RESEARCH ARTICLE

Brian S. Oommen · Ryan M. Smith · John S. Stahl The influence of future gaze orientation upon eye-head coupling during saccades

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Abstract Mammals with foveas (or analogous retinal specializations) frequently shift gaze without moving the head, and their behavior contrasts sharply with "afoveate" mammals, in which eye and head movements are strongly coupled. The ability to move the eyes without moving the head could reflect a gating mechanism that blocks a default eye-head synergy when an attempted head movement would be energetically wasteful. Based upon such considerations of efficiency, we predicted that for saccades to targets lying within the ocular motor range, the tendency to generate a head movement would depend upon a subject's expectations regarding future directions of gaze. We tested this hypothesis in two experiments with normal human subjects instructed to fixate sequences of lighted targets on a semicircular array. In the target direction experiment, we determined whether subjects were more likely to move the head during a small gaze shift if they expected that they would be momentarily required to make a second, larger shift in the same direction. Adding the onward-directed target increased significantly the distribution of final head positions (customary head orientation range, CHOR) observed during fixation of the primary target from 16.6±4.9° to 25.2±7.8°. The difference reflected an increase in the probability, and possibly the amplitude, of head movements. In the target duration experiment, we determined whether head movements were potentiated when subjects expected that gaze would be held in the vicinity of the target for a longer period of time. Prolonging fixation increased CHOR significantly from 53.7±18.8° to 63.2

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J. S. Stahl (⊠) Department of Neurology, University Hospitals of Cleveland, 11100 Euclid Avenue, Cleveland, OH 44106, USA e-mail: jss6@po.cwru.edu Tel.: +1-216-8443170 Fax: +1-216-8445066 $\pm 15.9^{\circ}$. Larger head movements were evoked for any given target eccentricity, due to a narrowing in the gap between the x-intercepts of the head amplitude:target eccentricity relationship. The results are consistent with the idea that foveate mammals use knowledge of future gaze direction to influence the coupling of saccadic commands to premotor circuitry of the head. While the circuits ultimately mediating the coupling may lie within the brainstem, our results suggest that the cerebrum plays a supervisory role, since it is a likely seat of expectation regarding target behavior. Eye-head coupling may reflect separate gating and scaling mechanisms, and changes in head movement tendencies may reflect parametric modulation of either mechanism.

Keywords Eye-head coordination · Gaze saccade · Ocular motor range · Human · Video oculography

Introduction

In humans and other mammals possessing a fovea or analogous retinal structure, each saccade may or may not be associated with movement of the head. This variable coupling stands in stark contrast to the behavior of many species whose retinas lack circumscribed regions specialized for high acuity; mammals such as the rabbit, guinea pig, and mouse tend to exhibit fairly rigid eye-head coupling, moving the head (or at least generating pulses of neck torque) for all gaze shifts or, correspondingly, making very few eye saccades when the head is held fixed (Collewijn 1977; Fuller 1980; Fuller 1981; Fuller 1992a; Gresty 1975; van Alphen et al. 2001). The dissociation of head and eye movements in mammals whose retinas are characterized by areas anatomically specialized for fixation (which we will loosely term "foveate" mammals) makes sense from a teleological standpoint. Foveate mammals must constantly shift the eyes during visual exploration. Moving the head with each saccade would be energetically wasteful or even impossible, as the inertial properties of the head would prevent

the realization of planned head movements when oppositely directed saccades come in close succession. The ability to shift the eyes without attempting to accelerate the head is thus an important part of the specialized ocular motor repertoire related to foveal vision. It may require specialized neural circuits, as do fovea-directing behaviors such as smooth pursuit and vergence.

Despite this ability to dissociate head and eye movements, there are indications that foveate mammals still retain the neural substrate for a more obligate coupling of eve and head movements. Coordinated eve and head saccades can be elicited by electrical stimulation of multiple areas responsible for organizing gaze shifts, including cortical eye fields (Martinez-Trujillo et al. 2003; Sparks et al. 2001; Tu and Keating 2000), superior colliculus (Corneil et al. 2002b; Freedman et al. 1996; Roucoux et al. 1980), and pontine reticular formation (Sparks et al. 2001). In fact, neck muscles can be activated by collicular stimulation that generates gaze shifts less than 5° in amplitude (Corneil et al. 2002a), possibly reflecting the existence of monosynaptic pathways from superior colliculus to the cervical spinal cord (Isa and Sasaki 2002; Robinson et al. 1994). Other evidence for inherent coupling of eye and head control in foveate mammals includes the tight linkage between eye movements and cervical EMG (Andre-Deshays et al. 1991), relationships between latency of eye and head movements (Zangemeister and Stark 1982a), and a clinical report that head movements can essentially replace saccadic eve movements when the latter are congenitally absent (Gilchrist et al. 1997). A parsimonious explanation for these findings is that coupled eye and head movements in afoveate mammals arise because outputs from gaze control are channeled to the premotor circuitry of both the eyes and the head, and foveate mammals retain these circuits.

Assuming the existence of pathways effectively linking control of eye and head, how does the foveate mammal execute saccades without generating head movements? The mechanisms by which the decoupling is achieved have received relatively little attention. Most models of eye-head coordination were developed for the purposes of understanding how saccade metrics are adjusted to maintain accuracy during concomitant head movements. These models assume a head movement for every saccade, take head trajectory as an external input, or incorporate a switch to gate head movement but do not specify how the switch is controlled (Galiana and Guitton 1992; Goossens and Van Opstal 1997; Laurutis and Robinson 1986; Phillips et al. 1995; Ron et al. 1994; Tomlinson 1990; Tweed et al. 1995). One exception is a model, also designed to explore intrasaccadic eye-head coupling, that uses a dead-zone nonlinearity to prevent head movements when the gaze shift amplitude is within a certain central range (Freedman 2001).

Existing physiological data provide limited clues to the location of the decoupling mechanism. Several authors have postulated that the divergence of head and eye control occurs in brainstem sites receiving input (directly or indirectly) from the superior colliculus (Corneil and

Munoz 1999; Freedman and Sparks 1997; Sparks et al. 2001). But while the decoupling mechanism may lie at the level of the brainstem, its operating parameters (e.g. gating thresholds, scaling slopes or intercepts) are quite likely to be defined by other structures. Head movement tendencies are strongly affected by the characteristics of the behavioral task. For instance, head movements are faster, or initiated more rapidly if the target displacement is highly predictable (Zangemeister and Stark 1982b), if the target will be the goal of a subsequent limb movement (Smeets et al. 1996) or direction of ambulation (Hollands et al. 2002), if a saccade is executed as part of a sequence of gaze shifts in which at least part of the sequence requires head movements (Fuller 1992b), or when gaze shifts occur as part of a process of scanning a wide field (Land 1992) or a line of text (Lee 1999). A common feature of all these situations is that the subject has expectations regarding future steps in the task, and thus a subliminal knowledge that orienting the head toward the new target will be advantageous or even required (for instance, if the gaze shift is part of a unidirectional sequence that would eventually require the eye to exceed the eye-in-orbit range). Cognitive activities such as expectation and prediction generally involve the cerebrum, and thus the effect of task upon head movement tendencies implicates the cerebrum in the control of eye-head coupling. Frontal cortical eye fields have been implicated in learning or executing programmed sequences of saccades (Isoda and Tanji 2002; Pierrot-Deseilligny et al. 2002) and could potentially supply information regarding future gaze direction to any mechanism controlling eyehead coupling.

The current experiments were contrived to test directly the idea that saccade-associated head movements are regulated so as to improve efficiency. As such, eye-head coupling should be stronger when gaze is to be directed in the vicinity of the new visual target for a relatively long period, or if a gaze shift will be followed by further shifts in the same direction and would carry the eyes beyond their customary range if unaccompanied by a head movement. We tested this prediction using reductionist stimuli that nevertheless evoke a naturalistic behavior in which saccades are variably accompanied by head movements. Preliminary results from pilot experiments have appeared elsewhere (Stahl 2001b; Stahl 2002).

Materials and methods

Subjects

Ten subjects (3 female, 7 male, ages 23–50 years) were studied under a protocol approved by the Institutional Review Board of the Cleveland Veterans Affairs Medical Center and complying with the ethical standards laid down in the 1964 Declaration of Helsinki. All subjects gave informed consent prior to inclusion in the study. All subjects were assessed for head movement propensities using the standard stimulus conditions and analysis methods previously described (Stahl 1999). The measures of propensity derived from this "ranging" test—particularly the eye-only range (EOR)—were used to customize stimuli employed in testing the influence of future gaze location upon eye-head coupling. All subjects participated in two different experiments designed to investigate this influence: the first experiment tested the effect of adding anticipatable secondary target steps, and the second tested the effect of altering duration of fixation. Five subjects were available to perform the first experiment twice; results (CHOR, EOR) from the two sessions were averaged to generate single values for each subject. All other subjects underwent each experiment once. All but 2 subjects were naive as to the purpose of the experiments, and the remaining two subjects (authors BSO and JSS) were unaware of their own performance until after each experiment was completed.

Recording apparatus

Eve and head movements were measured in the horizontal plane only. Eye movement was monitored using a video pupil tracking system (ISCAN, Burlington, MA) consisting of a light-weight CCD camera, infrared light source, and "heat" mirror mounted to the brim of a baseball cap. The complete cap apparatus weighed only 230 g, and its limp electrical lead was carefully looped and fixed so that it presented no detectable load or resistance over the entire range of head movements. The heat mirror, which was positioned relatively close to the subject's eye, yielded a clear visual field spanning approximately 50 degrees in the horizontal plane, and in fact was entirely invisible for the 2 subjects who could be recorded in darkness. Eight subjects could not be recorded in darkness owing to the excessive size of their dark-adapted pupils, which rendered the pupil tracking unreliable. For those subjects the edges of the mirror were visible and could potentially intersect the line of sight, but equally so in each of the stimulus conditions being compared.

The video image was processed online by the ISCAN software to determine the horizontal position of the pupil center relative to the center of the video image. Sampling rate was 60 Hz, and ISCAN claims a horizontal resolution of 1/3 of a video pixel for its proprietary tracking algorithm. The pupil position was converted to a proportionate analog signal and output for subsequent capture to a master computer, responsible for all data acquisition and stimulus control. Head movement was measured using a phase-detection magnetic search coil system with 2-m field coils (CNC Engineering, Seattle, WA). The search-coil, which was pre-calibrated on a protractor device, was taped to the front of the baseball cap. Eye and head movement signals were low-pass filtered (cutoff 90 Hz), and then digitized at 100 Hz and stored on the master computer. Note that analyses were restricted to measuring initial and final positions, which are essentially DC signals. Thus the filtering served primarily to prevent aliasing of high frequency noise from the search coil carrier frequency.

Eye position signals were converted off-line to eye-in-head angle, using a linear calibration equation established in each recording session from the eye positions recorded as subjects fixated a set of horizontal targets positioned every 10° between -40° and 40° . The equilibrium eye position signal for each fixation position was regressed against target angle to generate the conversion coefficients. This relationship was highly linear, with an r^2 value uniformly in excess of 0.99, and an RMS error of $1.3\pm0.3^{\circ}$ (mean \pm sd, n=5 subjects) over a $\pm40^{\circ}$ range. Gaze-in-space angle was calculated as the sum of the angular eye-in-head and head-in-space values (i.e., G = E + H). Zero eye-in-head and head-in-space positions were defined at the start of each experiment based upon the positions recorded as the subject aligned head and gaze with a central target.

Stimulus apparatus and paradigms

Subjects were seated at the center of a semicircular array (radius 97 cm) of LEDs spaced 1° apart, spanning 180°, and positioned at eye level. For all testing, subjects were instructed to fixate the illuminated target LED as quickly and accurately as possible,

moving the head or not as desired. Each of the three experimental paradigms required a full 35-min recording session to complete.

The experimental conditions for the "ranging" experiment have been previously described (Stahl 1999). As diagrammed in the top panel of Fig. 1, in each stimulus cycle the LEDs were illuminated in the following sequence:

- 1. Central LED, duration 1300 ms
- 2. Three to six "peri-zero" targets within $\pm 0\text{--}2^\circ$ of center, duration of each 650 ms
- 3. "Test" target, duration 1400 ms, eccentricity ranging $\pm 50^{\circ}$, with targets over $\pm 9-33^{\circ}$ appearing twice as often as those outside that range.
- 4. Two to five "peri-test" targets within $\pm 0-2^{\circ}$ of the test target, duration of each 600 ms
- 5. Central LED illuminates and cycle repeats

One ranging experiment typically yielded responses to 190 test targets. We customized the future target direction and future target duration stimuli (described below) for each subject, based upon the location of the junction points between the subject's eye-only range (EOR) and left and right eye-head ranges (EHR). The junction



Fig. 1 Variation of target position with time in a typical stimulus cycle for each of the three stimulus conditions—ranging, future target direction (onward/no-onward), and future target duration (long-dwell/short-dwell). In each panel, we study the head movement associated with the target transition marked with an asterisk

points were determined by qualitative evaluation of the plots of head amplitude vs. eccentricity of the target with respect to the head. Where left and right junction points differed, we chose an average of the two. Ranges for the test target, along with the qualitative EOR/ EHR junction points and measured EOR and customary head orientation range (CHOR, see below) are given for each subject in Table 1.

The future target direction experiment was designed to determine whether the probability of saccade-associated head movements differed depending upon whether or not the test target was followed shortly by a second target located at greater eccentricity (onward condition and no-onward conditions, respectively). As diagrammed in Fig. 1, in each stimulus cycle of the onward condition the LEDs were illuminated in the following sequence:

- 1. Central LED, random duration ranging continuously from 2000– 4000 ms
- 2. Test target, duration 1400 ms, eccentricity ranging $\pm 5^{\circ}$ about an average position chosen for each subject to be approximately 5° inward from the edge of the junction of the eye-only and eye-head ranges determined in the previously described ranging experiment. By choosing this range we could expect that the test targets were unlikely to evoke head movements in the no-onward condition, in which, like the ranging experiment, subjects should have developed expectations that gaze would be remaining in the vicinity of the test target.
- 3. Two to five peri-test targets, duration of each 600 ms, located within $\pm 0-2^{\circ}$ of the test target
- 4. Secondary target, duration 1400 ms, distributed uniformly at either $\pm 40-60^{\circ}$ or $\pm 50-70^{\circ}$. The more eccentric range was selected when the center of the customized test target range (see step 2) exceeded $\pm 25^{\circ}$. The secondary target ranges were designed so that there was a high probability that saccades to the secondary target would be accompanied by head movements.
- 5. Two to five peri-test targets, duration of each 600 ms, located within $\pm 0-2^{\circ}$ of the secondary target
- 6. Central LED re-illuminates and cycle repeats

The no-onward sequence was identical, except for the omission of steps 4, 5, above, i.e., the central LED re-illuminated immediately after completion of the peri-test targets in step 3. Each recording session consisted of a single block of approximately 150 stimuli of the onward type, and another block of approximately 180 of the no-onward type. The order of the blocks was determined at the start of the recording session by a coin toss. For the subjects who were available for a repeat session, the order of the blocks was reversed

Table 1 Head movement tendencies for all ten subjects derived from the ranging experiment, including customary ocular motor range (*COMR*), customary head orientation range (*CHOR*), eye-only range (*EOR*), and approximate T_H value of the junction between the EOR and the left and right eye-head ranges (*EHRs*) in plots of ΔH vs. T_H . The last column lists the test target range used in the future target duration experiment, chosen for each subject based upon the eccentricity of the subject's EOR/EHR junction

Subject	COMR	CHOR	EOR	EOR:EHR junctions	Onward/no-onward target ranges
1	58°	52°	38°	±15°	±5-15°
2	53	56	20	10	5-15
3	40	70	38	15	5-15
4	58	49	50	20	10-20
5	49	63	35	15	5-15
6	38	72	16	10	5-15
7	68	59	60	25	15–25
8	32	95	38	15	5-15
9	93	24	85	30	20-30
10	80	26	89	30	20–30

from the order used in the initial session. Prior to taking data, subjects were shown both stimulus sequences and instructed explicitly as to the differences. In this manner we insured that subjects had strong expectations that they either would or wouldn't be called upon to make a large secondary gaze shift within a few moments of fixating the test target.

The future target duration experiment was designed to determine whether the probability of saccade-associated head movements differed depending upon whether or not subjects were required to maintain gaze in the vicinity of the test target for several seconds (short-dwell and long-dwell conditions, respectively). As diagrammed in Fig. 1, in each stimulus cycle of the long-dwell condition the LEDs were illuminated in the following sequence:

- 1. Center LED, duration 1300 ms
- 2. Three to six peri-zero targets within \pm 0–2° of center, duration of each 600 ms.
- 3. Test target, duration 1400 ms, at a random eccentricity ranging straight-ahead to 30° beyond the qualitative EOR/EHR junction point, with targets occurring twice as often within $\pm 12^{\circ}$ of the left and right junction points.
- 4. Three to six peri-test targets, duration of each 600 ms, located within $\pm 0-2^{\circ}$ of the test target
- 5. Zero target re-illuminates and cycle repeats

In the short-dwell condition, the test target was illuminated for 750-1400 ms, extinguishing when head velocity neared 0°/s or 1400 ms was reached, whichever came first. By adjusting the duration of the illumination based upon actual head velocity, we maximized the likelihood that saccade-associated head movements would be recorded in their entirety, while still guaranteeing that the test target illumination period was as brief as possible. The shortdwell test target was followed by re-illumination of the center target, and the stimulus cycle repeated. Note that these stimulus conditions resulted in subjects being called upon to maintain gaze in the vicinity of each test target for 3-4 s in the long-dwell condition, as opposed to approximately 1 s in the short-dwell condition. As in the future target direction experiment, each recording session consisted of one block of short-dwell and one block of long-dwell stimuli. Order of the blocks was determined for all subjects in advance based upon a non-replacement draw from a randomized list of orders, thereby assuring that equal numbers of subjects were tested for each order. Subjects were instructed as to the difference between the two stimulus sequences to insure that they developed expectations regarding whether or not they would be called upon to maintain gaze in the vicinity of the test target.

Data analysis

Data files for all three experiments (ranging, future target direction, future target duration) were processed as previously described (Stahl 1999) to extract the initial and final eye-in-head and head-in-space positions associated with fixating the test targets. When no overt head movement occurred, final head position was taken as the head position at the conclusion of the gaze shift. As in the previous study, head movements were only considered to be associated with the eye saccade if they were initiated prior to 50 ms after the conclusion of the gaze shift. Responses were discarded if the head was in motion at the moment that the test target was presented, or if initial or final gaze positions were obscured by loss of video tracking (e.g., due to blinks). From the initial and final positions we calculated head movement amplitude (Δ H). We also calculated initial target eccentricity with respect to the head as $T_H = G_F - H_I$, where G_F and H_I are final gaze position and initial head position, respectively. Note that for our target distance, T_H is essentially equivalent to the predicted eye eccentricity (E_{PRED}=E_{I}+\Delta G) variable introduced in the referenced study. Plots of ΔH vs. T_H and $\Delta H/G_F$ vs. stimulus number were generated to allow qualitative assessment of subject responses.

As head movements are probabilistic events (Fuller 1992a), we used probability-based measures to quantify head movement

tendencies. These measures include the eye-only range (EOR, the range of T_H (or E_{PRED}) within which saccade-associated head movements were unlikely to occur) and the customary head orientation range (CHOR, the range of head eccentricities over which the head was likely to be found at the completion of orientation to the test target, i.e., at the moment at which H_F was measured). EOR was determined as previously described (Stahl 1999). Briefly, we used a Gaussian kernel method (Silverman 1986) to generate a curve proportional to the frequency of head saccade occurrence as a function of T_H, and then divided the curve pointwise by the curve proportional to the frequency of each $T_{\rm H}$ in the stimulus set. The resultant curve gives the probability of a head movement as a function of T_H. It was fit by a piecewise-linear, notch-filter profile and the EOR was defined as the central region of the fitted curve within which probability of head movement was less than 0.5. CHOR was designed to measure the range in which the subject was likely to maintain the head, and thus reflects both the likelihood of a head movement (quantified directly by the EOR) and the size of head movements when they occurred. The procedure for determining CHOR is diagrammed in Fig. 2, and proceeds as follows: First, we used the Gaussian kernel method (kernel standard deviation = 3° , width = 20°) to generate a curve proportional to the frequency of target-in-space angles generated during the experiment (Freq $[T_S]$). Next, we used the kernel method to construct the distribution of final head positions (Freq[H_F]), with the modification that for each saccade made in response to a target at T_S eccentricity, we scaled the kernel by $Freq[T_S]$, thereby correcting for the fact that target eccentricities were distributed non-uniformly. In other words,

 $Freq[H_F] = \sum_{i=1}^{N} \frac{K_i}{Freq[T_{S,i}]}$ where *i* is gaze shift number and K_i is a

Gaussian kernel centered on $H_{F,i}$. Finally, the customary head orientation range was defined as the range of H_F containing 90% of the area under the Freq[H_F] curve. Thus CHOR defines the range of positions within which the head is most likely to be found (probability = 0.9) at the end of the response to the test targets. CHOR is analogous to customary ocular motor range (COMR), but focuses upon the position of the head on the neck, rather than the eccentricity of the eye in the orbit. A subject with a narrow COMR will have a wide CHOR and vice versa. It should be noted, however, that CHOR is more dependent than COMR upon the range of target amplitudes that is tested. For any given subject tested in chest-fixed conditions, CHOR will become wider as the target distribution is broadened.

The significance of differences between head movement tendencies was determined using a 2-way ANOVA implemented in MATLAB (The Mathworks, Natick, MA), where one factor was subject and the other factor was experimental condition (i.e. onward and no-onward, or long-dwell and short-dwell). All average values are reported as mean±sd.

Results

The effect of expected future target direction on head movements

Subjects responded to the test [primary] target by generating head movements to a variable degree, but all subjects generally executed a head movement when fixating the secondary target in the onward condition. When a head movement accompanied the saccade to the test target in the onward condition, the head typically came to a full stop prior to the appearance of the secondary target. Thus, the head movement to the secondary target was initiated from a stationary condition. Of note, in pilot experiments in which the test target was not followed by the small peri-test targets, the head often executed a single



Fig. 2 Illustration of the calculation of CHOR. *Top panel:* curve proportional to distribution of target positions in space ($Freq[T_S]$), generated by summing a Gaussian kernel centered upon T_S for each test target. Freq[T_S] values for three selected targets are numbered. *Middle panel:* treatment of the head movement responses to the three targets whose $Freq[T_S]$ values are indicated in top panel. Standard Gaussian kernels centered on the H_F of the responses are scaled by the $Freq[T_S]$ before being added to an accumulator. The scaled kernels (thick Gaussians) are shown along with scaled kernels for 14 additional responses. *Bottom panel:* final accumulator contents (proportional to distribution of final head position, $Freq[H_F]$) after summing scaled kernels for 104 responses. Vertical cursors delineate CHOR, the region encompassing the central 90% of the area under the $Freq[H_F]$ curve

smooth movement from the straight-ahead position toward the future location of the secondary target. Such movements might be anticipatory head movements (Bizzi et al. 1972) related entirely to the future secondary target, as opposed to head movements made to the test target but potentiated by the expectation of the secondary target. Adding the peri-test targets removed this confounder, rendering it clear that the head movement accompanying the initial saccade was directed toward the test target.

Qualitative inspection of plots of Δ H/G_F vs. stimulus number indicated that in the onward condition, head movements were more likely and/or larger. A typical plot for one subject is shown in Fig. 3. Responses to leftward and rightward test targets are plotted separately, and in both plots, responses to the onward condition (first stimulus block) are plotted as triangles and responses to the no-onward condition are plotted as circles. In the onward condition, head movements exceeding 20% of G_F became common after approximately the tenth stimulus cycle. Once the no-onward condition began, $\Delta H/G_F$ declined almost immediately, with head movements exceeding 20% of G_F becoming rare. Similar effects were observed for both rightward and leftward targets. Figure 4 shows the distributions of final head position from which CHOR was calculated, for the same data shown in Fig. 3.

Figure 5a summarizes the behavior of all ten subjects, plotting CHOR in the onward condition vs. CHOR in the no-onward condition. The data fall uniformly above the unity relationship line, indicating that CHOR was always larger in the onward condition. Average values were 25.2 $\pm 7.8^{\circ}$ in the onward condition, vs. 16.6 $\pm 4.9^{\circ}$ in the noonward condition, and the difference was statistically significant (p<0.001, 2-way ANOVA, with subject and condition as factors). As discussed in Methods, CHOR reflects both the likelihood of a head movement and the amplitude of the movements when they occur. Figure 5b assesses the effect on head movement probability alone by plotting the probability of a head movement in the onward condition vs. the probability in the no-onward condition. Probability was calculated as the number of stimulus cycles in which the head moved divided by the total number of stimulus cycles, and a head movement was considered to have occurred when $\Delta H/G_F$ exceeded 0.1 (i.e. the amplitude of head movement was at least 10% of the final gaze eccentricity). This 10% threshold effectively



Fig. 3 Plots of head movement gain ($\Delta H/G_F$) as a function of stimulus number for one subject in the future target direction experiment. Each data point reflects the response to the appearance of one test target. Responses to rightward and leftward test targets are plotted separately, and responses gathered in the onward condition and no-onward condition are plotted as triangles and circles, respectively. Shifting to the no-onward condition was followed by an abrupt reduction in head movement gain

Fig. 4 Distributions of final head position in the onward and no-onward conditions, based upon data presented in Fig. 3. Vertical cursors delimit CHOR. CHOR expanded in the onward condition

Α

CHOR (deg), Onward



5.0

No-onward

Fig. 5A, B Comparison of head movement tendencies in the onward and no-onward conditions of the future target direction experiment. Dashed line in each plot indicates the 1:1 relationship. A Customary head orientation range (CHOR). B Probability of a head movement with amplitude exceeding 10% of final gaze eccentricity. The onward condition was associated with an increase in both CHOR and head movement probability in all subjects

excluded occasional tiny head movements that, being so much smaller than bona fide head saccades, appeared to represent a qualitatively different behavior (Stahl 1999). All subjects fell well above the unity relationship line, reflecting an increase in average head movement probability from 0.22±0.13 to 0.58±0.17 (2-way ANOVA, p < 0.0001). While head movement probability was strongly increased, the effect of the stimulus condition upon head movement amplitude was less clear. We assessed this effect specifically by determining for each subject and condition the average $\Delta H/G_F$ of all head movements that satisfied the $\Delta H/G_F > 0.1$ criterion. The average $\Delta H/G_F$ was larger in the onward condition for 8/10 subjects (the increase ranging 0.21 to 0.53), but smaller in the remaining two subjects (decrease of 0.07and 0.13), and the effect of stimulus condition on $\Delta H/G_F$ did not reach statistical significance (p=0.08). Thus, the increase in CHOR in the onward condition appeared to derive to a greater extent from the increase in the likelihood of a head movement occurring, rather than from an increase in head movement amplitude.



Fig. 6A–C Comparison of one typical subject's responses to longdwell (*top row*) and short-dwell (*bottom row*) conditions of the future target duration experiment. **A1, A2** Plots of head movement amplitude vs. target eccentricity with respect to the head (T_H). Fitted lines were generated by a piecewise linear least-square fit as previously described (Stahl 1999). Decreased target duration was associated with an increase in the central range over which head

The effect of future target duration on head movements

Longer target durations led to an increase in head movement tendencies. The effect is demonstrated for one typical subject in Fig. 6, which includes plots of ΔH vs. T_H, the distribution of final head eccentricity (basis for CHOR calculation), and plots of probability of head saccades vs. T_H (basis for EOR calculation) in the longdwell and short-dwell conditions. Note in the short-dwell condition the increase in the span of the central region in which test target fixations are accomplished without moving the head (compare panels A1, A2), and the corresponding decrease in CHOR (compare the distance between the vertical cursors in panels B1, B2) and the increase in EOR (compare distance between vertical cursors in figures C1, C2). Figure 7a summarizes the behavior of all ten subjects, plotting CHOR in the shortdwell condition versus the long-dwell condition. All subjects fell below the unity relationship, indicating that head eccentricity ranged more widely when subjects knew that gaze would be oriented toward the test target for an extended period. Average CHOR increased from 53.7 $\pm 18.8^{\circ}$ in the short-dwell condition to $63.2\pm 15.9^{\circ}$ in the long-dwell condition, and the difference was significant (p=0.0001, 2-way ANOVA, subject and condition as factors). Figure 7b shows the analogous scatter plot for EOR. All but two subjects fell above the unity relationship, indicating that some of the increase in CHOR in the long-dwell condition arose due to a decrease in the range of T_H over which head movements were *improbable*. EOR averaged 55.1±19.2° in the short-dwell condition and 40.7

movements did not occur. **B1**, **B2** Plots of distribution of H_{F} . Cursors delimit CHOR. Note that CHOR is narrowed in the shortdwell condition. **C1**, **C2** Plots of head saccade probability as a function of T_{H} . Cursors delimit EOR, the central region where the fitted probability curve (not shown) falls below 0.5. EOR expanded in the short-dwell condition

 $\pm 21.1^{\circ}$ in the long-dwell condition, and the difference was significant (*p*=0.0016, 2-way ANOVA).

The form of the ΔH vs. T_H plot in Fig. 6 (panels A1, A2) can be explained by postulating a mechanism that scales potential head movements based upon T_H . The scaling operation implies the determination of both slopes and intercepts of the eye-head ranges, the region in which head amplitude is a linear function of T_H . Changes in either could influence both CHOR and EOR. Fig. 8 assesses whether the duration of future target illumination influenced the x-intercepts, by comparing the differences between the left and right x-intercepts in the short- and long-dwell conditions. Nine out of 10 subjects fell above



Fig. 7A, B Comparison of head movement tendencies in the shortdwell and long-dwell conditions of the future target duration experiment. Dashed line in each plot indicates the 1:1 relationship. **A** CHOR; **B** eye-only range (EOR). The long-dwell condition was associated with an increase in CHOR and a corresponding decrease in the T_H range over which saccades were executed *without* head movements



Fig. 8 Comparison of the intercept gap (the range of T_H between the x-intercepts of the ΔH vs. T_H relationships for leftward and rightward saccades) in the short-dwell and long-dwell conditions. Dashed line indicates 1:1 relationship. Short-dwell condition was associated with enlargement of the intercept gap, accounting for the decrease in saccade-associated head movements

the unity relationship line, indicating that the intercepts shifted eccentrically in the short-dwell condition, i.e., when subjects knew that fixations would be of brief duration, the minimum target eccentricity required to plan a head movement of non-zero amplitude increased. The average size of the "intercept gap" was 31.2±18.3° in the long-dwell condition vs. 45.7±18.0° in the short-dwell condition, a statistically significant difference (p=0.0092, 2-way ANOVA, with subjects and stimulus condition as factors). In contrast, there was little effect of stimulus condition on the average of slopes of the left and right eyehead ranges. Slope averaged 0.98±0.45 in the short-dwell condition and 0.95±0.33 in the long-dwell condition (p=0.73). Thus the effect of target dwell upon CHOR and EOR reflects a change in the range of T_H over which head movements were planned, as opposed to the magnitude of a multiplicative factor coupling T_H and ΔH .

Discussion

Variations in target sequence affected the propensity of subjects to move the head, supporting the hypothesis that a subject's expectations or knowledge of the future orientation of visual attention modulates eve-head coupling. Subjects were more likely to move the head during a small gaze shift if they expected that they would be momentarily required to make a second, larger shift in the same direction. The tendency to execute a saccade-associated head movement was also increased when subjects expected that gaze would be held in the vicinity of the visual target for a longer period of time. Overall, the results are consistent with the idea that foveate mammals modulate head movements in the interest of efficiency, and support the speculation that they possess circuits that have knowledge of the future direction of visual attention and exercise supervisory control over connections between brainstem gaze control centers and the premotor circuitry of the head. These putative circuits allow the animal to align the head with the *future* center of visual attention.

While the circuits may have developed with the advent of the fovea and analogous structures, an alternative speculation is possible. Afoveate mammals could possess the supervisory connections, but fail to generate long-range plans for their gaze shifts. In such cases, differences could not arise between the next visual target and the long-range center of visual attention, and the head would tend to align with gaze at all times. A similar argument has been raised to reinterpret Land's finding (Land 1992) that humans performing a driving task exhibited tight eye-head coupling (Smeets et al. 1996).

Expectation may modulate head movement gating or scaling

Our previous work has suggested that head control may involve two different processes, both depending upon $T_{\rm H}$ (Stahl 1999; Stahl 2000). One mechanism generates the piecewise linear relationship between ΔH and T_H , i.e., sets the x-intercepts and slopes of the regions within which ΔH increases as a function of T_{H} . The second process acts as an all-or-nothing gate, determining whether the movement planned by the scaling mechanism actually occurs. The increase in head movement tendencies in the onward condition of the future target direction experiment corresponded to an increase in the probability of moving the head. Whether this increase in probability reflected a change in the putative head movement gate or the gap between the x-intercepts set by the scaling mechanism ("intercept gap") cannot be determined from our data, since test target eccentricities were quite limited, precluding the construction of a ΔH vs T_H plot and determination of x-intercepts. The onward target condition may also have exerted its effect by increasing the slope of the scaling mechanism (based upon the increase in the closely related $\Delta H/G_F$ value), although this effect was weaker and failed to reach statistical significance.

The target duration experiment did allow for construction of ΔH vs T_H plots, and they indicated that the decrease in head movements in the short-dwell condition corresponded to a change in the x-intercepts of the scaling mechanism, while scaling slopes were unchanged. In fact, the average increase in measured EOR (14.3°) was almost identical to the increase in the intercept gap (14.6°) , so the decrease in head movements in the short dwell condition could have come about through a parametric modulation of head movement scaling without any effect upon head movement gating. This result differed from that obtained in a previous study of head movements following prolonged neck restraint, in which the increase in measured EOR was best explained by a change in the range over which the gating mechanism blocks head movements (Stahl 2000). Together the studies support the existence of separable scaling and gating mechanisms, indicate that either are subject to parametric modulation, and argue that different behavioral conditions or experiences may act on one mechanism or the other in a selective fashion.

Relationship of experimental stimuli to more natural conditions

The current experiments were designed to control a subject's agenda regarding future direction of visual attention by creating expectations regarding the location of future target appearances. This sort of scenario, i.e., targets appearing suddenly at anticipated general locations, does occur in real life, and has been exploited in previous investigations of the saccadic system (e.g., Guitton et al. 1990). However, the more common scenario is probably one in which subjects make sequences of saccades between targets that are continuously visible. The benefits of directing the head based upon future visual attention would be expected to apply to this situation as well. If anything, the effect is expected to be stronger in this natural situation, since the subject has more information available regarding the location of visual targets, as well as some internally generated plan as to the sequence in which they will be explored.

Others have, in fact, strongly advocated studying eyehead coordination during behaviorally relevant tasks (Kowler et al. 1992; Pelz et al. 2001; Smeets et al. 1996; Steinman et al. 1990). But the attractions of this approach are offset to some extent by the bewildering variety of influences that might impact upon head control in a natural context. For instance, the current experiments demonstrated that reducing the duration of gaze deviation depotentiates head movement. But obviously, if the visual target lies beyond the limit of the full-scale ocular motor range, it must be fixated with a combined eye-head saccade, no matter how fleeting a fixation is planned. At intermediate eccentricities, lying outside the customary ocular motor range but within the full-scale range, the interplay between eye movement kinematics and the visual requirements of the behavioral task may become a factor in determining whether head movements occur. Eye movement kinematics, including the accuracy of smooth pursuit and the vestibulo-ocular reflex, as well as the stability of gaze holding, deteriorate as eye position becomes more eccentric (Stahl 2001a). This eccentricitydependent degradation of eye movements would also degrade visual acuity. Thus, the tendency to generate a head movement to an eccentric target may vary according to the clarity of vision required to accomplish the behavioral goals associated with fixating the new target. Eye-head coupling could also conceivably be influenced by past head movements. Although this issue has yet to be formally explored, the idea that head movements may potentiate further head movements was suggested by qualitative inspection of plots of $\Delta H/G_F$ versus stimulus number, in which subjects performing the no-onward block sometimes generated flurries of head movements lasting several stimulus cycles. Eye-head coupling would also be modulated moment-to-moment by the likelihood that the next visual target could become the goal of a limb movement (Smeets et al. 1996) or a change in the direction of ambulation (Hollands et al. 2002). All these modulating factors must play out in the context of a subject's innate

head movement tendencies. Different subjects exhibit differing propensity to move the head (Bard et al. 1992; Fuller 1992b; Stahl 1999). These variations do not simply reflect differences in strategy with which subjects execute the experimental task, since they are clearly manifest in an experiment in which targets appear randomly and singly, and no orienting strategy can be developed (Stahl 1999). Finally, while we have focused upon non-conscious influences upon eye-head coupling, head movements are also under voluntary control. It is easy to verify that one can voluntarily inhibit all head movements, or conversely, increase one's tendency to execute eye-head saccades.

Clearly, head control is subject to many influences, rendering it difficult to determine what governs individual head movements during a complex, natural behavior. Contrived, reductionist experiments performed in controlled laboratory settings remain important because their interpretation is more straightforward, and they are inherently easier to translate to physiological experiments aimed at defining the neuronal mechanisms of eye-head coordination. The current experiments, for instance, suggest that it would be profitable to perform recordings in monkey cortical areas that have been implicated in the control of sequences of gaze shifts, emphasizing a search for units that discriminate between eye-only and combined eye-head saccades.

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