THE VESTIBULO-OCULAR REFLEX DURING HUMAN SACCADIC EYE MOVEMENTS

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SUMMARY

1. Eye and head movements were recorded in normal humans during rapid refixations with the head still (saccades) or moving (gaze saccades) to determine if the vestibulo-ocular reflex was operating at such times. Subjects made self-paced refixations between fixed targets. Eye movements were recorded with the electro-oculogram for large saccades and with the eyecoil/magnetic field method for smaller movements.

2. The putative function of the vestibulo-ocular reflex during a gaze saccade is to adjust the movement of the eye for the movement of the head by adding the saccadic command and the vestibular signal. This action, referred to here as linear summation, would maintain gaze-saccade accuracy by making gaze velocity (eye in space) independent of head velocity. It would also preserve the duration of the eye movement. The present experiments show that these predictions fail badly for gaze saccades of about 200 deg. When a subject increased his head velocity voluntarily, for example, from 420 to 805 deg/s, mean gaze velocity rose from 540 to 820 deg/s and duration dropped from 380 to 250 ms. Linear summation did not occur.

3. By means of a yoke clenched in the teeth, the subject's head could be momentarily and unexpectedly slowed by collision of the yoke with a lead weight during a 180 deg gaze saccade. The perturbation decreased head velocity by about 150–200 deg/s, decreased gaze velocity by about the same amount and did not change eye velocity (in the head); another indication that the vestibulo-ocular reflex was not working. Nevertheless, gaze-saccade duration was automatically increased so that the over-all accuracy of the movement was not changed.

4. Subjects made saccades between targets at ±20 deg without attempted head movements. Simultaneously the experimenter struck the yoke, clenched in the subject's teeth, with a rubber hammer. The hammer blow caused a transient head velocity of about 70 deg/s. Gaze velocity transiently rose or fell, depending on the direction of the blow, by similar amounts and a quantitative analysis suggested that the vestibulo-ocular reflex was essentially absent. Again, duration was automatically altered so that saccade accuracy was not changed.

5. Subjects looked back and forth between targets 20, 40 or 60 deg apart as their head turned through the straight ahead position, actively or passively, at velocities up to 600 deg/s (active) or 300 deg/s (passive). In this way large head velocities were present throughout the duration of the gaze saccades. Peak gaze velocity rose linearly with head velocity reaching values from 800 to 1000 deg/s; about twice the velocity possible with the head still. This behaviour also indicates an absence of the vestibulo-ocular reflex. Again, duration decreased as gaze velocity increased in order to maintain accuracy.

6. Finally, subjects made saccades from primary position with the head initially at rest to targets 30 and 40 deg in the periphery with no, a moderate, or a rapid head movement. As head velocity increased, gaze velocity increased and duration decreased, contrary to the predictions of linear summation.

7. Evidence for a vestibulo-ocular reflex was not found during saccades or gaze saccades of 40 deg or larger. Accuracy of saccadic gaze changes was preserved by some mechanism that adjusted duration; an action beyond the purview of the vestibulo-ocular reflex. Such a mechanism is proposed. It suggests that an internal copy of eye and head position combine to estimate gaze position. The latter is then compared to an internal signal of desired gaze position. The difference, or error, drives burst neurones to produce the saccade. When the error becomes zero, the eye is on target and the saccade stops. Thus, duration is automatically adjusted. This model is compatible with the behaviour observed in these experiments.

INTRODUCTION

When we turn to look at something, we usually make a saccade and a head movement simultaneously in the same direction. The question has arisen whether the vestibulo-ocular reflex continues to act during such saccadic movements. The purpose of this reflex is to turn the eye in the head, automatically, in the direction opposite to a head movement, at nearly the same velocity, so that eye position in space remains approximately constant and the motion of images of the world on the retina is kept small during head movements. Put another way, eye position in space is made independent of head movements. If the reflex continued to work during saccades accompanied by a head movement, it would slow the saccade in the head by the velocity of the head so that eye velocity in space would not be altered by the head movement. Again, the purpose of the reflex would be to free eye movements in space from the potential disturbance of a head movement. Specifically, the reflex would allow the trajectory of eye position in space, called gaze position, to be the same whether or not the head also moved. (Current terminology defines eye position to be with respect to the head; gaze position, the position of the eye in space, is then the sum of head position and eye position. Further, a single saccade with a head movement will be called, for brevity, a gaze saccade. This usage is adopted throughout.)

Whether this happens has been the subject of controversy. There are theoretical reasons why one might suppose that the vestibulo-ocular reflex would or would not function during gaze saccades. Bizzi and colleagues (Morasso, Bizzi & Dichgans, 1973) pointed out that if the vestibulo-ocular reflex permitted gaze saccades to be

independent of head motion, the saccadic system could then programme saccades the accuracy of which would not depend on the velocity of a concomitant head movement cr whether the head moved at all. If the reflex were not to operate and the head movement were not otherwise compensated, gaze would be carried past the target. Since that does not happen, it seemed reasonable to suppose that the vestibulo-ocular reflex was active during gaze saccades. These authors provided evidence in the monkey that this was the case for saccades up to 40 deg in amplitude. Since this theory supposes that saccadic commands and vestibular commands simply summate in a linear fashion in their effects on the final eye movement, it shall be referred to as the linear-summation hypothesis.

On the other hand, several observations would argue against this hypothesis. One is that during saccades motoneurones of the antagonist eye muscle are inhibited and cease discharging (e.g. Schiller, 1970); a vestibular signal, unless very intense, would not bring these neurones out of inhibition so that half the vestibular command would be lost. Linear summation would appear only if the central nervous system took steps to compensate for this severe non-linearity.

Moreover, the neurones primarily responsible for passing the vestibular signal monosynaptically from the vestibular nucleus to the motor nuclei of the eye muscles, called vestibular plus eye position by King, Lisberger & Fuchs (1976) or tonic-vestibular-pause cells by Pola & Robinson (1978), cease firing (the pause) during all saccades in the monkey. This implies that the vestibulo-ocular reflex is literally disconnected during saccades. While the pause is not complete for some tonic-vestibular-pause cells (Scudder & Fuchs, 1981), the bulk of the evidence in primates would make the possibility of linear summation unlikely.

The results of behavioural experiments are perplexing. Linear summation was supported by experimental results in the monkey by Morasso *et al.* (1973) but Tomlinson & Bahra (1986) have found this to be true only for saccades less than about 20 deg; for saccades larger than about 40 deg, the vestibulo-ocular reflex, tested by rapid head perturbations, is absent. In humans, the data of Jürgens, Becker, Rieger & Widderich (1981) suggest the presence of a partial reflex for head velocities less than 125 deg/s. Data from the cat have been controversial. Saccadic gaze velocity increases when the head is free to move, contrary to the linear-summation hypothesis (Haddad & Robinson, 1977). Using sudden head perturbations, Guitton, Douglas & Volle (1984) and Blakemore & Donaghy (1980) found an intact vestibular reflex during saccades while Fuller, Maldonado & Schlag (1983) found none.

The present study continues these investigations in human beings. In the hope that the presence or absence of linear summation would become clearer with larger movements, the range of head velocities up to 800 deg/s and gaze shifts up to 200 deg were explored.

METHODS

Eye movements were measured with either the direct-coupled electro-oculogram (e.o.g.) or the eyecoil/magnetic field method. The latter method was used whenever possible but, since it measures the sine of the angle of gaze relative to the magnetic field, the e.o.g. had to be used beyond 40 deg. When that was necessary, subjects were adapted to the dim illumination used in the experimental room and frequent calibrations were made while subjects looked at targets at known positions.

Sensitivity and accuracy were about 1·0 deg. Head position was measured by attaching a tightly-fitting helmet worn by the subject to a potentiometer. In the e.o.g. experiments gaze position was created electronically by adding eye and head signals. In eyecoil experiments, where the sensitivity was 0·25 deg, head position was subtracted electronically from gaze position, recorded by the eyecoil, to measure eye position (in the head). In some cases, head position was changed passively by *en bloc* rotation of the subject with a motorized chair in which case chair position was equal to head position. Only horizontal movements were studied.

Head position was usually differentiated electronically to obtain head velocity over the band 0–25 Hz. Eye and gaze velocity were obtained similarly over the band 0–50 Hz. Otherwise, over-all system band width was limited by the pen recorder to 0–80 Hz. Between two and four subjects were used in various parts of the experiments. All were normal, adult males familiar with eye-movement recording and oculomotor physiology.

For sudden head perturbations, the subject clamped a plastic bar in his teeth that was attached to a yoke that encircled the head. At the back of the yoke was a metal spur. For perturbations with the head stationary, the spur was struck with a rubber hammer. During head rotations, the spur, covered with a foam cushioning material, was allowed to strike a one pound lead weight, suspended on the end of a string, thereby momentarily slowing the head. The plastic bar was not fitted to the teeth so that if forces became too large the bar could slip.

RESULTS

Behaviour during large gaze saccades

The following experiment shows that linear summation does not occur during large gaze shifts. Fig. 1 shows typical eye, gaze and head movements for gaze saccades (single saccades with head movements) with an amplitude of 205 deg. The targets were two white marks on opposite, black walls, the room lights were dim, and the subject made self-paced gaze saccades back and forth. Eye position was measured with the e.o.g. Once the saccade began, in the example of Fig. 1 *A*, eye velocity quickly reached a peak of about 425 deg/s and then began to decrease. Head velocity increased to a peak of 805 deg/s; when it reached gaze velocity, eye velocity, by definition, became zero. Eye velocity remained low for about the last third of the gaze shift. Very late in the gaze saccade the eye began to move back toward the centre. Then the gaze saccade ended (dashed line) and the vestibulo-ocular reflex stabilized gaze while the head completed its movement. A corrective saccade of 3·6 deg occurred 145 ms later. The head movements in Fig. 1 are only about 170 deg which is as large as was comfortable for this subject without turning the body as well. Consequently, the eye in the head started from a position about 15 deg in the direction of the old target and ended 15 deg in the direction of the new.

Fig. 1 *B* illustrates that gaze velocity and gaze-saccade duration depended on head velocity contrary to the idea of linear summation. In this example, the subject deliberately made a slower head movement. In *A*, peak head velocity was 805 deg/s; in *B*, 420 deg/s. In *A*, average gaze velocity was 820 deg/s, the duration (dashed vertical lines) was 250 ms. In *B*, average gaze velocity was 540 deg/s, duration was 380 ms. This behaviour means that a normal vestibulo-ocular reflex and linear summation were not operating. If they were, the time course of gaze would be independent of the velocity of the head movement and this was clearly not the case. The phenomena illustrated in Fig. 1 occurred in all subjects when they were asked to vary head velocity. It was not the intention to study the metrics of these movements so that no detailed analysis was performed. The only point was to illustrate that linear summation did not occur for such large displacements. The
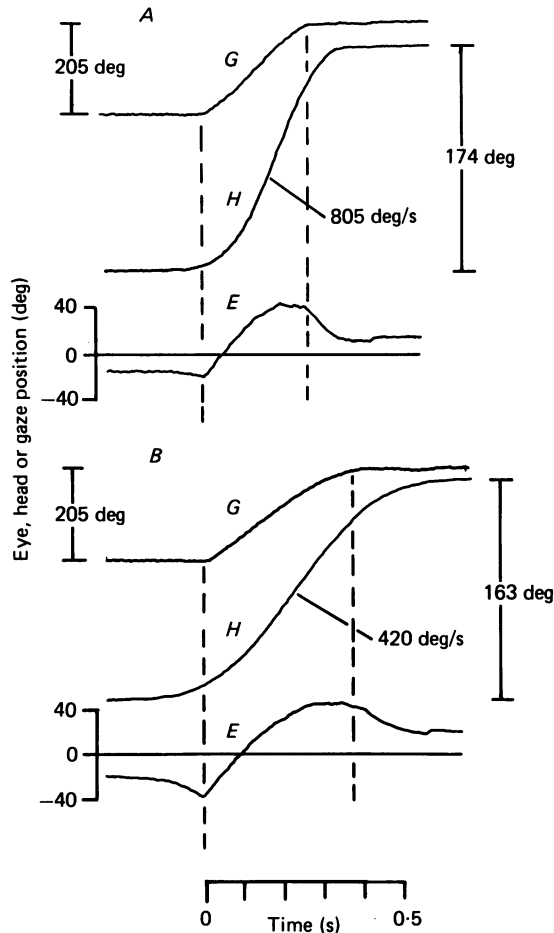
Fig. 1. Typical behaviour of eye, E, head, H, and gaze, G, during gaze saccades between targets 205 deg apart. In B, the subject deliberately moved the head more slowly. In A, the duration (vertical dashed lines) was 250 ms; in B, 380 ms.

increase in gaze velocity (52 %) and decrease in duration (34 %) shown in Fig. 1 were so large that statistical analysis was also unnecessary to make the point.

The accuracy of these gaze saccades to an initially unseen but remembered target was better than the accuracy of saccades between visible, jumping targets. In two subjects the mean value of twenty-five corrective saccades was $5 \cdot 7 \pm 2 \cdot 4$ deg (± 1 s.d.) and $3 \cdot 3 \pm 2 \cdot 1$ deg. This is a short fall of only 2–3 % of the total gaze shift; smaller than the 10 % typical of saccades in the range 0–40 deg (e.g. Becker & Fuchs, 1969). Consequently, 205 deg gaze saccades are not less accurate than saccades within the oculomotor range. Some mechanism is apparently operating to insure this accuracy in spite of variations in head velocity and this simple experiment shows that it is not the vestibulo-ocular reflex. This is not entirely unexpected since this reflex might not be able to cope with such large gaze shifts and high velocities.

Limitation of eye position

An obvious non-linearity is that eye position is normally limited to 45–50 deg in humans. Fig. 1 shows that when eye velocity became zero eye position was near 40 deg and was thus approaching this limit. The question arose as to whether eye velocity became zero because head velocity had caught up to gaze velocity and the vestibulo-ocular reflex had driven eye velocity to zero, or whether eye velocity became
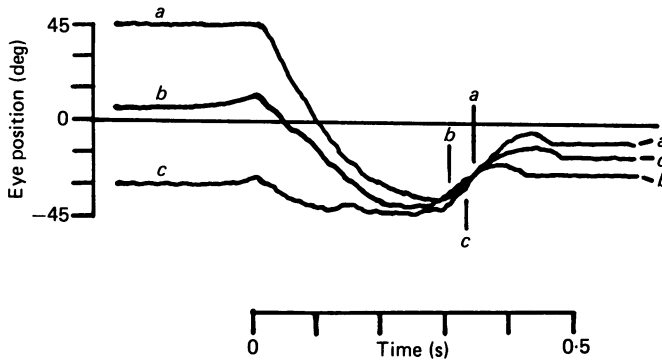

Fig. 2. Movement of the eyes from different initial positions. The task is similar to that shown in Fig. 1; head and gaze movements would be similar to the ones shown there. Vertical lines marked *a*, *b*, *c* indicate the termination of the three gaze saccades.

zero simply because the eye was close to a position limit. To investigate this, initial eye position was changed. The experiment illustrated in Fig. 2 is the same as that in Fig. 1 except that, with the head in its initial position, the target being fixated was moved 30 deg left or right. This changed initial eye position only approximately by 30 deg since the subject often unconsciously readjusted his head slightly. Ten trials were run from each initial position for two subjects.

Fig. 2 illustrates the major features of the results. From any of the three initial positions the eye moved quickly to a position that could vary from 35 to 45 deg in the orbit in the direction of the gaze shift. It reached this position in about 200 ms. For the final 150 ms the eye remained relatively stationary in the orbit.

There is a clear dependence of initial eye velocity on initial eye position. It was 225 deg/s in trace *c*, 391 in *b*, and 692 in *a*. It has already been demonstrated by Abel, Dell'Osso, Daroff & Parker (1979) that as the eye approaches the periphery, centrifugal saccades become slower than centripetal. This was tested in these two subjects; they were asked to make saccades between two targets 20 and 30 deg to the left and then 20 and 30 deg to the right. Both showed an obvious difference: 10 deg rightward saccades, for example, had average peak velocities of 214 deg/s in one subject if the saccades were centrifugal and 303 deg/s if centripetal. The numbers for the second subject were 256 and 366 deg/s respectively. This finding was expected and can probably be attributed to the length–tension properties of muscle. The effect seems to become more apparent when maximum effort is called for, as in these large gaze saccades. The initial velocities of traces *c* and *a* in Fig. 2 are 42 % less and 77 % larger, respectively, than the velocity of trace *b*. It is because of this that the eye

approached its extreme deviation at about the same time (200 ms) regardless of where it started since the further away it started, the faster it travelled.

That from various initial positions and with various head velocities, eye velocity always approached zero as the eye approached a zone near its limit, suggests, but does not prove, that eye velocity became zero because of some eye position limit and not because of the vestibulo-ocular reflex. Because eye velocity remained near zero for most of the last third of the movement, it would seem unlikely that the saccadic eye-velocity command and the vestibulo-ocular reflex just happened to cancel throughout this period and just in this small position range. The more likely explanation is that the eye starts off at such a high velocity that, regardless of initial eye position, it will approach this proposed limit well before the gaze saccade is over. Once in this limit the eyes appear to be simply carried by the head until the goal is near. If that is the case, it is easy to see why gaze velocity and gaze-saccade duration can be influenced by head velocity as shown in Fig. 1 since, with the eye in some sort of position limit, gaze velocity is determined solely by head velocity.

It is important to note that this limit is not mechanical since that is generally accepted to be normally at about 45–50 deg. One must thus hypothesize a limit imposed by the central nervous system, rather than the eye muscles, one that varies from trial to trial. Detailed analysis of this phenomenon was not performed because it could not prove, any more than can the traces in Fig. 2, the idea of a neural limit zone. It is an issue that lies to one side of the main thrust of these experiments and it is raised here as a potentially important yet unexplored aspect of oculomotor physiology.

Head perturbations during large gaze saccades

An eye-position or head velocity saturation could explain why the vestibulo-ocular reflex appeared to be inoperative in Fig. 1 but does not address the question of whether the vestibulo-ocular reflex might actually be turned off during the saccade. To examine this, the head was perturbed unexpectedly in the middle of a gaze saccade. The subject clenched in his teeth a bite bar connected to a metal spur behind the head. The spur struck a weight suspended on a string on some trials during gaze saccades of about 180 deg. Otherwise the methods were the same as for Fig. 1. A typical result is shown in Fig. 3. The point at which the spur struck the lead weight is indicated by a vertical line. Subsequently head velocity rapidly decreased, eye velocity did not increase (if anything, it decreased slightly) and gaze velocity slowed from 493 to 314 deg/s. Similar behaviour occurred in about fifteen trials (e.g. Fig. 3B) in each of two subjects and indicated that the vestibulo-ocular reflex, if present, was failing to compensate for the perturbation.

In the example of Fig. 3A, the collision caused a drop in head velocity, $\Delta\dot{H}$, of 144 deg/s. The drop in gaze velocity, $\Delta\dot{G}$, was 179 deg/s. The gain of the vestibulo-ocular reflex may be calculated from $1 - (\Delta\dot{G}/\Delta\dot{H})$. This gain, normally close to $+1.0$, was, in this example, -0.24. In one subject the mean gain of eleven perturbations was -0.12 ± 0.37. The difference $(\Delta\dot{H} - \Delta\dot{G})$ implicit in this formula is a small difference between two large numbers (each about 150–200 deg/s) which probably accounts for much of the large variability. Nevertheless, this value of gain suggests that the vestibulo-ocular reflex was not operating during these gaze saccades.
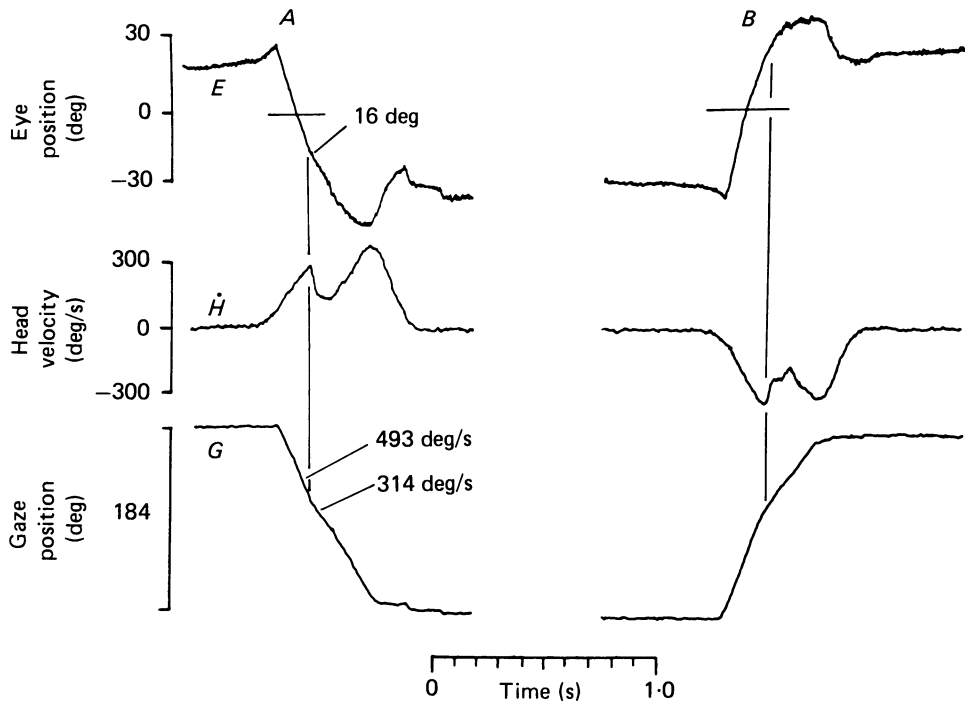
Fig. 3. The results of head braking. E is eye position, $\dot{H}$ is head velocity and G is gaze position. The experiment is similar to that illustrated in Fig. 1 but at the vertical lines, the subject's head struck an obstacle and slowed momentarily. If the vestibulo-ocular reflex were operating, gaze would not have slowed as head velocity dropped and the velocity of the eye would have increased. None of this happened as though the vestibulo-ocular reflex were absent. A and B show two examples from the same subject.

Care was taken to control for eye position. If the perturbation occurred during the period when the eye was presumably near some sort of limit, the absence of an increase in eye velocity due to a decrease in head velocity would not be surprising. Records, however, such as the one in Fig. 3A, showed that if the perturbation occurred when the eye was only 16 deg eccentric in the orbit, the result was still the same; there was no compensation for the sudden drop in head velocity.

The perturbation did not affect the accuracy of the gaze saccades. After the collision, gaze and head velocity decreased together but then began to increase, again together, and the duration of the gaze saccade was, of course, prolonged. Accuracy was assessed by the amplitude of corrective saccades. For ten trials similar to that in Fig. 3, the amplitude of corrective saccades was $4\cdot3\pm2\cdot5$ deg. For control trials, it was $3\cdot3\pm2\cdot1$ deg. These numbers are not statistically significantly different. This result indicates that despite an absent or deficient vestibulo-ocular reflex, some mechanism nevertheless compensated for the unexpected perturbation by adjusting duration to allow gaze to reach the same goal.

Head tapping

The apparent absence of a vestibulo-ocular reflex in Fig. 3 could still be due to a saturation at such high head velocities (300–500 deg/s) and need not indicate that
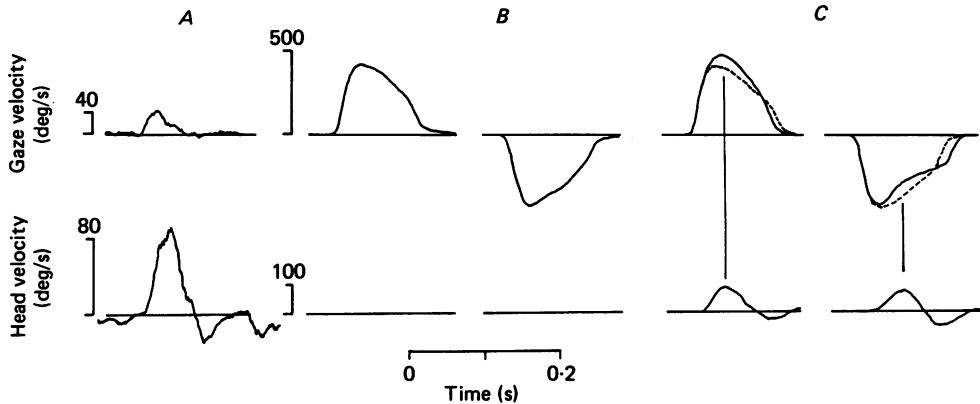
Fig. 4. The effect of tapping the head (with a rubber hammer) in the midst of saccades between ±20 deg. *A*, the head velocity created by a tap and the gaze velocity it created. *B*, the gaze-velocity profiles of one subject for 40 deg saccades in each direction. *C*, the same profiles disturbed by a tap in mid-saccade, one aiding, one opposing the saccade. The dashed lines are copied from *B* for comparison.

the reflex has been switched off centrally. Consequently, head perturbations were made during saccades without voluntary head movements. Two subjects made saccades between two visible targets 40 deg apart (±20 deg with respect to the head). Eye movements were recorded with the eyecoil method. The subject clapped his hands rhythmically at a rate of about 0·5–1·0 Hz and made saccades in time with the clapping while the experimenter tapped the spur of the bite bar with a rubber hammer, also in time with the clapping. This scheme caused taps to occur in mid-saccade with reasonable frequency. As controls, saccades were made without taps and vice versa.

Fig. 4 shows typical results. In *A*, where the subject was fixating straight ahead, the head perturbation (lower trace) did perturb gaze (upper trace). This was obvious to the subject who experienced oscillopsia. The reason is probably that the tap, which must be kept brief to be intrasaccadic, had a duration (positive half) of about 70 ms and so had significant spectral power above the upper end of the band width of the human vestibulo-ocular reflex, reported to be 15 Hz by Skavenski, Hansen, Steinman & Winterson (1979). Thus, the dynamics of the vestibulo-ocular reflex attenuated the pulse of head velocity, the resulting eye velocity was inadequate and a pulse of gaze velocity resulted. In Fig. 4*A*, the peak change in gaze velocity, $\Delta\dot{G}$, was 44 deg/s, that of head velocity, $\Delta\dot{H}$, was 88 deg/s so that the gain of the vestibulo-ocular reflex, calculated from $1-(\Delta\dot{G}/\Delta\dot{H})$, was 0·50. The average of ten such measurements was $0·59\pm0·05$ for the subject illustrated and $0·55\pm0·06$ for the other subject.

Fig. 4*B* shows the velocity profile of a typical 40 deg saccade in each direction for one subject. Note the large change in scales. It was found that self-paced saccades made between two continuously visible targets were more reproducible than visually triggered saccades as reported in the literature. For example, ten saccades, all in the same direction, had, for this subject, a peak velocity of 494 ± 11 deg/s in these experiments. The standard deviation was 2·2 % of the mean compared to 13 % reported for visually triggered saccades (e.g. Schmidt, Abel, Dell'Osso & Daroff,

1979). Because of this reproducibility, the curves in B, selected as typical, could be superimposed, as dashed traces, on those of C to observe the difference caused by a head perturbation. Typical examples are shown in Fig. 4C. This superposition shows that when the hammer tap moved the head in the same direction as the eye movement, gaze velocity was clearly increased (Fig. 4C, left) and was decreased for taps in the other direction.

The maximum difference between the dashed and continuous curves was the peak change in gaze velocity $\Delta\dot{G}$ and, as before, the gain of the reflex was calculated by $1-(\Delta\dot{G}/\Delta\dot{H})$ where $\Delta\dot{H}$ was peak head velocity. Unfortunately taps were restrained to changes in head velocities of less than 100 deg/s for fear of injuring the teeth. This means that $\Delta\dot{G}$ is a small difference between two large numbers so that small fluctuations in individual trials would cause large fluctuations in $\Delta\dot{G}$. Nevertheless, ten records similar to that in Fig. 4C gave an average gain of $0\cdot17\pm0\cdot21$. Despite the large variability, this number is significantly smaller than the value of $0\cdot59\pm0\cdot05$ obtained for this subject when saccades were not occurring. The values of gain for the second subject with and without saccades were $0\cdot11\pm0\cdot2$ and $0\cdot55\pm0\cdot06$ respectively. A more extensive, statistical analysis might indicate more firmly that the gain values measured during saccades are not statistically significantly different from zero, but they are certainly so small compared to control values that one can say that the vestibulo-ocular reflex has largely disappeared during 40 deg saccades. Since neither head velocity nor eye position was close to any saturating non-linearity, these results suggest that the reflex was disconnected centrally.

In this experiment gaze arrived on target despite the perturbation. In Fig. 4C, when the head tap caused a decrease in gaze velocity, it was made up by a subsequent increase in velocity, compared to the control trace, and an increased duration so that the area under the curve, gaze displacement, was preserved. When the head tap increased gaze velocity it was followed by a decrease in velocity and a decreased duration so that total gaze displacement was again preserved. To quantify this, the amplitudes of ten saccades each in the cases of no tapping, tapping in the same direction as the saccade and tapping in the opposite were measured. The mean values were $39\cdot2\pm1\cdot25$, $39\cdot7\pm1\cdot36$ and $38\cdot7\pm1\cdot58$ deg. These numbers are not significantly different. Again, it should be recalled that in this study, voluntary saccades between two fixed targets were found to be surprisingly reproducible compared to saccades triggered by a jumping target. The tap, with no saccade, displaced the head by about 4 deg. With a reflex gain of about $0\cdot14$, the same tap during a saccade could be expected to displace gaze by $3\cdot4$ deg, causing a $3\cdot4$ deg overshoot, or undershoot, if it were not corrected. Since this was not seen it appears that some internal mechanism subsequently corrected for the perturbation and allowed the eye to reach its goal in space.

Large active and passive head velocities

The finding that the vestibulo-ocular reflex was essentially absent during a saccade seemed at odds with the observation in humans (Jürgens *et al.* 1981) and monkeys (Morasso *et al.* 1973) that eye velocity in the head, during a saccade, slows down if the head also moves in the same direction, due, it has been presumed, to the vestibulo-ocular reflex. Consequently, this issue was re-examined with an effort to

increase head velocity throughout the duration of the gaze saccades. During normal eye–head reorientations head velocity rises slowly compared to eye velocity and, for small gaze shifts, the gaze saccade is over before head velocity becomes very large. To get larger persaccadic head velocities, four subjects were asked to rotate their heads sinusoidally, as well as they could, creating peak head velocities from 50 to 600 deg/s. Peak head excursion was about ± 50 deg. Eye position was measured with the e.o.g. The subjects were asked to look from one to the other of two targets, always visible, 20, 40, or 60 deg apart, when head position passed through straight ahead and head velocity was usually maximum. Fig. $5A$ shows an example.
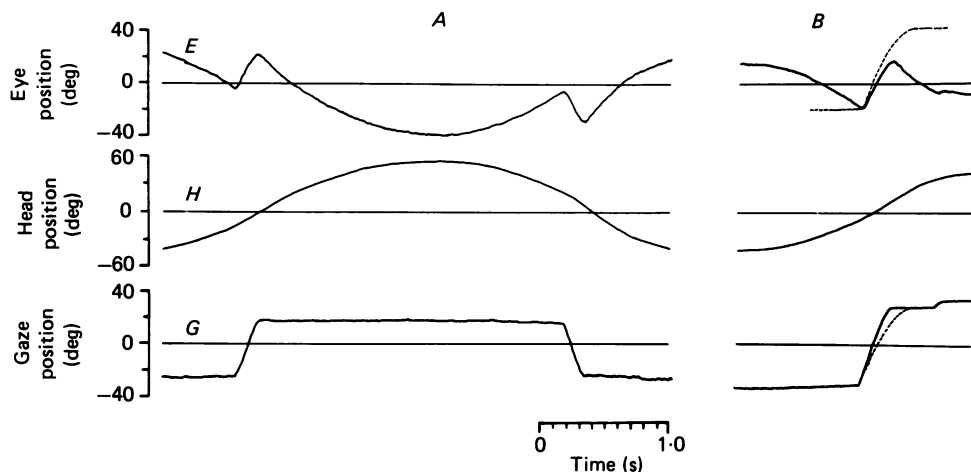

Fig. 5. Saccades during large, sinusoidal, active head movements. E, H and G are defined as usual. A, as the head passes approximately through zero at various self-generated velocities, the subject looked between targets at ± 20 deg. In B, a single movement between targets at ± 30 deg is compared to a similar saccade with the head still (dashed lines). Note that gaze velocity is increased and duration decreased by the head movement contrary to the linear-summation hypothesis.

In order to observe the behaviour of peak gaze velocity, $\dot{G}_p$, and peak eye velocity, $\dot{E}_p$, as $\dot{H}$ increased, it would seem natural to plot them against $\dot{H}$. For head velocities below about 350 deg/s where, with visible targets, the gain of the vestibulo-ocular reflex is close to one, this would be adequate. Above this value, however, the gain decreases significantly and it is appropriate to use slow-phase eye velocity at the time of the saccade as an index of that portion of the vestibular stimulus which is getting through to the eye and with which the saccadic command is supposed to sum in the linear summation hypothesis. Thus, $\dot{E}_s$, the magnitude of slow-phase eye velocity just prior to the saccade was chosen for the abscissa in Fig. 6.

The major feature of Fig. 6 is that above some slow-phase velocity, $\dot{E}_{so}$, 100 deg/s in this example, $\dot{G}_p$ rose linearly with $\dot{E}_s$ while $\dot{E}_p$ remained constant. If the vestibulo-ocular reflex had been working over this range, $\dot{G}_p$ would have stayed constant and $\dot{E}_p$ would have fallen as indicated by the dashed lines. This did not happen. If the vestibulo-ocular reflex had not been working at all, $\dot{G}_p$ would have risen linearly with $\dot{E}_s$ while $\dot{E}_p$ remained constant as was the case above $\dot{E}_{so}$. For the
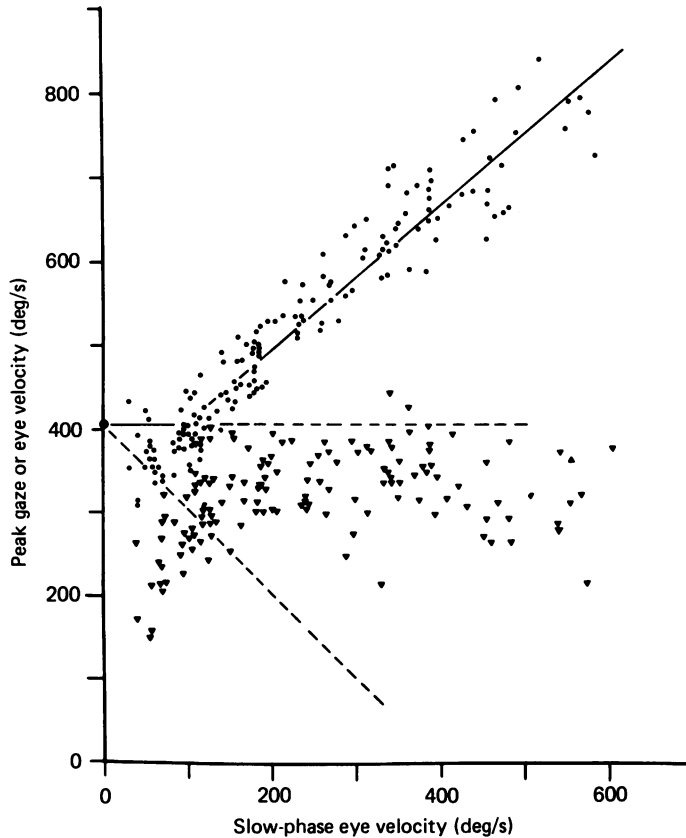
Fig. 6. Peak saccadic gaze velocity $\dot{G}_p$ (dots) and peak saccadic eye velocity $\dot{E}_p$ (triangles) as a function of the magnitude of slow-phase eye velocity $\dot{E}_s$ just before each saccade for subject D. Z. in the experiment depicted in Fig. 5. Upper and lower dashed lines show what $\dot{G}_p$ and $\dot{E}_p$ would have done, respectively, had the vestibulo-ocular reflex been working. The large dot on the ordinate is $\dot{G}_0$, mean peak saccade velocity when the head is still. Values of $\dot{G}_p$ for velocities of $\dot{E}_s$ above 100 deg/s were fit with a linear regression shown by the continuous line.

data in Fig. 6 the targets were 40 deg apart. The test was repeated with targets 60 and 20 deg apart with similar results.

To describe these results, $\dot{E}_{so}$ was estimated first by eye, and data points for larger values were fit by a linear regression shown by the straight line going up and to the right. $\dot{E}_{so}$ was then redefined as the intersection of that line with a horizontal line extended rightward from the mean gaze velocity, $\dot{G}_0$, found with no head movements. Values of $\dot{G}_0$, $\dot{E}_{so}$, and the slope and correlation coefficient of the linear regressions for the four subjects are shown in Table 1. The slopes are close to 1·0 showing an absence of a vestibulo-ocular reflex in the range above $\dot{E}_{so}$, and the correlation coefficients indicate an unambiguous relationship.

Fig. 5B illustrates the time course of these movements in more detail. To bring out the failure of linear summation more clearly, the targets were put 60 deg apart. In this example, peak head velocity was 96 deg/s and remained near this value

TABLE 1. An analysis of the data in the format of Fig. 6 for four subjects. $\dot{G}_0$ is mean peak saccadic velocity with the head still. The rising phases were fit with a straight line with slopes and correlation coefficients shown. $\dot{E}_{so}$ is the value of slow-phase eye velocity at which this line begins to rise above the value $\dot{G}_0$

Subject	$\dot{G}_0$ (deg/s)	$\dot{E}_{so}$ (deg/s)	Slope	Correlation coefficient
D.R.	470 ± 52	150	1·04	0·87
D.Z.	408 ± 25	100	0·86	0·95
S.C.	526 ± 37	80	0·93	0·92
A.L.	507 ± 31	45	0·82	0·62
Means	478	94	0·91	0·84

throughout the gaze saccade. Superimposed on the eye and gaze traces is a typical saccade (dashed line) made by this subject between continuously visible targets at ±30 deg with the head still. When the head moved, eye displacement in the head was, of course, greatly reduced. This reduction must take place whether or not linear summation was occurring, given that the movement had normal accuracy. The decrease must be, of necessity, the distance that the head moved during the duration of the saccade. If, however, linear summation had been at work, eye velocity would have decreased by just the amount of the head velocity so that gaze velocity would have remained as if the head had not moved and duration would have remained constant. None of these predictions occurred. Eye velocity did slow down, but not enough, so that gaze velocity increased and duration decreased, in this example, from 370 ms to 230 ms. Something was slowing the eye in the head but it was not what one would expect of the vestibulo-ocular reflex.

This test was repeated with passive whole-body rotation. The vestibular chair started to move clockwise from a sufficiently counter-clockwise, initial position that the chair could accelerate to the desired speed before it faced the target display. By that time the subject had acquired the left target and now made a saccade to the right target, 40 deg away, after which the chair decelerated to a stop and the process was then reversed. Fig. 7 shows results similar to those in Fig. 6. As slow-phase eye velocity increased, peak saccadic gaze velocity also increased, peak eye velocity stayed more or less constant and linear summation was not evident. Subject A.L. did, however, have lower velocities than the other subjects for both passive (diamonds, Fig. 7) and active rotations (Table 1).

For passive head rotations (Fig. 7), gaze velocity usually rose to even higher values than for active rotations. From Table 1, one can calculate that S.C., D.R. and D.Z. had mean, peak gaze velocities of 731, 626 and 580 deg/s respectively for active rotations at 300 deg/s but 980, 792 and 900 deg/s for passive rotations (Fig. 7). This is reflected in the slopes of the curves of peak gaze velocity in Fig. 7, for these three subjects, in that they are greater than 1·0. For these subjects, gaze velocity behaved not merely as though linear summation were absent but as though some extra source of innervation were available; similar to the 'activation' reported by Jürgens *et al.* (1981). A gaze velocity of 900 deg/s for subject D.Z., for example, when being passively rotated at 300 deg/s, is remarkable when compared to the 450 deg/s he made for 40 deg saccades, in these trials, when the head was still. Linear summation
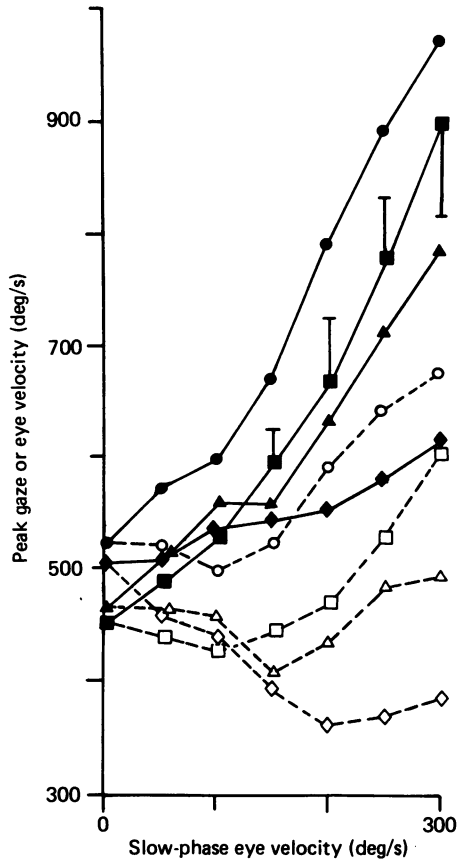
Fig. 7. These data are similar to those in Fig. 6 but head rotation is passive rather than active, from zero to 300 deg/s in steps of 50 deg/s. Peak gaze velocity (filled symbols) and peak eye velocity (open symbols) are shown for the four subjects. Targets were 40 deg apart. In all cases, gaze velocity rose rapidly with head velocity (or slow-phase eye velocity) indicating an absence of the vestibulo-ocular reflex. Subjects were S.C. (circles), D.Z. (squares), D.R. (triangles) and A.L. (diamonds). Note ordinate starts at 300 deg/s.
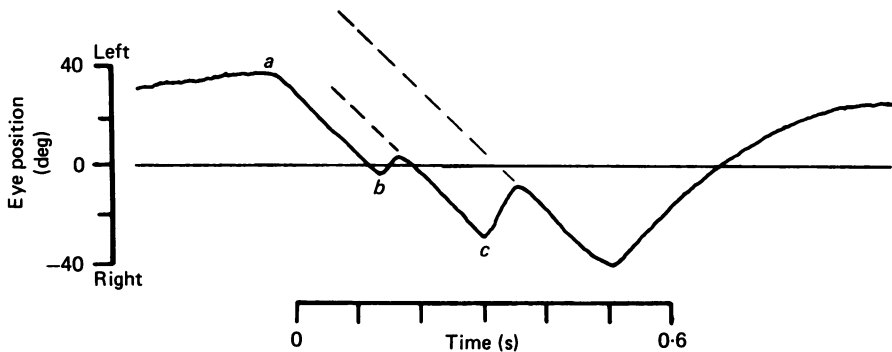

Fig. 8. An example of a saccade during passive rotation at 300 deg/s. The targets were 40 deg apart. The saccade at *c* is 34·8 deg in space (vertical distance between dashed lines). Its duration was only 50 ms during which gaze velocity was 816 deg/s. These values are quite incompatible with the presence of a vestibulo-ocular reflex.

would predict that peak gaze velocity should remain at 450 deg/s. A complete absence of the vestibulo-ocular reflex would predict a peak velocity of 750 deg/s (450 plus 300). A velocity of 900 deg/s is beyond the prediction of either hypothesis.

Fig. 8 shows another example of this behaviour. Prior to point *a*, the subject was suppressing the vestibulo-ocular reflex as he sought the right-hand target. At point *a* the vestibulo-ocular reflex commenced holding the eye on or near this target. Eye velocity was 258 deg/s rather than 300 deg/s; the gain of the reflex was only 0·86 at this velocity. At *b* and *c* the subject made two gaze saccades to the left target, 40 deg away. In general, this was a difficult task when chair velocity was 300 deg/s and significant saccadic dysmetria was the rule. Nevertheless, the amplitude of the gaze change at *c* was 34·8 deg (the vertical distance between the two dashed lines). Peak velocity in the orbit of this saccade was 516 deg/s. This is roughly the velocity with which this subject made 40 deg saccades with the head stationary (D.R., triangles in Fig. 7). Gaze velocity for this gaze saccade was 816 deg/s. In this example eye velocity was not slowed by a putative vestibulo-ocular reflex and gaze velocity was substantially increased over that with the head still. Further, the duration of a 35 deg saccade for this subject with the head still was about 136 ms (extrapolated from Table 2). With the head going at 300 deg/s, the duration was only 50 ms (Fig. 8), a decrease of 63 %.

Smaller saccades and gaze saccades

One impetus for this research was to test the idea of Morasso *et al.* (1973) that the vestibulo-ocular reflex did operate with a gain near 1·0 for gaze saccades 40 deg or less. All our experiments so far question this idea but the conditions were always somewhat removed from the natural situation. It seemed wise to repeat their experiment. A few changes were made in the following experiment from the conditions of Morasso *et al.* (1973): the subjects were human; the two targets were always visible rather than one light jumping back and forth; and subjects paced themselves. In addition, the eyecoil method was used. This method has little system noise and can be differentiated to obtain gaze velocity without introducing a lot of noise. Further, the method measures gaze directly (eye in space, not eye in head) so the time course $G(t)$ is not complicated by having to add $H(t)$ and $E(t)$ to get it. In this way changes in $\dot{G}(t)$ become more apparent.

Subjects made saccades from straight ahead to targets 10, 20, 30 and 40 deg in the periphery with and without head movements. They were asked to hold their head still, then move their head at a moderate speed and then rapidly in three sets of trials. They were told to bring their heads to a full stop before beginning the next gaze saccade. Fig. 9 shows some typical wave forms, and average values for the two subjects studied appear in Table 2.

For 10 and 20 deg saccades, the subjects began to move their heads either simultaneously with the saccade or slightly after and the saccade was over before head velocity reached any significant value. Obviously $\dot{G}(t)$ was the same with or without a head movement; a result irrelevant to the question at hand. For 30 and 40 deg, however, the head reached velocities large enough to affect $\dot{G}(t)$.

The dashed curves (E_0) in Fig. 9*A* and *B* show the time course of the saccade when the head was still. When the head moved, eye motion in the head was slower and
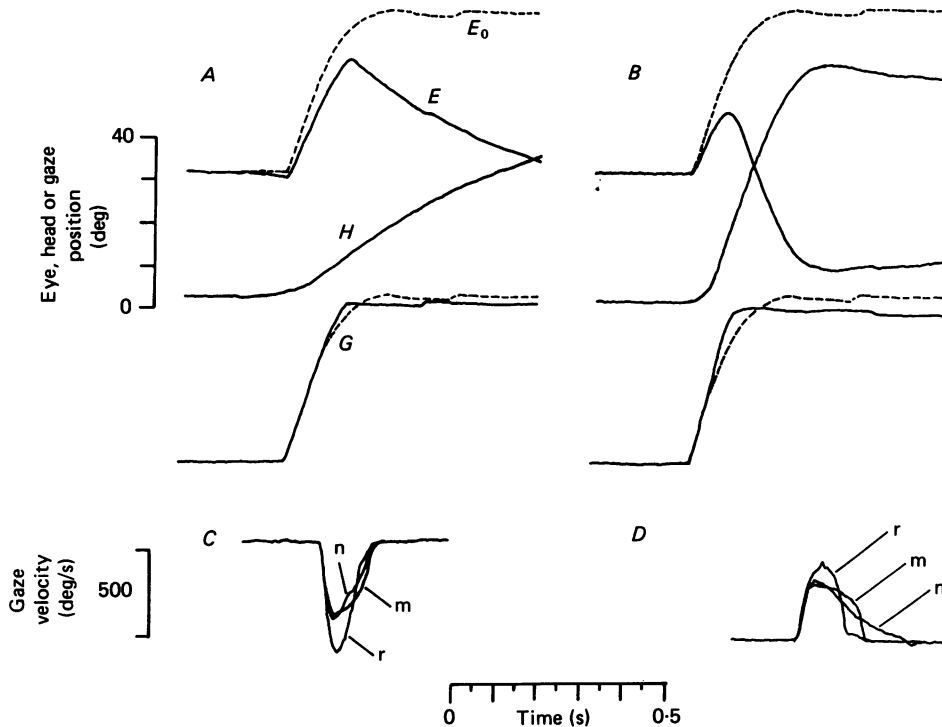
Fig. 9. *A* and *B* illustrate the time course of 40 deg gaze saccades made by subject D.Z. with moderate and rapid head movements respectively. Eye, head and gaze movements are indicated by *E*, *H* and *G* respectively. Dashed lines, E_0, show eye motion with the head still for comparison. Traces were chosen as representative of the mean values in Table 2. As head velocity increased, average duration decreased from 283 (dashed line) to 182 (in *A*) to 122 ms (in *B*) (see Table 2). In *C* and *D* curves of gaze velocity, $\dot{G}(t)$, are superimposed for two subjects (D.R. and D.Z. respectively) for the three conditions of no (n), moderate (m) and rapid (r) head movement. In all cases, this curve grew taller and narrower as head velocity increased. The curves in *D* are the velocities of the same gaze saccades shown in *A* and *B*.

the amplitude smaller, more so when the head moved rapidly. The decrease in $E(t)$ compensated for the presence of $H(t)$ so that the eye still got on target. This action has been attributed to the vestibulo-ocular reflex but if that were the case, durations and the profiles of gaze velocity would be the same regardless of head motion. That did not happen although the differences were smaller than in most of our other experiments.

For both subjects, Table 2 shows a consistent rise in peak gaze velocity, $\dot{G}_p$, when head velocity rose from moderate to rapid. The mean rise was 130 deg/s (range, 57–174). For subject D.Z., duration fell remarkably for 40 deg saccades; from 283 to 182 to 122 ms for the three head velocities. This is admittedly an extreme example. When D.Z. attempted a saccade from 0 to 40 deg with the head fixed, he appeared to near some limit of his oculomotor range. The eye (dashed lines, Fig. 9) slowed down and took an unusually long time (283 ms) to reach its end point. When his head was free to move, the eye was spared from this limit and the prolonged, low-velocity

TABLE 2. Eye–head behaviour for 30 and 40 deg saccades from primary position in the same direction for two subjects who made no head movement (zero), then moderate and finally rapid head movements. ΔG, actual mean amplitude of primary gaze saccade; D, duration; $\dot{G}_p$, peak gaze velocity; $\dot{H}(\dot{G}_p)$, head velocity at the moment when gaze velocity reached its peak; $\dot{H}_p$, typical peak head velocity; n, number of observations. Numbers following ± are 1 S.D.

		Subject D.R.			Subject D.Z.		
	Head motion	Zero	Moderate	Rapid	Zero	Moderate	Rapid
$0 \rightarrow 30°$ left	ΔG(deg)	26·1±1·5	27·8±2·1	27·7±2·2	29·8±0·8	28·3±1·0	27·9±1·4
	D(ms)	124±13	115±14	113±10	114±4	114±7	99±6
	$\dot{G}_p$ (deg/s)	427±14	437±27	599±42	430±28	387±13	444±26
	$\dot{H}(\dot{G}_p)$ (deg/s)	—	67±20	268±95	—	47±30	112±67
	$\dot{H}_p$ (deg/s)	—	95	380	—	65	380
	n	8	7	10	8	9	7
$0 \rightarrow 40°$ left	ΔG(deg)	32·7±1·4	35·5±0·5	38·0±2·3	39·1±0·7	38·5±1·7	34·7±1·3
	D(ms)	149±6	137±6	133±5	283±20	182±29	122±11
	$\dot{G}_p$ (deg/s)	450±11	456±31	630±45	358±19	303±39	427±25
	$\dot{H}(\dot{G}_p)$ (deg/s)	—	115±13	298±59	—	45±25	216±68
	$\dot{H}_p$ (deg/s)	—	145	450	—	80	335
	n	8	3	10	9	6	8

component disappeared. The limit notwithstanding, this behaviour is still incompatible with a vestibulo-ocular reflex summating linearly with a pre-programmed saccadic command. Further, as D.Z. increased his head velocity from moderate to rapid, duration decreased by another 60 ms (33 %) even though the possible complication of an eye position limit was no longer involved. Duration was not so obviously affected for 30 deg gaze saccades for both subjects and for 40 deg gaze saccades for subject D.R., but examination of the wave shape, $\dot{G}(t)$, in Fig. 9C and D shows the same trend toward higher gaze velocities and shorter durations as head velocity increased.

The individual traces of $\dot{G}(t)$ in Fig. 9C and D were selected as representative of the mean values in Table 2, superimposed for the three conditions of head velocity. Again, superposition of such curves was greatly aided by the repeatability of self-paced gaze saccades between two fixed targets as opposed to visually-triggered saccades. In a broad sense, as head velocity increased, the curves $\dot{G}(t)$ became taller and narrower. As head velocity went from zero to moderate, $\dot{G}(t)$ reached approximately the same peak but was more sustained, developing a plateau or a late shoulder, and remained higher than its value with no head movement (compare curves n and m in Fig. 9C and D). Thus, mean gaze velocity rather than peak gaze velocity, increased. As head velocity increased from moderate to rapid, the curves grew taller for both subjects. Since the area under these traces equals net gaze displacement which remained constant, the curves must become narrower and that is what happened (compare curves r and m in Fig. 9C and D). For D.Z. this led to a decrease in duration (Table 2). The only reason it did not for D.R. is that his profile developed a tail in this condition and, since duration was strictly defined by the time when $\dot{G}(t)$ re-entered the noise level, duration, technically, did not decrease.

In summary, increasing head velocity during 40 deg gaze shifts in this experiment led to an increase in mean or peak gaze velocity and a narrowing of the width of the

curve $\dot{G}(t)$. This behaviour is not predicted by linear summation. While this behaviour was evident for 40 deg saccades, it was less so for 30 deg saccades indicating that the ability to distinguish between the linear summation hypothesis and any other proposal for maintaining saccade accuracy (see Discussion) becomes more and more difficult as gaze saccades become smaller.

<div align="center">DISCUSSION</div>

In most of the experiments described, linear summation was absent. When head velocity increased, gaze velocity almost always increased and duration decreased contrary to the predictions of this hypothesis. The changes were not small. Fig. 1 shows a decrease in duration of 34 % when a subject doubled head velocity. Fig. 8 shows an increase in gaze velocity of 58 % and a decrease in duration of 63 % during passive head rotation at 300 deg/s. Even during the normal eye–head reorientations shown in Fig. 9, duration decreased 33 % when subject D. Z. increased his head velocity from moderate to rapid.

There were two situations in which linear summation and the vestibulo-ocular reflex could appear to have been playing a role. First, during 30 deg eye–head reorientations (Table 2) there was a rise in peak gaze velocity for rapid head movements but it was not dramatic and was not reflected in duration. If one looked only at 30 deg gaze saccades or smaller, with moderate head velocities, one would be more struck by the similarities rather than the differences in gaze velocity and duration and conclude, as did Morasso *et al.* (1973), that gaze-saccade accuracy was being preserved by the vestibulo-ocular reflex. A stricter interpretation of such data, however, is only that accuracy is achieved in some manner indistinguishable from linear summation for these small movements. Secondly, in Fig. 6 (but not in Fig. 7) there is a region below a slow-phase eye velocity of about 100 deg/s ($\dot{E}_{so}$, Table 1) where there was no clear trend. Gaze velocity did not rise linearly with head velocity in this region but there was so much scatter in the data that it is also difficult to claim that linear summation was present.

The head-tapping experiment (Fig. 4), however, indicates that even when intended head velocity is zero a vestibulo-ocular reflex is still absent, at least for 40 deg saccades. This evidence implies that the reflex is not attenuated by some sort of saturation but is deliberately disconnected as suggested neurophysiologically by the pause, during all saccades, in the discharge rate of the neurones that carry this reflex from the vestibular nuclei to the ocular motoneurones (King *et al.* 1976; Pola & Robinson, 1978). This suggests that linear summation is absent for all head velocities. The head-tapping experiment was done only for 40 deg saccades; unfortunately, smaller saccades were not investigated. Tomlinson & Bahra (1986) found that rapid head perturbations in monkeys did not elicit changes in eye velocity during large gaze saccades but did for saccades 20 deg or less. The present study does not indicate whether this is the case in humans as well.

Nevertheless, the evidence of the present experiments demonstrates that for gaze saccades of 40 deg and larger, the vestibulo-ocular reflex is shut off and the hypothesis of linear summation must be abandoned. This is the main conclusion from this study and in our view the evidence is unequivocal. That gaze saccades are still accurate
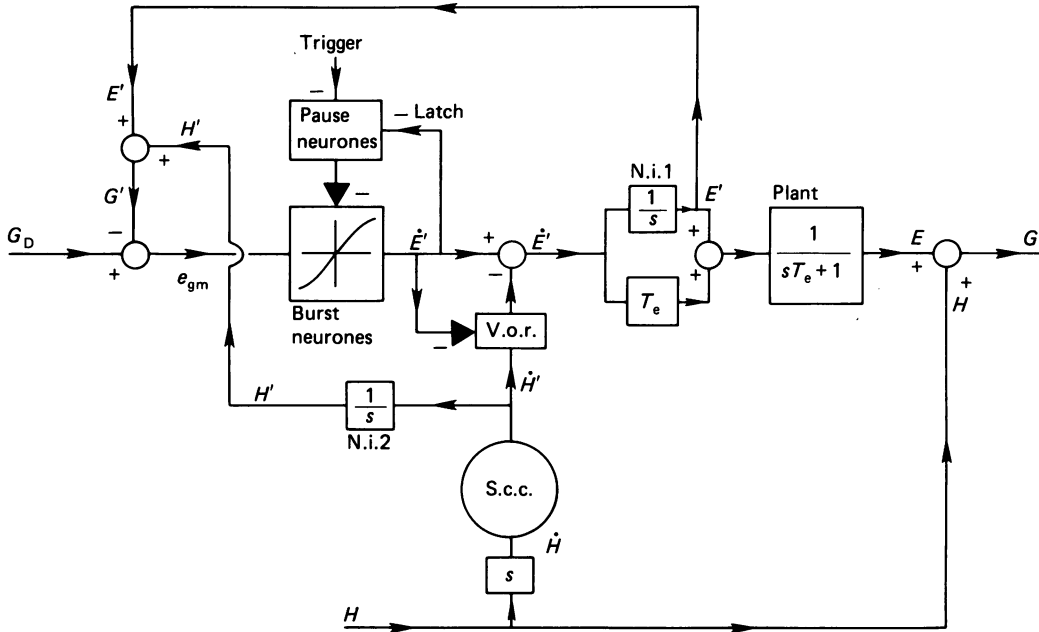
Fig. 10. A model utilizing local gaze feed-back. This is an extension of the local feed-back method of generating saccades described in Zee *et al.* (1976) and van Gisbergen *et al.* (1981). In this case, an internal copy of gaze position G' is found by adding internal copies of head position H' and eye position E'. This is compared to desired gaze position, G_D, and the difference drives the eye through burst neurones. The main advantage of the model is that regardless of what the head does, the eye will continue until it gets on target at which time the gaze saccade automatically stops. See text for details. Integration and differentiation are indicated in Laplace notation $1/s$ and s as is the lag of the oculomotor plant where s is complex frequency. T_e is the plant time constant, about 0·25 s.

means that some other system must exist to achieve this accuracy. This system usually slows the eye movement in the head and, of course, must decrease its amplitude when the head moves in the same direction, as shown in Fig. 5*B*. In doing so, its action bears a resemblance to that of a vestibulo-ocular reflex. When one notes, however, that gaze velocity has increased and duration decreased, often substantially, when the head moves, one can see that the resemblance is superficial. Duration is the most significant clue; the vestibulo-ocular reflex, by its nature, should not be able to vary the duration of a saccade; an action contrary to the whole idea of linear summation. Yet throughout these experiments duration is adjusted over a large range to attain accuracy. This adjustment is not pre-programmed since it still occurs when the head is perturbed unexpectedly in mid-saccade (Figs. 3 and 4). This system appears to keep a running account of eye position in space and be able to stop the eye automatically when it gets on target. The following proposal is offered as one way in which this might be done.

A gaze feed-back model

  The proposed hypothesis, shown in Fig. 10, is an extension of one proposed by Zee,

Optican, Cook, Robinson & Engel (1976) for saccades with the head still. They proposed that an internal copy of eye position be compared to an internal command for a desired eye position. The difference, motor error, should than be amplified by burst neurones to drive the eye at a high velocity (the saccade). The saccade would stop automatically when motor error reached zero; that is, when the eye was on target. The virtues and faults of this theory have been extensively debated (van Gisbergen, Robinson & Gielen, 1981; Henn, Hepp & Büttner-Ennever, 1982; Fuchs, Kaneko & Scudder, 1985) but at present it, or variations on it, remain the only specific theory, capable of quantitative predictions, for the generation of saccades. The extension is to include head movements. Let the internal copy of eye position (E', Fig. 10) be added to an internal copy of head position, H', to create a copy of gaze position G'. This should be compared to G_D, an internal command for a desired gaze position. The difference, gaze motor error, e_{gm}, drives burst neurones at high rates forming an eye-velocity command $\dot{E}'$. This moves the eye quickly until G' equals G_D. At this point, the eye is on target, e_{gm} is zero and the saccade stops.

   Other details are similar to those for the older model (e.g. van Gisbergen *et al.* 1981). Briefly, the burst neurones provide a high gain by firing very rapidly, even for only small motor errors, but the rate saturates for large errors thereby providing the main non-linearity seen experimentally between saccade amplitude and velocity. For very large saccades, the saturation limits eye velocity to about 500–600 deg/s regardless of how big e_{gm} might be. A timing circuit is also needed. Pause neurones inhibit burst neurones until they themselves are interrupted by a trigger signal which initiates a saccade. The pause neurones must be kept silent while a saccade is in progress and this is done by the latch pathway. These circuits simply insure that once a gaze saccade is initiated, it is free to run its course until the eye is on target. The eye-velocity command $\dot{E}'$ passes directly to the plant (the eyeball and muscles) with gain T_e and through the neural integrator n.i.1. The output of the neural integrator provides the signal E'. Again, these elements are described in more detail elsewhere (van Gisbergen *et al.* 1981). The vestibulo-ocular reflex is indicated by the path marked v.o.r. Its input is $\dot{H}'$, head velocity as reported by the semicircular canals (s.c.c.). This signal is integrated (n.i.2) to provide the signal H' needed in the calculation of G'. The v.o.r. path normally has a gain of about 0·9. During saccades of 40 deg or larger, it is proposed that this path is shut off, probably by inhibition from burst neurones.

   One might object to proposing neural correlates H' and G' of the physical variables H and G which have no upper bound. After many complete revolutions of the head, these variables would reach very large values. This can be avoided in several ways. One is to reset H' and G_D after each movement so that changes do not accumulate but, of course, this is only a problem if one supposes these variables to be encoded in proportion to the discharge rate of neurones. It is easy to imagine other methods of encoding (e.g. spatial) that avoid this problem. Such variations are not included in Fig. 10 to leave the model in its most simple and easily understandable form. Also, H' could be derived in part from neck proprioception but this has also been left out for simplicity.

Model behaviour

   The behaviour of this model during gaze saccades can be illustrated rather simply.
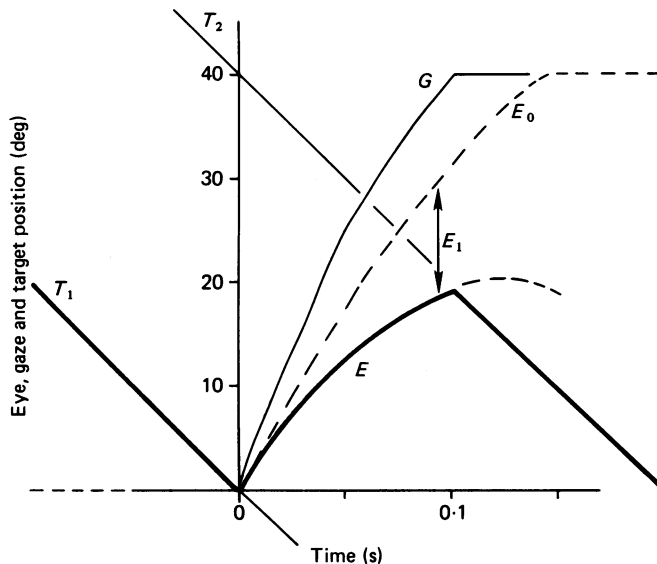
Fig. 11. The behaviour of the model during a constant head velocity of 200 deg/s. E_0 is the assumed trajectory of a 40 deg saccade with the head still. T_1 and T_2 are the old and new target motions with respect to the head. E_1 is the amount by which E_0 is decreased by the vestibulo-saccadic reflex to produce eye position E. G is the sum of E and H (the latter not shown explicitly). Note that E slows down creating behaviour similar to that of the vestibulo-ocular reflex but, in this example, for an entirely different reason. Duration decreases from 150 to 105 ms and gaze velocity increases, similar to the behaviour seen in much of this study.

The model can be linearized for this analysis by letting the gain of the burst neurones be a fixed constant A. Assume that the vestibulo-ocular reflex is disconnected during the gaze saccade (gain of v.o.r. zero). We are not concerned with how this model makes a saccade (amply demonstrated elsewhere) but what will happen to that saccade when the head moves. Consequently, we need only draw some wave form E_0 in Fig. 11 that resembles a typical saccade made with the head still without having to describe it analytically. As an example, a 40 deg saccade with a duration of 150 ms was chosen. When the head moves, the signal $\dot{H}'$ will cause $\dot{E}'$ and E' to decrease through the connexions n.i.2, the paths H', G', e_{gm} and out through the burst neurones to $\dot{E}'$. It is a decrease because of the minus sign between G' and e_{gm}. In other words, the head movement helps the eye towards its goal thereby reducing e_{gm} more quickly. This in turn decreases $\dot{E}'$ and so, of course, E. The amount of decrease can be calculated by superposition; it is the change in E caused by the H signal acting alone. To distinguish this change from E in general, call the decrease E_1.

The transfer function from H to E in Fig. 10, via the path H', G' and e_{gm}, taking into account the feed-back path E', is

$$\frac{E_1(s)}{H(s)} = \frac{-1}{(s(1/A)+1)},$$ (1)

in Laplace notation. By noting that 10 deg saccades have a peak velocity of about 200 deg/s (Schmidt *et al.* 1979), the value of A can be roughly estimated as 20/s so

the time constant $1/A$ in eqn. (1), which will be relabelled τ, is about 0·05 s. This equation shows that the decrease, $E_1(t)$, from the wave form $E_0(t)$ is equal to the increase in head position, $H(t)$, except that it is slowed by a 50 ms lag.

For the special case in which $H(t)$ is a ramp of head velocity with a value of $\dot{H}_1$, as in Figs. 5 and 8, the solution to eqn. (1) is

$$E_1(t) = -\dot{H}_1(t - \tau\,(1 - e^{-t/\tau})), \qquad (2)$$

where t is time. Values of $E_1(t)$ were calculated with $\dot{H}_1$ chosen as 200 deg/s. The curve E in Fig. 11 is the original saccadic wave form E_0 less E_1. T_1 and T_2 are the position of the old and new targets with respect to the head, travelling at 200 deg/s in the direction opposite to the head movement. When E intersects the line T_2, e_{gm} will have reached zero and the gaze saccade will terminate automatically. The sum of H and E is the new gaze trajectory G which now has a higher velocity and shorter duration than the curve E_0 with no head movement. The new duration, determined graphically, is 105 ms, down from 150, at which time the decrease in E is 12·5 deg. The new peak eye displacement is only 19 deg.

Fig. 11 resembles experimental curves such as those in Figs. 5B and 9. If this were an experimental record, casual inspection might suggest that the vestibulo-ocular reflex was operating since a head movement caused the eye to slow down, but, of course, the vestibulo-ocular reflex was disconnected for this simulation. If, for example, one did not notice the change in duration and gaze velocity in Fig. 11, one might note that the net displacement had dropped from 40 to 19 deg so that the mean velocity, mistakenly using a duration of 150 ms in each case, had dropped from 267 deg/s (40/0·15) to 127 deg/s (19/0·15). The decrease, 140 deg/s, could lead one to conclude that the vestibulo-ocular reflex was at work with a gain of 0·7 (140/200), a totally incorrect interpretation. The model, then, behaves in a way that superficially resembles a vestibulo-ocular reflex. This is not surprising in view of the path from H to E via H', G' and e_{gm}. This path has very different dynamics (eqn. 1) from the vestibulo-ocular reflex but nevertheless creates a link between head and eye movements. Since this link is established only during gaze saccades, the name vestibulo-saccadic reflex might be appropriate. All prior studies have automatically assumed that any modification of eye movement by head movement must be due to the vestibulo-ocular reflex: the proposed model indicates that this unquestioning attitude is not justified.

More important, the feed-back model in Fig. 10 is specifically designed to adjust duration automatically to maintain accuracy and consequently is compatible with the experimental results of this study. The vestibulo-saccadic reflex easily accounts for the behaviour shown in Figs. 1, 5, 8 and 9. When e_{gm} reaches zero, burst neurones cease firing, the latch circuit releases the pause neurones to insure that burst neurones remain off, the gaze saccade is over and the path v.o.r. is released from inhibition so that gaze stability may occur in the new position. If G' has been calculated correctly, the eye will be on target. As the head moves more rapidly, G' increases and e_{gm} decreases more rapidly so that duration is automatically reduced. The gaze feed-back also accounts for the behaviour shown in Fig. 3. If the head unexpectedly slows down, it takes longer for G' to equal G_D and duration is prolonged to get the eye on target. In Fig. 4, the same consideration applies except that G' could be increased

or decreased by the hammer blow and duration was accordingly decreased or increased. The model is also compatible with the data shown in Figs. 6 and 7. From eqn. (2) and Fig. 11 one can see that E_1 increases little, early in the saccade (for t less than τ) where eye velocity reaches its peak. Consequently, peak eye velocity is relatively independent of head velocity so that peak gaze velocity rises in direct proportion to head velocity (or slow-phase eye velocity).

It is worth noting that the scheme in Fig. 10 works whether the vestibulo-ocular reflex operates or not. If the reflex worked perfectly (v.o.r. left at 1·0), the gaze loop would not interfere. To see this, note that the signal processing in the path from $\dot{H}'$ through v.o.r., n.i.1 and back to G' is exactly that from $\dot{H}'$ through n.i.2, H' to G' except for the sign. Thus, these two paths would effectively cancel and G' would become independent of head motion as would duration. Consequently, linear summation is not precluded by this model, rather it is subsumed. If, as discussed above, the vestibulo-ocular reflex is able to get through the system for smaller saccades such as 20 deg, the over-all operation would not be disturbed and saccades would still terminate when gaze error was zero. It is not necessary to hypothesize two systems to maintain accuracy, one for small gaze saccades, another for large. If the vestibulo-ocular reflex does work during small saccades, it will simply be gradually replaced by the vestibulo-saccadic reflex as saccade size increases.

From a phylogenetic viewpoint, there are difficulties in trying to achieve gaze-saccade accuracy with the vestibulo-ocular reflex alone. Persaccadic cut off and saturation of motoneurones, mentioned in the Introduction, would distort and, for very large gaze saccades, block the reflex from getting to the eye. Even if this problem were solved, most subprimates have an oculomotor range of only ± 20 deg (e.g. cat, rabbit, goldfish) intensifying the problem illustrated in Fig. 2. During large eye–head–body reorientations in such animals, the eyes would soon be pinned into some limit, mechanical if not neural, and the vestibulo-ocular reflex would again be blocked. Finally, this reflex saturates in humans at 350 deg/s (Pulaski, Zee & Robinson, 1981). If it saturated at similar values during gaze saccades, it would again be blocked during many head movements at higher velocities. For these reasons it is unlikely that evolution would try to rely on the vestibulo-ocular reflex to achieve gaze-saccade accuracy. Fig. 1 shows that it did not.

Further, even within the range where position and velocity limitations might not block the reflex (e.g. 40 deg gaze saccades in primates), the vestibulo-ocular reflex would achieve accuracy at the cost of speed by preventing the head movement from helping the eye to get on target as quickly as possible. Thus, the vestibulo-ocular reflex would have prevented duration from decreasing from 370 to 230 ms in Fig. 5B, from 136 to 50 ms in Fig. 8 and from 182 to 122 ms in Fig. 9A and B. These savings in time are large and have obvious survival value. This is an additional reason for not choosing the vestibulo-ocular reflex as a method for achieving accuracy in gaze saccades. Some other method was needed and Fig. 10 is one possibility. If, however, the vestibulo-ocular reflex were left on, it could thwart the efficiency of the alternate method, as it would in the case of the proposed model, and prevent the desirable decrease in duration. This does not happen indicating that, as already suggested by the behaviour of tonic-vestibular-pause neurones, evolution has elected to turn this reflex off during most gaze saccades to prevent it from slowing them down.

It should be stressed that these experiments and the hypothesis proposed concern only a narrow aspect of eye–head co-ordination. They do not address, for example, the question of how head movements are generated or how the division of labour is decided between eye and head movement. No effort has been made to distinguish between gaze saccades and quick phases of nystagmus. The gaze saccades in this study were always between fixed targets. When the experiment illustrated in Fig. 6 was repeated using an illuminated target that jumped back and forth, it was found that peak gaze velocity did not increase linearly with increasing slow-phase eye velocity until the latter exceeded about 200 deg/s suggesting that visually triggered saccades and self-initiated saccades may differ in their interaction with head movements.

REFERENCES

ABEL, L. A., DELL'OSSO, L. R., DAROFF, R. B. & PARKER, L. (1979). Saccades in extremes of lateral gaze. *Investigative Ophthalmology and Visual Science* **18**, 324–327.

BECKER, W. & FUCHS, A. F. (1969). Further properties of the human saccadic system: eye movements and correction saccades with and without visual fixation points. *Vision Research* **9**, 1247–1258.

BLAKEMORE, C. & DONAGHY, M. (1980). Co-ordination of the head and eyes in the gaze changing behaviour of cats. *Journal of Physiology* **300**, 317–335.

FUCHS, A. F., KANEKO, C. R. S. & SCUDDER, C. A. (1985). Brainstem control of saccadic eye movements. *Annual Review of Neuroscience* **8**, 307–337.

FULLER, J. H., MALDONADO, H. & SCHLAG, J. (1983). Vestibulo-oculomotor interaction in cat eye–head movements. *Brain Research* **271**, 241–250.

GUITTON, D., DOUGLAS, R. M. & VOLLE, M. (1984). Eye–head coordination in cats. *Journal of Neurophysiology* **52**, 1030–1050.

HADDAD, G. M. & ROBINSON, D. A. (1977). Cancellation of the vestibuloocular reflex during active and passive head movements in the normal cat. *Neuroscience Abstracts* **3**, 155.

HENN, V., HEPP, K. & BÜTTNER-ENNEVER, J. A. (1982). The primate oculomotor system. II. Premotor System. *Human Neurobiology* **1**, 87–95.

JÜRGENS, R., BECKER, W., RIEGER, P. & WIDDERICH, A. (1981). Interaction between goal-directed saccades and the vestibulo-ocular reflex (VOR) is different from interaction between quick phases and the VOR. In *Progress in Oculomotor Research*, ed. FUCHS, A. F. & BECKER, W., pp. 11–18. New York: Elsevier.

KING, W. M., LISBERGER, S. G. & FUCHS, A. F. (1976). Response of fibers in medial longitudinal fasciculus (mlf) of alert monkeys during horizontal and vertical conjugate eye movements evoked by vestibular or visual stimuli. *Journal of Neurophysiology* **39**, 1135–1149.

MORASSO, P., BIZZI, E. & DICHGANS, J. (1973). Adjustment of saccadic characteristics during head movements. *Experimental Brain Research* **16**, 492–500.

POLA, J. & ROBINSON, D. A. (1978). Oculomotor signals in the medial longitudinal fasciculus of the monkey. *Journal of Neurophysiology* **41**, 245–259.

PULASKI, P. D., ZEE, D. S. & ROBINSON D. A. (1981). The behaviour of the vestibulo-ocular reflex at high velocities of head rotation. *Brain Research* **222**, 159–165.

SCHILLER, P. H. (1970). The discharge characteristics of single units in the oculomotor and abducens nuclei of the unanesthetized monkey. *Experimental Brain Research* **10**, 347–362.

SCHMIDT, D., ABEL, L. A., DELL'OSSO, L. F. & DAROFF, R. B. (1979). Saccadic velocity characteristics: intrinsic variability and fatigue. *Aviation Space and Environmental Medicine* **50**, 393–395.

SCUDDER, C. A. & FUCHS, A. F. (1981). Projections from the vestibular to abducens nuclei as revealed by spike triggered averaging. *Neuroscience Abstracts* **7**, 777.

SKAVENSKI, A. A., HENSEN, R. M., STEINMAN, R. M. & WINTERSON, B. J. (1979). Quality of retinal image stabilization during small natural and artificial body rotations in man. *Vision Research* **19**, 675–683.

TOMLINSON, R. D. & BAHRA, P. S. (1986). Combined eye–head gaze shifts in the primate. II. Interactions between saccades and the vestibulo-ocular reflex. *Journal of Neurophysiology* (in the Press).

VAN GISBERGEN, J. A. M., ROBINSON, D. A. & GIELEN, S. (1981). A quantitative analysis of the generation of saccadic eye movements by burst neurons. *Journal of Neurophysiology* **45**, 417–442.

ZEE, D. S., OPTICAN, L. M., COOK, J. D., ROBINSON, D. A. & ENGEL, W. K. (1976). Slow saccades in spinocerebellar degeneration. *Archives of Neurology* **33**, 243–251.