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Modulation of the Human Vestibuloocular Reflex During Saccades: Probing by High-Frequency Oscillation and Torque Pulses of the Head

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SUMMARY AND CONCLUSIONS

1. We probed the gain and phase of the vestibuloocular reflex (VOR) during the execution of voluntary gaze saccades, with continuous oscillation or acceleration pulses, applied through a torque helmet.

2. Small-amplitude (<1°), high-frequency (10–14 Hz) head oscillations in the horizontal or vertical plane were superimposed on ongoing horizontal gaze saccades (40–100°). Torque pulses to the head (''with'' or ''against'' gaze) were superimposed on 40° horizontal saccades. Eye and head movements were precisely measured with sensor coils in magnetic fields.

3. Techniques were developed to separate the oscillatory (horizontal or vertical) component from the gaze shift and obtain VOR gain and phase with Fourier techniques from the relation between eye-in-head and head oscillations. These involved either subtraction of exactly matching saccades with and without oscillation (drawback: low yield) or time shifting of successive trials to synchronize the oscillations (drawback: slight time blurring of saccades).

4. The results of these matching and synchronization methods were essentially identical and consistent. Presaccadic gain values of the horizontal VOR (typically about unity) were reduced by, on average, ~20 and 50% during horizontal saccades of 40 and 100°, respectively. These percentages may be truncated because of methodological limitations, but even after taking these into account (on the basis of simulation experiments with 2 different, theoretical profiles of suppression) our results do not support a complete saccadic VOR suppression for any substantial fraction of saccadic duration. Qualitatively similar changes were found when the vertical VOR was probed during 100° horizontal saccades.

5. Concomitantly with the reductions in gain, VOR phase was advanced by ~20° during the saccade.

6. In the wake of gaze saccades, VOR gain was consistently elevated (to ~1.0) above the presaccadic level (~0.9). We submit that this mechanism ensures stable fixation of the newly acquired target at a time when the head is still moving substantially.

7. Although the responses to head torque pulses showed idiosyncratic asymmetries, analysis of the differences in eye and head movements for pulses with and against consistently showed a sharp fall of VOR gain at saccadic onset, following an approximately exponential course with a time constant of ~50 ms. This decay may be assumed to reflect VOR gain for a period of ~50 ms, after which secondary gaze control mechanisms become dominant.

8. The time course of the gain decay and phase shift of the VOR suggest that suppression of the ''integrative (position) loop'' of the VOR circuit was more complete than suppression of the direct, ''velocity'' pathway.

INTRODUCTION

Natural shifts of gaze between different objects are often effected by combined eye and head movements. A frequently debated question is whether and how the vestibuloocular reflex (VOR) is modified during such gaze saccades. As long as the gaze remains aimed at the same object, the VOR is known to automatically turn the eye in the head in the direction opposite to any head movement, at nearly the same velocity, to hold gaze stationary. If the VOR continued to work during gaze saccades accompanied by an active head movement, it would slow the saccade in the head by the velocity of the head and consequently make eye movement in space independent of head movements. This latter type of behavior of the VOR was advocated in the early 1970s by Bizzi and colleagues (Bizzi et al. 1971; Dichgans et al. 1973; Morasso et al. 1973), who basically argued that eye movements in the head were programmed as an independent activity and that whatever the head did was irrelevant because all the head movements were compensated by the VOR. Under this ''linear summation hypothesis'' [a term introduced by Laurutis and Robinson (1986)], the velocities, amplitudes, and durations of gaze saccades should be unaffected by head movements, whereas eye-in-head velocities would be strongly affected. On the other hand, absence of such linear summation would permit the head movement to speed up gaze velocity, with faster acquisition of the target by combined eye and head movements as a useful result. Obviously, mechanisms other than the VOR would then be required to commensurately reduce the duration of the gaze movement and maintain saccadic accuracy.

Since the 1970s, continued work, especially on primates, has gradually eroded support for straightforward linear summation in favor of a (total or partial) suppression of the VOR during the saccadic, fast part of gaze shifts. The early work (Bizzi et al. 1971; Dichgans et al. 1973) concentrated on the later part of the gaze movement, when gaze is already on target but the head is still moving. The vestibular origin of the compensatory eye movements in this phase remains undisputed, but generalization of the linear summation hypothesis to the early part of the gaze shift has been shown to be untenable. Initially, Morasso et al. (1973) supported continuous linear summation in monkeys by showing that peak velocity and duration of gaze shifts were unaffected by the head being free or restrained, but only gaze shifts up to 40° were studied. The linear summation hypothesis could not logically account in any case for the dynamics of large gaze saccades that exceed the oculomotor range of the eye in the head, because head movements contribute to such large gaze shifts by definition. Already Jürgens et al. (1981)

have shown only a partial (~70%) summation of VOR and eye saccades in humans during passive head rotations at peak velocities of 125°/s. Tomlinson and Bahra (1986), using short, passive head perturbations in monkeys, found that the VOR was functional during saccades <20° but absent for saccades larger than ~40°. Absence of linear summation, except maybe for saccades <30°, was also supported by a variety of experimental evidence by Laurutis and Robinson (1986). Related experiments by other authors have also indicated that the VOR is operational during small saccades, but progressively turned off with increasing saccadic amplitude (Pélisson et al. 1988; Tomlinson 1990). Considerable idiosyncratic differences among human subjects in the degree of suppression, however, were demonstrated by Guitton and Volle (1987). Furthermore, the time course of the VOR suppression remains unclear. Laurutis and Robinson (1986) assumed an immediate switching between "on" and "off" conditions; Guitton and Volle (1987) proposed a more gradual VOR restoration; Pélisson et al. (1988) proposed an exponential VOR variation law; and, finally, Lefèvre et al. (1992) came up with a result arguing for a restoration of VOR gain from 0 to unity in the last 40 ms of the gaze saccade.

A problem with many of the experiments discussed above is that they interfered with the ongoing gaze motion by considerable alteration of the natural head movement; in this way, the object of the measurement (the gaze signal) was often disturbed in a rather crude way. In fact, it has been difficult to demonstrate suppression of the VOR during natural gaze movements when subjects were not forced to move the head very fast (Becker and Jürgens 1992; Pélisson et al. 1988; Smeets et al. 1996; Van der Steen 1992). A recent experiment with occasional, passive head perturbations during a sequence of natural gaze shifts (Epelboim et al. 1995) confirmed the maintenance of accuracy under such perturbations, but suggested considerable trial-to-trial variability in the contribution of VOR and non-VOR mechanisms to this accuracy.

In this study we probe the VOR during gaze shifts with the use of a helmet with torque motor (Tabak and Collewijn 1994, 1995) that enabled us to apply to the head either high-frequency (10–14 Hz), low-amplitude (<1°) oscillations or torque pulses, superimposed on gaze saccades. The ocular response to oscillation, which did not affect the gaze or head movements in a systematic way, could be extracted as an independent probe of the VOR. In this way it was, in principle, possible to evaluate the gain and phase of the VOR as continuous functions of time in relation to saccades, with minimum activation of non-VOR mechanisms correcting gaze accuracy. Analysis of the oscillations showed that VOR gain was indeed reduced during saccades. In contrast, VOR gain was enhanced in the wake of saccades. Furthermore, systematic advances in the phase of the VOR occurred along with the changes in gain. Changes in the VOR extended to the vertical VOR during horizontal saccades, and thus were not plane specific. The phase advances indicated, in addition to a decrease in gain, a change in the VOR dynamics, possibly due to a deficit in the integration of vestibular signals. To further explore this point, we administered, in complementary experiments, torque pulses to the head in conjunction with 40° gaze saccades. The difference in the responses of the eye to perturbations of the head in opposite directions (with or against the saccade) was similar for all subjects, although the responses themselves showed idiosyncratic asymmetries. The initial part of this difference could be approximated by an exponential decline of VOR gain, starting at saccadic onset, with a time constant of ~50 ms.

METHODS

Subjects and stimulation technique

Eleven healthy subjects, who had no known ocular or vestibular pathologies, served in the experiments. Three of the subjects wore spectacles (for mild refraction errors) but did not need these during the experiments. Passive, horizontal high-frequency head rotations were generated by a helmet, placed on the subject's head, with a torque motor (GEC Alsthom/Parvex; 120 W on top. The torque motor rotated a freely rotating flywheel. Acceleration of the flywheel caused a reactive torque of the helmet, which was transferred to the head. For a complete description of this method we refer to Tabak and Collewijn (1994, 1995). Vertical high-frequency head rotations were generated with another helmet, which had two similar but smaller torque motors (each 70 W) mounted coaxially and symmetrically on the right and left sides. The spindles of these torque motors were suspended in an aluminum U-shaped frame by means of two small ball bearings, such that their common rotational axis coincided approximately with a transverse axis through the center of the head. Each of the torque motors rotated a flywheel in identical directions about the transverse axis. The gravitational load of the helmet devices on the head was balanced by suspending them from the ceiling by a suitable spring. This suspension also left the subjects free to translate and rotate the head in all directions. The springs balanced the weight of the helmets but did not, of course, neutralize the extra mass attached to the head, which caused an additional inertial load on the head neck motor system. Moments of inertia (around the vertical axis) for the horizontal and vertical helmets were 0.03 and 0.45 $kg \cdot m^2$, respectively, whereas the moment of inertia of the head is ~0.2 $kg \cdot m^2$. The large inertia of the "vertical" helmet, caused by the two eccentrically placed torque motors with attachments, noticeably limited the subject's ability in making fast and large horizontal head movements.

All torque motors were powered by a driver [Soprel/Milano Transdriver (I) DB 425 W/R], which received a sinusoidally changing voltage as the control signal. For safety, control signals were high-pass filtered so that they returned exponentially to 0 in ~1 s; this prevented the buildup of high spinning velocities of the flywheels.

Recording technique

Eye and head movements were recorded with the scleral coil technique (Collewijn et al. 1975; Robinson 1963), relative to an earth-fixed, homogeneous magnetic field. The recordings should reflect only rotations and be invariant for any translations. To achieve this, the magnetic fields were made homogeneous in strength and direction over a space including any possible head position (see Collewijn 1977 for details on coil construction). An ocular sensor coil (Skalar, Delft, The Netherlands) was attached to one eye. To record the head movements, a second sensor coil was firmly attached to an individually fitted dental impression biteboard.

The sensor coils were connected to high-quality lock-in amplifiers (Princeton Applied Research, model 5210) to obtain their horizontal and vertical positions by amplitude detection. The sensitivity of the eye and head coils was calibrated before every experimental session with a protractor. The system's resolution was better than 1 min of arc. Each signal was digitized at 500 samples per second after antialias low-pass filtering at 125 Hz, and was stored into a

DEC PDP 11/73. Eye-in-head orientation was computed by subtraction of head orientation from gaze orientation.

Visual conditions

To obtain invariance for head translation of the gaze and head signals and of the angular viewing direction of the target, we placed the visual targets (2 light-emitting diodes) at optical infinity in the focal plane of a Fresnel lens (94 × 70 cm; focal length 118 cm). Unfortunately, the Fresnel lens was too small to cover the largest gaze saccades (100°). For this experimental condition the light-emitting diodes were placed at an distance of ~200 cm. This did not influence VOR gain, because this is not affected by optical infinity of the visual target in the frequency range from 2 to 20 Hz (Tabak and Collewijn 1994), but it probably did increase the variability of the size of our largest saccades somewhat. In both types of experiments the subjects were seated in the magnetic field, viewing the targets binocularly with the head unrestrained. All experiments were conducted in complete darkness, except for the two point targets.

Procedures in oscillation experiments

A first series of measurements concerned horizontal gaze shifts of various sizes with superimposed, high-frequency, horizontal head oscillations, i.e., combined eye head movements (gaze saccades) of 100 and 80° and saccades of 40° without active head movement. For the largest gaze saccades, subjects ($n = 11$) shifted gaze from the visual target 50° to the left to the target 50° to the right. In the next trial subjects made a gaze saccade from the right target back to the left target, and so on. Each trial lasted 4 s. The subjects were cued by an auditory signal to make the gaze saccades at the appropriate time. In addition, we imposed (in alternating fashion) a passive, horizontal head oscillation with a frequency between 9.0 and 10.5 Hz (6 Hz on 1 occasion) during 50% of the pairs of gaze saccades. We asked the subjects to make head movements in a natural way, with velocities that felt like normal, i.e., not at maximum attainable velocities. Subjects made between 30 and 40 gaze saccades in each direction, with and without head oscillation. Because of the shorter duration of the 80° gaze saccades and 40° saccades (without head movement), we had to apply higher oscillation frequencies (12 and 14 Hz) to accommodate a sufficient number of oscillation periods for analysis within the duration of the saccade. Head oscillation amplitudes (peak to peak) decreased when the frequency was increased, from ~0.5° at 10 Hz to ~0.3° at 14 Hz (Tabak and Collewijn 1994).

In a second series of measurements the subjects ($n = 9$) made horizontal gaze saccades of 100° but the head oscillation (frequency 5.8–6.8 Hz) was vertical, i.e., orthogonal to the plane of the gaze saccade. Each trial in this experiment lasted twice as long (8 s instead of 4 s); therefore subjects made fewer gaze saccades (between 20 and 35 to the right and left, with and without oscillation). Unfortunately, in this experiment the subjects found it very difficult to reach the normal head velocities associated with 100° saccades, because of the substantial increase in the moment of inertia by the helmet.

Procedures in torque pulse experiments

Subjects made saccades between the two continuously visible light-emitting diodes separated by 40°. Each trial started with a warning tone, followed after 4 s by a second tone, which was the signal for the subjects to make one saccade. In part of the trials, the torque motor started to rotate the flywheel just before the expected start of the saccade. The resulting head movements started ~100–150 ms before the saccade. The purpose of starting the head movement before the saccade was to obtain a substantial head velocity during the saccade. A disadvantage of this technique was that the relative timing between saccade and head movement was rather variable. Because the head perturbation started more than 100 ms before the saccade it is, furthermore, possible that subjects used information about the perturbation when they generated the saccadic command.

Three conditions of head movements were used in the experiment. In one condition (head static), the head did not move; in the other two the head was moved, either in the same direction as the saccade (head with), or in the opposite direction (head against). Because the response of the head to the torque differed between conditions (see RESULTS), we used a different timing of the torque relative to the go signal for the two perturbed conditions: pulses "with" were given 50 ms earlier than pulses "against." In this way, we ensured that the moment of maximum velocity of the head was near saccadic onset. Subjects made saccades in four to eight blocks of 20 trials. In each block, all saccades were in one direction; the head movement condition for each trial was unpredictable for the subject.

Data analysis of oscillation experiments

To analyze VOR gain it was necessary to separate the components in the head, eye, and gaze signals associated with the imposed head oscillation from the components related to the gaze saccade. For this purpose, we developed two methods, both yielding equivalent results. The first method (matching method) is conceptually simple, but can only be used to analyze a few saccades. The second method (phase synchronization) is more complex, but able to analyze all trials. Both methods started by synchronizing the recordings of all trials so that the start of the gaze shift (according to a velocity criterion of 50°/s) corresponded to $t = 0$.

The matching method treated the trials in which no perturbations (oscillations) were applied as reference saccades. For each perturbed trial, the set of unperturbed trials was searched for the single trial in which the gaze-related components best resembled the perturbed trial, assuming that the perturbation did not affect the dynamics of the saccade (this assumption is supported by the data). In a few initial experiments, this search for matching saccades was performed manually by overlying plots of saccades with and without oscillation. Later on, the search was computerized and performed by summing the squared difference between the signals (for both head and gaze) of a pair of trials from 50 ms before till 500 ms after the start of the saccade. For the best corresponding pair, the unperturbed signals were subtracted from the perturbed ones, and these difference signals were regarded as the perturbation (head) and the response to it (eye-in-head).

The phase synchronization method used only the trials in which oscillations were applied to the head, but used all of those. The phase of the oscillation of the head at $t = 0$ was random (see Fig. 1*A*). To enable the averaging of the perturbations, the signals were resynchronized on the phase of the head oscillation (determined by fitting a sine function to the head signal preceding the gaze shift). For trials with a phase between 0 and 180°, all signals were shifted backward in time so that the phase of the head oscillation at $t = 0$ became 0. For trials with a phase between 180 and 360°, all signals were shifted backward in time so that the phase of the head oscillation at $t = 0$ became 180°. This yielded two groups of trials, one with phase 0 and one with phase 180° (see Fig. 1*B*). For both groups, the gaze shift (for a 10-Hz oscillation) started somewhere between $t = -50$ ms and $t = 0$ ms (on average, $t = -25$ ms). After calculating the average signals for both groups, we could easily determine the average saccade and the perturbation. Because the perturbations have opposite signs in both groups, summing of the averages of both groups (and dividing by 2) removed all perturbations and isolated the saccadic components. On the other hand, taking the difference between the two groups divided by 2 removed the saccade and isolated the perturbation (head signal) and the response to it (eye-in-head signal). In this way,

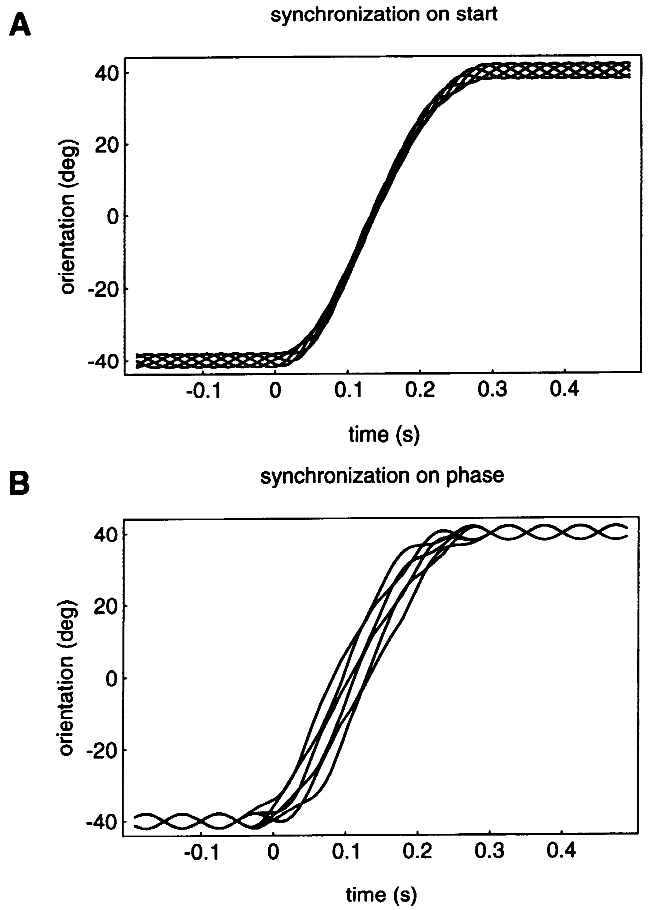

FIG. 1. Principles of the phase synchronization method. *A*: in a 1st step, starts of gaze displacements of all trials with head oscillation in a session are aligned at $t = 0$. *B*: in a 2nd step, phase of the superimposed oscillation is realigned to 0 or 180° at $t = 0$ (whichever is closest) by time shifting of the individual gaze records. In this way, phase is synchronized at the expense of some time blurring of the gaze movement.

the perturbation and the response could be determined very accurately in exchange for a decrease in the temporal resolution of the saccade (from 2 ms in individual trials to 25 ms in the phase-synchronized signals). In the experiment with vertical oscillation and horizontal saccades the separation was, in principle, much simpler because of the orthogonality of the signals. Nevertheless, we applied the same procedures in this case to ensure that the results of the analysis were comparable for all conditions.

After the perturbation was separated from the saccade by one of the methods mentioned above, VOR gain was determined as a function of time. For each instant, a Fourier transformation of the signals of head perturbation and eye-in-head response was calculated, with the use of data windowed by a Parzen window function ranging from 256 ms before until 256 ms after that instant. From the power and phase of the signals at the perturbation frequency, the gain and phase lag of the VOR was determined as a function of time. The rather long window was needed to be able to limit the analysis to a 2-Hz band around the perturbation frequency.

The two techniques we need to obtain the average response of all subjects (the phase synchronization and the Fourier transform) both blur the signal. To illustrate this artifact, we constructed artificial experimental data. One set of data was constructed with the use of a VOR gain that was equal to 0.9 until the onset of the saccade, was 0 during the saccade, and was restored immediately to 0.9 after the saccade (Fig. 2*A*). This would represent the maximum possible degree of intrasaccadic VOR suppression. A second set of data simulated a symmetrical, triangular decline and recovery of VOR gain, with a minimum (but not sustained) value of 0 (Fig. 2*B*). This case represents the minimum degree of VOR suppression in which complete suppression is reached at least at one moment: a conservative model. A phase lag of 0 between eye and head movement was used. The time course of phase and gain obtained after averaging the artificial trials and Fourier analysis are plotted in Fig. 2, *A* and *B*, for a simulated saccadic duration of 300 ms (about the duration of a 100° saccade). The time course of the VOR gain is blurred: instead of an immediate reduction to 0 at 0

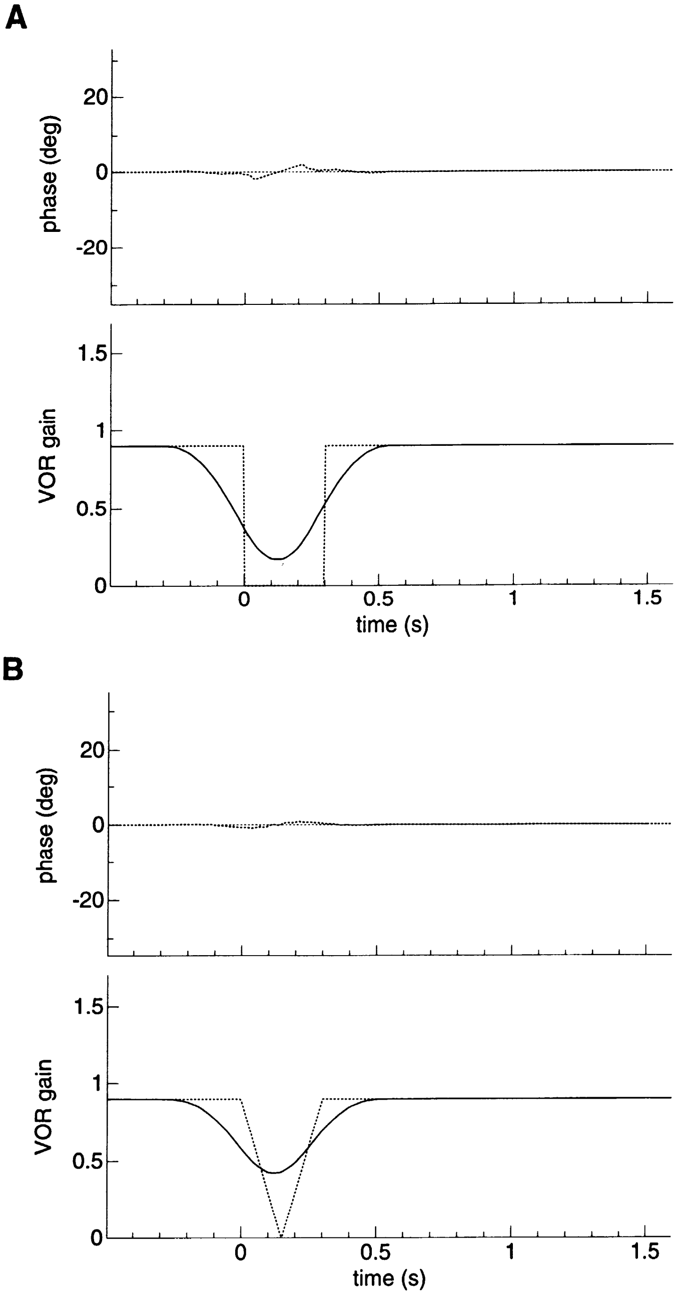

FIG. 2. Simulation of blurring effects of phase synchronization and window used in Fourier transform on the time course of phase and gain of the vestibuloocular reflex (VOR). Dashed curves: time courses for the (artificial) data. Solid curves: the relations obtained by analyzing these data with the use of the techniques described in the METHODS section. *A*: simulation of abrupt decline and recovery of VOR gain at saccadic onset and offset, with total suppression between (''square'' profile of suppression). *B*: simulation of linear decline and recovery of VOR gain, reaching total suppression only for a brief instant (''triangular'' profile of suppression). See text for further details.

ms, the gain reduces gradually before the saccade, reaching its minimum (0.17) at 124 ms, after which the gain restores slowly to its original value. One important artifact of the analysis technique is thus that a sudden change in VOR gain is blurred to a smooth change, which means that it is impossible to determine accurately the timing of the VOR suppression. In addition, the phase synchronization technique shifts the time of maximum suppression 25 ms forward (Fig. 2*A*). A further effect of our data analysis techniques is underestimation of the maximum amount of VOR suppression. The magnitude of this underestimation depends both on the duration of the suppression and on the shape of the suppression profile. For a simulated "square" profile of suppression to 0 gain, the minimum gain values yielded by the analysis for 400, 300, and 150 ms duration were 6.2, 18.7, and 51%, instead of 0%, of the presaccadic gain value. For a triangular profile, the corresponding values were 38, 47.1, and 65.8%, respectively. These numbers show the limitations of the estimates of time course and minimum value of VOR gain as obtainable with the techinque in its present version. It should be emphasized that, in contrast, distortions of phase were negligible (Fig. 2, *A* and *B*).

Data analysis of torque pulse experiments

Because the perturbations of the head could cause changes in the movements of the gaze, we had to determine the onset of the saccades carefully. Because the acceleration of the head was low near saccadic onset, we used a gaze acceleration criterion of 5,000°/s^2 to define saccadic onset and offset. This onset criterion was used in aligning gaze saccades in averages such as shown in Figs. 9 and 10. Saccades with amplitudes <30° were excluded from further analysis. Trials without perturbation in which the head moved by >2° during the trial were also excluded. For the perturbed trials, we had to check whether the perturbation during the saccade was sufficiently large. We used only trials in which the head moved >1.5° during the saccade with a velocity of >10°/s at saccade onset in further analysis. A total of 1,085 trials (75%) passed these criteria.

For the quantification of the effect of the head perturbation on the dynamics of the saccade, we calculated the instantaneous VOR gain, $G(t)$. This gain is an estimate of the effect of head movement on eye-in-head velocity during the saccade. It is calculated by dividing the difference in eye-in-head velocity between two head movement conditions (with and against) by the difference in head velocity between these conditions occurring 6 ms earlier

$$G(t) = \Delta V_{\text{eye}}(t)/\Delta V_{\text{head}}(t - 6)$$

Velocities were calculated as the position difference between two successive samples, divided by the sample interval (0.002 s); subsequently, this signal was low-pass filtered (effective cut-off 100 Hz) in both forward and reversed direction to prevent phase shift (Ackroyd 1973). The 6-ms time difference is our estimate for the delay of the human VOR. This delay is considerably shorter than the 14 ms determined by Lisberger (1984) in the monkey; our shorter estimate is based on our direct measurements of latency with helmet induced torque pulses in humans (ongoing experiments in our laboratory) and is in agreement with the few published data for humans (Maas et al. 1989). The total response of the head to the torque perturbation was measured by its orientation 200 ms after the onset of the saccade. For values that are averaged across subjects, the intersubject variability is indicated by the intersubject SD.

RESULTS

Probing the VOR with horizontal oscillation during horizontal gaze saccades

The basic result, obtained by the "matching" technique from a manually selected pair of saccades without and with head oscillation (in this particular case at 6 Hz), is illustrated in Fig. 3. Figure 3*A* shows the gaze, eye, and head displacements, all of which matched exceptionally well in this pair, except for the oscillations. Therefore subtraction of the "nonoscillation" from the "oscillation" records resulted in an almost perfect isolation of the oscillatory components (Fig. 3*B*). These difference signals show marked, characteristic changes during the saccade. The head difference signal shows that head oscillation continued with little change during the saccade. The gaze difference signal shows that before the gaze saccade (which started at t = 0) there was some modulation of gaze in phase with the applied head oscillation, indicating that the VOR was working at a gain below unity. Subsequently, during the fast displacement of gaze, there was a large increase in the amplitude of oscillation in the gaze signal, which now resembled the oscillation of the head. Simultaneously, there was a complementary decrease in the eye-in-head signal. This change indicates a marked reduction in VOR gain. The oscillatory modulation of the gaze signal was much reduced again around the time of the landing of gaze on target. In the last phase of the gaze saccade, when gaze

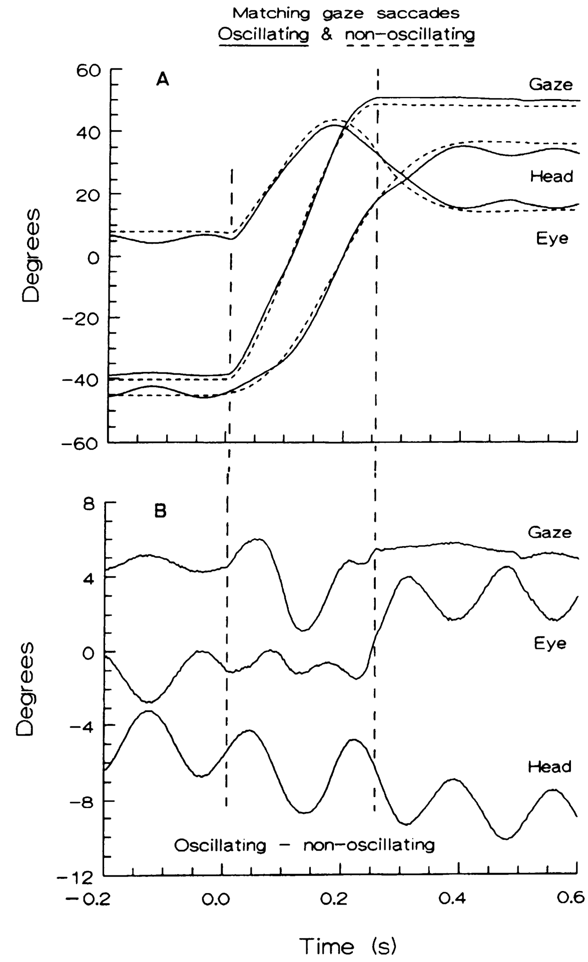

FIG. 3. Principle of the matching method. A pair of gaze saccades from 1 session was selected (1 with and 1 without head oscillation) in which gaze, eye, and head movements matched as well as possible, except for the oscillations. *A*: good match. *B*: subtraction of the nonoscillated from the oscillated trial isolated the oscillatory components. The modulations of the oscillation as a function of time show the changes in the VOR. (In this example the oscillation had an uncharacteristically low frequency of 6 Hz.)

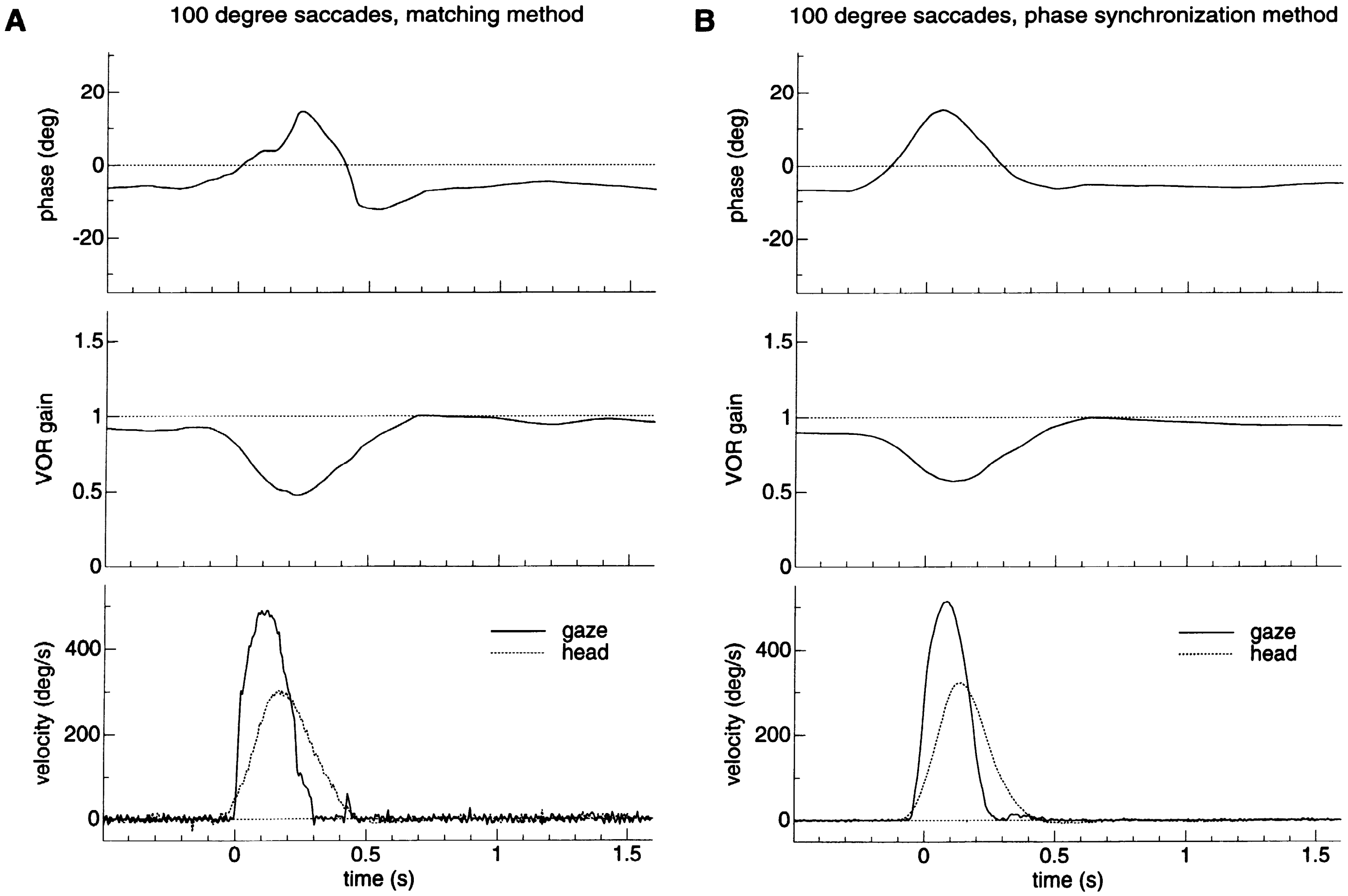

FIG. 4. *A*: example of the results of Fourier analysis, applied to a single matching pair of 100° saccades. *A, bottom*: saccadic components (as velocity profiles) of the gaze movements. *A, top 2 graphs*: phase and gain of the VOR, estimated from the oscillatory component (which is not shown here). *B*: results of Fourier analysis after application of the phase synchronization technique to all oscillated trials in the same session from which the single matching pair in *A* was derived. Notice the overall similarity between the results in *A* and *B*.

had landed but the head and eye continued to move in opposite directions, gaze showed even less oscillation and thus was more stable than just before the gaze saccade (again with complementary changes in the eye-in-head signal), indicating that the VOR functioned at a higher gain (closer to unity) after the gaze shift than before it.

These basic but somewhat qualitative findings (confirmed by a number of other manual matchings) were quantified by computerized matching and Fourier analysis of the oscillatory eye and head signals to determine gain and phase of the VOR. Figure 4*A* shows an example of such an analysis for a single pair of matched saccades (amplitude ~100°; oscillation at 9.6 Hz with an amplitude of ~1.0° peak to peak). The Fourier analysis shows that VOR gain was reduced from a presaccadic value of ~0.9 to slightly below 0.5 during the saccade, with a subsequent recovery to initially ~1.0 after the saccade followed by a gradual reduction to the presaccadic level. Remarkably, these changes in gain were accompanied by a temporary advancing of the phase by ~20°.

Thus the matching technique clearly demonstrates the existence of intrasaccadic changes in gain and phase of the VOR and suggests a characteristic time course for these phenomena. A limitation of these results is that matching pairs are rare and that the analysis is therefore based on few saccades. Fortunately, our second method of analysis, the phase synchronization technique, which uses all (oscillated) saccades, corroborated and refined the results of the matching method. Figure 4*B* shows the result of this analysis for all oscillation trials in the same session from which the single matching pair of saccades in Fig. 4*A* was derived. The graphs in Fig. 4*B* confirm that the VOR before the gaze saccades was working at a gain of 0.90. During the gaze saccades the VOR was partially suppressed, with an apparent minimum gain of 0.56, which is 62% of the presaccadic value. At the mean saccadic duration of ~400 ms, total suppression with a square or triangular profile (see METHODS, Fig. 2, *A* and *B*) would yield in our analysis apparent minima of 7.2 and 38% of presaccadic VOR gain, i.e., 0.07 and 0.34. Thus, for the subject illustrated in Fig. 4*B*, the limitations of our technique allow the conclusion that VOR suppression during 100° saccades was incomplete: the minimum gain of 0.56 was very much higher than the prediction of 0.07 for a complete suprression during the whole saccade, and also clearly higher than the predicted 0.34 for a triangular suppression profile with only momentary complete suppression (the most conservative assumption for suppression reaching 100% at any time during the saccade).

Strikingly, immediately after gaze landed on target the VOR was working at a supranormal gain (1.0). This supranormal VOR gain gradually returned to its normal, presaccadic value.

Finally, there was a significant intrasaccadic change in VOR phase. Before the start of the gaze saccades this subject showed a phase lag between compensatory eye movements and head oscillation movement of ~7°. This value progressively turned into a phase lead of 14° during the gaze saccade, and slowly returned to its original phase lag value. Figure 4*B, bottom,* shows the dynamics of the gaze and head movement velocities.

Figure 5, *A–C,* shows the means ± SD of the gain and phase relationship of the VOR as a function of time (obtained by the phase synchronization method) of all trials in all 11 subjects for the 100, 80, and 40° saccades, respectively. Mean VOR gains and phase lags preceding the gaze saccades were in agreement with the values of VOR gain and phase previously described for the applied frequencies (Tabak and Collewijn 1994). Specifically, VOR gain has been found to increase progressively for frequencies increasing above 8 Hz, up to values exceeding unity.

The average results for the 100° gaze saccades (Fig. 5*A*) strongly resemble the result of the single subject shown in Fig. 4. The mean VOR gain before the gaze saccade was ~0.94 with a phase lag of ~9°. During the gaze saccade, mean VOR gain reached a minimum of ~0.51 ± 0.13 (mean ± SD; $n = 11$), i.e., a VOR suppression by 47 ± 13% from the presaccadic level (see Fig. 6*A*). The total range of the percentage of suppression for 100° saccades was between 22 and 75% for individual subjects. Once again, the average and even the whole range across subjects seem incompatible with a total VOR suppression during the whole saccade (predicted suppression shown by our technique 93.8%; see METHODS). On the other hand, for a portion of the subjects, the data would not exclude a triangular (or maybe trapezoid) suppression profile reaching complete suppression for a brief fraction of the duration of 100° saccades.

Around the time when gaze landed on target, mean VOR gain became ~1.1, followed by a slow return to the presaccadic level. The averaged phase lag of ~9° before the gaze saccade changed into a phase lead of ~11° during the gaze saccade (phase shift of ~21°, see Fig. 6*B*), which also gradually returned to the original phase lag existing before the gaze saccade. Notice that the maximum VOR inhibition coincided with peak head velocity.

Saccades of 80 and 40° (Fig. 5, *B* and *C*) showed basically a similar course of VOR gain and phase as seen for 100° saccades, except for a less profound VOR suppression. Suppression amounted to 36 ± 11% (mean ± SD; $n = 7$) for 80° gaze saccades. Once again, this value is incompatible with a 100%, square suppression, which should yield a suppression by 81.3% in our analysis at the mean duration of 300 ms for 80° saccades. Even the theoretical, apparent reduction by 52.9% for "triangular" suppression reaching 100% momentarily was not reached, suggesting that complete VOR suppression, even momentarily, was only exceptionally reached in our experiments.

For 40° saccades, VOR gain reduction, as calculated in our analysis, was 19 ± 19% (mean ± SD; $n = 7$). One difference with the larger saccades was that there was no head movement during the 40° saccades (Fig. 5*C, bottom*). Another difference was the higher intersubject variability in VOR suppression for 40° saccades (see Figs. 5*C, middle,* and 6*A*). Two subjects showed a suppression of <1%, three subjects showed a suppression between 8 and 16%, and two subjects still had a substantial suppression of ~45%. At the mean duration for 40° saccades of ~150 ms, the theoretical outcome of our analysis would be an apparent gain reduction by 49 and 34% for a square and triangular profile reaching a maximum of 100% suppression (see METHODS). Once again, our mean results are not compatible with either of these cases; only the two (of 7) subjects with ~45% gain reduction during 40° saccades may have had a completely suppressed VOR at some time during the saccade.

The maximum phase shift of the VOR response during 40 and 80° gaze saccades amounted again to an advance of ~21° and was similar in magnitude for all subjects. A summary of the maximum saccadic reduction in gain and phase shift of the VOR (means ± SD of all subjects) is shown in Fig. 6 for the various saccadic sizes. Figure 6*B* shows a constant phase shift for all gaze amplitudes. Because we did not use the same head oscillation frequencies for the different gaze shift amplitudes, this constant phase shift does not imply a constant change in delay. Figure 6*A* shows that the reduction in VOR gain, as calculated with the Fourier technique, increases as a function of saccadic size. Given the filtering effects of this technique, as evaluated in our simulation experiments (see METHODS), part of this trend could be a calculation artifact (short-lasting suppressions being truncated more than long-lasting suppressions). To test this possibility, we performed a linear regression of calculated gain reduction on the duration of gaze shift (means for all subjects and saccadic sizes). Surprisingly, a correlation between the magnitude of gain reduction and gaze shift duration proved to be absent ($r^2 = 0.019$; $P > 0.5$). Therefore the possibility that the increase in gain reduction as a function of saccadic size, as shown in Fig. 6, is only an artifact, can be rejected.

The relations between head movements and VOR gain changes were analyzed quantitatively in Fig. 7, which shows scattergrams of mean values per subject and per gaze amplitude. In Fig. 7*A* we plotted the relation between the magnitudes of maximum VOR suppression and maximum head velocity, with a linear regression fitted through the data points. With an r^2 value of 0.514, this relationship was significant ($P < 0.0001$). We also plotted the relation between the time until maximum VOR suppression and the time until maximum head velocity after the start of the saccade (Fig. 7*B*). The diamond in Fig. 7*B* represents the only subject whose head velocity exceeded the minimum threshold of 5°/s during the 40° saccades. The linear regression in Fig. 7*B* had an r^2 value of 0.392 and was also significant ($P = 0.0041$). In the same way as described for the head movement, we also quantified the relation between magnitude and timing of VOR suppression and the gaze movement as well as the eye-in-head movement. Multiple regressions between the parameters of the VOR suppression and movement parameters of head and eye again showed that only the variations in head movement contributed significantly ($P < 0.05$) to the variations in VOR suppression.

Probing the VOR with vertical oscillations during horizontal gaze saccades

Figure 8 shows the averaged mean time course of vertical VOR gain and phase relationship of all subjects. During

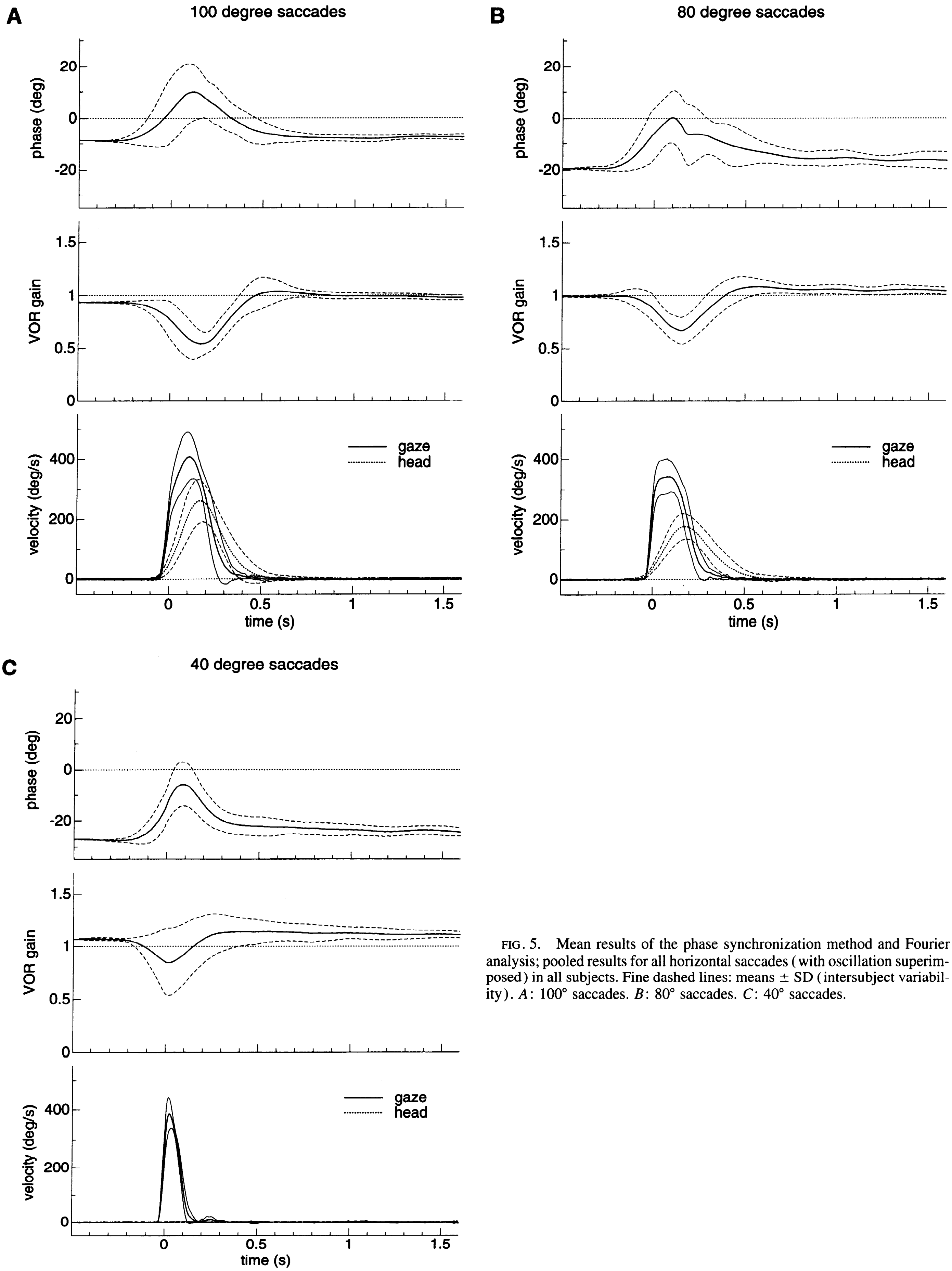

FIG. 5. Mean results of the phase synchronization method and Fourier analysis; pooled results for all horizontal saccades (with oscillation superimposed) in all subjects. Fine dashed lines: means ± SD (intersubject variability). *A*: 100° saccades. *B*: 80° saccades. *C*: 40° saccades.

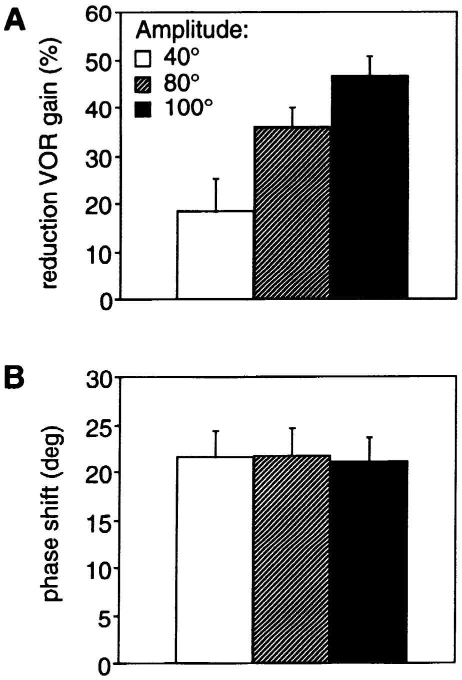

FIG. 6. Diagrams summarizing the mean changes (compared with presaccadic values) in gain (*A*) and phase (*B*) of the VOR during 40, 80, and 100° horizontal saccades for all subjects (mean ± SD of intersubject variability).

this experiment subjects had a higher head rotational inertia because of the large eccentric mass of the helmet used in this experiment. For this reason, subjects found it very difficult to make natural movements of the head. This is manifest in the low peak head velocity and the longer duration of the gaze saccade (see Fig. 8, *bottom*). Both the head velocity and the suppression were significantly ($P < 0.05$) smaller than for the 100° saccades obtained with the horizontally oscillating helmet. Despite this effect, which has been described before (Gauthier et al. 1986), there was a very consistent pattern of VOR gain reduction among the different subjects. Mean VOR suppression was ~37% at a maximum head velocity of 142°/s. The most striking dissimilarity between Figs. 8 and 5, *A–C*, is the difference in mean phase behavior, with higher variability during the gaze saccades with vertical oscillation. Mean maximum phase shift in comparison with the phase lag value just before the gaze saccade was only ~10°. The variability in phase behavior of the vertical VOR was, however, so high that this phase shift did not differ significantly from 0° or from 21° (the mean phase shift in the horizontal VOR).

Probing the VOR with horizontal torque pulses during horizontal saccades

In Fig. 9 we show the average result for two subjects; for these averages the individual records fulfilling the criteria were aligned on the onset of gaze movement (see METHODS). Head (thick lines) and gaze (thin lines) positions and velocities during a 40° gaze shift are shown for the unperturbed head and for head torque pulses with and against the gaze shift. Without perturbation, the head moved slightly (on average 0.3°) in the direction of the saccade. The responses of the head to the torque perturbations varied strongly between subjects: the total magnitude of the resulting head movement was on average 12° (range 3–22°), and about half of this occurred during the saccade. For all subjects, the amplitude of the head movement was larger when the perturbation was in the same direction as the saccade (13.3 ± 4.5°) than when the perturbation was in the direction opposite to that of the saccade (8.7 ± 4.4°). To compensate for these differences in response, the moment of onset of the head perturbation was made direction dependent (see METHODS). In this way, the part of the head movement that occurred during the saccades was made less dependent on the direction of the saccade: the head movements during saccades were 5.9° (head with) and 4.9° (head against) on average.

The head movement before the start of the saccade (8.2 ± 5.3°) caused a drift of the gaze of 0.7 ± 0.5° in the direction of the perturbation, which corresponds to a VOR gain of ~0.9. The response to the perturbation during the saccades varied strongly between subjects, as illustrated for two subjects in Fig. 9. For both subjects, the sign of the initial effect of the perturbation was independent of the perturbation direction: initial gaze velocity increased for *AL*, and decreased for *JF*, compared with undisturbed saccades. Despite this great variability in response, the difference in the re-

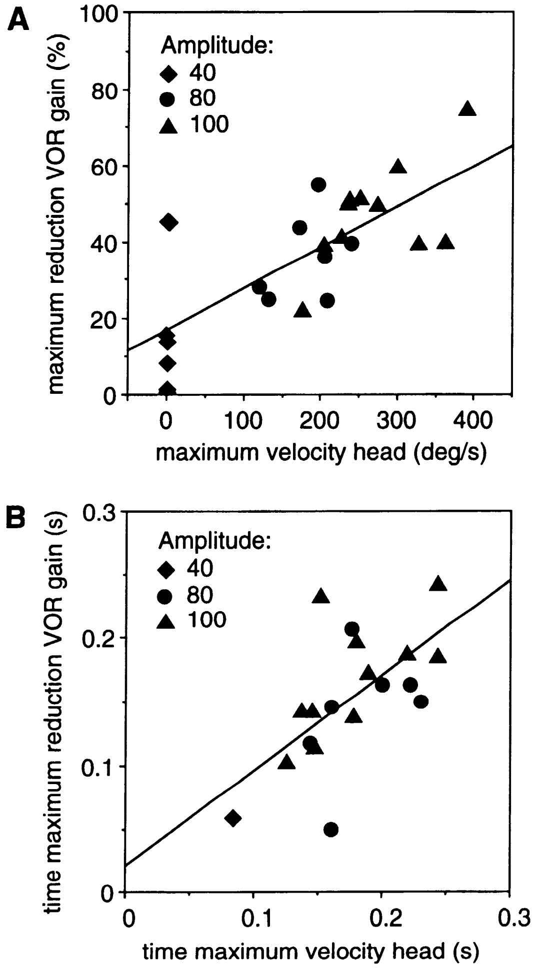

FIG. 7. Scattergrams showing results for all subjects. Each symbol represents the average result for horizontal saccades of 1 amplitude in 1 subject. Lines: linear regressions. *A*: relation between maximum reduction in VOR gain and maximum head velocity. *B*: relation between times of occurrence of maximum VOR suppression and maximum head velocity. Both correlations are significant; see text.

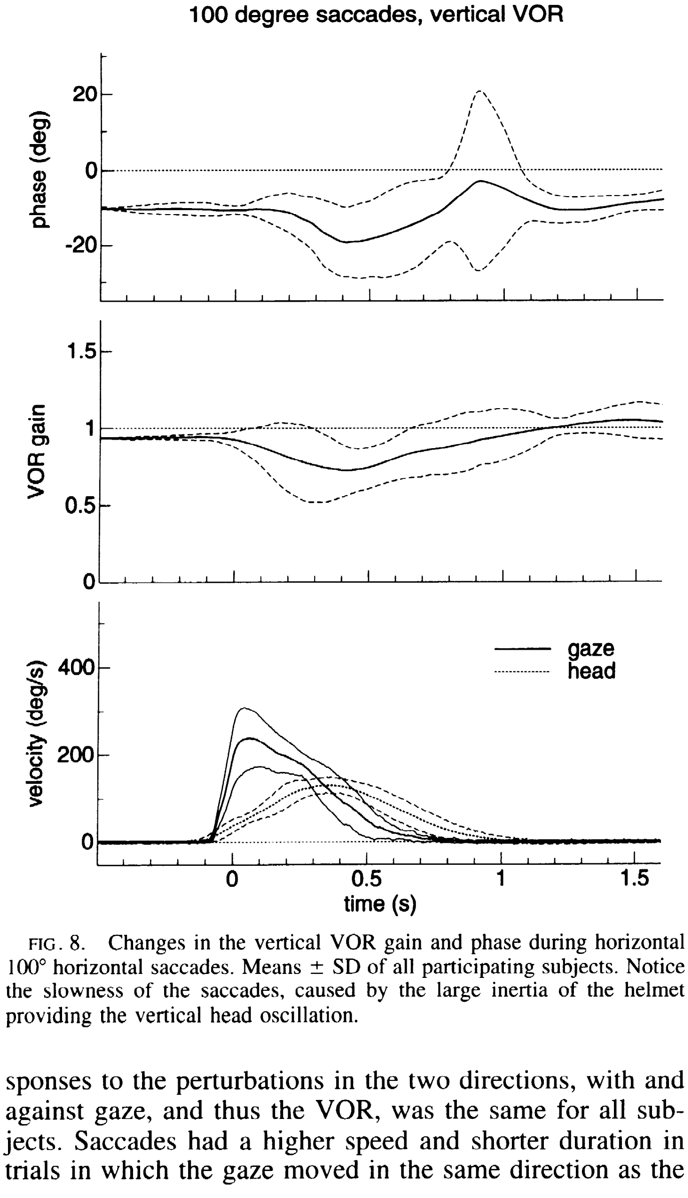

FIG. 8. Changes in the vertical VOR gain and phase during horizontal 100° horizontal saccades. Means ± SD of all participating subjects. Notice the slowness of the saccades, caused by the large inertia of the helmet providing the vertical head oscillation.

sponses to the perturbations in the two directions, with and against gaze, and thus the VOR, was the same for all subjects. Saccades had a higher speed and shorter duration in trials in which the gaze moved in the same direction as the perturbation than in trials with a perturbation in the opposite direction.

The duration of the gaze saccades was on average 137 ms. The duration varied between subjects (range 119–168 ms) and head movement direction (head with: 122 ms; head against: 150 ms). One would expect longer durations for saccades with larger eye-in-head amplitudes; this hypothesis was tested with the use of a linear regression analysis. For each subject, the duration of the (gaze) saccade correlated as expected with the eye-in-head amplitude, with a regression coefficient of 3.0 ± 0.5 ms/deg (averaged over the 12 experiments, $r^2 = 0.53$). For all subjects, the difference between the duration of the saccades with the two different perturbations was 28 ± 6 ms. For some subjects, mainly head movements opposite to the saccade induced a clear change (increase) in duration, whereas for other subjects, the duration was mainly changed (decreased) when the head moved with the saccade.

The perturbations of the head changed the maximum velocity of the eye-in-head movements. A perturbation in the direction of the saccade (head velocity 52°/s) decreased the maximum velocity from 402 to 391°/s; a perturbation opposite to the saccade (head velocity 45°/s) increased it to 431°/s. These changes in eye-in-head velocity were not enough to compensate for the head movements: the maximum speed of gaze increased from 403 to 444°/s when the head moved with the saccade, and decreased to 387°/s when the head moved against the saccade. For all subjects, a perturbation in the direction of the saccade resulted in higher gaze velocities and shorter durations than a perturbation in the opposite direction. Because the average magnitude of this difference in the responses to the two perturbations did not differ very much between subjects, we averaged the response over all subjects (Fig. 10). The gain of the VOR (calculated on the basis of the difference in the responses to the 2 perturbations) was ~0.95 before the saccade. When the saccade started, VOR gain dropped very quickly and stayed low till ~70 ms after saccadic onset. As shown in Fig. 10, this decrease in gain can be approximately described as an exponential decay with a time constant of 50 ms.

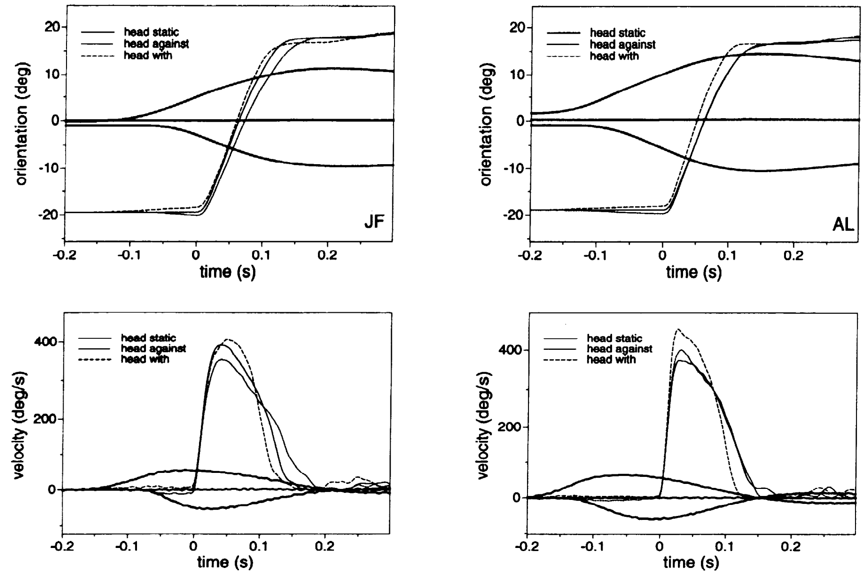

FIG. 9. Average movements of the gaze (thin lines) and head (thick lines) during saccades in 3 conditions of head perturbation (no perturbation, torque pulse in direction opposite to saccade, torque pulse in direction of saccade). For each condition, the average of all saccades to the left and to the right is plotted for 2 subjects (*AL* and *JF*). For 1 subject (*AL*), head perturbation increased gaze velocity during the initial 50 ms, whereas for the other subject (*JF*), head perturbation decreased gaze velocity during the initial 50 ms.

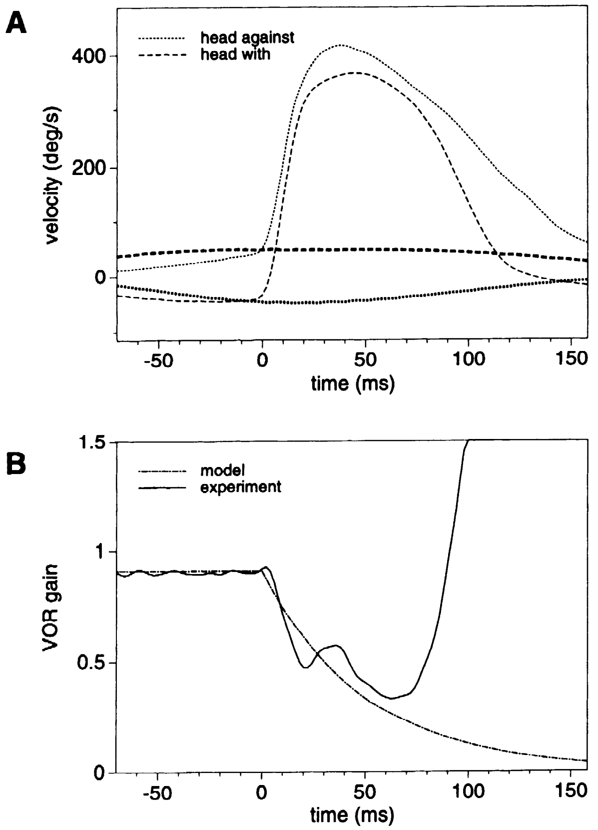

FIG. 10. Average movements of the head and eye for all subjects. Note the difference in time scale with Fig. 1. *A*: average velocity response of eye in head (thin lines) and head (thick lines) to the 2 types of perturbation of the head. *B*: VOR gain calculated from the difference in the responses to the 2 types of perturbations (——). Dot-dashed line: exponential decay of the VOR, with a time constant of 50 ms.

Thereafter, the gain of the VOR appeared to increase very fast but actually could not be further evaluated from the torque pulses, because non-VOR compensatory mechanisms clearly dominated at this stage.

Although the effect of the perturbations on saccadic dynamics differed between subjects, the gaze accuracy remained fairly constant for all subjects. Figure 11 shows the accuracy of the saccades with and without perturbations of the head. For unperturbed saccades, the saccade undershot the target by 2.3° (median value). Perturbations of the head increased the undershoot significantly (paired *t*-test, $P < 0.05$) to 2.9° (head with) or 3.3° (head against). The sign of the change in gaze amplitude was thus independent of the direction of the head movement. The SD of the undershoot was 1.9 ± 0.2°, independent of the perturbation. For all conditions, the undershoot of the first saccade was corrected to a large amount during the first 200 ms after the saccade.

DISCUSSION

Saccadic VOR changes revealed by head oscillation

Our previously developed method of "high-frequency" head oscillation (Tabak and Collewijn 1994, 1995) was successfully applied to probing the VOR during gaze saccades. Distinct advantages of the method in this application are as follows: *1*) the probing signal adds only a "dither" to the ongoing movements and does not systematically interfere with the gaze movement; *2*) the probe is easily applied and allows the continuous measurement of VOR gain and phase as a function of time, within limits imposed by unavoidable windowing techniques; and *3*) the high frequencies effectively exclude any high-level modulation of the VOR by visual or visually related effects such as smooth pursuit, VOR cancellation, and mental set (imagined targets and frames of reference).

Analysis requires the separation of the oscillatory component from the (very much larger) gaze shift component. Our first and most intuitive approach to this separation was to find matching pairs of gaze saccades among two subpopulations of similar gaze shifts with and without head oscillation. Simple subtraction of such pairs leaves only the oscillatory component. Unfortunately, the yield of this matching method is low: because the amplitude of the oscillation is only on the order of 1% of that of the gaze saccade, even the minor normal variability in the dynamics of successive gaze saccades is sufficient to restrict acceptable matches to a small fraction of the collected data. Successful matches do show the phenomenon of intrasaccadic VOR suppression in a convincing but qualitative manner (Figs. 3 and 4*A*), and a quantitative analysis technique that uses all the data is obviously preferable. A working solution was found in the phase synchronization method, in which all signals were slightly shifted in time around the moment of saccadic onset, to reset

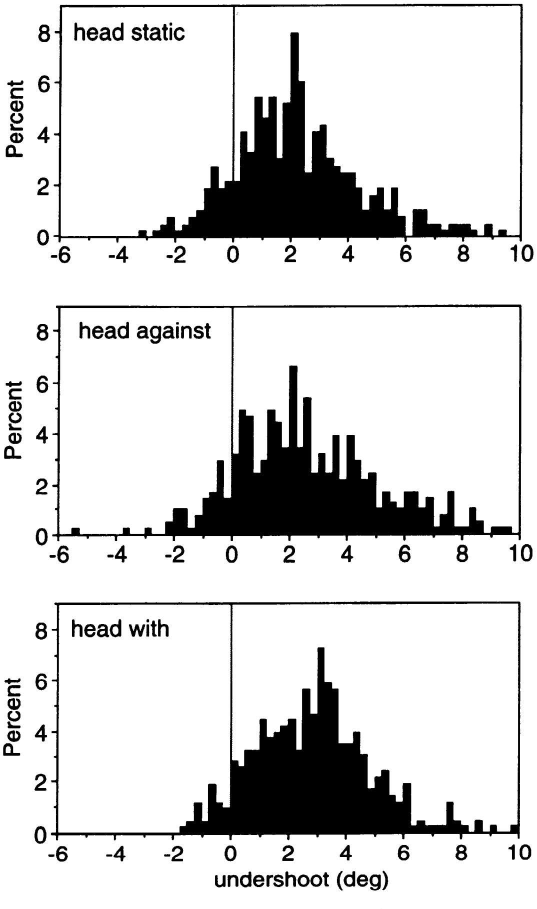

FIG. 11. Histograms of the error at the end of the primary saccade for the 3 conditions. Negative values: undershoot. Positive values: overshoot. All trials that passed the criteria mentioned in the INTRODUCTION for all subjects are used. Binwidth: 0.25°.

the phase of the oscillatory component of the head movement to 0 or 180° (whichever was closest). Subtraction and addition of the two synchronized groups isolated the oscillatory and saccadic motions, respectively, at the price of some blurring in time. Subsequent to the isolation of the oscillatory component by any of the two methods, gain and phase of the VOR as a function of time could be determined as a continuous function of time by Fourier techniques, with the use of a sliding window.

The consistent results obtained with both separation methods, for all subjects, corroborate the validity of the analysis, although the maximum suppression values found were truncated because of the blurring of time inherent to both the synchronization and the sliding window techniques. Similarly, this time blurring leads to some uncertainty in the exact timing of the changes in the VOR. The Parzen window extended over ±256 ms (±128 samples); this length is dictated by the frequency range of our oscillations (1 period having a duration on the order of 0.1 s). In this way, the obtained results are not contaminated by low-frequency components (drift) in the signals. Although the use of this window does not systematically shift events forward or backward, it smears events out in time so that it blurs the actual time course of gain and phase. Simulations with artificial signals (Fig. 2, *A* and *B*) showed that this blurring could shift the start and end of an instantaneous offset and onset up to 256 ms forward and backward, respectively. In this respect, the apparent start of VOR suppression ahead of the saccade, as visible in Fig. 5, *A–C,* is probably an (unavoidable) artifact of the Fourier technique. The timing of the minima and maxima of VOR gain should be correctly assessed by our technique, although sharp peaks in these values could be filtered out by the synchronization and windowing procedures. The amount of underestimation of the obtained peak values of suppression depends on the duration and the profile of the suppression. To assess the distortion of gains by the time blurring of our technique, we simulated the results for two theoretical profiles of saccadic VOR gain reduction that represent more or less extreme cases: *1*) total suppression during the entire saccadic duration (square profile) and *2*) gradual reduction and recovery (triangular profile) of VOR gain, with suppression reaching 100% only for a brief instant. As shown in detail in RESULTS, the outcome of our measurements, interpreted in the framework of these simulations, excludes the square profile of suppression in all cases, and suggests that even total suppression for a brief fraction of saccadic duration is the exception rather than the rule.

The suppression found with the oscillation technique is in general agreement with the conclusions from earlier work on saccadic VOR suppression, but adds further detail. The tendency for the depth of VOR suppression to gradually increase along with saccadic amplitude confirms earlier reports by several groups (Pélisson et al. 1988; Tomlinson 1990). The magnitude of the suppression has been variously estimated, probably depending on the methods used. Laurutis and Robinson (1986) found a virtually complete suppression for saccadic amplitudes >40°; Tomlinson (1990) reported an equally profound suppression in monkeys; Pélisson et al. (1988) found a slightly less strong suppression, whereas Guitton and Volle (1987) emphasized the variation of depth and time course of suppression among subjects. We confirm the existence of subject variability, especially for saccades of intermediate size, but in general we find a less complete suppression than have previous authors. A recent study by Epelboim et al. (1995), in which gaze movements of human subjects between close targets were occasionally perturbed by "pushes," also provided evidence for saccadic VOR suppression that was only partial and, moreover, variable among trials.

A new finding, which could only be obtained with the oscillation technique, is that VOR phase is advanced concomitantly with the reduction in VOR gain. This phase advance suggests possible mechanisms that could underlie the VOR suppression, as will be discussed later.

Another new and highly consistent finding in the oscillation experiments is the existence of a period of supranormal VOR gain after the saccadic gaze shift has ended. In the period when head and eye are still moving and even in the ensuing period when the gaze movements have been completed, VOR gain was higher than in the period preceding the saccade (Figs. 3–5). Because the purpose of a gaze shift is to fixate a new object of interest, it is important to carry gaze to the new object and then hold it very steady for some time. Gaze lands on target often long before the head reaches a steady position; thus perfect function of the VOR in the wake of the gaze shift is of considerable functional importance. We submit that, therefore, VOR gain in this period is tuned closer to unity to assist in the stability of fixation of the new target. In this respect it is important to emphasize that VOR gain is frequency dependent: we previously assessed (Tabak and Collewijn 1994) with the oscillated helmet that the horizontal VOR gain in normal humans is ~0.9 in the 2- to 4-Hz range, but rises to unity and higher in the 12- to 20-Hz range. This tendency is clearly reflected in Fig. 5, *A–C,* in which progressively higher probing frequencies were used for smaller saccades. Natural horizontal head movements (including such behaviors as running and vigorous head rotation) contain no energy >5 Hz (Grossman et al. 1988). Therefore it seems fair to conclude that for natural behavior the VOR has a baseline gain slightly below unity, so that the postsaccadic enhancement will bring VOR gain indeed closer to unity in the physiological frequency range.

Our experiments with vertical oscillation during horizontal saccades show the existence of VOR suppression in a plane orthogonal to the saccades. Thus VOR suppression was not entirely plane specific. This finding is somewhat at variance with the results of Tomlinson and Bahra (1986) who found, with the use of horizontal head perturbations, that during small (<10°) and large (30–40°) vertical saccades the horizontal VOR was on in monkeys. During large horizontal gaze shifts (>30–40°), Tomlinson and Bahra found that the horizontal VOR was completely switched off. Our findings are compatible with some degree of plane specificity; suppression of the vertical VOR was certainly smaller than that of the horizontal VOR (Figs. 5*A* and 9). However, the slowing of the head velocities by the larger inertial mass of the vertical helmet may significantly contribute to this difference. Statistical analysis (Fig. 7) suggests that VOR suppression is most tightly correlated with head velocity: the magnitude of suppression correlated best with the maximum head velocity, and the timing of the VOR gain minimum also correlated best with the time of maximum head velocity. This suggests that the amount of VOR gain reduction depends more on head velocity parameters than on saccadic size as such. Head movement was, however, not absolutely necessary to get VOR suppression, as shown by some subjects for our 40° saccades (Fig. 7*A*, diamonds).

Gaze control in relation to head torque pulses

In contrast to the oscillations, torque pulses biased the head position systematically in one direction and needed to be corrected somehow for gaze saccades to remain accurate. We investigated the effect of torque pulses for 40° saccades that hardly involved any voluntary head rotation. We found that such perturbations of the head reduced the amplitude of saccades slightly, independently of the direction of the perturbing head movement. This amplitude change, combined with the asymmetries found in the changes in speed and duration, supports the hypothesis that the saccadic command is changed by the perturbation. The accuracy of the unperturbed saccades in our experiment corresponds to the accuracy of saccades to stationary targets (in dark surroundings) as reported by Lemij and Collewijn (1989). The average undershoot of the saccades increased slightly in our experiment when the head was moved (independent of its direction), without an increase of its SD. Pélisson et al. (1988) did also find a slight increase of the undershoot of saccades due to head perturbations, but in their experiments variability increased as well. The increase in undershoot that we found for head perturbations may have a parallel in the increase in undershoot found when targets are not continuously visible (Lemij and Collewijn 1989): both changes might reflect that, in uncertain situations, the programming of saccades is changed in a conservative direction to have a larger safety margin.

A striking result in our experiments was the asymmetry in the effects on saccadic dynamics. Although one would expect that, given the presence of saccadic VOR suppression, gaze saccades would speed up for torque pulses with gaze and slow down for torque pulses against gaze, compared with the unperturbed condition, such a symmetrical response was not obtained in many subjects (see Fig. 9). Pélisson and Prablanc (1986) also reported an asymmetric response for some of their subjects in response to head perturbation during 30 and 40° saccades: complete compensation for perturbations against the saccade and almost no compensation for perturbations in the other direction. Tomlinson and Bahra (1986), studying VOR saccade interaction in monkeys, reported an asymmetry in the opposite direction for responses to head perturbations during 20° saccades. The various asymmetries the we found are thus not a peculiarity of our experiment, but were present as well (although not emphasized) in other experiments.

Subject-dependent asymmetries in the VOR could be accounted for in two ways. A first explanation would be that the VOR is really suppressed asymmetrically in a subject-dependent way. Suppression, however, cannot lead to an increase in gaze velocity when the head moves against the saccade (as for example in Fig. 9, *right*). Therefore asymmetric suppression of the VOR cannot explain the asymmetries we found. A second explanation is that the head perturbation changed the speed of the saccade. Such subject-dependent general changes in saccadic speed profiles have been also reported in other conditions. For instance, Collewijn et al. (1992) investigated the effect of fixing the head to a biteboard on saccadic velocity profiles. The effect of this fixation on these profiles was quite different for the two subjects studied by Collewijn et al., and was not directly related to the actual head movements the subjects made when the head was free. In a similar way, one could imagine that a head perturbation changes the saccade generation in a subject-dependent way.

A second asymmetry that we found was that the response of the head to the torque perturbation was direction dependent: perturbations opposite to the saccade were counteracted more effectively than perturbations in the direction of the saccade. A similar asymmetry was found by Tomlinson (1990) in monkeys for the response to torque perturbations during active head movements. Our result suggests that, even though our subjects did not move the head voluntarily, the motor output to eyes and head was coordinated. Possibly, this coordination involved a saccade-direction-dependent setting of the gain of the stretch reflex of the neck muscles. A similar coordinated change in reflex gain of muscles that are not causing movements themselves has been reported for muscles around the shoulder during elbow flexion movements (Smeets et al. 1995).

Saccadic VOR changes revealed by head torque pulses

The difference in the response to perturbations in opposite directions showed a time-dependent effect of head movements on eye-in-head velocity, which supports the hypothesis that the VOR is partially suppressed during saccades. The essential result (Fig. 10) is that VOR gain falls sharply at the beginning of the saccade and continues to do so at a lower rate till ~70 ms after saccadic onset. At that time (long before the saccade's end), the VOR becomes uninterpretable in this type of experiment, because of the interference of other mechanisms, as will be discussed later. Because this technique of estimating VOR gain is not corrupted by time blurring (which could not be avoided in the oscillation experiments), it probably provides the best estimate of the course of VOR gain around saccadic onset. In particular, it does not suggest any alteration of VOR gain preceding saccadic onset, a conclusion that is further supported by the raw results of the matching technique such as shown in Fig. 3 (not subjected to Fourier analysis).

We confirm that, despite this VOR suppression, gaze saccades remain approximately accurate. When no saccades are made, VOR gain is in general slightly lower than unity in the physiological range of frequencies (Tabak and Collewijn 1994). If the compensation for head movements were based on the VOR, a head movement would introduce a gaze error in the same direction as and proportional to the head amplitude. So, one would expect a larger gaze error (overshoot for head with, undershoot for head against) at the end of the saccade than at saccade onset. In our experiments, however, the gaze error introduced by the perturbation was smaller at the end of the saccade than just before the start of the saccade. Moreover, the direction of the error was independent of the direction of the head movement. The accuracy of the saccade was thus even better than could be expected on the basis of a working VOR alone.

In our experiment, in agreement with previous literature, head movements changed both the amplitude and the duration of the eye-in-head saccade. The variation in duration is actually one of the key arguments in favor of saccadic VOR suppression, because if the VOR compensated for head movements the duration of the saccade would be independent of the head movement. Actually, the changes in duration of the saccades with head perturbation appear to obey the classical duration-amplitude relation. Collewijn et al. (1988) reported, for head-fixed saccades up to 50°, a linear relation between the amplitude and duration with a slope of 2.7 ms/deg. We found a virtually similar relation between eye-in-head amplitude and duration: 3.0 ± 0.5 ms/deg. Our data on the accuracy and duration of the saccades corroborate the conclusion of many other authors (see INTRODUCTION) that it is not possible to model eye head coordination during saccades as the linear summation of a VOR and an unchanged saccade. In the next section we discuss the possible mechanisms responsible for the behavior of the VOR as probed with the two types of perturbation.

Mechanisms

Several authors (Guitton 1992; Laurutis and Robinson 1986; Pélisson et al. 1988; Tomlinson 1990) have proposed variations on the local feedback model (Robinson 1975) of saccade generation to account for the interaction between saccades and head movements. In these models, the inputs to the burst neurons and to the neural integrator are in gaze coordinates, instead of eye-in-head coordinates as in the original model. Without head movements, the models behave just as the Robinson (1975) model. If the head moves during the saccade, the effect of the head movement on the saccade will develop as follows. Because the initial activation of the eye muscles is only based on the gaze error at the start of the saccade, the initial part of the saccade will be independent of head movements and the VOR during the saccade. If the VOR functions at unity gain during the saccade, the error in gaze will be equal to the error in eye in head, so the gaze saccade will be the same as it would without head movements. If the VOR is (partially) suppressed during the saccade, the burst activity will gradually change on the basis of the larger (head against) or smaller (head with) motor error. This will change the saccadic dynamics, but the saccade will reach the target as accurately as without head movements.

According to these models, the response to a head movement during saccades consists of two components: one mediated by a ''short'' path (the actual VOR, which is supposed to be suppressed to a certain amount), and one mediated by a ''long'' path through the saccade generating circuitry. Importantly, the processing of vestibular signals through the long, ''saccadic'' path is supposed to take much longer than that in the short VOR. The difference in delay between these two paths has been estimated as ~50 ms (Laurutis and Robinson 1986). If this is correct, then the first 50 ms of the saccade would still show the changes in the response of the true, short path VOR to a torque pulse. As a consequence, Fig. 10 would be correct in showing that during this period the VOR gain decreases roughly exponentially toward 0, with a time constant of ~50 ms, leaving VOR gain at ~0.3–0.4 at 50 ms after saccadic onset.

The VOR pathway is assumed to contain two components. The shortest connection of the afferents from the semicircular canals to the oculomotor neurons is a disynaptic, three-neuron arc, the middle neuron being a secondary vestibular neuron in the vestibular nuclei. The VOR-related canal afferents are mostly in phase with head velocity for frequencies >0.1 Hz (see, e.g., Highstein 1988). Most of the involved vestibular neurons are of the position-vestibular-pause type, i.e., they carry signals related to head velocity and eye position, and they pause during saccades. The velocity signals on these neurons provide the appropriate velocity input to the oculomotor neurons, but to account for the input-output relations of the VOR throughout the frequency range, the VOR pathway must also carry an eye position control signal, which is created by integration of the velocity signals (Skavenski and Robinson 1973). This ''neural integrator'' function appears to be distributed among several parts of the brain stem, including the nucleus prepositus hypoglossi and the vestibular nuclei themselves (Cannon and Robinson 1987; for review see Keller 1991). Part of the integrated signal is also carried by the position-vestibular-pause cells, although probably not with a high enough gain to provide the oculomotor neurons with sufficient position information during the VOR (Tomlinson and Robinson 1984). A crucial role of the saccadic ''pause'' of vestibular neurons in mediating the VOR suppression during saccades in a graded manner has been postulated (see, e.g., Berthoz et al. 1989). Saccadic suppression of vestibular neurons is likely to affect the stream of both velocity- and position-related signals to the oculomotor neurons, possibly to different extents. Therefore a residual (partly suppressed) VOR during a saccade might have dynamic properties that differ from the normal VOR. Our finding that VOR phase is advanced by ~20° during saccades would be consistent with a complete suppression of the integrated signal, in addition to a graded reduction of the velocity signal. Thus saccadic suppression of the VOR cannot be described as a pure reduction in gain.

Conclusions

Our experiments show, in agreement with earlier work, that the VOR is suppressed during gaze saccades. VOR gain appears to fall sharply at saccadic onset, following approximately an exponential course with a time constant of ~50 ms. Our work strongly suggests, however, that this suppression is never complete, even for very large saccades. The transient reduction in gain is accompanied by a transient advance in VOR phase, suggesting that the neural integrator is suppressed more completely than the direct velocity pathway. At the end of the saccade, VOR gain is restored to a level (~1.0) that is consistently higher than presaccadic VOR gain (~0.9); a result that would strongly favor stable fixation of the newly acquired target.

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