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Eye-Head Coordination in Cats

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SUMMARY AND CONCLUSIONS

1. Gaze is the position of the visual axis in space and is the sum of the eye movement relative to the head plus head movement relative to space. In monkeys, a gaze shift is programmed with a single saccade that will, by itself, take the eye to a target, irrespective of whether the head moves. If the head turns simultaneously, the saccade is correctly reduced in size (to prevent gaze overshoot) by the vestibuloocular reflex (VOR).

2. Cats have an oculomotor range (OMR) of only about ±25°, but their field of view extends to about ±70°. The use of the monkey's motor strategy to acquire targets lying beyond ±25° requires the programming of saccades that cannot be physically made.

3. We have studied, in cats, rapid horizontal gaze shifts to visual targets within and beyond the OMR. Heads were either totally unrestrained or attached to an apparatus that permitted short unexpected perturbations of the head trajectory.

4. Qualitatively, similar rapid gaze shifts of all sizes up to at least 70° could be accomplished with the classic single-eye saccade and a saccade-like head movement. For gaze shifts greater than 30°, this classic pattern frequently was not observed, and gaze shifts were accomplished with a series of rapid eye movements whose time separation decreased, frequently until they blended into each other, as head velocity increased. Between discrete rapid eye movements, gaze continued in constant velocity ramps, controlled by signals added to the VOR-induced compensatory phase that followed a saccade.

5. When the head was braked just prior to its onset in a 10° gaze shift, the eye attained the target. This motor strategy is the same as that reported for monkeys. However, for larger target eccentricities (e.g., 50°), the gaze shift was interrupted by the brake and the average saccade amplitude was 12–15°, well short of the target and the OMR. Gaze shifts were completed by vestibularly driven eye movements when the head was released.

6. Braking the head during either quick phases driven by passive head displacements or visually triggered saccades resulted in an acceleration of the eye, thereby implying interaction between the VOR and these rapid-eye-movement signals.

7. Head movements possessed a characteristic but task-dependent relationship between maximum velocity and amplitude. Head movements terminated with the head on target. The eye saccade usually lagged the head displacement.

8. Results suggest that *1*) rapid gaze shifts utilize the integrated action of active and reflexive mechanisms, specifically visually triggered saccades and vestibular quick phases; and *2*) eye and head positions are monitored by corollary discharges that yield an internal representation of gaze.

INTRODUCTION

Coordinated eye and head movements represent an elegant example of how the nervous system accurately controls two simultaneously moving body segments. Such movements were first studied systematically by Bizzi and his colleagues (5, 14, 29), who showed that when a monkey orients to a randomly appearing visual target, it encodes the same saccadic-eye-movement signal in both the head-fixed and head-free conditions. In the head-free condition, the vestibularly induced compensatory eye movement produced by the head movement is added linearly to the saccade signal. Since the compensatory eye movement is in the opposite direction to the saccade, saccade velocity and amplitude for a given target eccentricity are reduced by amounts equal to the velocity and amplitude, respectively, of the head. This mechanism has been called the addition hypothesis (33). The elegance of this system is that a saccadic eye movement can be programmed independently of the head movement and that a high degree of accuracy is achieved because the vestibuloocular reflex (VOR), operating at unity gain, enables the gaze to reach and stay on target irrespective of whether the head motion is perturbed.

There are, at present, conflicting views (33) regarding whether eye-head coordinated movements in cats make use of this motor strategy. In support of the addition hypothesis, Blakemore and Donaghy (7) have observed interaction between the VOR and saccades made within the oculomotor range (OMR). However, Haddad and Robinson (23), have argued against addition on the basis of their observation that the velocity of a saccade of given amplitude is faster in the head-free cat than it is in the head-fixed cat. In support of this view, Fuller et al. (17) reported no summation between the VOR and saccades accompanying active head-free gaze shifts in the cat.

The cat has an OMR of only 25° (21, 36), which is considerably less than that of the monkey. If the addition hypothesis was valid in the cat, then gaze shifts larger than the OMR would either be impossible head-free or require that the animal program saccades larger than those physically possible with its head fixed. Harris (24) reported that cats do not make gaze shifts greater than 25°. However, Collewijn (9) and Roucoux et al. (34) have reported single-step gaze shifts greater than 25° in the head-free animal.

The possibility that the cat may use a motor strategy different from that of the monkey was reinforced by Guitton et al. (21) and Roucoux et al. (35), who studied eye and head movements evoked by collicular stimulation in the alert animal. These results have suggested that for large evoked gaze movements beyond the OMR, the eye and head trajectories are preprogrammed and proceed independently of each other with the vestibular signals appearing to be momentarily prevented from affecting eye velocity during the saccade. This lack of interaction between rapid eye movements and the VOR is plausible given that quick phases, which are the rapid eye movements generated by vestibular stimulation, have been regarded to be different from saccades on the basis that during the former, but not the latter, the VOR appears to be "disconnected" (33). Thus collicular stimulation suggested that the cat may be using quick phases when reorienting its gaze. In further support of this mechanism, it has been shown that passive whole-body rotation in cats and humans can lead to, after a short latency of ~20–75 ms, a quick phase that takes the eye beyond center to optimize looking toward where the head is turning (8, 20, 28).

The main objectives of the studies presented in this paper were *1*) to resolve the conflicting data and to clarify the motor strategy used by the cat to shift its gaze using coordinated eye and head movements, and *2*) to determine how active ("foveating" saccades) and reflexive (quick phases) mechanisms might interact so that gaze may achieve a specific target zone. Another objective was to describe quantitatively the spatial and temporal characteristics of rapid horizontal-orienting movements of the head, the eye movements relative to the head, and the sum of head and eye movements defined as gaze. Some preliminary results have been presented elsewhere (15).

METHODS

General

Head and gaze movements are defined as changes in the position of the head and visual axis, respectively, with respect to the earth reference. The term eye movement will be used to refer to displacements of the visual axis (or eye) relative to the head. Rapid displacements of each of the above will be called head, gaze, and eye saccades, respectively.

Five adult cats (avg wt 3.5 kg) were studied. Stainless steel bolts were permanently implanted in the skull and around them was formed a dental acrylic pedestal. A thin stainless steel U-shaped crown was imbedded in the perimeter. A stainless steel bracket was attached to the crown and served to attach the cat's head to the braking mechanism described below. To conduct an experiment, the cat was first placed in a loosely fitting cloth bag and then into a box that gently restrained the body but permitted unrestricted upward and horizontal head movements in the range ± 90°. Downward head movements were limited to −60°. In these experiments only horizontal movements were studied.

The total weight of the skull bolts, acrylic mount, crown, and stainless steel bracket was 60 g compared with the average weight of a cat's head, which was ~300 g. The estimated (by calculation) moment of inertia of a cat's head about the C1–C2 junction, where rotation was assumed, was 5,300–10,000 g cm^2 depending on the animal's weight. Our calculated value of head inertia is in agreement with that experimentally determined by Peterson and Goldberg (30, and private communication) and can be compared with a value of 750 g cm^2 for the added components including the braking device (see next section). The effect on the head movement of this added inertia was negligible, as suggested by Fig. 4 (see next section).

Recording of eye and head movements

The results will show that the amplitude of ocular deviations in cats with head-free range from about 8° in 10° gaze shifts to 18° in 60° gaze shifts. Thus for large gaze shifts, important errors may arise when subtracting two large signals, gaze and head, to obtain a smaller one, the eye. Accordingly, considerable effort was made to assure that the gaze and head records were highly accurate.

Both head and gaze movements were measured with the search coil in magnetic field technique. The demodulating circuitry was adapted from McElligott et al. (27) (bandwidth 1.8 kHz, 3 dB; noise < 4 min). The field coils were 92 cm in diameter, which provided a cube-shaped region 8 cm on edge, where the field strength varied less than 2%. Cat head movements of ±60° horizontally (maximum deviation studied) covered a range of 8 cm.

The cats were implanted with a scleral eye coil of three turns and an identical coil was attached to the acrylic explant. To accurately measure large head and gaze deviations, it was necessary to take account of the fact that a coil's signal is proportional to the sine of its angular deviation. The appropriate calibration of the two coil signals was obtained by oscillating horizontally at 0.3 Hz, through an angle of ±70° the field coil arrangement about the animal whose head was fixed. The field coil angular deviation was obtained from a potentiometer. During this calibration procedure, the head, gaze, and potentiometer signals were sampled at 4-ms intervals and stored on a high-capacity disk drive. A linearized calibration was obtained off-line by first selecting a saccade-free segment of data and then storing in memory a look-up table of the head coil and eye coil (gaze) signals, respectively, vs. the field coil angular deviation calculated from the potentiometer signal. Thus the gaze and head signals obtained during the experiments could be transformed into angular deviations, the accuracy of which is discussed below.

The signal obtained by rotating the field coil about a stationary eye coil is not necessarily the same as that obtained in the actual experiments when the field was stationary and the head carried a simultaneously rotating eye coil. This is due to small signals induced in subcutaneous leads, connectors on the explant, and wire leads to the signal demodulators. To minimize this irrelevant pickup, the subcutaneous leads were formed of carefully twisted wire; connectors on the head were kept very small and were oriented such that a plane through the two pins was nearly horizontal. Also, the wire leads were made with special low-pickup cable (Perfection Mica). The calibration of the head coil could be easily verified independently of the cat by placing the same coil on a calibration device and turning it through known angles. Verification of the eye coil calibration was more difficult. In one animal, this was done by anesthetizing the cat and, with threads attached to the conjunctiva, moving the eyeball through known angles calculated by projecting the blind spot onto a tangent screen. With the eyeball fixed in the orbit, the head was also moved through known angles. No significant difference was found between these two different eye coil calibration procedures and those obtained by simply rotating the field coils. Since all cats were prepared in the same way, a similar result was assumed true for all subsequent animals.

Behavioral conditions

The behavioral conditions under which the cats were tested were determined with two major objectives in mind: *1*) to obtain rapidly and reliably in an alert animal behaving as naturally as possible, a large number of coordinated eye-head displacements having a wide range of amplitudes; and *2*) to obtain with reliable latency visually triggered gaze displacements to targets with eccentricities varying between 10 and 60°.

The first objective was met by placing in front of a hungry cat an opaque screen, with either its left or right vertical border in line with the cat's central gaze position, and protruding some food randomly on one side or the other. By varying the width of the screen, a wide range of amplitudes of horizontal gaze movements could be produced as the highly aroused animal eagerly looked to and fro from one side of the screen to the other. In the text, this behavioral condition will be referred to as the search mode.

Three of the cats were also trained to orient to one of a number of light-emitting diodes (LEDs) spaced symmetrically on a horizontal semicircular perimeter arc. The LEDs were spaced symmetrically from the center position at angles of 10 to 60°. The cats were trained to look at a spoonful of food placed near center and to orient to a LED following its unexpected illumination. Following a correct orienting movement, food was advanced from immediately above the LED on a holder. This behavioral mode will be referred to as the visually triggered mode. It was thought to be very lifelike because food appeared proximal to a prior sensory stimulus. Accordingly, the technique permitted very rapid training (2–4 20-min sessions). The cat whose data is presented here oriented accurately with a SD of about ±1° to a LED at 30° and ±2° to another at 50°. Note that in the data analysis the effective target eccentricity was taken as the angle between the LED and the gaze's starting position.

In the behavioral tasks described above, the perimeter arc was placed at a distance of ~50 cm in front of the plane passing through the center of rotation of each eye, whereas the distance between this plane and the center of rotation of the head was ~7 cm. For this ratio of distances (7/40 = 0.14), the theoretical VOR gain of the compensatory movement should be ~1.1 if gaze is to remain fixed on the target with no retinal slip (4, 7, 10). Blakemore and Donaghy (7) have reported actual gains lower than the theoretical values in cats performing coordinated eye-head movements to proximal targets. During such active movements, our cats always had VOR gains close to unity.

Braking of head movement

The three trained cats, in either the search or visually triggered modes, were tested on an apparatus that permitted unexpected braking of the head movement shortly before or after its initiation. This procedure can reveal the influence of the VOR on saccades by taking advantage of the fact that *1*) visual feedback takes an order of magnitude longer than the VOR to affect eye movements, and *2*) neck proprioception as expressed by the cervicoocular reflex has negligible effects on eye movements (1, 16, 29, 30). To perform these tests, the cat's head was attached via a universal joint to a shaft equipped with an electromagnetic brake (static torque = 40 kg cm) and a potentiometer for recording head movements. The center of rotation could be adjusted to provide the cat with maximum comfort and the least impediment to normal head motion. In general, the axis of rotation was above the C1–C2 junction, whose position in turn was estimated by measuring from the lambdoidal crest. In the apparatus, the cat maintained its head at ~20–30° below the stereotaxic plane, which corresponds approximately to normal head posture (13, 19).

In the experiments, the brake was applied randomly in 1 of about every 10 movements. The brake onset was triggered either after a fixed delay from the onset of the target light or when the head or eye velocity signals exceeded a predetermined threshold value. The data were sampled by the computer at intervals of 2–4 ms.

The restrictive effects of the braking system on head motion were negligible in the trained cats. For example, Fig. 4*B* shows that head-orienting movements are like eye saccades in that they show a specific relation between peak velocity and amplitude. This figure shows, with open circles, the characteristics of movements made during a period of ~2 min by an aroused cat with its head totally free and not attached to the shaft of the braking system as it searched for food occasionally presented from behind the opaque screen. By comparison, the filled circles correspond to movement made immediately afterward, when the cat's head was placed in the holder. The slight restraint and added inertia of the braking system had no effect on the characteristics of the head movement.

Data analysis

The characteristics of gaze, head, and eye movements were studied in five cats when their heads were either completely free or in the holder of the braking system. Braking experiments were performed on three of the cats. All data were stored on the computer disk and digital magnetic tape. During off-line analysis, the movements were viewed on a large screen oscilloscope. A semiautomatic analysis routine was used in which cursors were placed about selected movements. Gaze, head, and eye characteristics, as well as other quantities presented in RESULTS were automatically measured. The operator scrutinizing the data could overide any measurement made by the automatic analysis.

RESULTS

We will first present a general description of large and small gaze shifts in the cat, followed by a more quantitative analysis of the eye, gaze, and head trajectories when the head was braked at different times relative to the rapid eye movement. To facilitate an overview, all figures will show data obtained from the same cat (*cat L*). All cats yielded comparable results, and Table 1 shows a quantitative comparison between them.

General features of horizontal coordinated eye and head movements

In our experimental paradigms, cats never produced solitary saccades unaccompanied

TABLE 1. *Linear regression equations for eye, gaze, and head saccades*

Cat	$\dot{E}_m$ vs. E		$\dot{G}_m$ vs. G	$\dot{H}_m$ vs. H
			4	5
	Head free	Head fixed	Head free	
1	2	3		
B	$\dot{E}_m = 10.8\ E + 44.3$ $r = 0.82\ n = 32$	$\dot{E}_m = 10.4\ E + 16.0$ $r = 0.90\ n = 49$	$\dot{G}_m = 7.1\ G + 60.0$ $r = 0.76\ n = 32$	$\dot{H}_m = 6.1\ H + 24.8$ $r = 0.81\ n = 56$
C	$\dot{E}_m = 15.9\ E + 15.0$ $r = 0.89\ n = 66$	$\dot{E}_m = 11.9\ E + 4.0$ $r = 0.92\ n = 48$	$\dot{G}_m = 11.9\ G + 20.0$ $r = 0.86\ n = 66$	$\dot{H}_m = 7.4\ H + 19.2$ $r = 0.93\ n = 93$
H	$\dot{E}_m = 19.1\ E + 59.0$ $r = 0.83\ n = 48$	$\dot{E}_m = 14.4\ E + 47.0$ $r = 0.80\ n = 86$	$\dot{G}_m = 15.5\ G + 56.7$ $r = 0.90\ n = 48$	$\dot{H}_m = 8.1\ H + 45.1$ $r = 0.92\ n = 85$
S	$\dot{E}_m = 14.4\ E + 36.3$ $r = 0.92\ n = 72$	$\dot{E}_m = 11.2\ E + 10.3$ $r = 0.83\ n = 92$	$\dot{G}_m = 10.6\ G + 37.9$ $r = 0.89\ n = 72$	$\dot{H}_m = 4.9\ H + 34.2$ $r = 0.80\ n = 130$
L	$\dot{E}_m = 18.8\ E + 83.9$ $r = 0.74\ n = 49$ Fig. 2*A*, open circles	$\dot{E}_m = 14.7\ E + 88.7$ $r = 0.73\ n = 122$ Fig. 2*B*	$\dot{G}_m = 15.3\ G + 83.0$ $r = 0.84\ n = 49$	$\dot{H}_m = 6.8\ H + 109.0$ $r = 0.84\ n = 70$ Fig. 4*B*, open circles

G, H, E, gaze and head, relative to space, and eye, relative to head, respectively (degrees). G_m, H_m, E_m, gaze, head, and eye maximum velocities (degrees per second). *n*, no. of data points. *r*, correlation coefficient. Column 1: data presented in figures are from *cat L*. Columns 2-4: because of cats' limited oculomotor range, no saccade starting from central position and contributing to regression lines in column 3 has an amplitude greater than 25°. To permit comparison, regression lines in columns 2 and 4 are through points for which $G < 25°$. Note also that regression lines in columns 2 and 4 are, for each cat, taken from same experimental session. Column 5: these data obtained with cat in search mode when head was totally free and not in holder.

by a head movement even for 10° target offsets that are well within their OMR (~25°). Similarly, rapid head movements without a saccade were never seen. Typically, rapid eye movements occurred just after (see next section) the head began its characteristic saccade-like trajectory. In agreement with Collewijn (9) and Roucoux et al. (34) but not Harris (24), all of our cats could produce large single-step gaze shifts of amplitude greater than their OMR. The maximum single-step gaze shift observed had an amplitude of ~70°. Figure 1*A* shows an example of a coordinated eye and head movement associated with a 10° gaze shift made by one cat in the visually triggered mode. Gaze (G) is the position of the visual axis in space and is the sum of the eye movement relative to the head (E) plus head movement relative to space (H). $\dot{G}$ and $\dot{E}$ represent gaze and eye velocity, respectively. The movement resembles the classic pattern of eye-head coordination as described by Bizzi and colleagues (5, 14, 29). Once the visual axis was on target, the gaze trace was flat since the effect of head movement was canceled by the VOR (see next section). Figure 1*B* shows an example of an orienting movement to a visual target situated at an eccentricity of 30° left of center, whereas Fig. 1, *C* and *D,* shows movements to targets at 50°. These traces look qualitatively similar to those of the small amplitude movements. However, one characteristic difference of the larger displacements (including 30°) was that the gaze velocity ($\dot{G}$) vs. time plot (Fig. 1, *B–D,* but not *A*) frequently did not exhibit the usual "bell-shaped" profile generally seen in the small gaze shifts. Rather, the profile was much flatter with peak velocity held over a proportionally longer time interval. Another interesting and unusual feature of the large gaze shifts was that the associated rapid eye movements were frequently composed of two regions (Fig. 1*D*): an initial high-velocity saccade-like region followed by a period of significantly lower velocity. This characteristic will be understandable in light of the subsequent results.

EYE-SACCADE CHARACTERISTICS: HEAD-FREE VS. HEAD-FIXED. It is well known that for the head-fixed cat there exists an approximately linear relationship between a saccade's

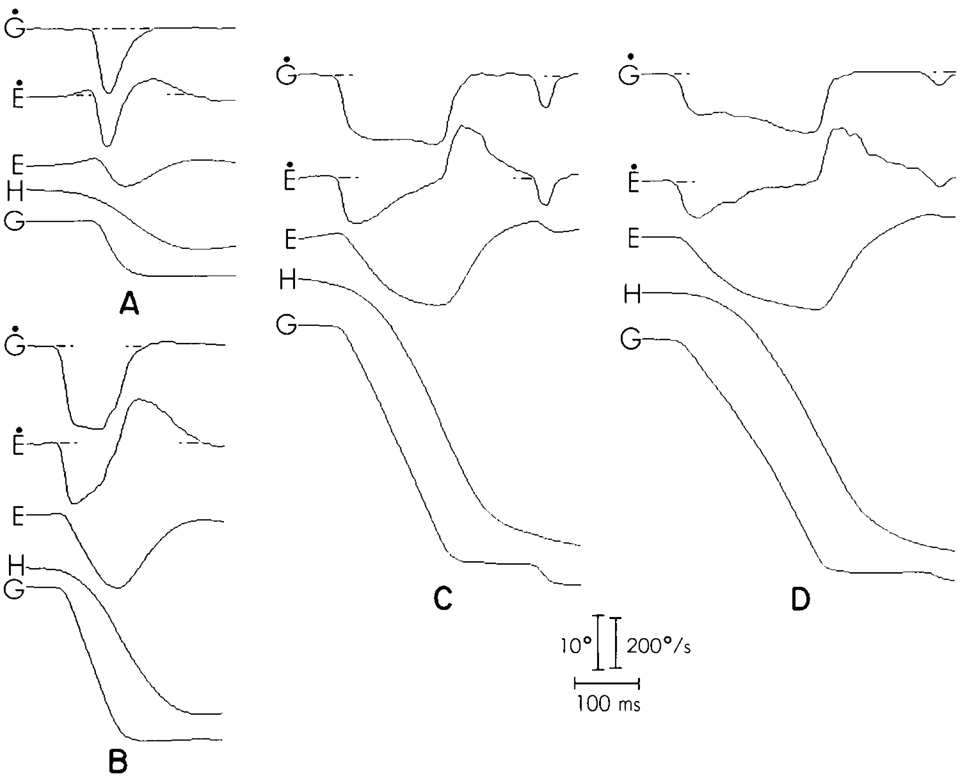

FIG. 1. Examples of "simple" coordinated eye-head movements made by a trained cat as it oriented to a small light spot. *A*: 10° gaze shift. *B*: 30° gaze shift. *C* and *D*: 50° gaze shifts. Latter 3 examples are for targets outside cats' oculomotor range (OMR). See text for further details. E, angular rotations of eye relative to head. H and G, head and gaze angular rotations relative to space. G = E + H. $\dot{E}$, $\dot{H}$, and $\dot{G}$, eye, head, and gaze velocities. Horizontal dash-dot lines on velocity traces indicate zero velocity.

maximum velocity ($\dot{E}_m$) and its amplitude (E) (22). To compare saccades in the head-free and head-fixed cat, it should be recalled that this relation is quite labile in the latter condition, being susceptible to the animal's state of alertness (12). Because the head-free cat orienting to LEDs for food was always very aroused, the head-fixed animal was also kept as alert as possible by presenting food and making novel sounds. For comparison, $\dot{E}_m$ and E are plotted for both the head-free (Fig. 2*A*) and head-fixed (Fig. 2*B*) conditions tested some 5 min apart when the cat was in the visually triggered mode. Because it was sometimes uncertain when head-free saccades ended (e.g., Fig. 1*D*), E was measured at the point where the eye trace had reached its fullest deviation, just before the compensatory phase. However, the precise choice of this point did not significantly affect the estimate of saccade amplitude. Because the head-fixed saccades in Fig. 2*B* never exceeded 20° in amplitude, the head-free data of Fig. 2*A* were divided into two groups: open circles correspond to head-free saccades that accompanied gaze shifts less than 20°, whereas filled circles represent saccades in larger gaze shifts. For comparison, the straight line in Fig. 2, *A* and *B*, is the linear regression line through the head-fixed data. For gaze shifts less than 20°, there was a tendency for saccades with head-free cats to be faster for a given amplitude than saccades with head-fixed cats. This difference, although small in this cat (*cat L*), was consistent in all cats tested (see Table 1) and is in agreement with previous reports (7, 23). The difference still existed when the cat was in the search mode for which head

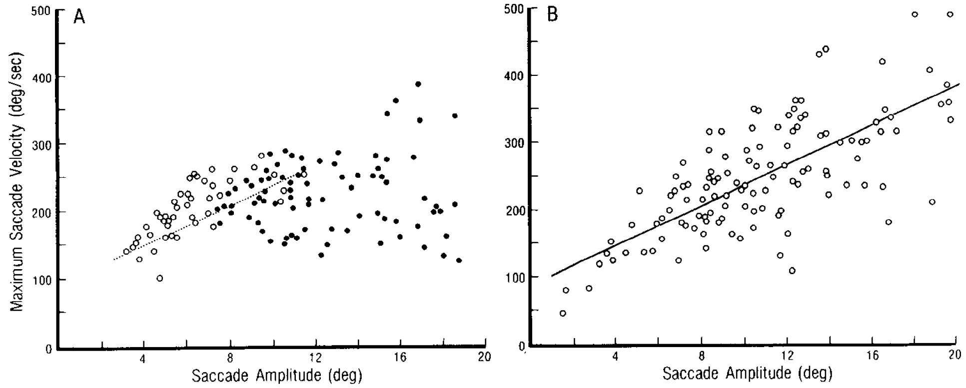

FIG. 2. Main sequence relationship linking maximum saccadic-eye velocity to saccade amplitude for visually triggered orienting movements. *A*: head free. Open circles are for saccades accompanying gaze shifts < 20°. Closed circles are for saccades accompanying gaze shifts > 20°. Dotted line through open circles is same as linear regression line through the head-fixed data shown in *B*. *B*: head fixed. Solid line is linear regression line: slope = 14.7/s, intercept = 88.7, n = 122 points, r = 0.73.

velocity was faster than in the visually triggered mode (Fig. 4). For gaze shifts larger than 20°, $\dot{E}_m$ in the head-free condition saturated at an average value of ~220°/s.

EYE LAGS HEAD. Contrary to the observations of Blakemore and Donaghy (7), the vast majority of saccades in all of our cats lagged the head movement. This was true in both the visually triggered and search modes and was independent of the amplitude of the gaze shifts. Obvious examples of this phenomenon are seen in Figs. 1 and 5. The average latency was ~40 ms. When the head began to move, there first appeared a slow phase followed by a saccade. This pattern is qualitatively similar to the one evoked by vestibular signals during passive head displacements (2, 8, 20, 28). There was no correlation between latency and head amplitude, nor between latency and starting eye position.

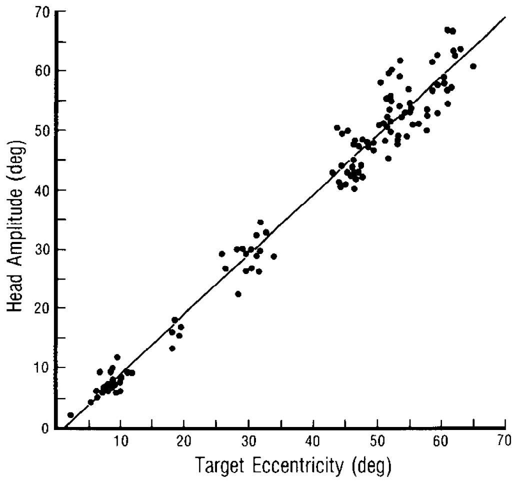

FIG. 3. Comparison between the amplitude of a head displacement and the target eccentricity for visually triggered movements. The solid line is the linear regression line through the data points: slope = 1.0, intercept = −1.2, n = 133 pts, r = 0.99.

HEAD-MOVEMENT AMPLITUDE. Figure 3 shows a typical relation between head amplitude and target eccentricity obtained when the eye began its saccade from a position in the orbit no greater than 1° from center. The linear regression line has a slope of 1.0 and an intercept, near zero, of −1.2. Thus on average an eye-head movement terminated with the head aligned on target and therefore with the eyes at center. The same conclusions applied to the search mode and for movements made with the head either in the holder or totally free. Very few movements began with the eye more than 2° from center, and therefore we could not accurately assess the effect of starting eye position on overall head-movement amplitude.

HEAD-MOVEMENT CHARACTERISTICS. Head displacements were very stereotyped movements whose saccade-like nature was reflected by rapidity and a high correlation between maximum velocity (H_m) and amplitude (H)

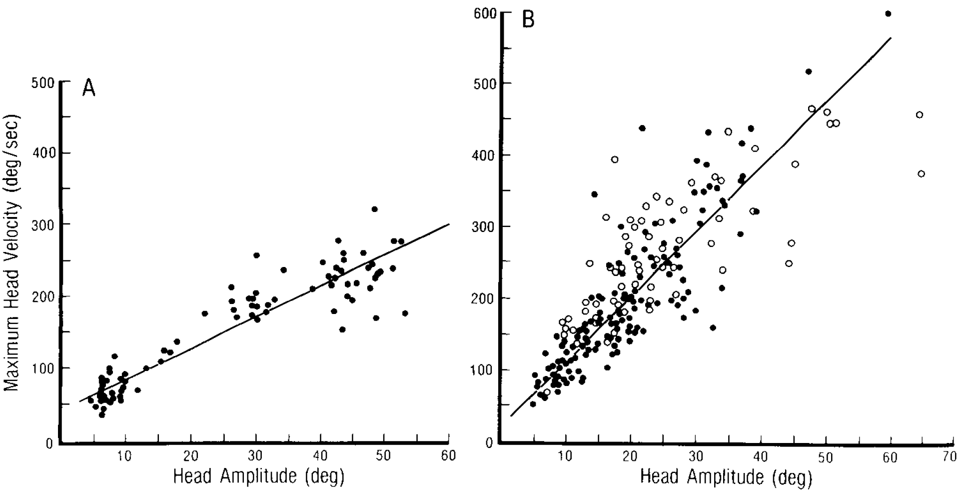

FIG. 4. Main sequence relationship linking maximum head velocity to head amplitude. *A*: cat orienting to visual targets (visually triggered mode) with its head in the holder. Solid line is linear regression line: slope = 4.3/s, intercept = 43.3, n = 83 points, *r* = 0.93. *B*: cat searching to and fro about room (search mode). Open circles represent movements for which cat's head was completely free and not in holder. Closed circles indicate movements made with head in holder. Linear regression line is through filled circles: slope = 9.1/s, intercept = 23.6, *n* = 146, *r* = 0.86.

in both the search and visually triggered behavioral modes. Figure 4*B* shows this relation obtained when the cat was in the search mode with its head either totally free (open circles) or attached to the holder (filled circles). Over most of the amplitude range, the small restraint and added inertia imposed by the holder resulted in an insignificantly lower head velocity. Figure 4*B* also illustrates the rapidity of head saccades: the slope of the regression line through the head-free data is about 50% of that for eye saccades when the head was fixed (Table 1 and Fig. 2). Note, however, that the slope of the linear regression line through the $\dot{H}_m$ vs. H data was less in the visually triggered mode (Fig. 4*A*).

COMPLEX GAZE DISPLACEMENTS. For rapid gaze displacements greater than ~30°, the pattern of coordinated eye-head movements in ~75% of the movements studied was not always as simple as that shown in Fig. 1. Figure 5 shows selected examples that typify the various frequently seen patterns. Figure 5*A* shows a slow (100°/s) head displacement associated with a 35° gaze shift characterized by a series of rapid eye movements in the same direction, separated by compensatory movements that frequently but not always (Fig. 5*A*, see * on G trace) stabilized gaze. This category of movements corresponds to the "multiple step gaze shifts" of Fuller et al. (17). Another feature of the movements of Fig. 5*A*, also shown in Fig. 5*B*, was that the head displacements were not as simple as those shown in Fig. 1. These more complex head trajectories had one or more points of inflection or "notches" characterized by repetitive decelerations and accelerations of the head (see Fig. 1, $\dot{H}$ traces and oblique arrows on H traces). Each new head acceleration was associated with a rapid eye movement.

When the head moved faster than 100°/s, the same general eye movement pattern was frequently seen. For example, in Fig. 5*B* there are two obvious rapid eye movements separated by only a short 20-ms plateau (Fig. 5*B*, oblique arrow on E trace). The first saccade also has an irregularly shaped velocity profile. The acceleration in the gaze trace also reflects the presence of the "overlapping" rapid eye movements. In Fig. 5*C*, the eye movement relative to the head (E) shows essentially the same characteristics as in Fig. 5*B* but with the two high-velocity segments more blended together (oblique arrow on E trace). The associated reacceleration of the G trace (marked by filled triangle) is also more difficult to perceive in this case. Indeed,

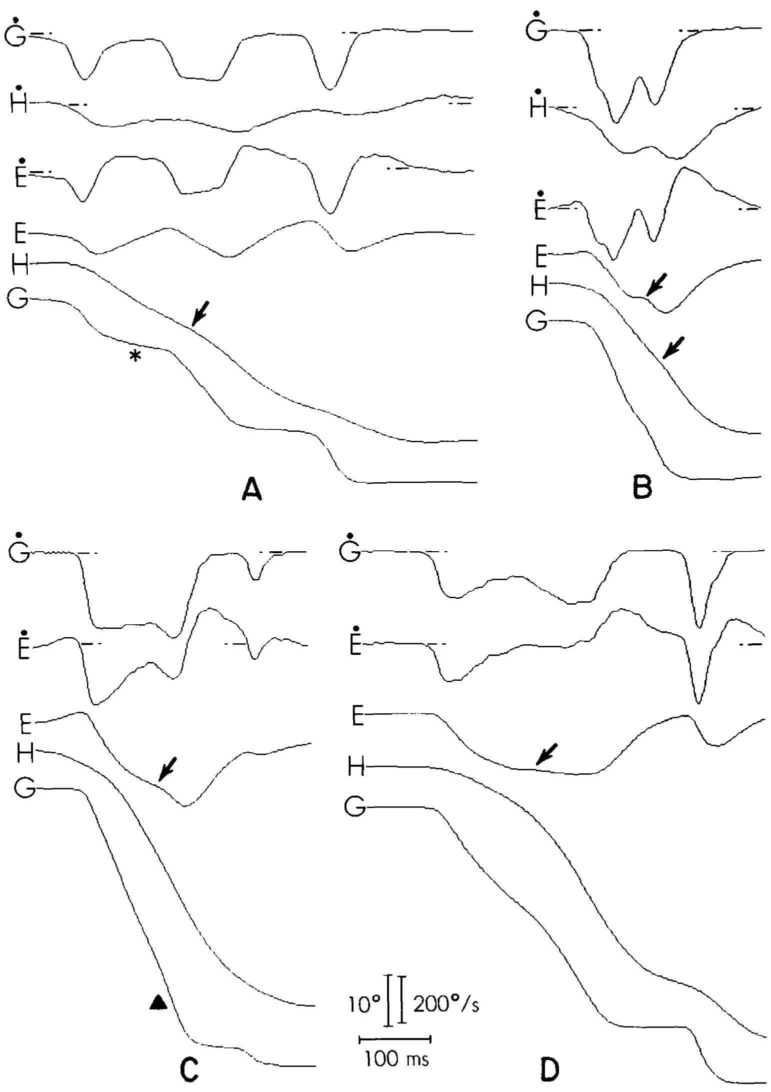

FIG. 5. Examples of "complex" coordinated eye-head movements made by a trained cat as it oriented to light spots outside OMR *A*: slow gaze shift (maximum head velocity ~ 100°/s) used a steplike sequence of small gaze displacements. Asterisk marks example where gaze velocity between steps frequently did not have zero velocity. Oblique arrow on this and other H traces shows examples where head accelerated in synchrony with an eye movement. *B-D*: fast gaze shifts (maximum head velocity > 200°/s). Oblique arrows on E traces indicate a transition between 1 rapid eye movement and another. This transition is barely perceptible in *D*. Gaze movement accelerated in synchrony with second rapid eye movement. This is indicated by filled triangle in *C*. Other symbols are as in Fig. 1.

in many of the visually triggered movements to targets at 50°, there was just a subtle hint (Fig. 5*D*, oblique arrow on E trace) of a reacceleration, but to casual inspection and without examples like those in Fig. 5, *A-C*, this would generally be attributed to noise.

The examples of movements shown in Fig. 5, *A-D*, show that gaze shifts of the cat can be accomplished with a series of very closely spaced rapid eye movements. In the context of the addition hypothesis, a plateau region in the E trace, like that shown in Figs. 1*D* and 5*D* could result if the saccade signals were nulled by the VOR signal. The following experiments were designed to reveal the visual and vestibular mechanisms implicated in generating such gaze trajectories.

Effects of preventing head motion: "early-brake" condition

With the well-trained cat in the visually triggered mode, the onset of the head movement could be predicted reasonably well, thus allowing the timing of the brake to be adjusted to just prevent head motion. Three examples obtained in this "early brake" paradigm are shown in Fig. 6 for a 50° target eccentricity and for a progressively increasing brake duration. The trace labeled *B* indicates when the brake was applied. The first striking feature of these results is that the visually triggered saccade did not attain the limits of the OMR (~23° in this cat), even though the target was at 50° but terminated at about 10–12°. This is not consistent with the main premise of the addition hypothesis whereby the nervous system codes a saccade of amplitude equal to target offset.

The second feature is that there were no additional corrective saccades (3) up to ~200 ms after the first saccade's termination. For longer brake durations, the eye frequently returned to central position. Never in ~200 observations in two cats were the closely spaced overlapping saccades of Fig. 5, *B* and *C*, ever observed. However, the visually triggered saccade frequently did not terminate with zero velocity but continued for about 100 ms in a ramplike movement (see also Figs. 10 and 12).

The third point of interest is that when the brake was suddenly and unexpectedly released, the head and gaze quickly attained the target zone. Following brake release, the eyes initially moved in the compensatory direction with a VOR gain less than unity since the gaze also accelerated synchronously with the head. The eye movement soon reversed direction, thereby suggesting the programming of a quick phase. Subsequent results will show that there probably was interaction between the VOR and the quick-phase signal, and the very slow quick phases shown in Figs. 6 and 10 are probably the result of a strong rapid-eye-movement signal being attenuated by an equally strong VOR associated with the very rapid head movements that followed the brake's release.

Figure 7 shows that the relation between maximum velocity and amplitude was similar for saccades made in the early-brake experiment and those made with the head fixed. In the early-brake experiments, the saccade amplitude was measured at the beginning of the ramp, but measuring at the end did not significantly change the interpretation, be-

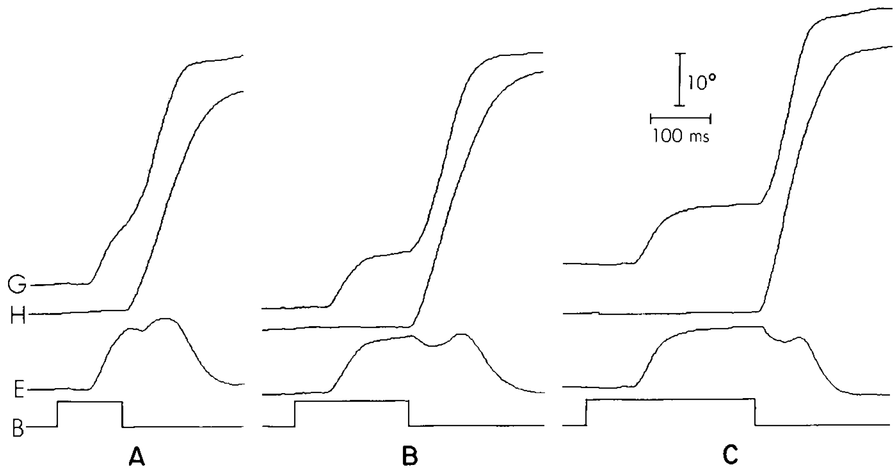

FIG. 6. Examples of visually triggered 50° orienting movements in which head motion was prevented. Early-brake condition. Brake duration increases progressively from *A* to *C*. Note that eye does not attain limits of OMR. See text for further details. *B*: brake marker pulse. Other symbols as in Fig. 1.

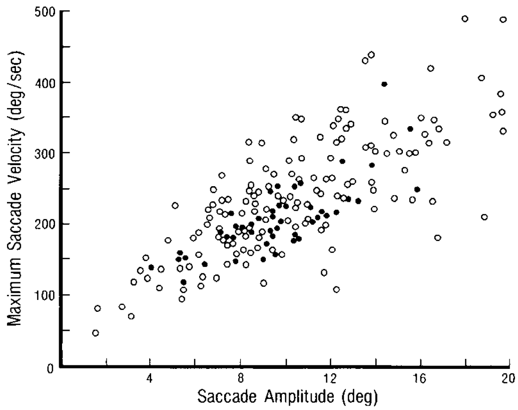

FIG. 7. Comparison between maximum velocity-amplitude relationships of saccades in head-fixed and early-brake conditions. Open circles: head fixed. Closed circles: early-brake condition in which head motion was just prevented.

cause most brake durations were short (<200 ms) and the ramp amplitude was correspondingly small. The slight difference between the two families was not significant, based on a covariance analysis comparing slopes and intercepts of linear regression lines through the two populations. This result suggests that proprioceptive feedback, associated with suddenly preventing head motion, did not influence the saccade signal.

It should be noted, however, that there was one difference between the head-fixed and early-brake saccades: the existence of the postsaccade ramp seen in Fig. 6. This slow movement appeared frequently between head-free gaze saccades (Fig. 5*A*) but was observed only rarely in the head-fixed cat.

Figure 8 compares the amplitude of saccades in the head-free and early-brake conditions for different target eccentricities (cat in visually triggered mode). Note that the braking trials were interspersed, 1 in about every 10, with regular trials (head unperturbed) in the same experimental session. Furthermore, when measuring the head-free saccades, only those showing a single saccade, like the profiles of Fig. 1, *A–D*, were considered. Saccades exhibiting evident notched trajectories like those of Fig. 5, *B* and *C*, were discarded, but examples like that in Fig. 5*D*, where velocity variations could have been due to noise, were included in the sample. It is of interest that for a target at 10°, the amplitude of the saccade when the head was braked (mean = 8.0°) tended to be larger than in the head-free condition (mean = 5.1°). This is compatible with the addition hypothesis. Conversely, for a target at 50° the amplitude of saccades with head-free cats (mean = 15.4°) tended to be larger than those in the braked trials (mean = 11.8°). This is very surprising. What would have been expected, due to the addition hypothesis in the head-free condition, are saccades of amplitude less than ~12°.

Whether head-free saccades were larger than head-fixed ones depended on the head velocity. The open circles of Fig. 9*A* replot the same data as shown by the open circles in Fig. 8. The filled circles were obtained in the search mode when the cat looked anxiously from one side of an opaque screen to another. Figure 9*B* shows that for about the same head displacement, the animal produced considerably faster head movements in the search mode than in the visually triggered mode. (To evaluate potential magnitude of VOR's influence on a saccade in addition hypothesis, we have plotted concurrent head velocity, which is velocity of head measured at saccade's maximum velocity point.) Figure 9*A* shows that saccades in the search mode were smaller than those in the visually triggered condition. Furthermore, saccades in

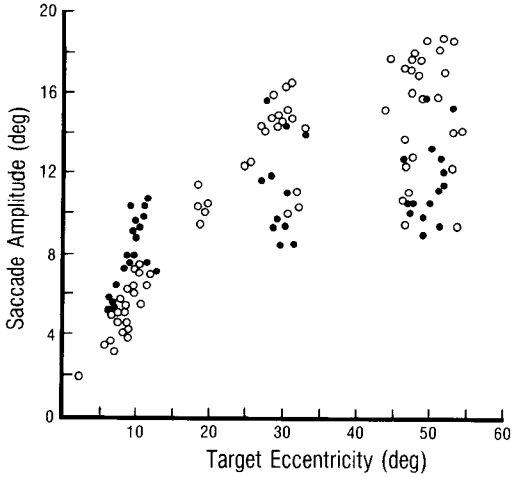

FIG. 8. Saccade amplitude associated with gaze shifts to visual targets (visually triggered mode) at eccentricities within (<25°) and beyond (>25°) cat's OMR. Open circles: head motion unperturbed. Closed circles: early brake. See text for further details.

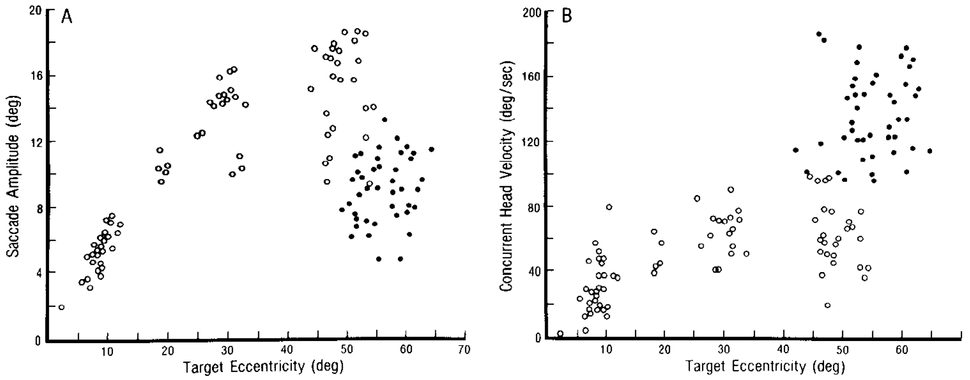

FIG. 9. Effect of head velocity on saccade amplitude in an unperturbed eye-head movement. Open circles: cat in visually triggered mode. Closed circles: cat in search mode. *A*: cluster of closed circles indicate that group of orienting movements made in search mode have smaller saccade amplitudes, for about same gaze shift, than orienting movements made in visually triggered mode. *B*: concurrent head velocity (CHV) is velocity of head at saccade's maximum velocity point. For about same amplitude of gaze shift, CHV is larger in search mode. See text for further details.

the search mode were frequently smaller than those in the early-brake condition.

Effects of braking head during saccade: "late-brake" condition

If the head were to be suddenly immobilized during a saccade, thereby removing the VOR signal, the addition hypothesis would predict that the rapid eye movement should accelerate. This hypothesis was tested by unexpectedly braking 1 in about every 10 large head movements made in either the search or visually triggered modes. No differences were found between these two modes except for the fact, as seen in the previous section, that in the search mode the head velocities tended to be faster and, consequently, the attenuating effect of the VOR on the saccade tended to be larger. The effects of the braked-head motion on the eye movement were therefore more evident in this mode and some typical results are shown in Fig. 10.

In Fig. 10, the vertical dashed line indicates when the head was immobilized by the brake (B) (data obtained with computer sampling every 2 ms). Before the brake onset, the head in each example had attained a considerable velocity (200°/s or greater), and when suddenly braked the head rebounded slightly (see H trace) because of flexibility in the head-holder assembly.

As might be expected from the early-brake results, in this late-brake condition the saccades also terminated well before the eye reached the limits of the OMR, even though the intended gazed displacement was 50–60°.

The gaze trace (G) in each example of Fig. 10 shows that suddenly immobilizing the head had no obvious effects on the gaze trajectory (marked with a filled triangle) associated with the first saccadic eye movement. This gaze saccade retained the bell-shaped velocity profile characteristic of the small gaze shifts shown in Fig. 1*A*. By contrast, the eye saccade accelerated in synchrony with the brake. The speed-up of the eye is visible on the E trace (oblique arrows) but is most evident on the Ė trace. In Fig. 10*B*, the eye's acceleration is more difficult to see because the brake occurred near the saccade's maximum velocity point. These results, in conjunction with those of Fig. 9, strongly suggest that the VOR is active during saccades and that it combines with the saccade command to attenuate the movement.

The examples of Fig. 10, *A–D*, were also chosen to illustrate the effects of progressively increasing the brake duration. These data corroborate two observations associated with Fig. 6: *1*) no additional saccades, other than the first, were evident in the braked condition except for recentering saccades (none in Figs. 6 and 10) occurring ~200 ms after the first saccade; and *2*) the intended overall gaze shift was completed only when the brake was released and consisted of a short compensa-

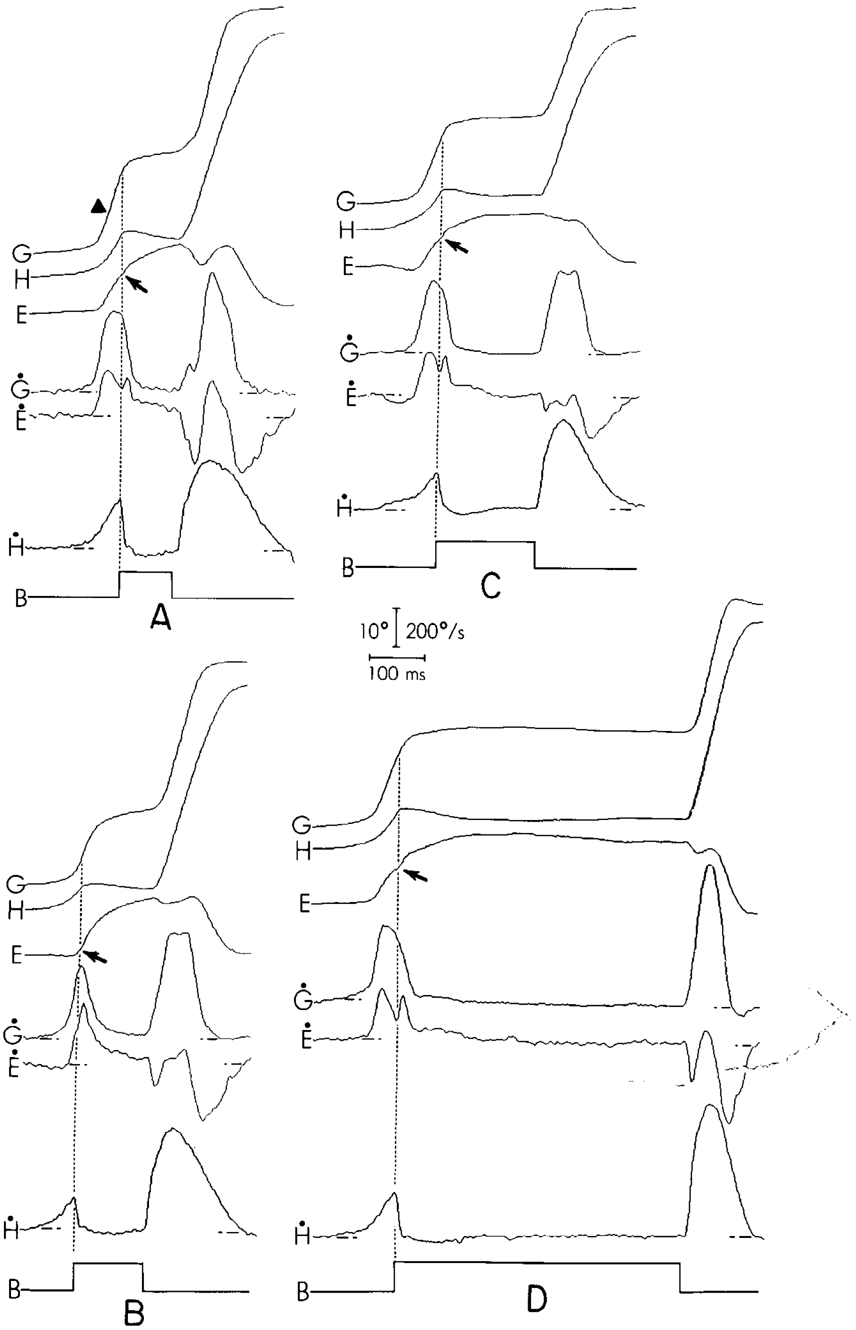

FIG. 10. Examples of eye-head movements, made in search mode, in which during a saccade head motion was suddenly interrupted by a brake. When head suddenly decelerates (vertical dotted line), there is a synchronous acceleration in eye movement (marked by oblique arrows on E traces) seen clearly on eye velocity (Ė) trace. Note that no visible perturbation of gaze saccade occurs (marked by filled triangle in *A*). Symbols are as in Fig. 1.

tory eye movement (see E trace) followed by an eye movement in the direction of the head motion. In light of the data of Fig. 11, the latter is interpreted to be (see next section) a quick phase attenuated by the VOR. It is also of interest to note, in light of the examples of Figs. 6 and 10 and the model presented in DISCUSSION, that this quick phase seldom brought the eye more eccentrically in the orbit than 2–4° past the terminal position of the first saccade.

When gaze was displaced head-free with a steplike sequence of saccades, the visual axis frequently was not fixed in space during the intersaccadic periods but continued on with a ramplike motion in the direction of head movement (Fig. 5*A*). The examples of Fig. 10, like those in Fig. 6, show that this ramp was present even when the head was braked, although in this case the postsaccade motion of the eye was faster because of an additional VOR signal induced by the head's rebound. Figs. 10, *C* and *D,* and 6*C* suggest about a 100-ms duration for the ramp.

Effects of braking the head during passive movements

The results associated with Figs. 6 and 10 strongly suggest that vestibularly induced rapid eye movements, or quick phases, play an important role in completing the gaze shift once the head brake is released. Furthermore, the very slow velocity of these movements has suggested that the originally strong rapid-eye-movement signal has been attenuated by the VOR. To gain more insight into this possible interaction, the head of the cat was displaced passively in the light, with respect to its fixed body, with a time course similar to that of the active head movements. These movements could also be braked.

Fig. 11*A* shows an unperturbed passive head (H) displacement. The vertical dashed line on the left indicates the start of the head movement. Note the VOR-induced compensatory eye (E) movement that resulted in an approximately flat gaze (G) trace until the vertical dashed line on the right. At this point the gaze accelerated rapidly, but the eye continued to move in the compensatory direction and finally reversed direction and continued with a very slow velocity. Fig. 11, *B* and *C,* show that when the head was braked suddenly during the gaze saccade (vertical dashed line on right), the eye virtually instantaneously accelerated in the direction of a quick phase. This result suggests that the VOR is active during quick phases and that it adds with the quick-phase command. Thus in Fig. 11*C* the quick-phase signal presumably started when the gaze trace suddenly accelerated (oblique arrow), but the eye, as in the example of Fig. 11*A,* still moved in the compensatory direction: quick-phase-VOR interaction therefore yielded reversed quick phases.

Effects of braking the head during compensatory phase of eye motion

Normal coordinated eye-head movements consist of one or more saccadic eye movements, each followed by a compensatory

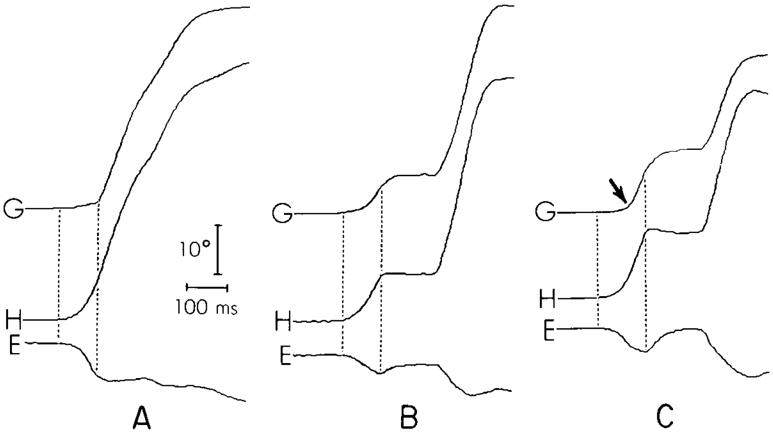

FIG. 11. Passive head displacements relative to fixed body, with trajectories resembling active movements. *A*: movement unperturbed *B–C*: movement interrupted by brake. In each example, left vertical dotted line indicates start of head motion. Right vertical dotted line in *A* indicates start of saccadic gaze displacement. In *B* and *C* right dotted line indicates point where head suddenly decelerates. See text for further details and Fig. 1 for symbols.

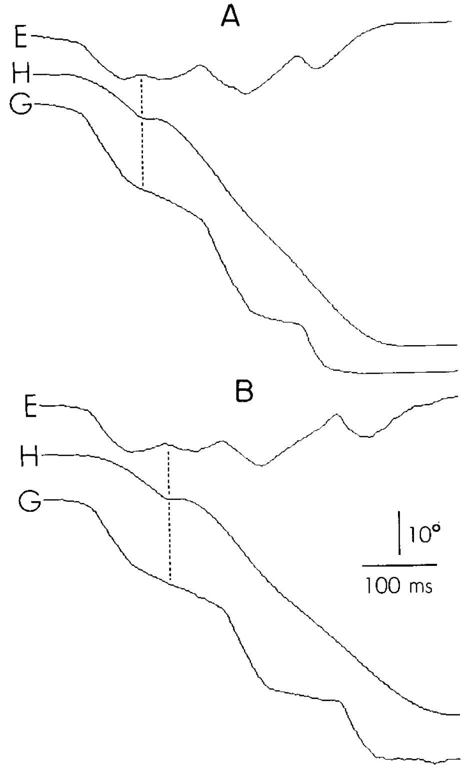

FIG. 12. Examples of braking head motion during a compensatory movement of eye. Eye immediately reverses direction, thereby suggesting that ramplike gaze displacement is due to a signal added to VOR-induced compensatory eye movement. Symbols are as in Figs. 1 and 6.

movement of the eye toward center. Dichgans et al. (14) showed that this compensatory phase in monkeys was due to the VOR, but Fuller et al. (17) have claimed that during rapid head displacements in cats the compensatory phase is frequently unaffected by changes in head velocity and is therefore preprogrammed. The present results do not corroborate the findings of Fuller et al. (17). As shown in the two examples of Fig. 12, suddenly immobilizing the head (vertical dashed line) had no effect on gaze but always immediately stopped the compensatory movement with the eye (E) trajectory assuming the ramp discussed above in relation to Figs. 5*A*, 6, and 10.

DISCUSSION

Head movements

In the cat, most head trajectories were saccade-like displacements for which there was, like eye saccades, a strong correlation between maximum velocity and amplitude. Such a relationship is a classic property of movements associated with step-tracking tasks. Other characteristics of these movements are trajectories with monophasic, "bell-shaped," velocity and biphasic acceleration profiles. Examples in the literature are head movements in humans (38) and limb movements in humans (11) or cats (18). The slope of the linear regression line linking the head movement's maximum velocity to its amplitude in cats depended on the task being accomplished and the animal's level of arousal. Cooke (11) has shown that the slope of the linear regression between maximum velocity and amplitude for arm movements depends on how subjects were instructed. As might be expected, moving as "accurately as possible" yielded slower movements than moving "as fast as possible." Similarly, our cats moved their heads more slowly when they oriented accurately to LEDS than when they were in the search mode. Such behavioral factors influenced the head movement characteristics much more than the added restraint imposed by the head-braking system (Fig. 4).

In the head-fixed cat, there is a tight linkage between eye position and neck EMG activity, such that when the eyes move from center to one side there is a proportional increase in the EMG of neck muscles on that side (21, 37). The functional importance of this mechanism in the head-free situation is not known but could underlie the clear accelerations in head movements (Fig. 5, *A* and *B*) that frequently occurred in synchrony with saccades.

In Blakemore and Donaghy's (7) experiments, the saccade normally preceded the head movement. In our experiments, the eye lagged the head either when the cat's head was totally free (not in holder) or when the animal was highly accustomed to the head-holder arrangement. However, during the initial phases of training in the holder, our cats frequently made saccades that either preceded the head or that were unaccompanied by a head movement.

In the visually triggered mode, the cats aligned their heads with the target. This differs from humans (2) but could be due to our training procedure whereby food was made available at the position of the LED. However, in the search mode, the amplitude of the head and gaze displacement were also always about equal, even though food was infrequently presented.

When the head was braked for a short period lasting up to 500 ms and then released, the intended final position was still achieved, suggesting that the head motor program was not interrupted (6).

VOR-saccade interaction: addition hypothesis

In monkeys it has been argued that the VOR slows visually triggered saccades. This has been called the addition hypothesis (33). There is some controversy regarding how, in cats, a rapid eye movement signal interacts with a vestibular slow phase signal during an active head movement. Blakemore and Donaghy (7) passively displaced cats' heads during saccadic eye movements and noted interaction. Guitton et al. (21) and Roucoux et al. (34, 35) suggested, primarily on the basis of microstimulation of the superior colliculus, that the addition hypothesis is valid for eye movements within the OMR but that for larger gaze shifts, the VOR is momentarily disconnected during the rapid eye movement. By contrast, Fuller et al. (17) have suggested that the VOR does not interact with any saccades that accompany an active head movement.

In the present experiments, we tested for interaction by braking the head during the first saccade that accompanied a head movement. In using this experimental approach, it is assumed that any influence on the saccade of perturbing the head motion is due to sensory feedback from the semicircular canals and not to, for example, neck muscle proprioceptors. There is no evidence to date suggesting extravestibular effects. Neck or other proprioceptors have no effect on the saccade characteristics in monkeys (29) and in normal cats the cervicoocular reflex has negligible gain (16, 30). Furthermore, the present results (Fig. 7) show that the characteristics of saccades were similar when the head was unexpectedly prevented from moving (early-brake) and when the head was continuously fixed in space.

By assuring low noise signals and high sampling rate, it was possible to reveal, in nearly all trials in which the head was braked during a saccade, an acceleration of the saccade coincident with the head's sudden deceleration (Fig. 10). Since there was no significant synchronous change in the gaze trajectory, it follows that $\Delta\dot{E} = \Delta\dot{H}$, suggesting that the VOR gain was close to unity during the saccade. Interestingly, gaze was not momentarily stabilized when the head was released unexpectedly. It was difficult to estimate the gain at this point, because quick phases were visually triggered after ~25 ms and one had to allow ~10 ms for the semicircular canal signal to adequately rotate the eye (26). Measuring between 10 and 20 ms following brake release gave an average VOR gain of 0.39 (SD = 0.16).

We did not directly test for interaction between the VOR and what we have hypothesized to be the vestibular quick phases that also participate in active eye-head displacements (Fig. 5). However, the remarkably slow maximum velocity of quick phases seen after head release in Fig. 10, *B–D*, suggests that the output of the burst generator, responsible for driving these rapid eye movements, might have been attenuated by the strong VOR signal associated with the rapid head motion. In concurrence with this interpretation is the observation (Fig. 11*A*) that during passive head rotations resembling active head displacements, the quick phases were also very slow and even occasionally reversed. If the passive head movement was suddenly interrupted (Fig. 11, *B* and *C*) these slow quick phases accelerated in synchrony with the onset of head deceleration. As shown for saccades, there was little or no change in the gaze trajectory (Fig. 11*C*), thereby suggesting that the VOR operated at unity gain during quick phases.

Our observations, suggesting that the addition hypothesis holds for quick phases, contradicts a number of studies that used comparative measurements of amplitude and duration in head-fixed saccades and quick phases and showed that in humans and cats there exists no interaction between vestibularly driven quick phases and the VOR (22, 25). However, in agreement with the present results, unusually slow quick-phase trajectories have been reported during high-velocity passive head rotations in humans (31).

Are compensatory phases VOR induced or preprogrammed?

Fuller et al. (17) have reported that whenever the gaze shift is rapid ($\dot{H}_m > 200°/s$) and large (>40°), the compensatory phase that follows each rapid eye movement and rotates the eye in a direction opposite to head rotation is preprogrammed and not vestibularly induced. This observation was not confirmed by our experiments in which braking the head not only halted the compensatory phase but revealed an oppositely directed eye movement whose driving signal must have been added to the vestibular signal (Fig. 12). Thus the ramplike slow (~50°/s) movements that frequently linked orienting-gaze saccades were not due to a VOR of gain less than unity. It is of interest that this ramp motion was only present in active eye-head movements and was hardly ever seen with head-fixed saccades.

Amplitude of coded saccade as a function of target offset

Central to the classic model of eye-head coordination (5, 14, 29) is the observation that the same saccade signal is coded, and therefore the same gaze trajectory occurs, irrespective of whether the head moves. Our results suggest that cats use this motor strategy only when orienting to targets at eccentricities of ~10° or less. For these small gaze shifts, there was the classic pattern of gaze, head, and eye trajectories (Fig. 1*A*), and when the head motion was unexpectedly prevented, the eye nevertheless attained the target zone.

For gaze shifts to targets between 10 and 30°, there was an apparent transition zone that began to reveal mechanisms more readily observed in larger gaze shifts. For orienting movements to targets outside the OMR, the trajectories shown in Figs. 1 and 5 suggest a great variety of possible eye-movement patterns that, in combination with a head movement, permitted the accurate displacement of gaze. With regard to these large movements, the most striking result emerged in the early-brake trials for which the eye saccade terminated with an amplitude of 10–12°. Thus, contrary to the predictions of the classic model, the eye was never driven to or near the limits of the OMR.

A further surprising feature of the large gaze shifts appeared for movements to target eccentricities of 50°. In these trials, the saccades tended to be larger when the head motion was unperturbed than when the head was unexpectedly immobilized. If the saccade had been programmed to drive the eye to ~12° and the head had moved simultaneously, then based on the addition hypothesis one would have expected a saccade smaller than 12°. Why a larger saccade? The eye trajectories shown in Fig. 5 coupled with the early-brake results suggest that the rapid-eye-movement amplitude was increased in the unperturbed head trials by the coalescence of a number of sequential rapid eye movements. Indeed, one objective of showing Fig. 5 was to emphasize that there can be a continuum of shapes in the E trace between the distinctly spaced rapid eye movements of Fig. 5*A*, the closely spaced movements in Fig. 5*C*, the plateau with a small dip of Fig. 5*D*, and possibly the movements of Fig. 1, *C–D* where there was no evident inflection point in the eye trajectory.

Four other relevant observations to this "saccade-coalescence" hypothesis resulted from the early-brake experiments (Fig. 6). First, "notched" eye velocity ($\dot{E}$) profiles like those in Fig. 5, *B* and *C*, were never seen following brakes that lasted 200 ms or longer (to give ample time for a visually triggered saccade to terminate), thereby suggesting that the second movement in the sequence was not a corrective saccade (3). Second, the possibility that braking aborted corrective saccades is considered unlikely because of the lack of effect of neck afferents on saccades (previous section) and the lack of corrective saccades following late brakes applied near the end of saccades. Third, only when the head was released did gaze begin moving toward the target and this via a sequence of eye movements starting with one in the compensatory direction followed by another in the direction of head motion. The latter observation suggests that the postbrake completion of gaze was due to vestibular mechanisms, specifically, that gaze acquired the target with quick phases. Fourth, for very short brake durations (e.g., Fig. 6*A*) the vestibularly driven quick phase coalesced with the initial visually triggered saccade, thereby producing an eye movement trajectory similar to that seen with unperturbed head movements (Fig. 5*B*). On the basis of these observations, it is tempting to assume that the overlapping rapid eye movements frequently seen in large gaze shifts, when the head was unimpeded, (Fig. 5, *B* and *C*) were caused by quick phases summing with the first visually triggered saccade. This is considered further below.

Quick-phase mechanisms

The hypothesis that large (>30°) gaze shifts in cats are accomplished partly with quick phases raises the question of how, in an active orienting movement, these rapid eye movements are triggered and terminated. Indeed, for passive whole-body rotations of a cat, the model of Chun and Robinson (8) and other corroborating experiments (20, 24) have shown that quick phases start and stop at specific points in the orbit (a craniotopic coordinate system), whose respective distances from central gaze position depend on the head velocity. In support of the use of quick-phase mechanisms in eye-head coordination, the results of collicular microstimulation have suggested that in large gaze shifts the saccade is driven to a specific craniotopically coded point in the orbit (21, 35). Do quick phases observed in the active gaze shifts start and end at orbital positions compatible with the Chun-Robinson (8) model? In the present observations of unperturbed movements, it was difficult to establish the start and stop positions of quick phases because examples where these hypothesized movements stand out, like the one that follows the first saccade in the E trace of Fig. 5*B*, were infrequent. In the early-brake and late-brake experiments, the starting positions of the quick phases evoked after brake release were far from central gaze position, thereby suggesting a triggering mechanism different from that proposed in the Chun-Robinson model. Furthermore, the terminal positions varied considerably. In the 50° gaze shifts, the quick phases evoked after brake release terminated in the zone 8–18° from central gaze, corresponding to that where rapid eye movements ended when the head was unperturbed (open circles in Fig. 8). However, for 30° gaze shifts the quick phases terminated short of the corresponding zone for that target defined by open circles in Fig. 8. Qualitative inspection of the records suggested that the terminal point of quick phases was determined primarily by when gaze was on target: in 30° gaze shifts the gaze following brake release got on target more quickly than for 50° gaze shifts and the quick phases in the former condition did not travel as far.

Eye saccade characteristics

The maximum velocity of saccades in the head-free (Fig. 2*A*) condition tended to saturate at a value (220°/s) corresponding to the maximum velocity of those head-fixed (Fig. 2*B*) saccades with amplitudes in the range 10–12°. This observation is compatible with the proposition that a saccade with a maximum amplitude of ~12° is coded in even the largest gaze shifts. It may appear surprising that the maximum velocity of these 12° saccades is similar in both the head-free and head-fixed conditions since the addition hypothesis would have suggested otherwise. However, a saccade had its maximum velocity at a time in the head-free movements when the head velocity was low, thereby minimizing the effect of the VOR on the saccade signal.

In agreement with Haddad and Robinson (23) and Blakemore and Donaghy (7), there was a tendency in gaze shifts less than 20° for a given saccade amplitude to have a higher saccadic eye movement maximum velocity when the head was actively moving than when it was stationary (Table 1). It has been argued (23, 33) that such a result speaks against the addition hypothesis, but this may be erroneous. Indeed, as noted previously, the maximum velocity of saccades is not greatly affected by the head movement. However, as the head velocity increased rapidly throughout the saccade, the level of the compensatory VOR signal constituted a larger percentage of the average velocity than of the peak velocity. Thus the amplitude, which is the product of the average velocity and saccade duration, was reduced proportionally more than the maximum velocity. This could have produced the steeper peak velocity vs. amplitude relationship seen in the head-free case.

Conceptual model of oculomotor organization

On the basis of our experimental observations, we propose that gaze, in an eye-head movement of the cat, is controlled by mechanisms that integrate both visually and vestibularly triggered eye movements. However, the complex and variable eye movement patterns that accompany large gaze shifts suggest that to achieve accuracy in the orienting movement it is important that the system controlling eye movements "know" the instantaneous gaze position relative to the target. This consideration supports the existence of a modified version of Robinson's (32) local feedback model in which not only eye position relative to the head is monitored internally by a corollary discharge but also head position so that the sum of the two provides an internal representation of gaze (33). A possible qualitative schematic of how the oculomotor system may be arranged is suggested in Fig. 13. The proposed scheme is based almost entirely on the Chun and Robinson model for quick phase generation (8, 20). The only novel features proposed are *1*) that a visually determined desired eye position can access an element in their model, and *2*) that the VOR is not switched off during the rapid eye movements.

An internal representation of target position relative to the eye (T/E) is assumed to be first converted to target position relative to the head (T/H) and then passed through a saturation element (S) where, based on the early-brake experiments, a is ~12°. Note that we could equally have assumed that T/E is passed through S since, in our experiments, cat saccades always started near central position. However, unpublished experiments in our laboratory of human eye-head coordination have shown that when the eye starts from an eccentric position in the orbit, the maximum saccade amplitude is determined by a limiting position in the orbit (S) rather than by a limit on the saccade amplitude itself. The output of S is then added to Chun and Robinson model's (8) value of C. In accordance with this, model noise (n_c) is also added. The quantity C is a head velocity (vestibular) and time-dependent (time constant ~1 s in passive condition, Refs. 8, 20) "center of interest" measured with respect to the head. The sum of C plus the output of S yields a desired eye position relative to the head (E_d/H). This quantity is then compared to instantaneous eye position, relative to the head (E/H), in the manner of the local feedback model (32), and the pulse generator (PG) is driven until $e = E_d/H - E/H = 0$.

The system requires two switches between e and the PG. The left-hand switch is necessary in both the quick-phase (8) and saccade (32) local feedback models. The error signal e serves as the trigger source (via Q) that closes the left switch, which is then held closed by the PG output until e = 0. Q is the threshold device (8) that triggers the OR gate whenever e exceeds a head-velocity-dependent threshold. The right-hand switch is necessary to prevent an input to PG from the quick-phase generator once gaze error (T/E) = 0. One other specific feature of this

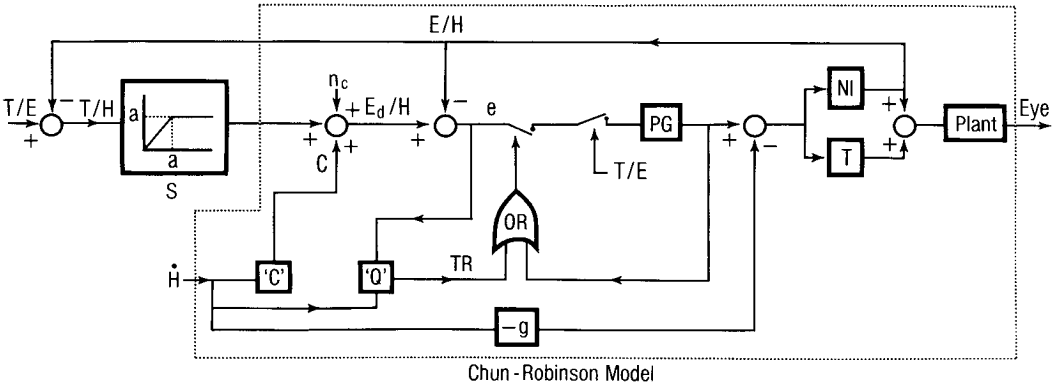

FIG. 13. Schematic model summarizing the experimental results and suggesting, qualitatively, how visually triggered saccades and quick phases might be combined. Proposed system assumes an extended version of Robinson's local feedback model combined with Chun and Robinson (7) model for quick phase generation. S, saturation element whose output never exceeds value a ≈ 12°; C, box which generates a position; C, in the orbit where quick phases terminate. C, a function of head velocity; Q, box which triggers (TR) a quick phase based on the current error (e) between desired eye position (E_d/H) and actual eye position (E/H). See text for further explanation.

model is worthy of note: the addition, after PG, of the saccade and head-velocity signals in accordance with the experimentally suggested validity of the addition hypothesis. The gain (g) of the VOR during its interaction with the output of PG was ~1.0 in the present experiments.

A typical flow of signals through this conceptual model is as follows. With the eye at center, the presence of a visual target at 50° from the area centralis yields an equivalent T/H signal that is then reduced by S to a signal specifying that the eye should rotate 12°. Simultaneously, the head motor system (not shown) begins turning the head, almost a velocity step, toward the target. The vestibular signal causes a buildup of C such that $E_d/H = 12° + C$. The resultant value of e in conjunction with a low threshold at Q triggers the OR gate, and the saccade very quickly (much faster than the buildup of C) drives the eye until $e = 0$ and the left switch opens, putting the system in the slow phase mode. The head keeps turning and C still builds up. The error e eventually surpasses the threshold Q and another quick phase is triggered. Note that noise may trigger quick phases spontaneously and that in the active case, C and Q could have properties different than those measured (8, 20) in the passive system. The ramp (Figs. 5, 12) between rapid eye movements is not considered in this model.

In summary, the scheme of Fig. 13 explains some crucial experimental findings. *1*) The threshold element (S) truncates visually triggered saccades at 12° when the head is fixed. *2*) Since E_d/H can be bigger than the limit imposed by S, it is possible to have head-free rapid eye movements terminating further in the orbit than those in the head-fixed condition. *3*) If the head moves very rapidly, the gaze can reach the target before the saccade reaches E_d/H. *4*) The resumption of head motion following a brake can lead to quick phases that bring gaze onto the target. *5*) There is interaction between the VOR and either saccades or quick phases. *6*) The existence of postsaccade plateaus in the eye-position trace (Fig. 5*D*) is due to the pulse generator output being nulled by the VOR.

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