

VESTIBULO-OCULAR FUNCTION DURING CO-ORDINATED HEAD AND EYE MOVEMENTS TO ACQUIRE VISUAL TARGETS

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SUMMARY

1. Experiments have been conducted on human subjects in an attempt to establish the role of the vestibulo-ocular reflex in the co-ordination of head and eye movements during visual target acquisition.

2. When the subject moved head and eyes to acquire visual targets in the horizontal plane, the eye movement consisted of an initial saccade in the direction of head movement followed by a slower return towards orbital centre which compensated for remaining head movement.

3. When the head was moved either voluntarily or passively in the dark the pattern of eye movement was very similar to that seen during target acquisition.

4. The mean latency between the start of head acceleration and the onset of the saccadic eye movement was greater in the dark (108 msec, s.D. 85 msec) than for the visually induced responses (14 msec, s.D. 59 msec), in which eye movement often preceded head movement when moving to small ($< 45^\circ$) target offset angles.

5. In all experimental conditions gaze displacement at the end of the initial saccade was normally related in a predictive manner to final head position, but when fixating visual targets offset by more than 60° from the central position there were often large errors, 22% of responses undershooting the target by more than 15° .

6. A highly significant ($P < 0.001$) linear relationship was found between gaze displacement and head velocity under all experimental conditions. During target acquisition head velocity was normally positively correlated with amplitude of target offset. The large errors in gaze displacement in response to the larger target offsets occurred at levels of head velocity lower than normally associated with such target offsets.

7. The results have led to the suggestion of a dual mode of control for head-eye co-ordination. In one mode, normally associated with small target offsets ($< 45^\circ$), control is mediated by retinal error information. In the other mode, associated with larger target offsets, gaze displacement is generated as an automatic response to head turning.

8. The observation of similar relationships between head and eye movement during passive head turning implicates the vestibulo-ocular reflex in the secondary mode of control, and provides support for the hypothesis that the role of the vestibular saccade is to induce a rapid offset of the eyes in the direction of head movement, thus facilitating rapid search and target location.

INTRODUCTION

Man, in common with other vertebrates, has evolved a powerful system of hierarchical control mechanisms for the stabilization of the image of the external visual scene on the retina of the eye. The afferent information necessary for effective control is derived from three principal sources, the visual system, the vestibular apparatus and, to a lesser extent, the kinaesthetic sensory system.

It has long been recognized from the work of Breuer (1889) and Dodge (1923) that the ocular movements with respect to the head induced by stimulation of the semicircular canals are of a compensatory nature, so that the eye is, to a great extent, rotationally stabilized in space whilst the head is in motion. The compensatory nature of the vestibulo-ocular reflex response is most evident when the subject has a visual target upon which to fixate during head movement. However, when the vestibular system is stimulated in the absence of vision the resulting eye movement is most frequently of an oscillatory nature (nystagmus). It consists of two distinct components: the compensatory component (or slow phase) described above and the fast phase, or saccadic component, which is generally of opposite polarity to the compensatory component. Whereas the velocity of the compensatory component reflects the varying velocity of head movement, the saccadic components are of approximately constant velocity (up to $400^\circ/\text{sec}$) and provide fast re-positioning.

An indication of the possible significance of the saccadic component of nystagmus became apparent from observations made by Melvill-Jones (1964). During repeated high-rate turning movements of the head in man, the saccadic component became the dominant feature of the response, turning the eye in the same direction as the head. It was suggested that the role of the saccade might be to induce a rapid offset of the eye in the direction of head rotation during voluntary head movement. Such a manoeuvre would have obvious advantages, since the eye can be moved with greater initial acceleration than the head. The compensatory component of the response would play its part following the end of the saccade by stabilizing the eye in its new offset position. Subsequently, this concept of the function of the saccade was given further support by attempts to model the mechanism of saccadic generation in the vestibulo-ocular reflex (Barnes, 1973).

In accordance with this concept it has been shown (Bartz, 1966) that during a voluntary co-ordinated movement of the head and eyes to acquire a visual target fixed in space the eye movement does consist of an initial saccade in the direction of head movement followed by a slower return to orbital centre. However, it is not certain that the saccade is of vestibular origin and it was the aim of the experiments to be described to investigate the role of the vestibular apparatus during visual target acquisition. The response of the eyes to head turning in the lateral plane has been compared in three experimental conditions; first, when the subject made voluntary movements in the dark, secondly, when the subject's head was forcibly turned in the dark, and thirdly, when the subject made voluntary movements to fixate discrete visual targets.

METHODS

Apparatus

The subject sat in a dental chair which could be easily adjusted to suit different subjects. The chair was positioned at the centre of a semicircular periphery of radius 1.2 m, the inner surface of which was painted matt black.

Embedded into the periphery were thirteen light-emitting diodes, which were used as target sources. The light output of the diodes had a rise time of 5 μ sec, thus enabling short pulses of light to be presented to the subject. Each target source subtended approximately 0.2° at the eye, with little dispersion and a high contrast edge when viewed in darkness. The diodes emitted red light with a luminance of 2.5 cd/m², a level which is well above the threshold for perception by the peripheral retina but sufficiently low to reduce the effects of light scatter.

The lights were placed at approximately equal intervals (15°) around the periphery to left and right of a centre light. Any small errors in target position were of no consequence in assessing the accuracy of eye and head positioning since calibration was carried out on these same targets.

A specially designed helmet was made from strips of aluminium alloy formed into the shape illustrated in Fig. 1. It was lined with a high density polyester foam (Tempafoam, Dynamic Systems Inc), which has a high resistance to impact loading combined with a high level of long-term compliance. The lining conformed easily to the contours of the head, thus reducing the occurrence of pressure points, whilst providing a firm interface between the head and the helmet. However, in order to establish a more rigid connexion, a stiff U-shaped bar was connected to the head band of the helmet and to a dental bite at its centre. The total weight of the helmet was 0.7 kg.

The crown of the helmet was attached to a rotary potentiometer by a metal bellows coupling (Fig. 1) which was extremely rigid in torsion but provided very little resistance to lateral movements of the head. This was found to be important in maintaining the head responses as normal as possible, by absorbing the initial rolling movement which frequently accompanied rotation of the head in yaw.

It was found, by repeated alignment of a helmet-mounted sight (see Fig. 1 and Barnes & Sommerville (1978) for description) with each of the target lights, that the head-position signal contained an error of no more than $\pm 0.2^\circ$, even for head rotations as large as 75°.

An angular accelerometer was also attached to the underside of the dental bite as shown in Fig. 1 to measure the acceleration of the head about the axis of rotation. The angular velocity of the head was obtained by integration of the acceleration signal.

Eye movements were recorded using a conventional electro-oculographic technique (resolution approximately $\pm 0.5^\circ$). For this purpose two silver-silver chloride suction electrodes were placed on the skin beside the external canthus of each orbit as shown in Fig. 1. The potentials were amplified by a DC differential amplifier with negligible drift and passed through a second order low pass filter with a 50 Hz corner frequency to reduce noise.

The presentation of the target lights was made in a random sequence under the control of a programmable calculator (Tektronix 31). Recordings were made on a multi-channel analogue tape recorder (Philips Analog 7).

The laboratory in which the experiments were carried out was almost entirely light-proof and all instrument lights were covered to eliminate visual positional cues other than the target lights.

Subjects

Six subjects, five of them male, participated voluntarily in the experiment. None had any known visual, vestibular or spinal defect; all had normal mobility of the head and neck and were able to use a dental bite without discomfort.

Experimental procedure

The subject was prepared for electro-oculographic recording by cleaning the skin over the external canthi with alcohol and abrading the site with electrode jelly. Subject preparation was carried out in a very low level of illumination and took some 20 min. It was thus expected that the subject would be reasonably well dark-adapted by the beginning of the experiment (Gonshor & Malcolm, 1971).

Each of the six subjects participated in the following four experimental conditions.

(1) *Continuous target presentation (CT condition)*

The subject was instructed to move the head and eyes to fixate offset target lights which appeared at randomized positions around the periphery. Thirty sequences of target presentation were given; each sequence consisted of an initial 3 sec period during which only the centre light was on, followed by a further 3 sec period when one offset target light alone was presented. Each sequence was separated by a period of 1 sec. The subject was instructed to fixate the targets as they appeared in as natural a manner as possible. The number of sequences and presentation periods used were designed to enable fixation to be achieved without stressing the subject but with changes occurring frequently enough to alleviate the boredom associated with such an experiment.

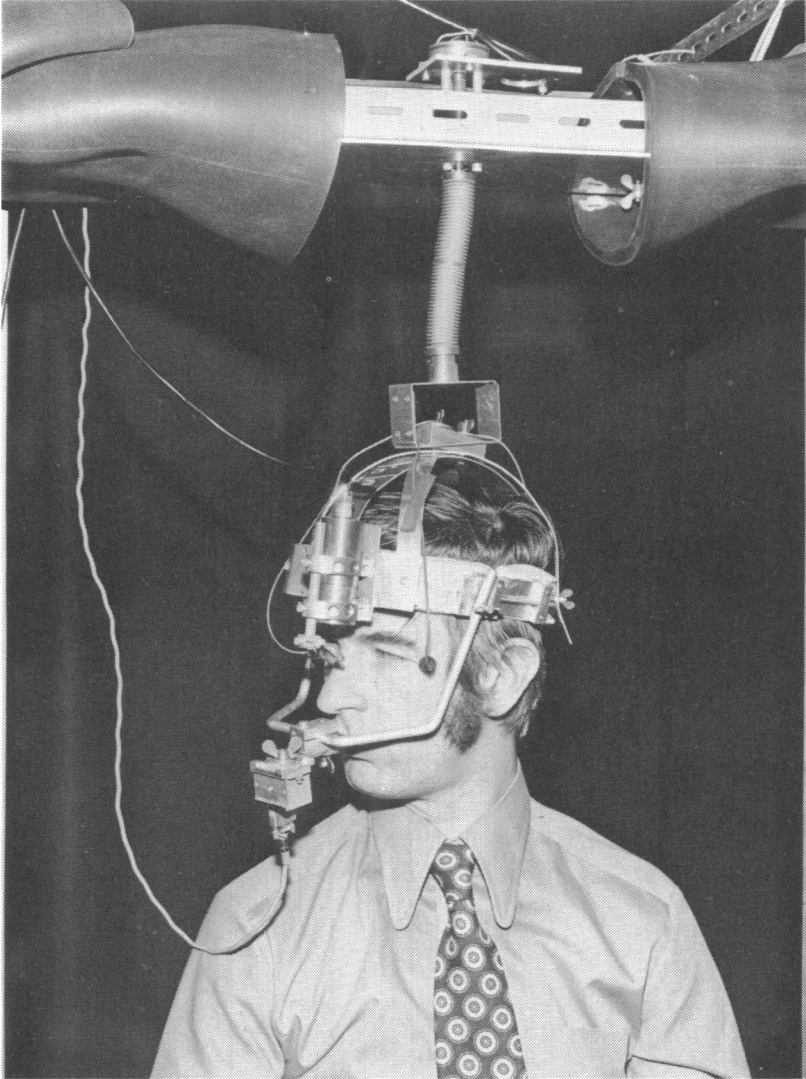


Fig. 1. The apparatus used to transduce head and eye movement. The helmet, which was attached to the head by a dental bite, was connected by a flexible metal bellows to an angular potentiometer. Attached to the helmet were a sighting system and an angular accelerometer.

(2) *Target flash presentation (TF condition)*

The target flash condition was similar to the continuous target presentation. However, following extinction of the centre light, the randomly determined offset light appeared for a period of 100 msec only. This was followed by a period (2 sec) of complete darkness, after which the same offset light reappeared for a further 2 sec. A period of 1 sec elapsed before the start of the next sequence. As before, thirty sequences were presented. The subject was instructed to fixate the centre light and when the offset target flash appeared, to turn head and eyes in a normal manner to the estimated position of the target. When the offset target reappeared the subject was instructed to make a final fixation without further head movement.

(3) *Voluntary head rotation in the dark (VR condition)*

In this experimental condition the subject voluntarily rotated the head about the yaw axis in the dark, with the eyes open. The movements were made in a set sequence, starting from the central position with respect to the body, moving to a random offset position and then returning to centre. There was no instruction to make voluntary eye movements. Rather, subjects were told that the objective was the achievement of a broad range of velocity and amplitude of head movement. Each subject made fifty or more individual head movements.

(4) *Passive head rotation in the dark (PR condition)*

During passive head rotation the head was turned manually about the yaw axis by the experimenter who gripped a point on the top of the helmet and applied a sudden torque. In this manner it proved possible to achieve relatively high levels of angular acceleration in simulation of the normal voluntary movements. The subject was instructed to relax the neck muscles and to stare blankly ahead into the darkened room. Altogether fifty or more individual responses were obtained from each subject.

The four experimental conditions were conducted in two sessions. In session *A*, continuous target presentation was followed by passive head rotation. In session *B*, target flash presentation was followed by voluntary head rotation. Three of the subjects completed session *A* first and three session *B* and no subject completed more than one session on any one day. It was found desirable in each session to complete the target-seeking conditions (1) and (2) first since these were self-calibrating, and to allow the effects of dark-adaptation on the electro-oculogram to stabilize for the conditions in which there was no visual stimulus. Calibrations of head and eye movement were carried out at the beginning and end of each experimental condition by allowing the subject to align the head-mounted sight (Fig. 1) or the eyes with selected targets.

RESULTS

Qualitative features

The responses of the head and eyes in the four experimental conditions were qualitatively very similar as shown by the examples in Fig. 2. In general, each of the oculographic records exhibited a pattern of eye movement in which there was initially a high-velocity saccade of large amplitude in the direction of head movement followed by a slow return towards orbital centre. The final eye position was normally offset in the direction of head rotation. The slow phase component provided adequate compensation for remaining head displacement after the end of the saccade as indicated by the gaze displacement in these examples.

The most noteworthy features of these responses may be summarized as follows.

(1) The latency of the saccadic eye movement with respect to head acceleration was generally greater for the experiments conducted in the dark than during visual target acquisition. During target seeking the saccadic eye movement was frequently initiated before head movement could be detected on the accelerometer record.

(2) In all four experimental conditions there were examples of response patterns in which more than one saccade occurred during head movement. These appeared to be associated with a lower than normal head velocity (see Fig. 2 (ii)).

(3) The saccadic eye movements observed during passive and voluntary head movements in the dark were as sharply defined as, and of comparable velocity to, those seen during target seeking.

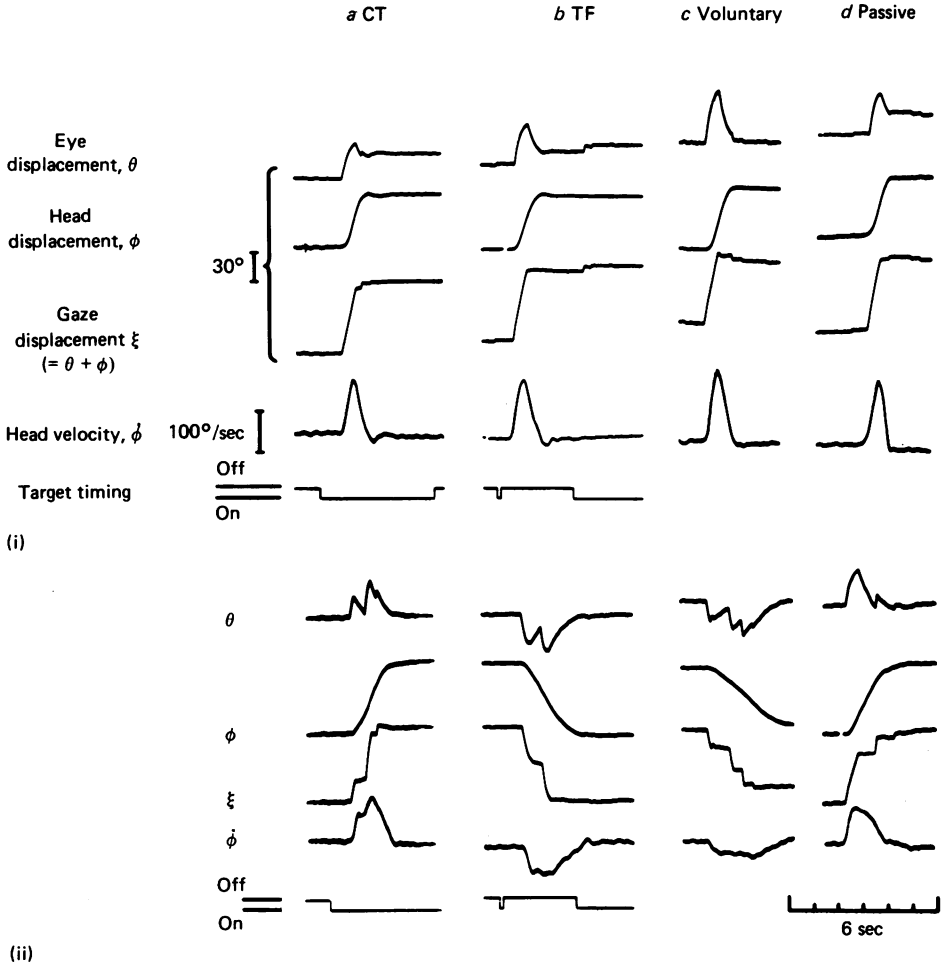


Fig. 2. Typical responses of the head and eyes during visual target acquisition (*a* and *b*) and during head movements in the dark (*c* and *d*) for approximately equivalent gaze displacements of 75° from centre. The head movements in the lower set of traces (ii) had peak velocities which were lower than normal as compared with the responses shown in the upper set (i).

(4) The initial velocity of the saccade was generally constant at about 200–300°/sec, but during high velocity head movements the eye velocity commonly fell during the latter part of the saccade to produce a ‘rounding effect’ before its termination (see ‘eye displacement’ in Fig. 2 (i)).

(5) During both voluntary and passively induced head movements the range of

peak head velocities for each subject was generally wider (typically 25–200°/sec for a 60° head displacement) than during visual target acquisition (typically 75–160°/sec for $\phi_2 = 60^\circ$). In addition, during passive head rotation it was rarely possible to achieve initial head angular accelerations comparable to those observed during voluntary head movements.

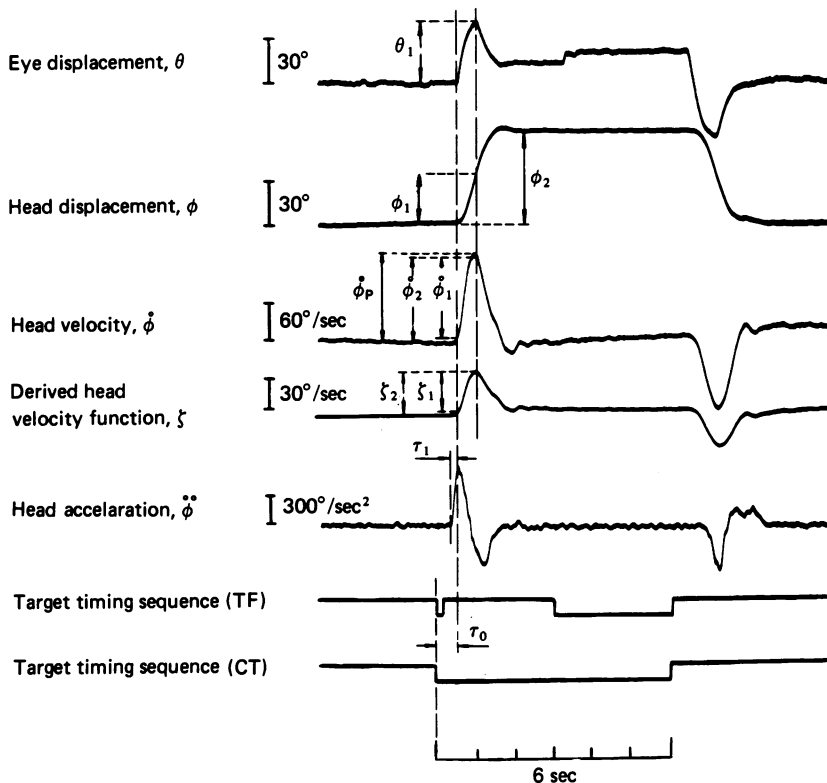


Fig. 3. A typical example of the response of the head and eyes during visual target acquisition, indicating the manner in which the defined variables were derived from the traces plotted on a multichannel recorder. Subscript 1 (e.g. ξ_1 , ϕ_1) refers to the difference in the variable between the start and end of the saccade. Subscript 2 defines values of the variable referred to its initial value.

Quantitative relationships between measured variables

Data reduction

The objective of the quantitative analysis was to determine whether the qualitatively similar responses in the different experimental conditions could be distinguished by any measured criteria. Accordingly, measurements of the characteristics of the head and eye movements were made by writing out the recorded signals on an ultra-violet galvanometer recorder. Discrete movements of head and eyes were then marked out in the manner illustrated in Fig. 3, where the variables used for subsequent analysis are defined. In the continuous target and target flash conditions the target offset angle (ψ) formed a further variable. The derived head velocity function (ζ) was obtained by transforming the recorded head velocity signal according

to an analogue transfer function to be described later. A further derived variable, the gaze displacement (ξ), was defined as the sum of head and eye displacement. The following relationships between the measured variables have been considered in detail for each subject.

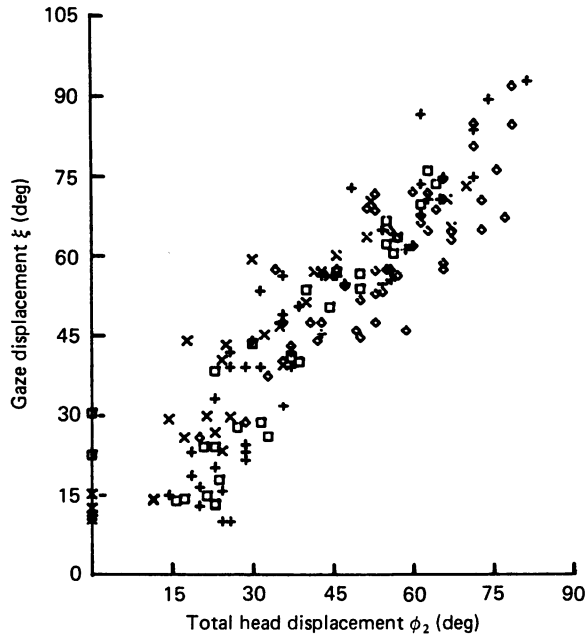


Fig. 4. The relationship between gaze displacement (ξ) at the end of the first saccade and total head displacement (ϕ_2), during visual target acquisition (CT, \times ; TF, \square) and during head movements in the dark (VR, $+$; PR, \diamond).

The relationship between gaze displacement (ξ) and total head displacement (ϕ_2)

The relationship between gaze displacement at the end of the saccade and the total head displacement is illustrated in Fig. 4 for each of the experimental conditions. The results from only one subject (S5) are illustrated as all were similar in form. The individual results were fitted using the functional relationship technique (a technique similar to linear regression analysis in which there is assumed to be error in both the dependent and independent variables) to an equation of the form

$$\xi = m_1 \phi_2 + c_1. \quad (1)$$

It was found that a linear relationship best described the majority (80%) of the responses obtained from all subjects. Values lying along the ordinate were rejected since these represented eye movements without head movements. The values of the coefficients m_1 and c_1 and of the associated correlation coefficients (r_1) for each of the experimental conditions are set out in Table 1 together with the r.m.s. error about the line of best fit (s_1).

On the basis of the values of r_1 it is possible to say that during voluntary and passive head rotation in the dark, the probability of eq. (1) not being the describing function for these results is less than 0.001. Similarly the correlation coefficients for the continuous target and target flash conditions were, in general, very high

($r_1 > 0.89$ for eight of the twelve) with an associated probability of less than 0.001. Sets of data exhibiting low values of r_1 were found to contain a number of responses of the type illustrated in Fig. 2 (ii) in which more than one saccade was executed during the course of the head movement. It will be shown later that there is a plausible explanation for the occurrence of such responses.

TABLE 1. The coefficients (m_1 and c_1) of eq. (1) with the associated correlation coefficient (r_1) and r.m.s. error about the line of best fit (s_1)

Subject ...	S1	S2	S3	S4	S5	S6	All Ss
CT							
m_1	1.09	1.16	1.18	0.58	1.00	1.06	1.03
c_1 (deg)	-0.8	-4.6	4.9	15.5	10.6	0.8	4.4
r_1	0.46	0.98	0.95	0.63	0.93	0.95	0.83
s_1	7.5	1.7	2.9	8.0	3.6	2.9	3.8
TF							
m_1	1.33	1.20	0.90	0.69	1.14	1.06	1.07
c_1 (deg)	-2.4	-4.4	-1.2	7.0	-0.4	-2.4	-1.7
r_1	0.97	0.98	0.98	0.71	0.89	0.82	0.85
s_1	1.7	1.5	1.8	6.8	4.1	5.3	3.9
VR							
m_1	1.41	1.27	0.99	0.95	1.30	1.45	1.24
c_1 (deg)	-0.1	-12.2	-7.8	3.2	-6.8	-8.5	-5.8
r_1	0.85	0.90	0.90	0.84	0.93	0.78	0.83
s_1	3.8	3.6	4.4	5.6	3.2	4.7	4.0
PR							
m_1	1.01	0.98	1.19	1.49	1.01	1.26	1.17
c_1 (deg)	16.1	3.0	-5.3	-13.3	2.6	-11.1	-3.1
r_1	0.88	0.82	0.71	0.81	0.85	0.75	0.77
s_1	3.6	5.2	5.0	3.6	3.8	5.0	4.2
All conditions							
m_1	1.39	1.13	1.09	1.07	1.06	1.17	
c_1 (deg)	-3.3	-3.5	-4.1	0.3	3.1	-3.5	
r_1	0.83	0.92	0.83	0.76	0.91	0.82	
s_1	3.6	3.2	3.4	4.1	3.7	4.3	

Analysis of variance revealed no significant difference in the values of the slope (mean 1.1, s.d. 0.2) or intercept (mean -0.7, s.d. 7.8) between any of the four stimulus conditions. The similarity of the responses to all four conditions is indicated by the large correlation coefficients ($r > 0.76$) obtained by combining the responses from all conditions (Table 1).

The relationship between total head displacement (ϕ_2) and target offset (ψ)

It has been demonstrated that gaze displacement is highly correlated with total head displacement during head movements in the dark. If the mechanisms responsible for this relationship were to function during visual target acquisition it is apparent that there should be a well defined relationship between head displacement and the amplitude of target offset.

Regression analysis revealed that the relationship between total head displacement and target offset (Fig. 5) could be represented by a linear equation with a slope of 0.80 for continuous target presentation and 0.78 for the target flash condition.

These values compare well with those obtained by Gresty (1974) (0.75 and 0.82 respectively) using similar experimental methods but are less than those obtained by Bizzi, Kalil, Morasso & Tagliasco (1972) in monkeys (0.92 for continuous target presentation only).

An analysis of variance was also carried out on the data which showed that total head displacement was correlated with target offset in a linear manner with a high level of significance ($P < 0.001$). However, there was no significant difference between the continuous target and target flash conditions, mainly because of the large inter-subject variance. This finding is in contrast to that of Gresty (1974) who found that the amplitude of head movement was significantly higher in the target flash condition.

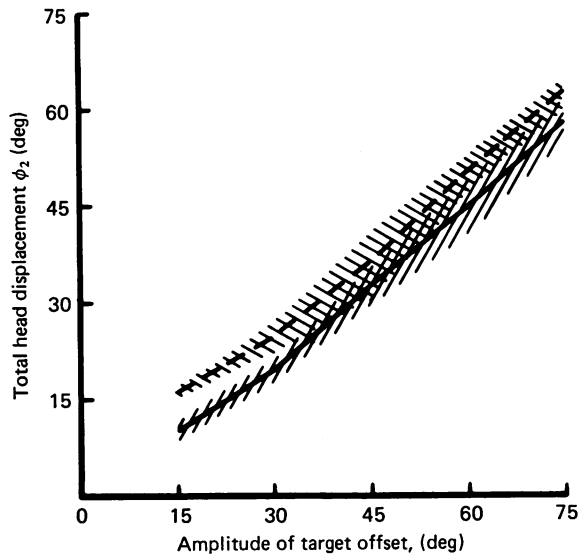


Fig. 5. The relationship between total head displacement (ϕ_2) and the target offset angle (ψ) during visual target acquisition (mean of six subjects; hatching indicates ± 1 S.D.). —, continuous target; ---, target flash.

The relationship between gaze displacement (ξ) and target offset (ψ)

One objective of the experiments was to consider the magnitude of errors in gaze displacement arising during the two target-seeking conditions. The results have been presented as the relationship between gaze displacement at the termination of the first saccade and target offset. It is important to emphasise that gaze was calculated for the first saccade only, as the object was to investigate whether the saccade is based on a predictive estimate or on a more precise retinal error signal. Representative results from two subjects are shown in Fig. 6.

There was a considerable difference between the response patterns of individual subjects and between the two experimental conditions. The feature common to all was that for the smaller values of target offset (15 and 30°) the gaze displacement showed little percentage error (generally $< 10\%$) whereas for the larger target angles the error in the initial gaze displacement was frequently large (50% and

greater). An indication of the magnitude of errors is given by the fact that 22% of all responses to 60 and 75° target offsets were in error by more than 15°.

The type of response which produced such large errors in gaze displacement (see Fig. 2 (ii)) appeared to be associated with low velocity movements. Consequently the relationship between gaze displacement and head velocity has also been examined.

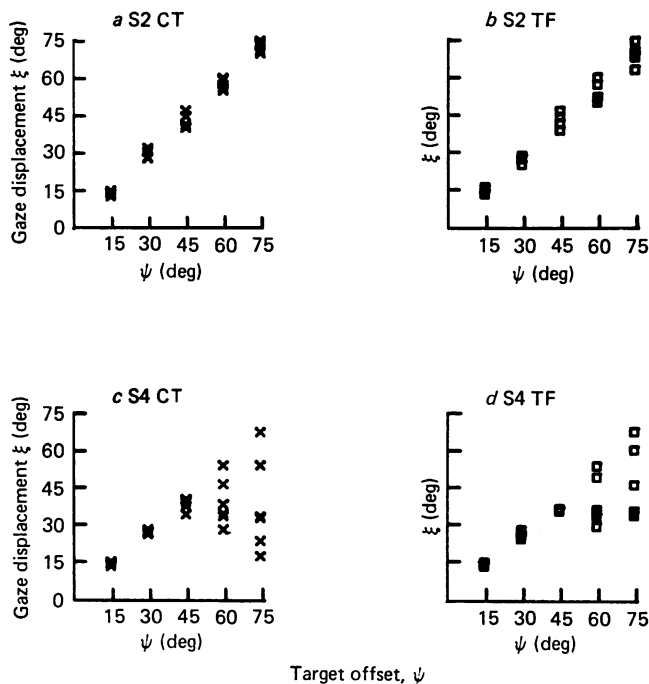


Fig. 6. The relationship between gaze displacement (ξ) at the end of the initial saccade and target offset angle (ψ) during visual target acquisition (CT, x; TF, □); a comparison of the responses of S2, who displayed little error in ξ , with those of S4 who made large errors in initial gaze displacement.

The relationship between gaze displacement (ξ) and head velocity ($\dot{\phi}_1$)

The responses of all subjects gave a positive correlation of gaze displacement with head velocity but many of the correlation coefficients were very low. Examination of the results showed that it was head movements of very high velocity ($> 100^\circ/\text{sec}$) and short duration (< 0.3 sec) which were contributing the largest part of the variance and these occurred mostly in the dark.

Therefore an attempt was made to derive a function of the head velocity which would produce significant attenuation of the short duration movements but which would not greatly reduce the degree of phase advance on head displacement.

The derived function (ζ) which was found to fit approximately for the majority of subjects had the form

$$\zeta(s) = \frac{1 + 0.25s}{1 + s} \dot{\phi}(s) \quad (2)$$

and specific values of $\zeta(t)$ were obtained by feeding the recorded head velocity signal through an appropriate analogue filter.

Fig. 7 illustrates the results obtained for the relationship between gaze displacement (ξ) and the derived velocity function (ζ_1) (see Fig. 3) for one of the six subjects (S5) under all experimental conditions. The technique of analysis used was that of deriving the functional relationship defined by the equation

$$\xi = m_2 \zeta_1 + c_2. \quad (3)$$

The associated correlation coefficients (r_2) together with the values of the slope and intercept are given in Table 2.

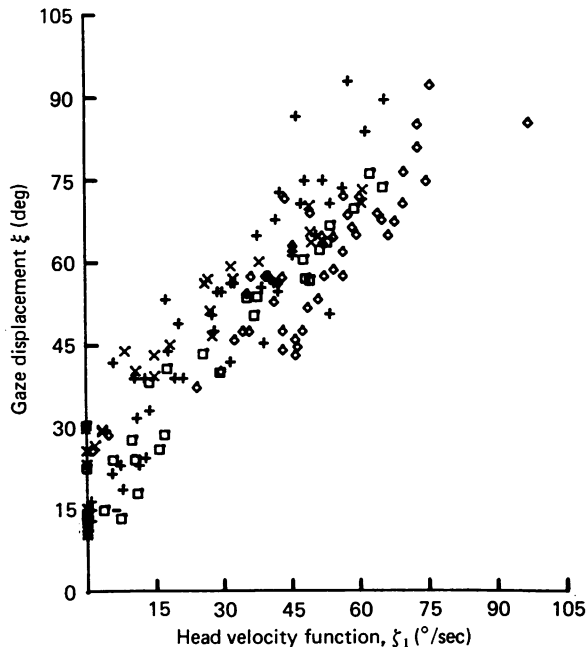


Fig. 7. The relationship between gaze displacement (ξ) at the end of the initial saccade and the derived head velocity function (ζ_1), during visual target acquisition (CT, \times ; TF, \square) and during head movement in the dark (VR, $+$; PR, \diamond).

The probability that eq. (3) does not fit the experimental data is very low ($P < 0.001$) for all subjects under all four experimental conditions. Comparison of the coefficients of eq. (3) by analysis of variance indicated no significant difference in the slope (mean 1.2, s.d. 0.3) or in the intercept (mean 12.6, s.d. 6.6) between the four experimental conditions.

For those responses in which there were large errors in initial gaze displacement and consequently a low level of correlation between gaze displacement and target offset there was a much higher correlation between gaze displacement and the derived head velocity function (ζ_1). Examination of the individual results showing large errors of undershoot revealed that these were mostly of the response type illustrated in Fig. 2 (ii), in which there was more than one saccade executed during the head movement and in which the head velocity was lower than normal for such a target offset angle.

A more positive indication of the fidelity of the relationship between gaze displace-

ment and the derived velocity function (ζ_1) can be obtained by correlating the values obtained at each individual target offset angle during target acquisition. Analysis revealed that for the 60 and 75° target angles there was always a positive correlation, even for those responses in which there was a relatively low level of error in initial gaze displacement. However, for the 15, 30 and 45° target angles the correlations were not consistently positive.

TABLE 2. The coefficients (m_2 and c_2) of eq. (3) with the associated correlation coefficient (r_2) and r.m.s. error about the line of best fit (s_2)

Subject ...	S1	S2	S3	S4	S5	S6	All Ss
CT							
m_2	2.01	1.02	1.25	1.30	0.93	0.94	1.12
c_2 (deg)	13.6	16.6	16.7	22.0	20.4	18.6	12.9
r_2	0.81	0.97	0.94	0.87	0.94	0.94	0.88
s_2	2.3	2.8	2.9	2.8	3.9	3.5	2.9
TF							
m_2	1.44	1.19	1.29	1.43	0.84	1.24	1.06
c_2 (deg)	-2.8	11.2	4.3	22.5	14.7	14.1	19.3
r_2	0.88	0.97	0.90	0.85	0.97	0.95	0.92
s_2	4.0	2.1	3.4	2.9	3.1	2.5	3.0
VR							
m_2	1.08	0.95	1.15	1.78	1.13	1.51	0.95
c_2 (deg)	8.6	7.8	6.8	13.5	10.6	6.2	14.0
r_2	0.54	0.78	0.91	0.93	0.93	0.89	0.76
s_2	13.9	8.8	3.8	1.8	3.8	3.4	4.8
PR							
m_2	0.99	1.28	1.27	1.03	0.87	0.87	1.08
c_2 (deg)	26.6	13.0	10.2	10.8	7.3	8.1	11.7
r_2	0.80	0.89	0.78	0.79	0.89	0.83	0.79
s_2	5.8	3.4	4.9	6.8	4.0	6.5	4.9
All conditions							
m_2	1.18	0.96	1.29	1.00	0.86	0.96	
c_2 (deg)	11.6	16.2	7.8	20.7	15.1	13.9	
r_2	0.69	0.87	0.87	0.85	0.91	0.84	
s_2	6.2	4.5	3.5	3.2	3.8	3.9	

An attempt has been made to optimize the function ζ for each of the subjects. A multiple linear regression analysis was carried out to find the best fit, for the data, to the equation

$$\xi = m_3 \zeta_1 + m_4 \dot{\phi}_1 + c_3. \tag{4}$$

The analysis was carried out for each subject using combined data from all four experimental conditions and the values of m_3 , m_4 , c_3 and the associated correlation coefficients r_3 are presented in Table 3. It is apparent from these results that the variance has been considerably reduced for some subjects, particularly S1.

The coefficients of eq. (4) can be used to derive an estimate of the optimum function of head velocity for each subject which is given by the equation

$$\zeta'(s) = \frac{1 + \tau s}{1 + s} \dot{\phi}(s), \tag{5}$$

where

$$\tau = (0.25 m_3 + m_4) / (m_3 + m_4)$$

and the new relationship between ξ and ζ_1 is given by

$$\xi = \alpha \zeta_1 + c_3,$$

where values of α are defined in Table 3. The values of τ were found to differ considerably between subjects.

TABLE 3. The coefficients (m_3 , m_4 and c_3) of eq. (4) with the associated correlation coefficient (r_3) and the values of the coefficients (τ and α) associated with the optimized velocity function (ζ') expressed in eq. (5)

Subject . . .	S1	S2	S3	S4	S5	S6
m_3	1.36	0.66	1.00	0.87	0.88	1.04
m_4	-0.27	0.03	-0.00	-0.04	-0.05	-0.10
c_3 (deg)	27.4	22.0	15.2	26.6	21.5	23.8
r_3	0.86	0.88	0.87	0.85	0.92	0.87
τ (sec)	0.06	0.28	0.25	0.22	0.20	0.17
α	1.08	0.69	1.00	0.83	0.83	0.93

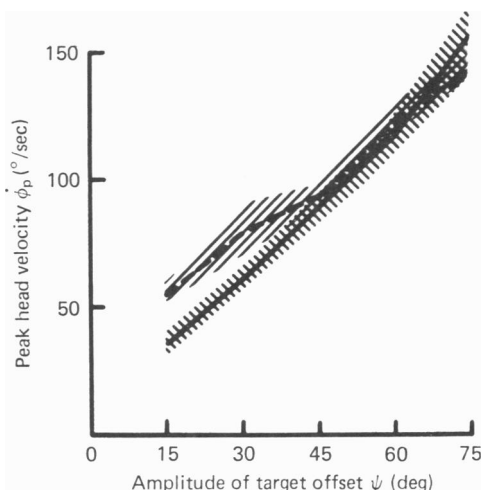


Fig. 8. Peak head velocity (ϕ_p) as a function of target offset angle (ψ) during visual target acquisition (mean of six subjects; hatching indicates ± 1 S.D.). —, continuous target; ---, target flash.

The relationship between peak head velocity (ϕ_p) and target offset (ψ)

The hypothesis that the amplitude of gaze displacement is determined by head velocity carries with it the assumption that head velocity is related to target offset for the majority of normal responses. Such a relationship has been demonstrated by Gresty (1974) in an experiment similar to the one reported here and by Bizzi *et al.* (1972) in monkeys.

In the present experiment movements to larger amplitude target offsets were generally made at higher velocity, as indicated in Fig. 8. Analysis of variance indicated that there was a highly significant ($P < 0.001$) linear correlation between ϕ_p and ψ . However, there was no significant difference in ϕ_p in the continuous target and target flash conditions, largely because of the differing behaviour of each subject. This is in contrast to the findings of Gresty (1974) who reported higher velocities

in the target flash condition from target offsets of 15 to 90°, but it may be significant that his recorded velocities were somewhat higher throughout the range.

The latency (τ_1) of eye movement with respect to head acceleration

A further objective of this experiment was to establish whether, during target seeking, the eye movement was initiated at an earlier stage with respect to head movement than during head movements performed in the dark.

The results have been compared by considering the latency (τ_1) as a function of gaze displacement (ξ) for each of the experimental conditions. Negative values of the latency (τ_1) indicate eye movement before head movement.

The three important factors which emerge from these results are as follows.

(1) Correlation analysis failed to reveal any meaningful relationship between the latency (τ_1) and gaze displacement for any of the stimulus conditions, the correlation coefficients being very low for all subjects. However, the latencies meaned over all subjects, were found to be ordered in relation to the stimulus condition in the following manner:

- | | |
|-------------------------------------|--------------------------|
| (i) continuous target presentation: | - 1 msec (S.D. 58 msec); |
| (ii) target flash condition: | 30 msec (S.D. 57 msec); |
| (iii) voluntary head rotation: | 78 msec (S.D. 74 msec); |
| (iv) passive head rotation: | 140 msec (S.D. 85 msec). |

Analysis of variance indicated a highly significant ($P < 0.001$) difference between all pairs of conditions.

(2) The distribution of negative latencies is of considerable interest. First, only rarely (eight times out of a total 300 movements) did saccadic eye movement precede head acceleration during head rotation in the dark and never during passively induced movements. On the other hand, during target seeking a considerable number of negative latencies were observed (thirty-nine out of 180 during continuous target presentation; twenty-seven out of 180 for the target flash condition).

A feature of particular interest is that, with the exception of one subject, the negative latencies were exclusively found in response to gaze displacements of less than 50°. A large number of these (twenty-nine in all) were responses in which the eye movement had been completed before the start of head movement or in which there was no head movement at all. These discrete movements were frequently observed for the smaller target angles (15 and 30°) and exceptionally for 45° displacements. However, one subject (S5) showed negative latencies during continuous target presentation even for amplitudes of gaze displacement up to 75°, although the latencies in the target flash condition obeyed the general rule expounded above.

(3) Frequently during voluntary head movement in the dark, and occasionally during passive stimulation, it was observed that the saccadic eye movement was initiated simultaneously with head acceleration, a point which will be considered in more detail in the Discussion.

The latencies in the continuous target and target flash conditions have also been examined in relation to target offset (ψ) (Fig. 9). Analysis of variance revealed that the values of the latency were significantly lower ($P < 0.001$) during continuous

target presentation. Note, however, that the mean values of τ_1 in the continuous target condition are positive for target offset angles greater than 45° .

The latency (τ_0) of eye movement initiation with respect to target presentation

The latency (τ_0) between illumination of the offset target light and onset of the saccadic eye movement is illustrated in Fig. 10, as a function of target offset.

The responses during continuous target presentation showed a positive correlation ($P < 0.001$ for all subjects) between the latency (τ_0) and target offset. The mean

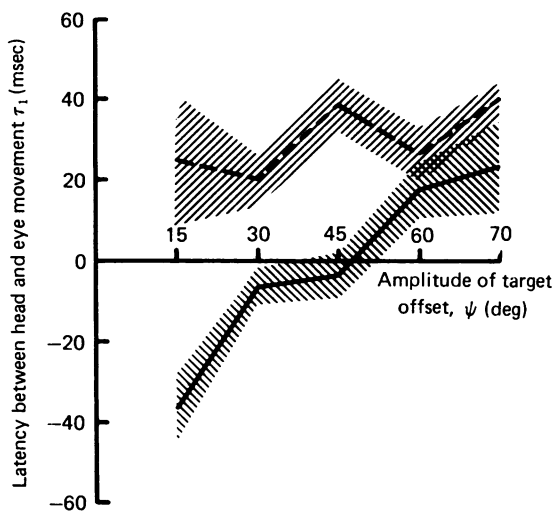


Fig. 9

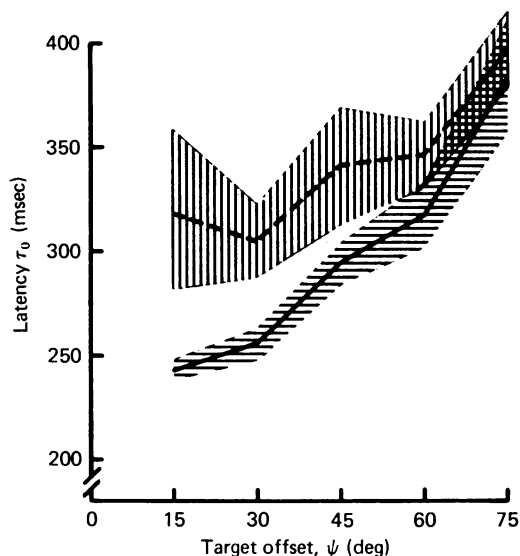


Fig. 10

Fig. 9. The latency (τ_1) between head movement and saccadic eye movement initiation as a function of target offset angle (ψ) during visual target acquisition (mean of six subjects; hatching indicates ± 1 S.D.). —, continuous target; ---, target flash.

Fig. 10. The latency (τ_0) between target presentation and saccadic eye movement initiation as a function of target offset angle (ψ) during visual target acquisition (mean of six subjects; hatching indicates ± 1 S.D.). —, continuous target; ---, target flash.

latency increased from a value of 243 msec at 15° to 383 msec at 75° , in contrast to the findings of Gresty (1974) who found no such increase. The responses to the target flash condition also showed a positive correlation, though with a lower level of significance, with mean latency rising from 317 to 396 msec. An analysis of variance revealed, rather surprisingly, no significant difference between stimulus conditions, a factor which was attributable to the significant interaction of subject with condition.

The latency of head movement initiation (τ_2) with respect to target presentation

The final variable to be considered is the latency between target presentation and the start of head movement (Fig. 11). Analysis of variance revealed a highly significant positive correlation ($P < 0.001$) between the latency (τ_0) and target offset for both stimulus conditions, the latencies in the target flash condition being significantly longer ($P < 0.05$). There was a highly significant difference between

subjects and a study of the results revealed that one subject (S5) contributed the largest part of the variance in the target flash condition.

The differences between the latencies τ_0 and τ_2 in the continuous target and target flash conditions brings out an interesting point concerning the differing performance of different subjects which may be summarized as follows. Three of the subjects (S1, S2, and S4) showed little or no difference between conditions in

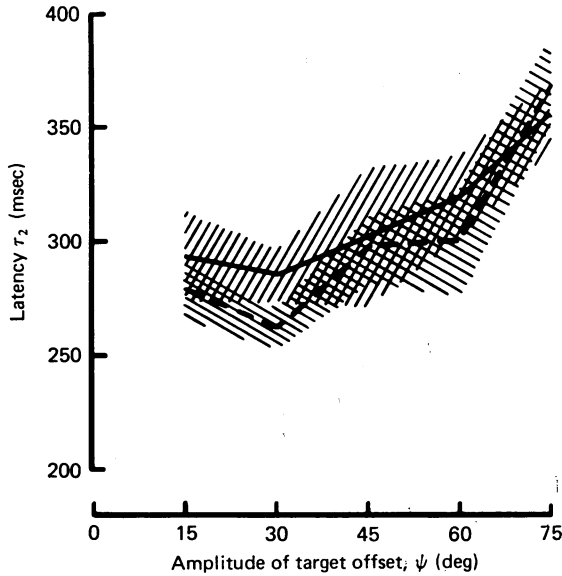


Fig. 11. The latency (τ_2) between target presentation and the start of head movement as a function of target offset angle (ψ) during visual target acquisition (mean of six subjects; hatching indicates ± 1 S.D.). —, continuous target; ---, target flash.

the latency (τ_0) to the start of the eye movement (mean differences 8 msec). Two of the subjects (S3 and S6) exhibited longer latencies to the start of eye movement (τ_0) in the target flash condition (mean difference 92 msec) but very little difference in the shortest latency (τ_3) to the start of either head or eye movement (mean difference 12 msec). These two subjects also showed little or no difference between conditions in the latency to the start of head movement (mean difference 5 msec). In other words, in both conditions, the head was moved within the same period after the stimulus but in the target flash condition saccadic initiation was delayed. Finally, one subject (S5) exhibited considerably longer latencies (τ_3) to the start of any movement (of either head or eye) in the target flash condition (mean difference 120 msec). It is of particular interest that S5 exhibited the greatest tendency to initiate the eye movement before the head movement and even in the target flash condition, where both head and eye movement were considerably delayed, 70% of all eye movements started before or simultaneously with head movement.

DISCUSSION

The most important fact to emerge from the experimental results is that when the head is moved either voluntarily or passively (see also Barnes, 1975) in complete darkness, the pattern of eye movement is similar to that observed during visual target acquisition. This fact alone calls into question the role of retinal error information in the determination of the amplitude of gaze displacement.

If the head is fixed then the gaze displacement is accomplished by a saccadic eye movement alone and its amplitude is presumably determined by the retinal error. When the head is free to turn, the gaze displacement still appears as a maximum velocity saccade (see Fig. 2), but the eye movement relative to the head is no longer of constant velocity because it is modified by the slow phase component of the vestibulo-ocular response, which leads to the 'rounding' of the saccade before its termination. However it has been demonstrated that during both voluntary and passive rotation of the head in the absence of any retinal error information the eye movement contains a saccadic component and it is clearly necessary to explain how such a saccade might interact with one determined by retinal error information.

One possible explanation is that retinal error information is used not to determine gaze displacement but to determine the amplitude of head movement. In order that such a system should function effectively it would be necessary for the peak gaze displacement to be functionally related to the amplitude of head movement. Evidence for such a relationship is provided by the high correlation between gaze displacement at the end of the initial saccade and total head displacement, which is apparently independent of stimulus condition.

The similarity does not necessarily imply that it is the vestibular system which is responsible for the generation of the saccade during target acquisition. It may merely demonstrate the ability of one system to mimic another so that whichever system is being used the nett response will be similar in form and will not lead to difficulties in, for example, spatial orientation. The usefulness of the relationship between head and eye movements in the dark is evident. If there were no saccadic component the eye would remain stabilized in space. The introduction of a saccade enables the subject to view, and possibly search, the visual field towards which the head is being turned.

No quantitative test of the adequacy of slow phase compensation was carried out, but qualitatively it appears that compensation is normally very precise, since gaze displacement remains essentially constant following the end of the initial saccade (Fig. 2). Peak gaze displacement is, in general, achieved before the end of the head movement and its relationship to total head displacement is thus a predictive one. For such a relationship to exist during passive stimulation in the dark the oculomotor system must have access to a predictive estimate of final head position.

The head turning movement is a very potent stimulus to the lateral semicircular canals, which effectively transduce head angular velocity in the range of frequencies normally associated with voluntary movements (Goldberg & Fernandez, 1971). Head velocity is phase advanced on head position and, to that extent, predicts it. It is therefore not surprising to find gaze displacement to be closely related to a function of head velocity. The particular function (ζ) defined by eq. (5) has been

shown, through modelling of the vestibulo-ocular reflex (Barnes, 1976*b*, 1978*b*), to be capable of providing just such a predictive estimate of final head position within the specific frequency band of normal head movement.

In general, the results of Table 1 indicate that the predictive gaze displacement is greater than the total head displacement, so that, in its final position, the eye is offset in the direction of head displacement, a feature which has been found by other authors during target acquisition (Bartz, 1966; Bizzi *et al.* 1972; Gresty, 1974). The gaze displacement is shared between the head and eyes; clearly a functionally advantageous manoeuvre since the head and eyes are individually limited to lateral angular excursions of approximately $\pm 75^\circ$ and $\pm 45^\circ$ respectively.

One of the most important factors in assessing the relative contribution of the vestibular and visual mechanisms during visual target acquisition is the latency of eye movement with respect to head movement. The saccadic eye movement was initiated before head acceleration in some responses to the visual target presentation; a finding that, necessarily, rules out the concept of saccadic initiation by the vestibulo-ocular reflex in those responses.

The negative values of the latency (τ_1) were mostly confined to responses to target angles of 45° or less, in which the errors in gaze displacement were very small. Conversely, there were very few responses to the 60° and 75° target offsets in which the eye movement preceded head movement. It was precisely in the latter group of responses that large errors were made in initial gaze displacement and in which gaze displacement was positively correlated with head velocity. Thus, for the smaller target offsets (up to 45°) it appears probable that control is mediated principally by retinal error information; for movements to the larger target offsets control is probably achieved by the system that is responsible for head-eye co-ordination in the dark. This conclusion must be tempered in view of the finding that the mean latency between head and eye movement was greater during head movements in the dark than during visual target acquisition. However, in all subjects a large proportion of the latencies during head movements in the dark were comparable to those during target flash presentation for the 60° and 75° target offsets. From visual inspection of the responses, the longer latencies appear to be associated with the lower levels of head velocity (see Fig. 2 (ii)) which were encountered infrequently during target acquisition.

During voluntary head movements in the dark there were a small number of responses in which the eye movement started before head acceleration and considerably more in which the two started simultaneously. A possible explanation is that during voluntary movements the saccade may be initiated by a central command. A collateral of the pathway responsible for neck motor activity relaying information directly to the saccadic generating mechanism could give shorter latencies between head and eye movement than those to be expected from vestibular stimulation (10 msec). In support of this concept Bizzi *et al.* (1972) have shown that when the eyes are moved to a target with the head clamped there is e.m.g. activity in the muscles of the neck which would produce movement of the head if it were free. It has also been demonstrated that stimulation of the superior colliculus, an area known to be intimately involved in visuomotor control (Goldberg & Wurtz, 1972; McIlwain, 1973), often results in head rotation as well as eye displacement (Faulkner & Hyde,

1958). This effect may be the result of stimulation of direct tecto-spinal fibres (Anderson, Yoshida & Wilson, 1971) or of more indirect pathways through the reticular formation.

However, this hypothesis is brought into question by results obtained when voluntary head movements were made during the period of a separate co-existent vestibular response induced by (a) a stopping stimulus (Barnes, 1976*b*), and (b) by spontaneous activity of peripheral pathological origin (Barnes, 1978*a*). The timing of saccadic initiation was dependent upon the superposition of the compensatory components of the head turning response and the existing nystagmus, so that when these were of opposite polarity, the saccade was delayed. Central initiation of saccadic activity during head turning would be unlikely to give such a result.

During visual target acquisition it is possible that the saccade of vestibular origin may be suppressed. Evidence of the ability to suppress has been obtained from comparison of two experimental conditions involving voluntary movements of the head (Barnes, 1976*b*). It was found that if the target light was fixed to the head it was difficult to suppress either the fast or slow phase components of the evoked eye movement. However, when the head was moved whilst fixating a target in space, the fast phase component was never seen, no matter how quickly the head was moved. In the latter condition, the slow phase is appropriate and the resultant retinal error is small, whilst in the other condition it is inappropriate since no movement of the eye is required. If the eye movement is inappropriate then it can only be suppressed if the slow phase velocity is low enough for the visual tracking mechanism to be effective (Barnes, Benson & Prior, 1978). Otherwise, the slow phase will break through and the fast phase will be an automatic response of the saccadic mechanism. It would appear that it is the retinal error, or perhaps the rate of change of error, which is responsible for determining whether the saccade is present or not. It is possible that such a suppressive mechanism could be responsible for eliminating the vestibularly generated saccade during visual target acquisition.

The information available from the various experiments described has been used to compile a revised model of the mechanisms of oculomotor control (Barnes, 1976*b*; Benson & Barnes, 1978). This has led to the concept of a hierarchical system for the generation of the saccadic component of eye movement, in which retinal error information forms the most important and accurate input to the oculomotor nuclei. However, in the absence of adequate retinal information, the vestibulo-ocular reflex provides an estimate of future head position, thus allowing the more rapidly moving eye to anticipate the head movement, and aid the process of visual search.

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