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Human ocular counterroll: assessment of static and dynamic properties from electromagnetic scleral coil recordings

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Summary. Static and dynamic components of ocular counterroll as well as cyclorotatory optokinetic nystagmus were measured with a scleral search coil technique. Static counterroll compensated for about 10% of head roll when the head was tilted to steady positions up to 20 deg from the upright position. The dynamic component of counterroll, which occurs only while the head is moving, is much larger. It consists of smooth compensatory cyclorotation opposite to the head rotation, interrupted frequently by saccades moving in the same direction as the head. During voluntary sinusoidal head roll, cyclorotation compensated from 40% to more than 70% of the head motion. In the range 0.16 to 1.33 Hz, gain increased with frequency and with the amount of visual information. The lowest values were found in darkness. The gain increased in the presence of a visual fixation point and a further rise was induced by a structured visual pattern. Resetting saccades were made more frequently in the dark than in the light. These saccades were somewhat slower than typical horizontal saccades. Cyclorotatory optokinetic nystagmus could be induced by a patterned disk rotating around the visual axis. It was highly variable even within a same subject and had in general a very low gain (mean value about 0.03 for stimulus velocities up to 30 deg/s). It is concluded that cyclorotational slip velocity on the retina is considerably reduced by counterroll during roll of the head, although the residual cyclorotation after the head has reached a steady position is very small.

Key words: Eye movements – Counterroll – Cyclorotation – Torsion – Scleral coil technique

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Introduction

Ocular rotation around the visual axis (cyclorotation, roll or torsion)[1] in response to roll of the head (counterroll) or to rotation of the visual surroundings has been a difficult and controversial subject for over a century, due to a variety of reasons. Cyclorotations are hard to record and most reports rely on rather indirect measurements, based on subjective or objective orientation of afterimages, the blind spot or the axis of astigmatism, or superimposition of iris photographs. Obviously, it is hard to acquire a high sampling rate with such techniques, and accordingly, studies have mostly been concentrated on static or slow phenomena.

As it turns out, the static effects amount to only a small fraction of the head and eye rotations in space and thus are sensitive to relatively small errors of measurement, distortions of perspective and unsteady fixation. Notwithstanding these problems, even by the end of the 19th century a reasonable consensus had been reached, concisely summarized by Nagel (1896), that static ocular counterroll after head roll in the human amounted to about 20% compensation for head rotations on the order of 20 deg, diminishing to about 10% for 90 deg head rotation. These findings were confirmed again by Fischer (1927), who in addition supported Mulder's (1875) assertion that a much larger compensation could be transiently observed in the orientation of an afterimage during the dynamic phase of the head roll. This is probably due to activation of the semicircular canals, whereas static counterroll is generally attributed to an input from the otolith organs, although an additional input from neck proprioception is likely (Fischer 1927).

1 In this paper the terms roll, torsion and cyclorotation will be considered as synonyms for rotation of the eye around the visual axis

More recently photographic confirmation of static counterroll of similar magnitude in humans was provided by Woellner and Graybiel (1959), Miller (1962), Nelson and Cope (1971) and Miller and Graybiel (1971), who also showed augmented responses due to increased gravity-forces as well as an approximately sinusoidal modulation of counterroll during full (360 deg) rotation of a subject, in support of control by shearing gravity forces acting on the otoliths. Many further photographic confirmations provide overwhelming evidence for human counterroll, although new denials (Jampel 1981) and reconfirmations (Kushner and Kraft 1983) continue to be published, and more direct recordings of ocular counterroll would seem to be useful.

This is of course especially true for the dynamic aspects of cyclorotation which are largely unknown. Counterrolling during continuous rotation of the subject (at 3 deg/s constant velocity), measured photographically, has been reported to be more consistent, conjugate, smooth and symmetrical than during static tilt (Diamond et al. 1979, 1982; Diamond and Markham 1981, 1983). The overall low gain of counterroll was unchanged by this procedure, which constitutes a low frequency dynamic stimulus for the otolith organs but does not activate the canals.

The dynamic response of the human otolith-ocular reflex has been tested with linear sinusoidal and step accelerations (Young et al. 1981; Lichtenberg et al. 1982). Low-pass characteristics with a dominant time constant of 0.33 s were found. Although these results are important for the understanding of otolith function, they can only partially account for counterroll during natural head rotation. The latter will cause significant rotatory accelerations which will activate the semicircular canals. Merton (1956, 1959) observed and filmed large compensatory rolling movements of the eye during sinusoidal oscillation of a subject around the optic axis of the eye, and succeeded in recording such movements (Davies and Merton 1958) using an ingenious optical method. Unfortunately, these results were only reported in a brief abstract. Petrov and Zenkin (1973) recorded torsional eye movements using a suction cap combined with a photokymograph. Although non-linearities of their recording technique hampered a straightforward quantitative analysis, their results are firm evidence for an effective, smooth counterroll with considerable gain during head movements. This counterroll was regularly interrupted by saccades in the opposite direction; these left only a comparatively small residual torsion which was maintained during static tilt.

For a more systematic, quantitative evaluation of dynamic counterroll, better instrumentation is needed. Although real-time systems based on video techniques are being developed (Young et al. 1981; Hatamian and Anderson 1983), a more simple electromagnetic technique which can be easily combined with recording of horizontal and vertical eye movements has been described by Robinson (1963). We have improved this technique and in the present article describe results obtained during active head motion under several lighting conditions and also during optokinetic stimulation. It will be shown that compensatory counterroll under dynamic circumstances, activating the canals as well as the otolith organs, is well developed, and that in addition to the labyrinth the visual input contributes significantly to this stabilizing reflex.

Methods

Technique of measurement

Angular positions of eye and head around three earth-fixed orthogonal axes (transverse, vertical and sagittal) were measured with sensor coils in a.c. magnetic fields by either amplitude (Robinson 1963) or phase (Collewijn 1977) detection of the induced a.c. potentials.

A large, homogeneous magnetic field (frequency 5000 Hz) was created with a vertical and transverse component in spatial and phase quadrature, by means of arrays of field coils as previously described (Collewijn 1977). This field essentially consisted of a magnetic vector of constant magnitude, rotating at constant angular speed in the frontal plane at 5000 c/s. Horizontal and vertical eye and head movements were detected by sensor coils, approximately aligned with the frontal plane in the straight ahead position and connected to dual-phase lock-in amplifiers. When an appropriate phase reference (derived from the field) was provided, the output of these amplifiers reflected the horizontal and vertical orientations of the sensor coil independently, at least in first approximation (with increasing angular deviations, progressive errors occur in these signals; see Robinson 1963). To detect cyclorotation (in the frontal plane, around a sagittal axis) a horizontal sensor coil was used; since such a coil is perpendicular to the (frontal) orientation of the field a maximal a.c. potential is induced in it; the phase of the signal is linearly related to the orientation of the coil around the sagittal axis, and thus reflects cyclorotation. The phase was detected as described by Collewijn (1977).

To measure head motions, a block with two orthogonally mounted coils was firmly strapped to the subject's head. By rotation through known angles this device was calibrated prior to the experimental sessions. Vertical and horizontal motion of one eye was measured with a scleral induction coil embedded in a silicone annulus, adhering firmly to the limbus (Collewijn et al. 1975). To measure ocular torsion, a special version of this annulus was constructed by one of the authors (T. C. J.) according to a principle described by Robinson (1963), but since then apparently never applied to human subjects. Effectively, this coil is wound around a vertical axis (Fig. 1). One turn follows first the inner (anterior) margin of the superior half of the annulus, returns following the outer (posterior) margin, then crosses to follow the

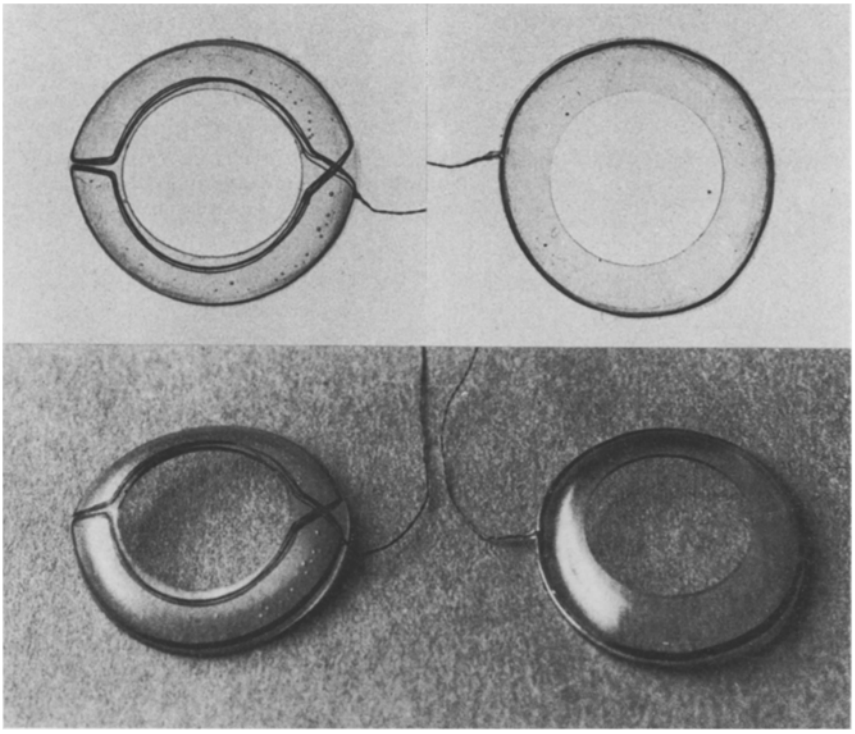

Fig. 1. Top: frontal view of the cyclorotational (left) and standard (right) coil in upright position, as they would be seen when facing a subject with the coils mounted. In some experiments, cyclorotational coils were mounted on both eyes. Bottom: oblique frontal view of the same coils. Dimensions: the diameter of the central hole was 11.3 mm

anterior margin of the lower half of the annulus, and returns to the origin along the posterior margin of the lower half of the annulus.

When the coil is placed with the crossing points of the windings oriented horizontally (as in Fig. 1, top), the coil has a horizontal plane of symmetry. The projection of the windings on this plane looks like a regular horizontal coil, wound consistently in one direction, and flattened in the antero-posterior direction. In contrast, the projections of these turns on the sagittal and frontal plane consist of two halves wound in opposite directions, which cancel each other. Therefore, this configuration behaves effectively as a horizontal coil. The coil was embedded in the usual way in an annular silicone carrier with the same shape as the usual annulus containing a frontally wound coil (Fig. 1). The coil was connected through an impedance-matching transformer and a preamplifier to the phase detection system. The use of the phase-detection method in the case of torsion had the specific advantage of absolute calibration. Voluntary torsion steps cannot usually be made on command; therefore calibration with the coil in situ was not possible. Compression of the coil in the antero-posterior direction might occur during the mounting on the eye; this would change the cross section in the horizontal plane and invalidate a previous calibration based on the *amplitude* of the induced signal. However, changes in the effective cross-section of the coil will not change the *phase* of the induced voltage.

The annulus with the torsion-sensitive coil is stiffer than a normal annulus; therefore, the fitting on the eye is more critical. Whereas the normal annulus adapts to almost all adult eyes, the torsion coil did not adhere well in some subjects. In the two subjects used in the present work (HS and HC, two of the authors) the adherence was entirely satisfactory; once mounted the annulus had no tendency to become loose, and could not be shifted or rotated on the eye unless first deliberately detached by lifting the edge with a blunt forceps. In some sessions, cyclorotation of both eyes was measured; in others cyclorotation of the left eye and horizontal and vertical motion of the right eye were recorded. (In the future it may be possible to embed the two types of coils into a single annulus.)

The overall performance of the ocular torsion measurement system was assessed with a calibration device. For cyclorotation, deviation of the torsion signal from linearity and symmetry was less than 1% for angles up to 20 deg. Crosstalk from horizontal or vertical motion alone was minimal when the effective orientation of the coil was in the horizontal plane. Any combination of horizontal and vertical deviations resulted in apparent cyclorotation, because a vertical deviation will be projected as cyclorotation on the frontal plane in the case of a simultaneous horizontal rotation. An exact theoretical treatment of this type of crosstalk is difficult, since it depends not only on the choice of the coordinate system but also on the geometry of the coil, which is not circular. Empirically it was found that a combination of 10 deg horizontal and 10 deg vertical rotation resulted in an apparent torsion of 1.5 deg. As in the conditions of our experiment horizontal and vertical gaze rotations were not larger than about 1 deg in dynamic conditions and much smaller in static conditions, we conclude that crosstalk artifacts are insignificant in our material. Translation along the right-left axis produced a very small artifact in torsion (0.04 deg/cm) due to small inhomogeneities in the field.

Procedure

Two subjects were investigated. They viewed either only a single red (HeNe laser) spot, the spot plus a checkerboard pattern (30 deg high × 40 deg wide; checks 3 × 3 deg), or were in complete darkness. The targets were placed in the focal point of a large Fresnel lens to make them appear at optical infinity. In this way, the translations of the eye associated with head roll did not induce horizontal or vertical eye rotations. For the measurement of static counterroll, subjects tilted their head to different static positions (spaced between about 20 deg left and 20 deg right); eye and head

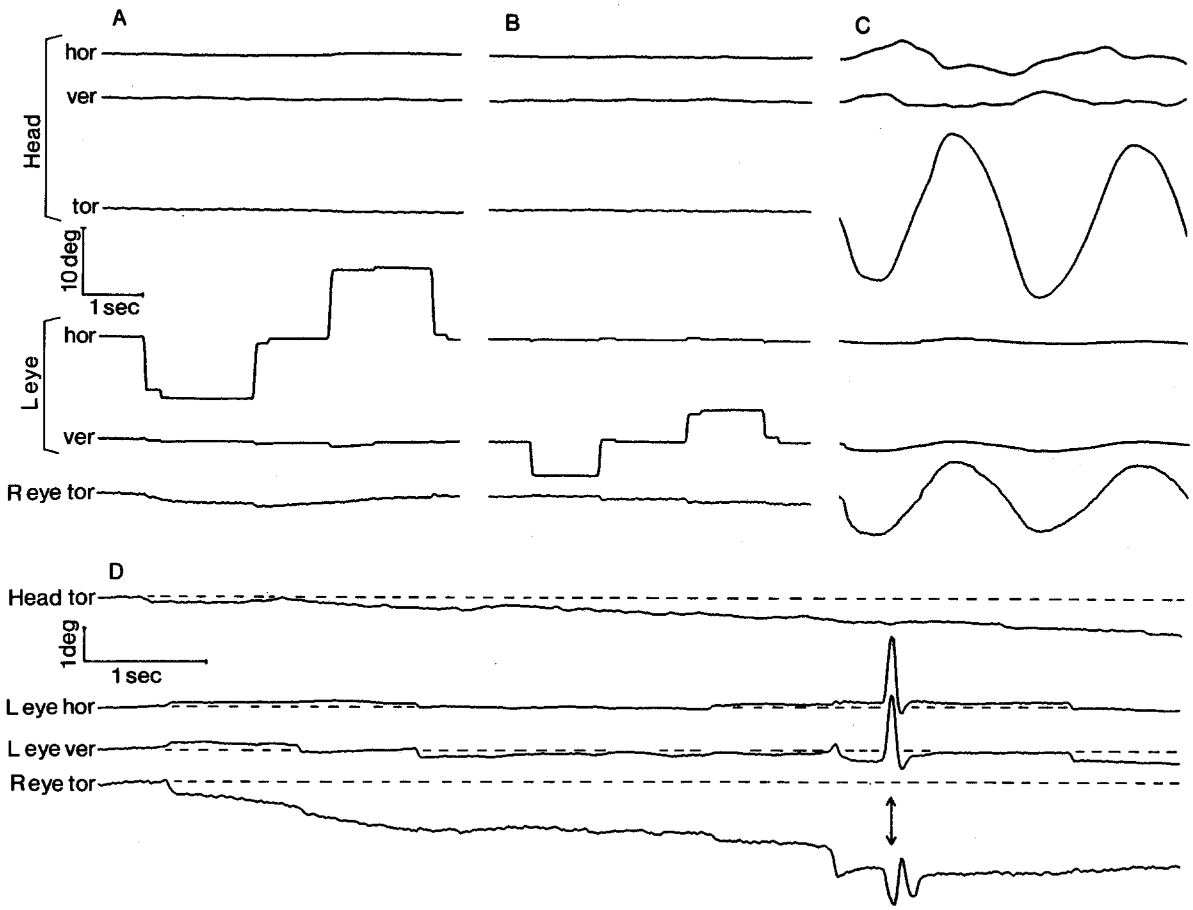

Fig. 2. Illustration of the specific sensitivity of the recordings for rotations in the horizontal (hor), vertical (ver) and torsional (tor) directions (**A–C**; upper calibration bars). Head and eye positions in space (gaze) are shown; in this and all other figures downward deflection of the traces represents horizontal motion to the left, vertical motion upwards and torsion with the upper pole of the eye moving to the right. **A** horizontal gaze calibration (10 deg steps); **B** vertical gaze calibration (5 deg steps); **C** voluntary oscillation of the head in roll with fixation of a spot surrounded by a checkerboard at optical infinity. **D** spontaneous eye movements and torsional head movements during fixation of a point target, plotted at higher magnification (lower calibration bars). Arrow: blink. Interrupted lines mark the initial positions

positions were measured for 20 successive steady positions. For the measurement of dynamic counterroll, subjects moved the head actively, pseudo-sinusoidally in roll at frequencies of 0.16, 0.33, 0.66 and 1.33 Hz, paced by a metronome, and amplitudes of about 10 deg. They continuously fixated the red spot alone or in combination with the checkerboard, or were in complete darkness. Finally, a disk provided with a random dot pattern and filling almost the entire visual field was rotated in front of the subject at various steady velocities (1.2–30 deg/s) to induce cyclorotational optokinetic nystagmus. The disk had a diameter of 70 cm and stood about 30 cm in front of the subject, who fixated the center.

All signals were observed on a penrecorder and sampled on line at a rate of 135/s, digitized with 12 bit precision (over a 50 deg peak-to-peak range) and stored on disk by a PDP 11/10 computer. Head and gaze positions were sampled for 8 s in each of 20 successive different tilt positions. Mean values were calculated off line over each 8 s period. In the dynamic conditions, periods of 16 s were sampled while the subject produced a continuous, steady head oscillation. Off-line analysis started with detection of saccades and separation of the eye movement into a cumulative smooth and saccadic component. Any bias and trend in the cumulative smooth eye position (caused by asymmetric distribution of smooth and saccadic components) were removed. Subsequently, cumulative smooth eye and head positions were Fourier transformed with a fast Fourier transform routine. The frequency component with the highest energy level was always located very close to the frequency of the metronome, and contained typically 50–90% of all the energy in the signal. Gain (ratio of peak-to-peak amplitudes of eye-in-head versus head position) and phase of this frequency component was then calculated.

The signals produced by the recording equipment represent the positions of the head and eye in space (gaze). In many cases, the position of the eye in the head (eye) was derived off-line as the difference between these signals (eye minus head).

Results

Performance of the recording system

In a first series of experiments, cyclorotation of the right eye, and horizontal and vertical motion of the left eye were recorded, to confirm the steady angular orientation of the visual axis in space and the specific sensitivity of the compound coil to cyclorotation.

Figure 2 shows examples of the typical performance of the system. Horizontal and vertical saccades to calibration points at 10 and 5 deg eccentricity did not cause crosstalk in the other channels (Fig. 2A and B), although the torsion signal showed some saccadic and drift activity of its own.

The latter is shown at higher resolution in Fig. 2D, taken from a period of fixation of the point target with the head upright (but unsupported). Horizontal and vertical gaze showed the usual amount of drift and small saccades. The torsional gaze was considerably less stable and drifted over a larger angle than torsional head position. The torsional eye-in-head position changed spontaneously over an angle of about 2 deg in a period of 7 s. Although the change in this example was rather large, fluctuations in a range of about 1 deg were commonly seen. These could not be explained by simultaneous horizontal or vertical eye movements, or torsional head movements. They also were unrelated to blink activity; Fig. 2D (arrow) also shows a typical blink with its associated transient vertical (downward) and horizontal (nasal) eye displacement (Collewijn et al. 1985). The blink also caused a (multiphasic) torsional eye movement, but this was transient and caused no net torsional displacement of the eye (or the coil). Figure 2C shows typical examples of voluntary, sinusoidal roll movements of the head with continuous fixation of the point target. The roll movements had an amplitude of more than 20 deg peak-to-peak and were unavoidably accompanied by some horizontal and vertical head motion. Horizontal and vertical gaze was relatively steady, with deviations not exceeding about 1 deg from the fixation point. The torsion trace (eye in space) showed cyclorotation in phase with the head roll, however, at a considerably lower amplitude. This means that a significant amount of counterroll of the eye in the head occurred. The major part of this counterroll, derived by subtracting the head curve from the eye-in-space (gaze) curve, proved to be transient in nature.

The absence of significant slip of the annulus on the eye around the torsional axis is of course crucial to the quality of these recordings. The most obvious cause for such slip would be mechanical friction of the eye lids with the annulus or its lead wire, sufficient to overcome its adherence to the eye. Any significant slip would be likely to show up in the recordings as deformations, discontinuities and irregular changes in the zero position; in the case of binocular recording of torsion such changes would

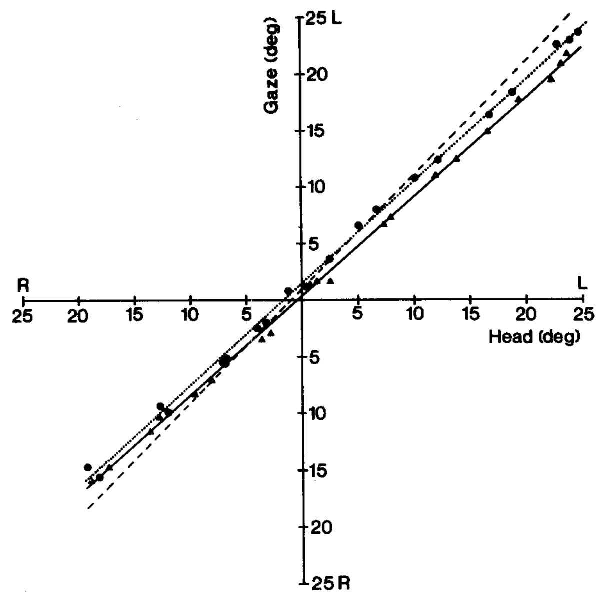

Fig. 3. Typical example of relation between static eye and head torsion. Orientation of the eye in space as a function of the orientation of the head in space has been plotted for 20 positions with the subject viewing a single fixation spot (round dots) and 20 positions viewing the spot surrounded by a checkerboard (triangles). All points were obtained in one session (subject HS, left eye). The calculated regression lines (dotted line: spot only; continuous line: spot and pattern) have a slope smaller than unity (interrupted line). The intersections are meaningless in view of arbitrary zero settings

Table 1. Gain of static ocular counterroll for head roll in the range 20 deg left to 20 deg right. Each gain figure was calculated from the slope of a linear regression line through 20 static head and gaze positions (fitting of this line indicated by r^2); each of these 20 data points was the mean position over a sampling period of 8 s. Subjects viewed either only a red spot or the spot surrounded by a checkerboard pattern

Subject	Session	Eye	Spot gain	Spot + pattern gain
HS	1	R	0.190[a]	–
HS	2	R	0.120	–
HS	4	R	0.115	0.133
HS	4	L	0.101	0.124
HC	3	R	0.089	0.084
HC	5	R	0.087	0.093
HC	5	L	0.087	0.090
Mean ± S.D.	3–5	R&L	0.096 ± 0.012	0.105 ± 0.022

[a] Calculated from 7 tilt positions only

most probably be uncorrelated for the two eyes. Zero positions (measured with the head upright) were recorded at regular intervals throughout the sessions. Within a series of 20 static tilt positions, zero eye-in-head position varied over ±1 deg; most of this was conjugated. The same was true for dynamic oscilla-

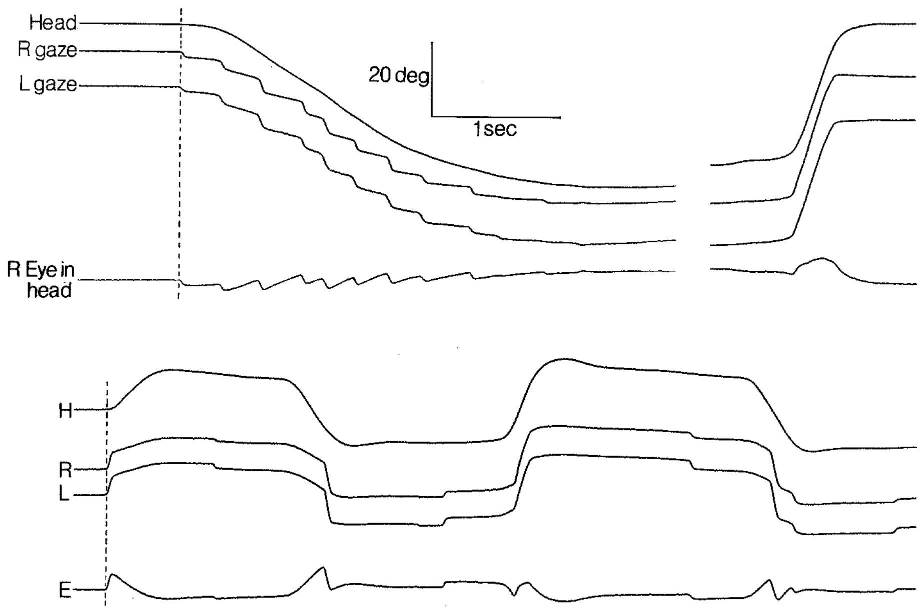

Fig. 4. Slow and fast steps of the head in roll, with recordings of cyclorotation in space of both eyes, and cyclorotation with respect to the head of the right eye. The subject (HC) viewed the fixation spot surrounded by the checkerboard pattern. Maximal head velocities are about 25 (top, left), 50 (bottom) and 125 (top, right) deg/s

tion at 0.16–0.66 Hz. Since such variations of torsional angle are also seen in the eye at rest (Fig. 2D), we consider these as genuine fluctuations of torsion. Larger shifts (up to 3 deg) in zero position were recorded after half of the trials with head oscillation at 1.33 Hz. The possibility of some slip during these rather violent motions can thus not be discounted, although even in this case the shifts were largely conjugated. Further arguments against any serious interference of slip are the high degree of conjugacy of eye torsion during steps (Fig. 4) and dynamic oscillation (Fig. 5), the occurrence of crisp torsional saccades and the magnitude and smoothness of the torsional eye movements relative to the head during oscillation (Figs. 5–7).

Static counterroll

Static counterroll was evaluated in systematic series of head tilt at angles spaced between 20 deg left and 20 deg right, in a pseudo-random sequence. Figure 3 shows an example of 40 successive measurements (20 with the point target only and 20 with in addition a checkerboard pattern) obtained in one session. Eye orientation in space (gaze) was plotted as a function of head tilt, and linear regression lines were calculated for the two visual conditions. Although a certain scatter of the points around these lines was noticed, the coefficients of determination (r^2; r being the correlation coefficient) were 0.997 to 0.999 which indicates an extremely good fit. The findings are summarized in Table 1.

The slopes were on the order of 0.9 and differed significantly from unity (the value to be expected in the absence of systematic counterroll). The gain of the counterroll is given by the difference between the calculated slopes and unity (Table 1). (The intersection points of the regression lines have no significance as the settings of the zero points are arbitrary.) For the three sessions in which both visual conditions were included (Table 1, 5 lower rows), the mean gain (2 subjects, 2 eyes) for static counterroll was 0.096 ± 0.012 (S.D.) when a single point target was fixated. A very small but systematic (i.e. in 4 out of 5 cases) increase to 0.105 ± 0.022 (S.D.) was found when the fixation point was surrounded by the checkerboard pattern. However, the variability of the data suggests a cautious interpretation of this effect until a larger amount of data has been collected. Differences between the two eyes or the two subjects were small. The data did not show asymmetry for tilt to the right or left; both eyes responded conjugately and equally in the two directions. Static tilt in darkness was not investigated since unsteady fixation in the horizontal and vertical direction in combination with low gain values would severely detract from the reliability of the data.

Transient phenomena during steps in head-tilt

Figure 4 shows the rotations of the two eyes and the head in space around the visual axis when the head was moved slowly or quickly from one steady position in roll to a new one. During a slow head roll

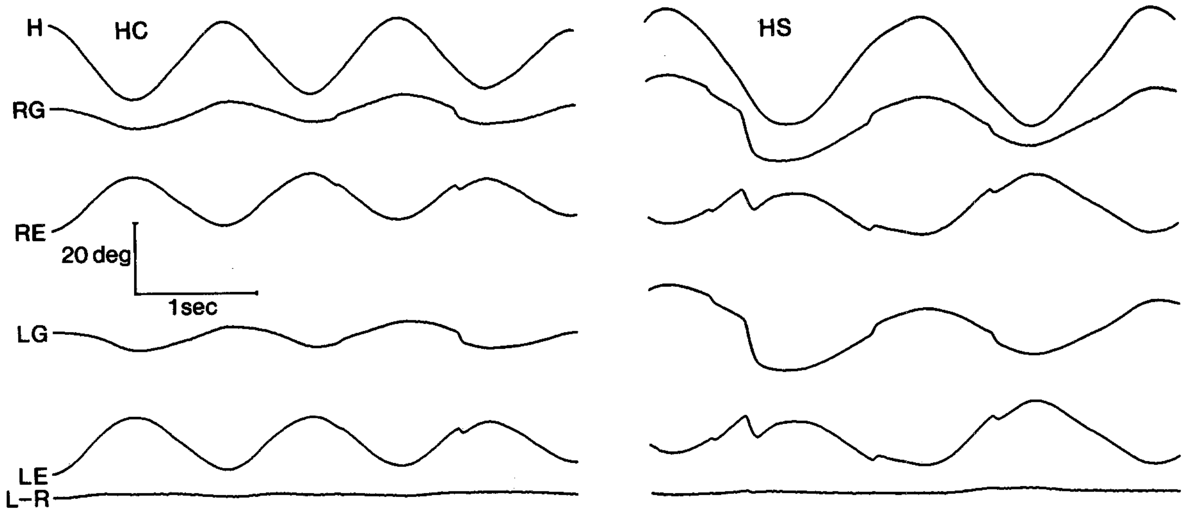

Fig. 5. Binocular recordings of cyclorotation during voluntary head oscillation in two subjects (HC and HS) viewing the spot surrounded by the checkerboard. H: head position; RG, LG: position of right and left eye in space; RE, LE: position of right and left eye in head (obtained by subtracting head from gaze); L–R: difference between cyclorotation of left and right eye

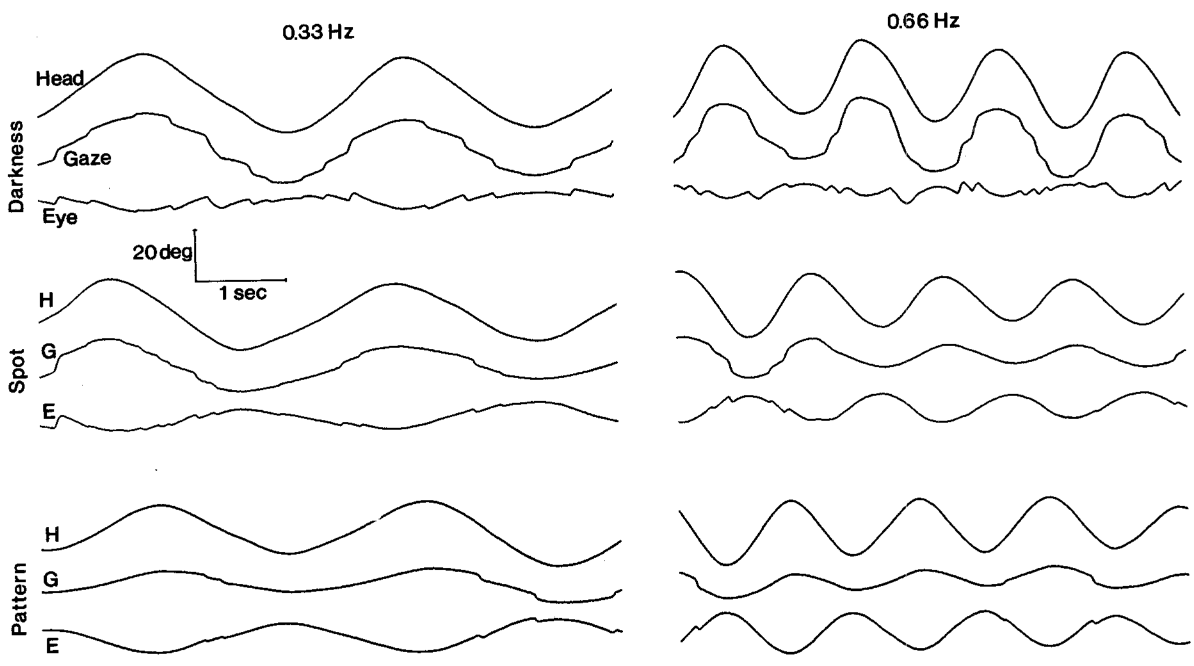

Fig. 6. Dynamic counterroll. Positions of head, eye in space (Gaze) and eye in head (Eye) during voluntary oscillation of the head in roll at about 0.33 and 0.66 Hz in darkness, viewing a spot or the spot and the checkerboard pattern. Subject HC

(about 25 deg/s; Fig. 4, upper left graphs) there was a regular sequence of periods during which the eyes remained relatively stable in space, interrupted by saccadic cyclorotation in the direction of the head roll. With respect to the head, the eyes showed a nystagmus consisting of slow phases in the direction opposite to the head roll and saccades moving with the head. These motions were almost perfectly conjugated for the two eyes. They resembled horizontal or vertical compensatory eye movements, although the stability achieved was generally lower for torsion. Saccades, occurring at a rate of 2–4/s reset the smooth counterroll largely, but not entirely: a small residual deviation of the eye in the head

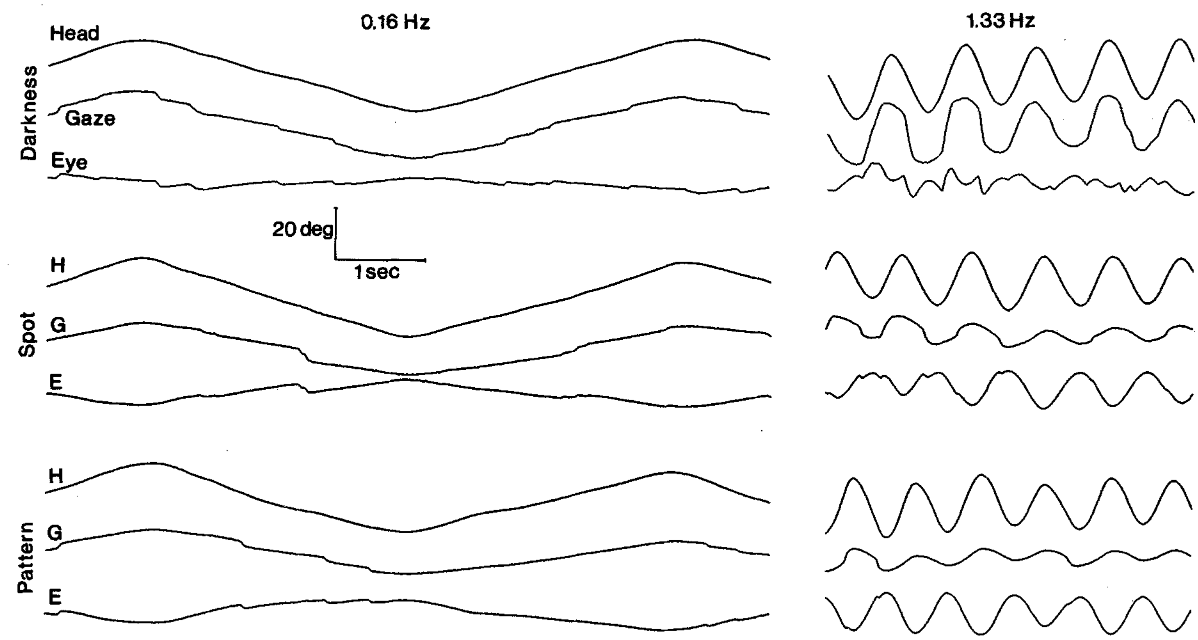

Fig. 7. Dynamic counterroll. As Fig. 6, for frequencies of about 0.16 and 1.33 Hz

accumulated (Fig. 4, top left graphs). This was the static component of the counterroll, which has been studied in most investigations of cyclorotation until now.

The bottom traces in Fig. 4 show eye-head coordination in roll during steps in head tilt with velocities of about 50 deg/s. The combination of smooth compensatory and saccadic forward gaze control is evident, but several instances of conjugate, spontaneous cyclorotatory saccades are also seen. Sometimes the cyclorotation was even initiated by a saccade (Fig. 4, bottom traces, first step); evidently cyclorotatory saccades do not occur only secondarily to smooth deviations. The expected systematic residual counterroll, opposite to the head displacement, was present after all steps. During very fast head tilt (Fig. 4, right top traces; head velocity about 125 deg/s) no compensatory counterrotation was seen except in the final stage; initially the eye was moving faster than (and thus leading) the head.

Dynamic counterroll

During continuous, pseudo-sinusoidal, voluntary oscillation of the head in roll, very considerable counterroll was always present. The two eyes cyclorotated in virtually perfect conjugacy in both subjects (Fig. 5). Recordings for the several frequencies (0.16 to 1.33 Hz) and visual conditions are shown in Figs. 6 and 7.

After computer elimination of saccades, the gain and phase of the cumulative smooth components of the eye-in-head displacements relative to the head movement were calculated. The mean values (and their S.D.) have been plotted in Fig. 8.

The data showed two major trends: gain increased with the frequency of head oscillation and also with the amount of visual information. Even in darkness and at the lowest frequency tested (0.16 Hz) gain of the compensatory smooth component (i.e. amplitude of cumulative *smooth* counterroll in the head/amplitude of head roll) was about 0.4, while values better than 0.7 were reached for 1.33 Hz in the presence of a stationary, structured visual pattern. Paired t-tests showed that the gain with a fixation spot present was significantly higher than in darkness ($p < 0.0005$); a further significant increase was induced by the checkerboard ($p < 0.0005$). The phase errors with respect to ideal compensation (exactly out of phase with the head) were slight (smaller than 10 deg except for one data point in Fig. 8). All standard deviations were relatively small. Even in darkness the gains were high enough to make them relatively unsensitive to the increased unsteadiness of fixation. A marked effect of darkness was the increased rate and size of saccades, limiting the range of torsional excursion of the eye in the head compared to the conditions containing visual information. With vision, the eyes moved in the orbit over a peak-to-peak range up to about 17 deg.

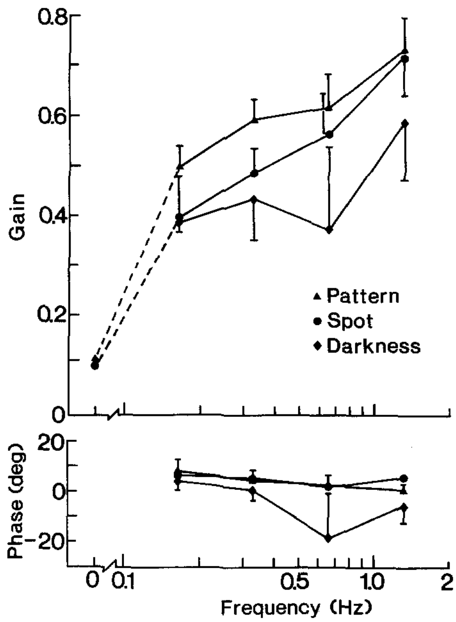

Fig. 8. Mean gain and phase relations for the smooth components of dynamic counterroll under three visual conditions. Averaged values for 2 subjects, 2 eyes and 2–3 sessions. The bars indicate one S.D.; each data point is the mean of 8–14 measurements. The gain for static counterroll have been inserted for comparison

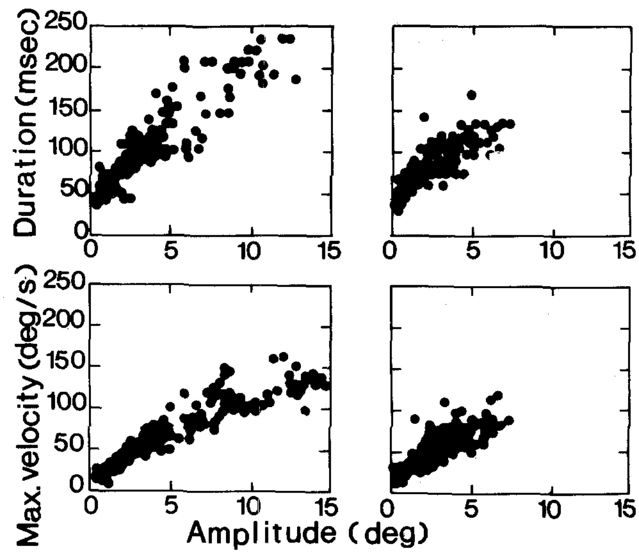

Fig. 9. Peak velocities and durations as a function of amplitude of a sample of torsional saccades, made during pseudo-sinusoidal head oscillation at 0.33 and 0.66 Hz. Subject HS. Left graphs: relations determined for the saccadic displacements of the eye relative to space; right graphs: relations for same set of saccades for displacement of the eye relative to the head

Torsional saccades

Maximal velocities and durations were calculated for a number of cyclorotatory saccades during voluntary head oscillation at 0.33 and 0.66 Hz, and are plotted as a function of saccade amplitude (Fig. 9). For the same set of saccades, the amplitude-duration-maximal velocity characteristics have been calculated for the motion of the eye in space (gaze; Fig. 9, left column) as well as for the motion of the eye in the head (eye-in-space minus head-in-space; Fig. 9, right column). Both of these relations are of interest: gaze saccades reflect the displacements of the retinal image, whereas eye-in-head saccades reflect the characteristics of the oculomotor system in the narrow sense. Of course, these two relations are reduced to a single one when the head is immobilized, which is the condition under which virtually all data in the literature for human saccades have been obtained. The eye-in-head saccades were not larger than about 8 deg, and the majority was smaller than 5 deg. For saccades with an amplitude of 5 deg the mean duration was about 120 ms and the maximal velocity about 75 deg/s, but the data showed a large variability. There was no difference between intorsional and extorsional saccades; therefore they have been pooled in Fig. 9. For the gaze-saccades, the amplitudes were larger, up to about 15 deg during pseudo-sinusoidal head oscillation, with the possibility for larger amplitudes during steps of the head in roll (Fig. 4). For the common amplitude range, the plots for gaze and eye-in-head saccades overlapped completely (Fig. 9). Maximal velocity of gaze saccades seemed to show soft saturation at about 150 deg/s for saccades larger than 10 deg, whereas duration continued to increase. For the gaze saccade of 32 deg shown in Fig. 4 (top, right) maximal velocity was 110 deg/s, with a duration of 320 ms. (Too few of such large saccades were recorded for a systematic analysis.)

Cyclorotatory optokinetic nystagmus

Optokinetic cyclorotatory responses were quite variable and in general had a low gain. Examples from the session with the largest responses are shown in Fig. 10.

The visual stimulus was highly effective in inducing subjective cyclorotatory vection and disorientation in the subject, but these were not necessarily paralleled by a strong cyclorotatory nystagmus. Especially for the higher stimulus velocities (12 and 30 deg/s) the head was also tilted in the direction of the stimulus. Although the nystagmus during stimulation at 30 deg/s in Fig. 10 seems very lively, the velocities of the slow phase did not exceed about 5 deg/s.

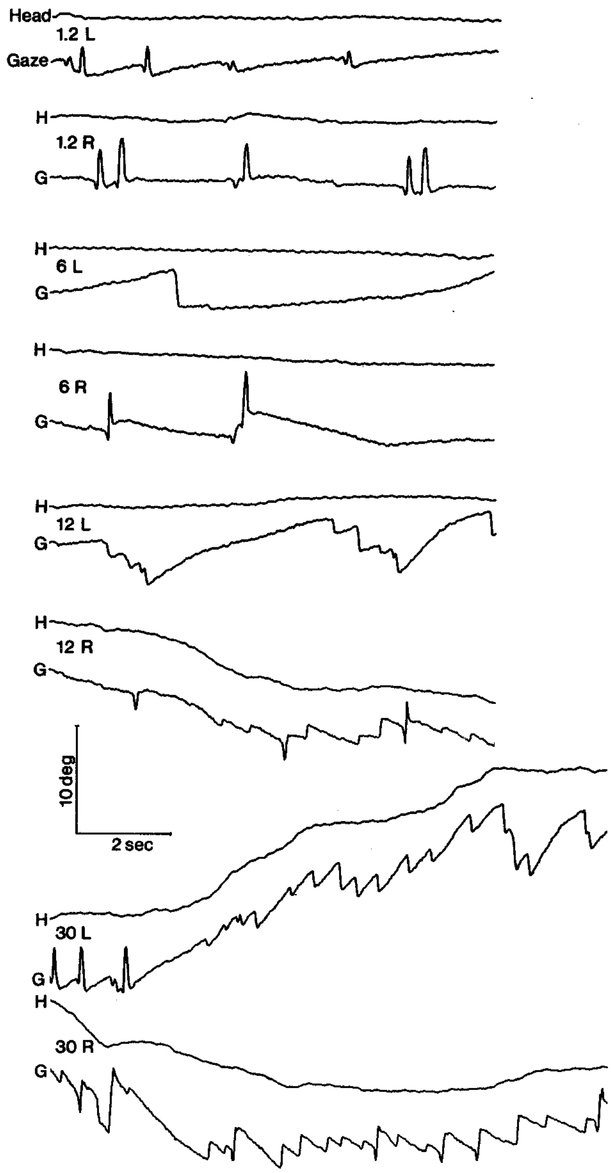

Fig. 10. Examples of cyclorotational optokinetic nystagmus. H: head roll; G: eye roll (in space). Stimulus velocities are indicated in deg/s with the upper pole of the disk rotating to the right (R) or left (L) as seen by the subject (HS)

Although the responses were often weak and irregular, they always had the form of a nystagmus and did not consist of a tonic deviation without fast phases. Mean slow phase velocity gains were calculated by computer for periods of 16 s optokinetic nystagmus with stimulus velocities of 1, 2, 6, 12 and 30 deg/s in both directions. As no systematic difference was seen between eyes, directions or subjects, Table 2 shows the mean (±S.D.) gains of the pooled data (12 measurements at each velocity). The gain was on the order of 0.03; the higher mean value of

Table 2. Mean cyclorotational optokinetic gain (±S.D.) for pooled data of 2 subjects, 2 eyes, 2 sessions and 2 directions

Stimulus velocity	Gain ± S.D.
1.2 deg/s	0.106 ± 0.212
6 deg/s	0.035 ± 0.041
12 deg/s	0.033 ± 0.046
30 deg/s	0.035 ± 0.050

0.106 for the lowest velocity (1.2 deg/s) may not be real since at this low velocity gain was extremely variable and sometimes even negative. This is probably due to the spontaneous drift of the eye, which often had a velocity of 0.1 deg/s or higher.

Discussion

Our results corroborate the occurrence of substantial compensatory cyclorotation during voluntary head movements. These are largely controlled by labyrinthine or other extra-retinal sources, but visual information definitively contributes to the generation of counterroll during head oscillation.

Our measurements confirm the presence of a small but highly consistent static counterroll. The gain was on the order of 0.1 (range 0.084–0.190) for static head tilts up to 20 deg. This is quantitatively in agreement with the results of the large majority of investigations undertaken in the last century, and further debate on the reality of this phenomenon seems unnecessary. Our results confirm it with a new technique of measurement.

However, these static deviations are only a small part of the compensatory motion, the major part of which is transient and can be recorded only *during* a head movement involving rotatory accelerations, and therefore stimulation of the canals. In agreement with Petrov and Zenkin (1973) we find substantial counterroll during head tilting with relatively good stabilization of the eye in space over short periods, alternated by saccades which reset the eye largely, but not entirely to the midposition. As a result, a residual static deviation accumulates. These transient compensations were noticed over a century ago in experiments with afterimages (Mulder 1875). When the head is steadily oscillated, the dynamic compensatory counterroll continues indefinitely with considerable gain and over a considerable spatial range, as has been found previously by Davies and Merton (1958).

The occurrence of a combination of smooth compensatory and saccadic reset movements is one of the causes of variability of torsional eye positions as a function of head tilt; torsion will be quite different before and after a torsional saccade although head tilt may be almost unchanged. This variability around a mean position – on the order of at least one degree – has been noticed by most investigators of cyclorotation. It is also caused by spontaneous torsion movements, without head movements (Fig. 2D). Miniature torsional eye movements were also recorded by Fender (1955) with a contactlens technique; Balliet and Nakayama (1978) have shown that with suitable training a large repertoire of voluntary cyclorotations can be developed.

The small amount of static counterroll suggests a weak connection of the otolith organs with the human cyclorotatory system, in contrast to the situation in rabbits and many lower vertebrates and invertebrates. In the past, the contribution from the otolith organs has been emphasized. The most constant results for counterroll have been obtained with continuous rotation at constant velocity (Diamond and Markham 1981, 1983). However, the amount of counterroll (gain) under those conditions remains as low as about 10% of head rotation. Our present findings show that a higher gain is only reached when the canals are effectively stimulated by a rotatory acceleration. The gain and phase relations of this dynamic component in humans highly resemble those for dynamic torsion in the rabbit (Van der Steen and Collewijn 1984). One marked feature of these relations is the increase of gain at higher stimulus frequencies, without larger changes in phase, in the range between 0.1 and 1.0 Hz. Another common feature of oscillatory counterroll in rabbit and man is the enhancement by visual information.

The interaction between the retinal and extraretinal information in man is not simple. The presence of a fixation point led to a considerable increase in dynamic counterroll compared to darkness, although a single point contains no orientational information. A further enhancement was induced by a pattern with many vertical and horizontal contours. Also static counterroll seemed to be marginally improved by this structured pattern, but this could be interpreted as a somewhat larger remnant of an enhanced dynamic counterroll during the head tilt, as the pattern was viewed continuously. On the other hand, Diamond and Markham (1981) found in two subjects being rotated at 3 deg/s (constant velocity) that there was no difference in counterrolling profiles with and without visual stimuli. An increase in static counterroll in the presence of structured, earth fixed patterns could also partly be due to a tendency of the vertical meridian of the retina to align with vertical contours. A systematic "optostatic" cycloversion has been described by Crone (1975), but maximal amplitudes were 1 deg or less. A larger effect of static visual contours occurs in the case of fusional cyclovergence when stimuli containing cyclodisparity are presented. Such binocular stimuli induce considerable cyclovergence (Crone and Everhard-Halm 1975; Sullivan and Kertesz 1978). Whereas the orientation of static tilted (non-horizontal or non-vertical) visual contours without a cyclodisparity component appears to be a weak stimulus for cyclorotation, rotating contours are quite effective in inducing ocular torsion (Brecher 1934; Howard and Templeton 1964; Kertesz and Jones 1969; Crone 1975; Merker and Held 1981). In most cases, only the static aspects of this torsion have been investigated, but Brecher (1934) observed a true cyclorotatory nystagmus in 16 of his 26 subjects. Torsional optokinetic nystagmus has been recorded in the rabbit (Collewijn and Noorduin 1972). Our present recordings in two humans showed a true torsional optokinetic nystagmus, but the gain was extremely low and variable, even tough the subjects consistently experienced strong cyclovection. A low-rate sampling of the nystagmus (such as by photography) would suggest a tonic deviation. Truly tonic deviation of the eye in the head was not prominent in our recordings of torsional optokinetic nystagmus, although a tonic deviation of the eye together with the head in space was often seen at higher stimulus velocities (Fig. 10).

Cyclorotational saccades were frequently made. Their occurrence was under some visual control. During pseudo-sinusoidal oscillation of the head in the dark they were made frequently, whereas their frequency and amplitude were considerably lower in the light, especially when a pattern was present (Figs. 6 and 7). Although retinal slip velocities can be equally reduced by short or long intersaccadic periods of stabilization, constancy of orientation (rotatory position) is much better maintained when saccades are avoided. For dynamic head oscillation in the range tested (0.16–1.33 Hz, peak-to-peak amplitudes about 30 deg) subjects were apparently able to suppress most of this saccadic activity, and make virtually smooth torsional compensatory eye movements with peak-to-peak amplitudes up to about 16 deg. During step displacements of the head in roll, this strategy was apparently not followed (Fig. 4).

In our material, torsional saccades of the eye in the head as well as of the eye in space followed an orderly peak velocity – duration – magnitude sequence, of the kind that has been extensively documented for horizontal saccades, but torsional saccades were slower (Fig. 9). Typical values for a 5 deg torsional saccade were about 120 ms duration and about 75 deg/s peak velocity. This contrasts with the higher velocities given in the literature for 5 deg horizontal eye-in-head saccades as 190 deg/s (Boghen et al. 1974); 180 deg/s (Baloh et al. 1975) and even 261 deg/s (Bahill et al. 1981). Balliet and Nakayama (1978) studied voluntary torsional saccades made by highly trained subjects (with the head fixed) and found comparable peak velocities as for horizontal saccades. However, their values were scaled up by a factor 1.43 in an attempt to compensate for a low sampling rate (64/s), which may have led to an overestimate in the case that torsional saccades are indeed relatively slow.

In conclusion, counterroll around the visual axis *during* natural head movements is a well developed reflex in humans, even though little of this compensation is retained in static conditions.

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