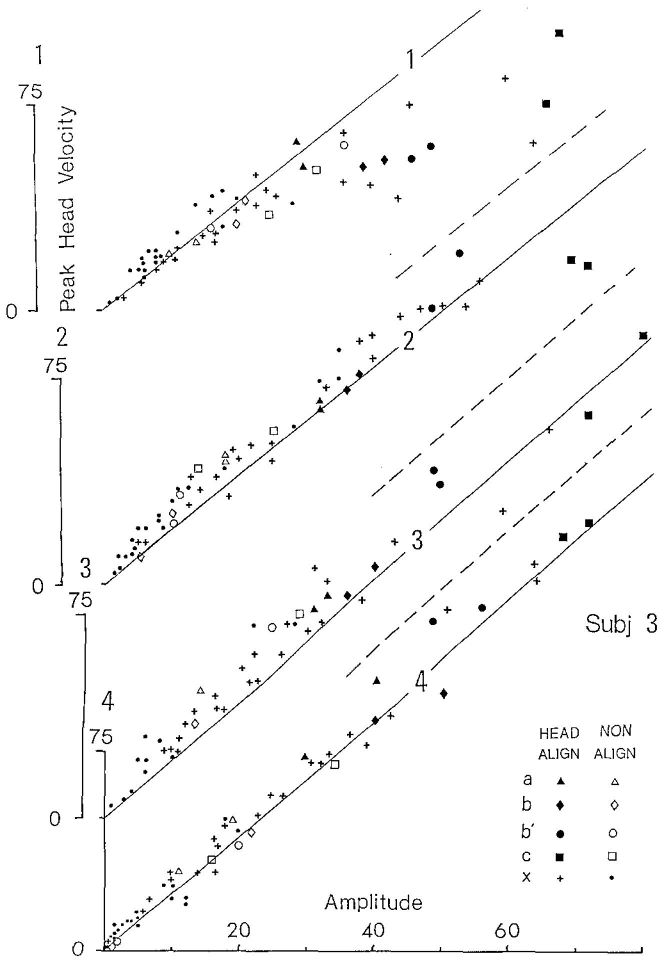

Fig. 7. Effects of restraint on movement profile. Data from four sessions in one subject (subject 3) with freedom of movement increased progressively. In session (Sesn) 1 *(top plot)*, the subject's head was coupled to the apparatus by a bite bar and one translatory bellow. In Sesn 2, the subject wore an occlusal bite plate, and a second bellow was added to the shaft. In Sesns 3 and 4 the chair was translated 2.5 cm foward and the back reclined (backward) to recenter the head beneath the potentiometer. Each data set includes two head-aligned and two non-aligned blocks, with the exception of Sesn 3, which includes only one non-aligned block. The four primary jumps of each block are plotted with a different symbol shown in the *inset* and are the same as those used in previous figures. Eleven additional points per block (extra, *x* in the inset) are represented by *crosses* (head-aligned) and *dots* (non-aligned). The *solid reference lines* are the same for each Sesn and represent a slope of 2.14°/s per degree, with an intercept of 0; the *broken lines* separate the data points of each session. Amplitude *(abscissa)* is in degrees and each of the four vertical axes is in degrees per second

secondary jumps per block, and 4 blocks per session ($n = 60$). In this case the changes were made in three steps, allowing the comparison between the bite bar and plate to be separate from the reduction of translation. The effect of the bite bar was to increase the number of jumps with no head movement (42% versus 28%). Addition of a second bellow (doubling translation freedom) increased the proportion of large amplitude jumps (from 3–8% to 14–17%).

Table 1. Percentage distribution of head movement amplitudes in subject 8

Procedure	Session	Amplitude of movements			
		0°	1–10°	10–30°	30–60°
Bite-bar	1	42	26	24	8
Occlusal plate	2	28	42	27	3
2 bellows	3	28	33	25	14
2 bellows	4	30	32	21	17

Total number of head movements ($n = 60$/session) in each session were placed in bins of four amplitudes (0° = no head movement) in three different conditions of movements: (1) in session 1 a bite-bar was used; (2) in sessions 2–4 an occlusal plate was used; (3) in sessions 1 and 2 only one bellow was used, whereas two were used in sessions 3 and 4

Limits of eccentricities. The possibility of physical impediment to eccentric NADs was examined in another way. In Fig. 8A Subj 9 continuously fixated the central light; as always, the instructions were only to maintain fixation, with no reference to head movements. The platform was rotated with increasing amplitude until the subject was finally producing 80° (peak to peak) oscillatory head movements. This is 10 times the amplitude the subject produced in the non-aligned c jump (Fig. 8B), and, relative to how much the subject crossed the midline in the head-aligned c jump, almost 10 times that amplitude (Fig. 8C). This lays to rest any notion that non-movers do not (or cannot) ever voluntarily move their heads to the same eccentricities seen in head-movers. (There was no correspondence between rank and the extent of head-in-space stabilization: Subj 2, 3, and 5–7, executed this task with gains of less than 0.3, and in platform rotations of less than 80°, performed the fixation almost entirely by eye movements; on the other hand, Subj 1, 4, 8, and 9, had gains of 0.5 or more, and as shown, the fixation was performed with combined eye and head oscillations, regardless of amplitudes.)

The NAD trace (Fig. 8A) is flattened at the peak of rotation, which again might suggest some impediment at extreme eccentricities. Note, however, that it is also flattened at smaller amplitudes. This characteristic was seen in all subjects (1, 4, 8, 9) who had sufficient NAD modulation to describe a sinusoidal pattern; at most it accounted for 70% of the cycles, more typically for about 50% or less.

It is possible that "non-movers" are translating the head; in this case the flattened NAD signal would be a harbinger. Translation MLT, APT will not only shift the gaze in a way not recorded by the NAD signal (M–L or side-to-side translation) but also alter the amplitude of angular movement necessary to complete the shift (A–P or fore–aft translation). (A geometric consideration can be found in Viirre et al. 1986.) This is partially so: the minute oscillations in the "Gaze" signal (Fig. 8A) confirm the proper contribution of the small MLT (0.8 cm) and APT (0.7 cm) movements; however, they are insufficient to account for the NAD signal flattening.

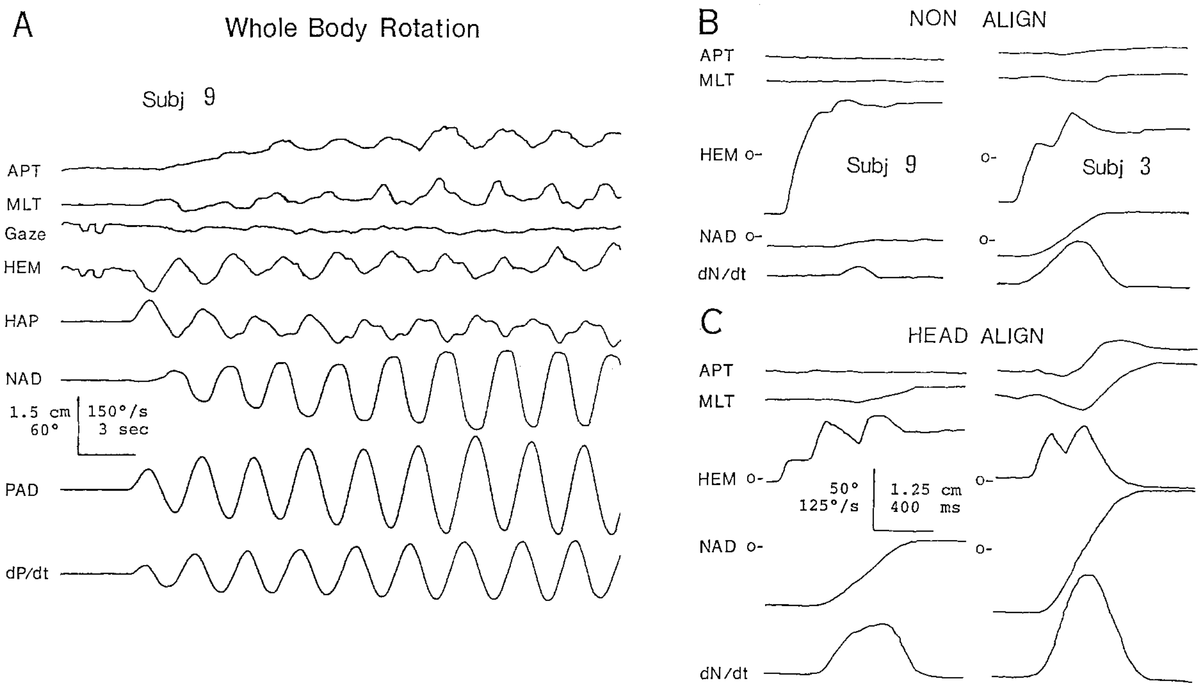

Fig. 8A–C. Head mobility in two paradigms. Head movement in subject 9 *(Subj 9)*, an extreme non-mover, is shown during whole-body rotation (**A**) while fixating a central light and compared with the standard non-aligned (**B**) an head-aligned (**C**) jumps. For comparison, data from subject 3 (*Subj 3;* a head-mover) is provided for identical jumps. **A** The platform was manually rotated at 0.32–0.36 Hz through angular deviations (*PAD*) up to 110°, resulting in head-on-trunk movements (*NAD*) of from one-half to three-fourths of PAD amplitude (i.e., gains of 0.50–0.75) for a maximum of 80° NAD amplitude. Head position in space (*HAP*), or "head gaze", is the difference between PAD and NAD; this is the amount by which the eyes must move in the head (*HEM*) to achieve stability in space (*Gaze*; sum of HAP and HEM). The flattened appearance of the NAD peak position, which is in part explained by periodic translation of the head (*APT* and *MLT*), is not reflected in the PAD velocity trace (*dP/dt*). **B** Same subject during the c jump task (80° symmetric step) in the non-aligned mode: the gaze shift was largely completed by eye movement; the head moved from −5 to 0°. In contrast, the head-mover *(right)* made a 28° head movement (−10–+18°) in the same task. **C** In the head-aligned mode Subj 9 moved their head from −39 to +5°, while Subj 3 executed an 82° head movement. Calibration in **A** applies to all traces in **A**, while calibration in **C** applies to **B** as well. Traces in **B** and **C** begin 100 ms after the target jump. Abbreviations (and conventions): *APT*, anterior–posterior translation (anterior movements are *upward deflections*); *MLT*, medial–lateral translation (*rightward* is positive); *Gaze* (position of the eyes relative to space; *right* is positive); *HEM*, horizontal eye movement (position of the eyes relative to the head); *HAP*, head angular position; *NAD*, neck angular deviation (head relative to trunk); *dP/dt*, platform angular deviation (*PAD*) velocity; *dN/dt*, *NAD* velocity

There is also relatively little translation during the jump modes. In fact all subjects, movers and non-movers alike, do incorporate translation in large gaze shifts; and the amount of the translation, regardless of rank, is proportional to rotational amplitude, as shown in Fig. 8B, C. The same subject (9) is shown in a jump task and compared with Subj 3. In both cases the translation is insignificant. Since Subj 9 does not reach anywhere near the eccentricities seen in whole body rotation (Fig. 8A), there is no physical basis for the low head saccadic gain in the 80° (c) jump. Therefore, non-movers simply rotate their heads less in gaze shifts.

Discussion

In most tests concerning head movement a constant starting position is used; or in other cases if the starting position is varied, only the amplitude of the jump is considered (see Fuller 1992a). In contrast, in the present test, the starting (fixation) position is given as much consideration as the amplitude and stopping (target) position. Thus, of the four jumps (and the gaze steps they evoked) studied, three ended with a constant target position at 40°, whereas the fixation point varied from 0° (sagittal plane, or straight ahead) to 20° or 40° on the opposite side; the jumps were 40°, 60°, and 80° in amplitude, respectively. On the other hand the fourth jump was symmetrical, starting and ending 20° on opposite sides of the midline; this can be compared with the equal-amplitude 0–40° jump, and with the 80° symmetrical jump. With these four jumps it was shown that both starting and stopping positions of the jumps can dramatically affect the extent to which the head participates in the gaze shift.

Another factor that influences head movement amplitude is the position of the eyes in the head (ocular orbital eccentricity) at the time of the gaze step. The threshold for eliciting mandatory head movements has been operationally defined (Introduction) as any gaze shift that takes the eyes beyond 40° (eye-in-head, or ocular-orbital eccentricity). Gaze shifts requiring less than 40° would be subthreshold for mandatory head recruitment, and those greater than 40°, suprathreshold.

Thus, in the present study if there were no requirement for head-alignment, a subject could position their head close to the midline and execute all jumps, including the 80° jump, by eye movements alone. Moving their heads slightly toward the fixation position in either the 60° or 80° jump would convert it to a suprathreshold jump.

Many of the jumps employed in the present study were designed to require exactly 40° of ocular eccentricity; as such, these jumps would elicit juxtathreshold gaze shifts (i.e., they bordered between discretionary, subthreshold, and mandatory, suprathreshold, shifts). By manipulating the starting position within the spatial ±40° window, and/or by requiring head alignment to control ocular eccentricity, the head movement threshold could be systematically varied. In two of four head-aligned jumps the gaze shift was suprathreshold, requiring a 60° or 80° gaze step: with the head and the fixation point aligned, and with the eyes therefore centric in the orbit, the subjects had to move their heads. Conversely, in the two 40° jumps, depending on the mode, the gaze step could be subthreshold (e.g., the symmetrical jump in the non-aligned mode) or juxtathreshold.

Based initially on the average gain of two non-aligned jumps, the behavior of the nine subjects distinguished an index of head movement propensity based on their mover/non-mover rank. This initial criterion was chosen because it is the most common mode (non-aligned) and because midline-eccentric jumps are contrasted with symmetrical jumps, each 40° in amplitude. Several other observations and generalities were offered to distinguish further the behavior of subjects in both the non-aligned and head-aligned modes. It is emphasized that, taken alone, the initial criterion (Fig. 2) is absolute only in distinguishing extreme head-movers from non-movers; it does not provide a priori the exact order within each group. Similarly, not all subjects obey each criterion used to distinguish head-movers from non-movers. Finally, it is emphasized that this study is not a population study (and therefore an absolute gain is not diagnostic of propensity in the general population); it is intended to show why these nine subjects chose to execute gaze shifts with or without head movements.

Three effects on head movement amplitude

In all subjects there is a "midline-attraction" effect described by the first and second generalities in Results (Head movement patterns). When the head is moved off the midline, and the gaze is stepped to the opposite side, there is a high certainty that the head will be moved ipsiversively, unlike when the jump is initiated with the head on the midline or centric position. In fact, the head position of all subjects ended closer to the target when the jump eccentricity was varied: the pooled mean gain for the a jump was 0.51 (or a stopping position of 19.6° from the target) compared with 0.73 for the b jump (or 10.8° from the target). This suggests a "resetting" of the end position. This second effect can be thought of as a "momentum" effect, in which the head is carried closer to targets.

These two effects – midline attraction and resetting – can have opposite influences on gain in head-movers and non-movers. For example, contrasting the two 40° jumps in the *non-aligned* mode (first generality) segregated the subjects for inverse reasons: in head-movers the 40° symmetric shift will evoke juxtathreshold movements; the gains were higher than the centric–eccentric jump in three of four subjects, augmented by the above two effects. However, in non-movers the symmetric shift is subthreshold, due to their maintenance of head position close to the midline (midline attraction) and the gain was lower in three of five subjects, while the centric–eccentric shift is juxtathreshold, forcing the non-movers to enter the realm of discretionary head movements, making the centric–eccentric gain the higher of the two jumps.

A third effect on head movement gain was similar in head-movers and non-movers alike. It is identified by exclusion of the midline-attraction and resetting effects. This is possible by comparing gains in the head-aligned and non-aligned modes in the a jump (which originates from the midline). This third "awareness/arousal" effect is attributed to the intrinsic behavioral context of the jump: the subject was made aware of head position and/or made more alert by an alignment requirement. As shown in Figs. 3 (gain) and 4 (normalized velocity), when head alignment was required, seven of nine subjects moved their heads more and slightly slower (24% slower) than in the identical jumps in the non-aligned mode, in which the head is moved with "gay abandon" (less and faster) in keeping with the absence of any attention to head movements. The two exceptional subjects, both non-movers (Subj 5 and 9), who moved their heads less in the aligned mode, also moved faster, emphasizing the linkage of awareness/arousal, gain, and, in this restricted case, normalized velocity.

Basis for low or high gains

The marked difference in overall average gains for all subjects (0.67 for head-aligned, 0.27 for non-aligned; Fig. 5A) is a reflection of all three effects in all subjects due to the head-alignment procedure. The head-aligned mode provided further differences between head-movers and non-movers by accentuating the midline-attraction and resetting effect. Thus, a partial reason for the marked differences between laboratories (Fuller 1992a) may be the instructions which alter the awareness/arousal effect (i.e., "Move your head to the target as quickly and accurately as possible", versus, "Look directly at the target as..."). This will be compounded if the fixation points are eccentric, bringing into play either or both of the first two effects. Such an explanation was given in the intriguing recent study of Delreux et al. (1991) in which the non-aligned jumps (which averaged 0.65 gain) were preceded by a head-aligned jump; they also reported that the gain for a 30° head-aligned jump was 0.51 if executed away from the midline, but was 0.97 when executed toward the midline, demonstrating, as in the present study, the midline-attraction effect. (It is added that their study was conducted in complete darkness, and this may also have contributed to their and others' higher gains.) Other subtle differences may arise from the method of light presentation, as described below.

The simplest variant of stimulus presentation is the interval during which the fixation/target lights are on: the longer the interval, the more likely the subject is to align his head with it, especially if the ocular eccentricity is beyond 20° or 30° (unpublished observation). Incorporation of a discrimination test and a reaction time response is typically employed to encourage continuous fixation in animals; for example, the target light may dim (Goldberg and Wurtz 1972) or the target may change color or orientation (Bizzi et al. 1972). If the discrimination requirement is coupled with no-jump fixations (i.e., the light dims without jumping), the alignment is even greater. For example, in monkeys, Tomlinson and Bahara (1986) used neither discriminations nor no-jump fixations, whereas Bizzi et al. (1972) used both. The gains of the former were much lower than the latter (see Fuller 1992a).

Another possible reason for differences in gain between laboratories could be the effect of repeated testing or extended training sessions. Head-movers could simply alter their behavior more adroitly and rapidly to suit the environment. This result was in fact found in one subject in some experimental conditions (Fig. 6), and therefore this effect can not be excluded. However, in all other subjects there was little evidence of enhancement or habituation of head movements.

The final and most obvious reason for low gains could be physical: the equipment did not allow anatomically normal and/or comfortable movements. It was found that intentionally imposed restrictions had no effect on the gain of movements [although if calculations include "no movements" in the 1–10° range (Table 1), gain would in fact be lower; but only for these small movements]. Therefore, another measure (apart from gain) was sought to at least quantify the effects of these encumbrances; such a measure was peak velocity of head movements.

Velocity of head movement

Ocular saccadic peak velocity as it relates to amplitude is among the most fundamental measurements in ocular motor research (Becker 1989). However, it is also known that ocular saccadic peak velocity varies between laboratories (Becker 1989); therefore it is no surprise that peak head velocity as a function of amplitude also varies. For example, Guitton and Volle (1987; their Fig. 1) found a slope of 4.4°/s per deg, with a y intercept of +106°/s, whereas Barnes (1979) found a slope of 2.6°/s per deg, intercept of +18°/s (from his Figs. 5, 8), which is closer to the present mean slopes of 2.8°/s per deg and 3.1°/s per deg (head-aligned and non-aligned, respectively) and a y intercept of +4°/s (e.g., Fig. 7). The gains of Barnes' study were much higher (0.75) than the present gains, whereas those of Guitton and Volle were much lower (average 0.22 for 30–60° amplitudes). This underscores the finding in the present report that there is no relationship between normalized velocity (the "instantaneous slope," as it were) and gain, nor was it affected by experience. The only relationship of velocity appeared to be with physical characteristics (high normalized velocity in robust males, low in gracile females), although differences in motivation cannot be excluded.

Effect of physical restrictions

Manipulations in the equipment were tested for the following reasons: (1) The discomfort of the standard bite bar may prevent or discourage some subjects from moving their heads. (2) Limitations in translation (in the horizontal plane and vertical axis) and rotation (about the pitch and roll axes) may restrict smaller movements in which head recruitment is comfortably optional, resulting in movements only in large gaze shifts. (3) Misalignment of the cervical-thoracic column relative to the axis of rotation may result in an anatomically suboptimal head attitude.

It was found that large movements (more than 30–40°) were most affected by reduction of translational freedom, whereas small movements (less than 10°) were most affected by the mouthpiece used to secure the head holder. The large movements are not affected in gain but have slower peak velocities. The smaller movements were not affected in velocity, only in relative number. By whole-body rotation it was additionally shown that non-movers are in fact capable of the same head-on-trunk eccentricities as head-movers; the former simply choose not to do so in the jump tasks.

The most surprising result was also the least detectable: when the whole chair was moved 2.5 cm forward (or backward) and the back then reclined (or inclined), to recenter the head, the angle of the cervical and possibly the upper thoracic vertebral column was slightly altered [estimated flexion (extension) of 1° at the cervicothoracic junction]. There is additional evidence that an optimal cervicothoracic angle is desirable: during platform rotation there is frequently a relatively sudden translation (about 1 cm in the initial APT trace in Fig. 8A); when the jump mode is resumed (not shown), there is a slow (5–10 min) return to the previously chosen position. Extending this observation, note that if there is misalignment of the craniocervical axis as well as reduced freedom of horizontal and vertical translation, then large amplitude movements would be most affected. This is due to the fact that the eccentric head axis would be drawn toward the recording axis at progressively larger eccentricities.

Despite several attempts to demonstrate the effects of physical impediments on the gain of head movement amplitude, the main effect was on peak velocity: the subjects moved their heads to the same place, but varied how they got there. Therefore, the third effect (awareness/arousal) and its corollaries (instructions, testing methods) at present seem the most likely reasons for variations in gain between laboratories. A similar suggestion has been made by others (Delreux et al. 1991).

The awareness/arousal effect may be reflected even at the basic level of superior collicular stimulation (Seagraves and Goldberg 1992): in contrast to earlier studies, head movements were indeed evoked by electrical stimulation if monkeys were working in a juxta- or suprathreshold gaze-shifting task, but were not evoked if the monkeys were executing a subthreshold gaze-step task. The implication in the present text is that priming the subject (or changing the "set") for head recruitment in gaze shifts (awareness/arousal) may have its correlates in set at the brain stem level.

Head-movers versus non-movers

Non-movers represent more a diversification of behavior and less a deficiency in adaptation to experimental restraints. There are nonphysical influences on movement gain, but there is also an idiosyncratic propensity to recruit the head. It is not due to the methods of recording. Individuals simply have a relatively innate behavioral trait which determines their propensity to move their head; this may in part reflect the individual's method of constructing central nervous coordinate systems. Current studies from the present laboratory on auditory-evoked head movements (in preparation), and recent reports (Delreux et al. 1991; Droulez and Berthoz 1991; Fuller 1992b; Pozzo et al. 1992) address this possibility. If head-movers initially chose extrinsic spatial or earth-fixed coordinates and non-movers chose intrinsic or head/body-oriented coordinates, the recalcitrance of the latter individuals to move their heads off the midline may be to reduce the necessary recalibration relating internal to external coordinates with the reorientation of the head. However, it is likely that the choice of reference coordinates is not fixed or absolute. Rather, in the continuous spectrum of head-movers and non-movers, there may be a bias towards either extreme (extrinsic versus intrinsic), which is idiosyncratic to both the individual and the conditions under which the gaze is shifted.

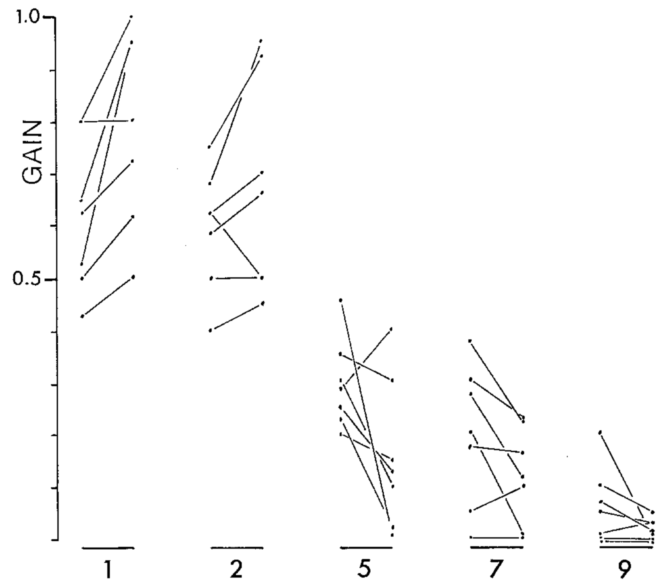

Fig. 9. Raw gains for five subjects in the non-aligned 40° jumps. Gains *(vertical axis)* of two head-movers *(1, 2, horizontal axis)* and three non-movers *(5, 7, 9)* are shown for the a (0–40°) and b (20–20°) jumps *(left and right points* for each subject, respectively). The trends shown (increase in gain in head-movers, decrease in gain in non-movers) were one of four criteria distinguishing the two groups. The first seven jumps (of the first seven blocks) taken from the first two or three sessions are shown for each subject. Gains from the same block are connected by *lines*

Appendix

Statistical results leading to the forgoing statements will be provided in approximately the order of presentation in the Results section. Four abbreviations will be used: head-mover (HM), non-movers (NM), head-aligned (HA), and non-aligned (NA). As the SDs suggest (Figs. 2, 5), there is typically some fluctuation in DC bias (see below) between blocks, which introduces variance in gain unrelated to the trends being examined. Such variance renders the trends described unsuitable for statistical tests of mean differences; in these instances, conclusions are based on comparison of gain changes within blocks from raw data. For the benefit of those unfamiliar with the analysis of such raw data, Fig. 9 (see below) shows examples.

Three generalities (see Fig. 3) were made in regard to the gain trends for each of the four jumps (a, b, b', c). The first generality contained two statements. Regarding the first statement (HAb > HAa in all subjects), Student's *t*-test for each subject showed a highly significant difference ($P<0.01$) in Sub 2, 3, 8, 9 and a significant difference ($P<0.05$) in Subj 4–7. In Subj 1 eight of nine pairs of jumps showed an increase, but the difference was insignificant ($P=0.21$). Regarding the second statement (NAb > NAa in HM and NAb < NAa in NM), differences in mean gain between b and a were insignificant in most subjects; Fig. 9 shows why. Temporarily ignoring the connecting lines, note that the overlap between a and b in all five examples is sufficiently great to render differences in means insignificant. The extent of overlap is partly due to the aforementioned DC-bias fluctuations. However, when the connecting lines (indicating measurements made in the same block) are considered, it is clear that the two HMs (Subj 1, 2) have a trend toward increased gain and the NMs (Subj 5, 7, 9) toward decreased gain irrespective of DC biases in gains. Differences in direction trend (up versus down) can be tested by chi-square. Comparing three HMs and three NMs showed the trend difference between the two groups to be significant (Fisher exact test, two-tail, $P=0.019$; Yates corrected chi-Square, $P=0.029$).

The third generality (HAa > NAa in seven of nine subjects) is based on differences between blocks; thus, means can be compared. Analysis of mean differences between HAa and NAa (Student's *t*-test) showed the difference to be highly significant ($P<0.01$) in Subj 1, 3, 4, 8 and significant ($P<0.05$) in Subj 7. Due to changes with experience, data for Subj 6 were culled to include only matched blocks (blocks conducted in adjacent times in each session and between sessions, as done in Fig. 6); the significance was marginal (t-test, $P=0.06$). In the last of the seven, Subj 2, the two jumps were not significantly different, although plotting as in Fig. 9 showed a trend similar to others.

In the second generality, and in analogous data in Fig. 5A, it was suggested that there was a differential trend in which the slope of the first series (a, b', c) was steeper (Fig. 5A) in NM than HM. This was tested by comparing the differences in each set of jumps. The mean increase in gain from a to b' among NM was highly significantly greater than HM (t-test, $P<0.001$). The increase in gain from b' to c among NM was significantly greater than HM ($P=0.03$). Differences in the second series (HAc < HAb in HM, and HAc > HAb in NM) were evaluated according to direction, since the directional trend is relevant, as in the case of Fig. 9. The trends in the two groups were significantly different (Yates, $P=0.019$; Fisher, $P=0.017$).

Differences in the normalized velocity (Figs. 4, 5) were originally found in seven of nine subjects (NA > HA) by analysis similar to that shown in Fig. 9 (the other two of nine subjects, Subj 5 and 9, had opposite trends and are not considered here). Statistical analysis (Student's t-test) revealed significant differences (NA > HA) in b, b', and c in Subj 4 and 6; in b and c in Subj 1, 7, and 8; and in b in Subj 2 and 3. Pooling of data for b and c (as in Results) resulted in a significant difference between the two modes (NA > HA) for both b and c ($P<0.05$). The pooling was done in two ways: first, paired samples of NA and HA for each subject were entered (the number of NA and HA blocks were rarely equal within each subject, resulting in the rejection of unpaired data); second, the means of NA and HA of each subject were entered, using both paired and unpaired data. As before, the two modes (NA and HA) were compared for b and c separately. Finally, if the b and c data are combined for all subjects, the difference (NA > HA) is highly significant ($P=0.006$).

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