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# The contribution of the horizontal semicircular canals to the response to off-vertical-axis rotation in the cat

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**Summary.** The response to off-vertical-axis rotation (OVAR) was measured in cats under circumstances in which the signals from the horizontal semicircular canals and otoliths were opposed. Opposition was achieved by sudden acceleration or deceleration during constant velocity OVAR. The degree of opposition was expressed as a canal/otolith ratio where a ratio of unity indicated agreement. For a canal/otolith ratio of 1, the OVAR gain (eye velocity/stimulus velocity) was 0.73 (±0.13). The steady-state OVAR response was, however, reduced if the canals and otoliths were opposed. The reduction depended on the degree of opposition with a fall-off of 0.15 gain/(unit of canal/otolith ratio). These findings are discussed with respect to the central velocity store and the mechanism underlying the generation of the OVAR response.

**Key words:** Eye movements – Vestibulo-ocular reflex – Otoliths – Off-vertical-axis rotation – Cat

## Introduction

Prolonged head rotation in the cat evokes a compensatory nystagmus of the eyes the effect of which is to keep the retinal image relatively stable. Several systems (e.g. canals, otoliths, vision, proprioception) contribute to the generation of these eye movements. This paper deals with the canal and otolith contributions. The canals' response to a step change in velocity of head movement, as measured in the VIII nerve, decays rapidly (time constant 5 s: Goldberg and Fernandez 1971). However, the eye movement response declines more slowly (time constant 16 s in the cat: Harris and Cynader 1981a) revealing a stored representation of the velocity of the head movement that continues to drive the eyes beyond the duration of the input signal.

If rotation is not about an earth-vertical axis, the pattern of stimulation of the otoliths (which detect linear acceleration: here gravity) convey information about the continually changing direction of tilt during the rotation and a continuous, sinusoidally modulated horizontal nystagmus is evoked which, in the cat, can represent a very considerable compensation (up to 73%; Harris 1987a). It seems that both the canal signal and the otoliths feed into a common velocity store (Raphan et al. 1979; Harris 1987b, c; see Fig. 3).

Normally, in the initial response to a step of velocity about a tilted axis, these signals (canals' and otoliths') are in agreement, and both contribute to the velocity that is stored. The otoliths' contribution can be examined in isolation. This can be achieved for example by tilting the table after the canals' response has decayed to zero (Harris 1987a and see below), or by rotating about an off-vertical axis (OVAR) with the horizontal canals plugged (Correia and Money 1970). In isolation the otolith component takes time to build up and to decline after the rotation (time constant about 5 s in the cat, Harris 1987a) suggesting the otoliths' access to a velocity store. But the gain (eye velocity/head velocity) of response finally achieved in the absence of a compatible canal signal is rather less than when the canals are co-activated (see below). This suggest an interaction between the canals' and otoliths' signals (Correia and Guedry 1966). In this paper I put the canals and otoliths into more marked disagreement and reveal that, in order to achieve the optimum response to OVAR, the canals and otoliths must give compatible information. The experiments also suggest that the effect of conflicting signals from the canals and otoliths is before the velocity storage stage. Some of the data reported here have been presented in preliminary reports (Harris 1985, 1986).

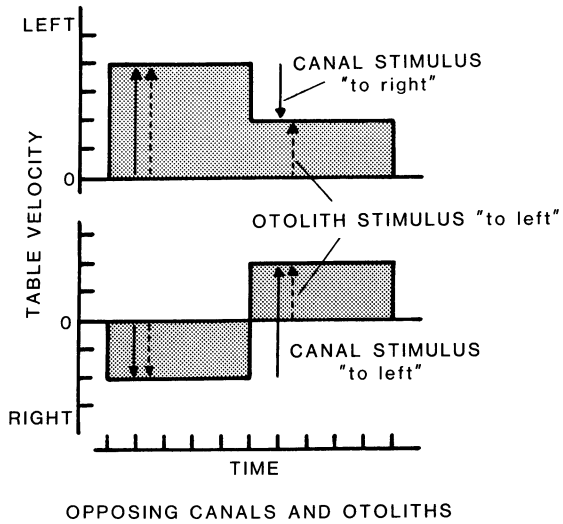



**Fig. 1.** Diagram to illustrate the pattern of off-vertical-axis rotation (OVAR) used to oppose signals from the canals and otoliths. The traces represent the velocity of rotation which is suddenly changed. The top example shows the consequences of slowing to half velocity. In this case the canals indicate movement to the right, whereas the otoliths persist in giving veridical information that rotation is to the left. This corresponds to a canal/otolith ratio of –1 (see text). In the lower example canals and otoliths indicate the same direction of rotation but different velocities (canal/otolith ratio of 2: see text)

## Methods

### *Maintenance and preparation of the cats*

The methods have been described in detail elsewhere (Harris and Cynader 1981a, b; Harris 1987a). Briefly, four adult cats were selected for their docility and implanted under Saffan anaesthesia (16 mg/kg: supplemented as required) and full sterile operating conditions with a scleral eye coil for measuring horizontal and vertical eye position (after Judge et al. 1980) and head-restraining tubes (Kopf).

### *Experimental procedure*

Animals were held on a two-axis vestibular stimulation table by means of the implanted head restraining tubes. They were held in a feline restraint bag (Jensen-Salsbery, Kansas). The properties of the system have been described in a previous paper (Harris 1987a). The animals were rotated about an axis perpendicular to their horizontal canals by tilting them 23 deg nose down with respect to the Horsley-Clark stereotaxic frame (Blanks et al. 1972). The entire apparatus (cat, eye position recording apparatus, motor for rotation) could be tilted so that the rotation could be about an off-vertical axis. All the OVAR data described in this paper were obtained with a tilt of 45 deg. The rotation of the animal was under the control of a PDP 11/23 computer which also recorded the eye movements onto disc for later analysis.

In order to oppose the signals from the canals and otoliths, the table could suddenly change velocity (acceleration 100 deg/s/s). This is shown diagrammatically in Fig. 1. In the first part of the procedure the table starts from stationary and, within 1 s, reaches a constant velocity. For this initial step in velocity the stimulation of the canals and otoliths is compatible. The canals' response decays rapidly, so that within 25 s there is no response due to the canal signal (see for example, Harris 1987a, Fig. 2a). The velocity of the table is then quickly changed to a new speed. The canals respond to the angular acceleration of this jump: that is the change in velocity. The otoliths, however, should provide veridical information about the new rate of rotation. If, as in the upper example of Fig. 1, the final speed is slower than, and in the same direction as the initial one, then the canals' and otoliths' signals are absolutely opposed since the canals convey information to the effect that the animal has changed direction. If, as in the lower example of Fig. 1, the final speed is faster or in the opposite direction, then the canals and otoliths give the same information as in the direction of rotation but differ in the velocity signalled.

### *Data analysis*

Again the method for analysing the eye movements has been reported in full previously (Harris 1987a). The data presented here represent sinusoidal curves fitted to differentiated eye position records during steady-state rotation: that is starting 15 s after any change in velocity of rotation. Gain is defined as eye velocity/stimulus velocity using the mean of the best fit to eye velocity.

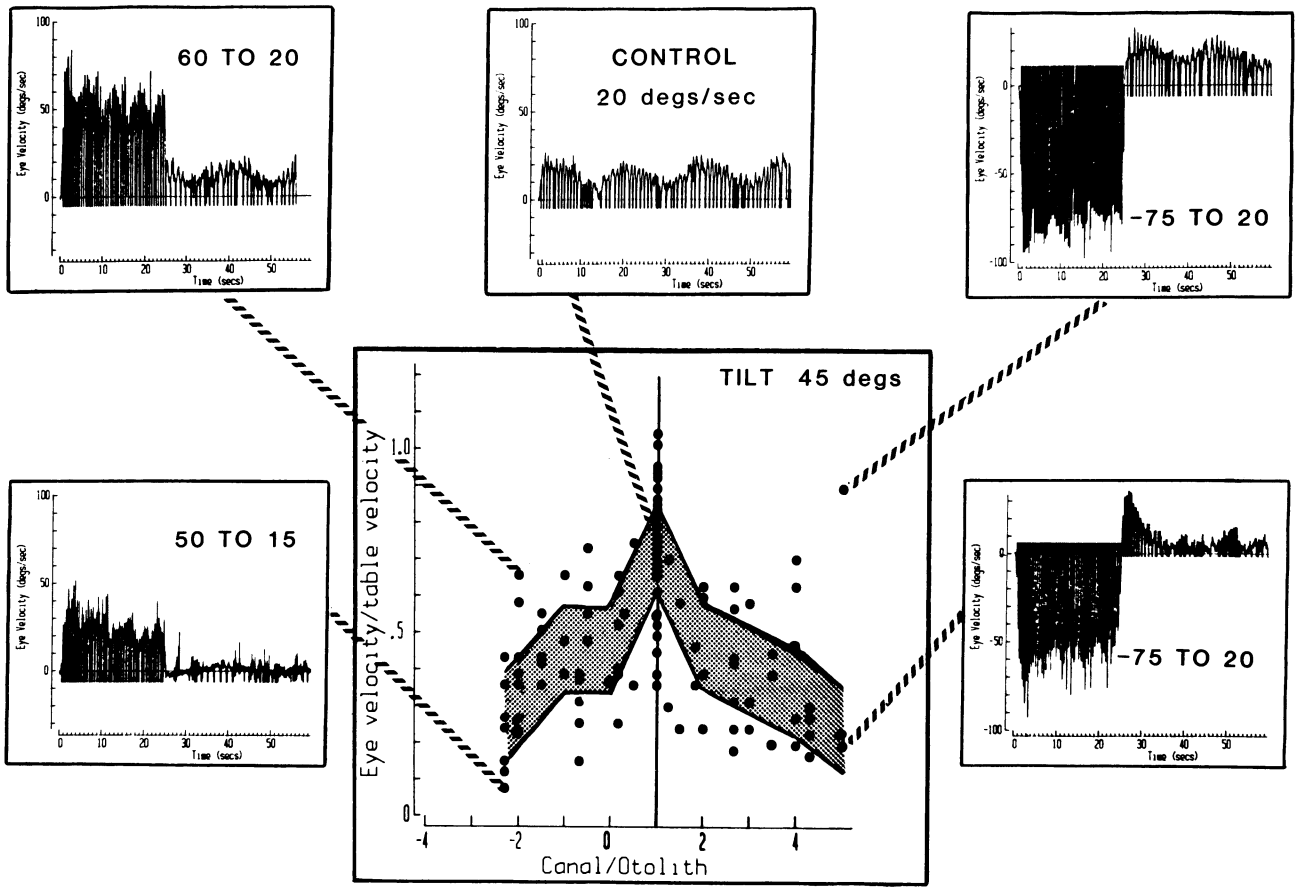
The degree of compatibility of otoliths and canals is expressed as the ratio between the presumed canal signal (change in angular velocity) and the otolith signal (rate of rotation). This ratio is assigned a positive sign if the two are in the same direction and negative if they are in opposite directions. Thus, changing speed from 60 deg/s left to 20 deg/s left is associated with a canal signal of 40 deg/s right and an otolith signal of 20 deg/s left yielding a ratio of –2. If there is no canal signal (as referred to in the introduction) this, of course, yields a ratio of zero. In the case of compatible stimuli (as from stationary to a particular speed) both the canals' and the otoliths' signals have the same value yielding a ratio of 1.

## Results

### *Effect of opposing canals and otoliths*

The effect of having different signals from the canals and otoliths is summarized in Fig. 2. The horizontal axis of the graph is the ratio between the canal signal and the otolith signal (see Methods). A positive ratio indicates that both the canals and otoliths convey information about rotation in the same direction. A ratio of 1 indicates that they were both the same amplitude, i.e. started from stationary. When the canals and otoliths are in disagreement (ratio not equal to 1), the gain (average eye velocity/stimulus velocity) of the response is diminished from 0.73 ± 0.13. The effect, surprisingly, is symmetrical about a canal/otolith ratio of 1: whenever the velocities signalled by the two systems differ, the gain of the response is diminished independent of agreement in direction. The modulation component is also reduced keeping a constant relationship to the average velocity of 0.13 (deg/s) modulation/(deg/s) bias velocity.

The slopes of the fall off in gain are symmetrical; slope = 0.15 gain / unit of ratio. They predict that the OVAR response would be completely suppressed at ratios of 6 and –4, corresponding for example to




THE EFFECT OF OPPOSING CANALS AND OTOLITHS

**Fig. 2.** The effect of opposing signals from the canals and otoliths on the steady-state eye velocity. All experiments were performed using off-vertical-axis rotation (OVAR) about an axis tilted by 45 deg. Whenever the signals from the two systems do not agree, there is a reduction in the gain of the eye movements. The shaded area represents ±1 standard deviation (0.13) from the average response gain for each ratio of canal/otolith (see text). Also shown as insets are some representative records connected to the points on the graph that they have produced. Regression lines from the canal/otolith ratio of 1 each have slopes of 0.15 gain/unit of ratio

changes in velocity from –100 to 20 deg/s (ratio = 6); or from 100 to 20 deg/s (ratio = –4).

An obvious feature of Fig. 2 is the large amount of scatter of the data points. Examples of the raw data that produced some extreme points are illustrated as insets. Standard deviations are high, but not higher than when the canal/otolith ratio is 1 (±0.13). The patterns of stimulation were arranged so that the final velocity was kept within the range 15–25 deg/s. This may explain the smaller standard deviation than that obtained with velocities in the range 5–72 deg/s (0.23, Harris 1987a).

### *Effects of otoliths in isolation (canal/otolith ratio of zero)*

By tilting the axis of rotation after the canal response has declined to zero, the effect of otolith stimulation by a rotating gravity vector can be seen in isolation. A nystagmus builds up with a time constant of 5 s and, if the axis is returned to vertical, declines with the same time constant. This is equivalent to a canal/otolith ratio of zero which Fig. 2 predicts should reduce the gain by 0.15 to 0.6. This was found but is less than two standard deviations (±0.26) and is therefore not significantly different from the control condition (starting from stationary) with a canal/otolith ratio of 1.

### *Effect of modifying the gain of the vestibulo-ocular reflex*

The gain of the vestibulo-ocular reflex (VOR) is very plastic and can easily be modified (see for example Harris and Cynader 1981b). This modification is thought to operate by means of changes in the

velocity storage system (Demer 1981). To test the effect of such modification I reduced the gain of the canal-driven VOR by forced rotation about an earth-vertical axis in the light with a fixed visual surround, to 0.4 within the hour (see Harris and Cynader 1981b). Reducing the gain to 0.4 introduces a canal/otolith ratio of 0.4. The slope of the regression lines of Fig. 2 (0.15) predicts that the gain should be reduced to 0.65. This is again less than 2 standard deviations from the control level of 0.74. Although insignificant, the gain does in fact fall by approximately this amount (on average from 0.81 to 0.73, see also Harris 1986).

## Discussion

This study has shown that by altering the compatibility of the information transduced by the canals and otoliths the amplitude of the off-vertical-axis rotation (OVAR) response is decreased. The fall-off of the response is however, relatively small. That is, the otolith response system has quite a high degree of tolerance for an inappropriate canal signal. There are two aspects to the results of this study: *1*) for relatively compatible signals from the canals and otoliths, the otoliths dominate the response but *2*) when these signals from the canals and otoliths are wildly different, the OVAR response is significantly attenuated.

### *Normal range of canal/otolith ratios*

Under what conditions could the canal signal be unreliable such that it would be appropriate instead to rely on the otoliths for information about rotation? The gain of the canal-driven vestibulo-ocular reflex (VOR) is vulnerable to various factors such as adaptation, habituation and alertness. The instruction set in man can also alter the gain from near unity if the subject is asked to imagine an earth-stationary target, to near zero if he is asked to imagine an object moving with him (Baloh et al. 1984; McKinley and Peterson 1985). The gain of the VOR can be further altered in response to geometric demands imposed by the distance between the axes or rotation of the two eyes and the head. This depends on the fixation distance. For objects closer than infinity eye movements that compensate exactly for a head movement actually can require a gain (eye angular velocity/head angular velocity) of 2 (Biguer and Prablanc 1981). So the canal-alone response can vary over the range 0 (VOR suppression) to around 2 (viewing a close object) under normal conditions. Interestingly a variation in canal/otolith ratio of $\pm 1$ produces a change in OVAR gain of only 0.15: close to the standard deviation ($\pm 0.13$). That is there is no significant alteration in the response over this range.

The VOR modification experiment represents an example of the gain of the canal-only VOR being manipulated within its normal range. The canals-alone response was incorrectly calibrated to suggest that the speed of rotation was less than it actually was. This recalibration was almost completely ignored when otolith information was also available: the OVAR response being insignificantly reduced whilst the canal-alone response was reduced from 0.95 to 0.4. The otoliths give more accurate and reliable information since the timing of a complete revolution can be obtained with respect to absolute reference points, i.e. how long it takes in between the periodic optimal stimulation of each otolithic unit tuned to a particular orientation of the animal.

### *Abnormal canal/otolith ratios*

So, over the normal range of variability that could be physiologically expected in the canal-response, the otolith signal dominates. But outside this range, the eye movements are indeed significantly attenuated by incompatibility between the canals and otoliths. Incompatibility between the canals and otoliths is also produced when a sudden tilt is imposed during post-rotatory nystagmus – under these circumstances *actual* rotation around the newly-tilted axis would have been accompanied by otolithic stimulation (see Harris 1987a for extensive discussion). The absence of such a signal from the otoliths reveals to the animal that rotation is not actually occurring and the velocity store is consequently discharged (Raphan et al. 1981; Waespe et al. 1981; Hain et al. 1987). Notice that the discharge of the velocity store by tilt is not always complete but depends on the extent of the tilt, i.e. the degree of incompatibility (Hain et al. 1987). This paper indicates that other grossly incompatible patterns of canal and otolith signals (e.g. canals indicating 150 deg/s when the otoliths indicate 20 deg/s) that also could not be expected to occur naturally tend to discharge the velocity store.

### *Mechanism of canal-otolith interaction*

The symmetry of the fall-off of the gain on the OVAR response shows that it does not matter whether the canals are tending to charge (same direction: positive ratio) or discharge (opposite direction: negative ratio) the central velocity store

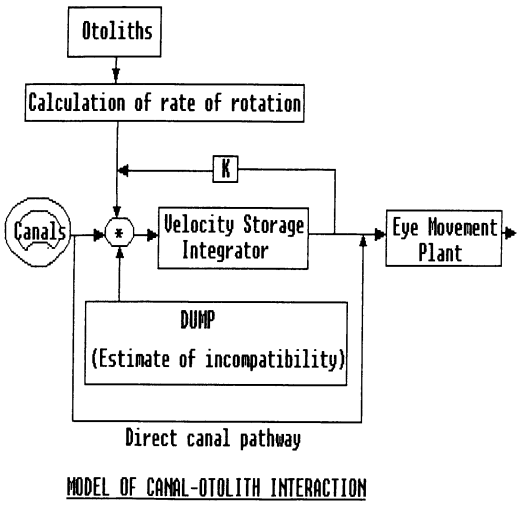



**Fig. 3.** Model of otolith-canal interactions. The point marked (*) shows the point of entry of the otolith signal, optokinetic system (not shown), the velocity storage feedback and the dumping facility

involved in the generation of eye movements in that direction. This observation suggests that the interaction I have revealed must occur before the store itself. Otherwise one might have predicted an "overcharging" of the store in response to positive ratios resulting in an increase in the OVAR gain instead of the decrease actually found. This is illustrated diagrammatically in Fig. 3. Notice that there is no otolithic influence when the velocity store is deactivated (Harris 1987b, c) and thus there can be no 'direct' otolithic pathway in contrast to the direct pathways of the optokinetic (not shown) and canal systems.

The entry point preceding the velocity store (* in Fig. 3) is also the site of entry of the optokinetic indirect pathway (Waespe et al. 1983; Raphan and Cohen 1985). However, the otolithic and canal systems differ in a fundamental way from the optokinetic system since they are both open loop: that is, neither the otolithic or canal signals are reduced by the eye movements they evoke. Thus, there *cannot* be a simple algebraic addition of the otolith and canal systems or the result would, under most physiological conditions when both the canals and otoliths give the same information, be too large. The results presented above show that the problem also cannot be solved by weighting of the canal and otolith signals since inappropriate canal/otolith signals always result in an *attenuation* of the response suggesting that it is the degree of incompatibility between them rather than the actual difference that is significant. Both these new results and the effect of tilt during post-rotatory nystagmus (Hain et al. 1987) suggest that the degree of incompatibility of information from different sources is taken into account at this stage (the input to the velocity store) and that a significant incompatibility results in an appropriate dumping of the store.

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## References

Baloh RW, Lyerly K, Yee RD, Honrubia V (1984) Voluntary control of the human vestibulo-ocular reflex. Acta Otolaryngol (Stockh) 97: 1–6

Biguer B, Prablanc C (1981) Modulation of the vestibulo-ocular reflex in eye-head orientation as a function of target distance in man. In: Fuchs AF, Becker W (eds) Progress in oculomotor research. Elsevier, North Holland, pp 525–530

Blanks RHI, Curthoys IS, Markham CH (1972) Planar relationships of semicircular canals in the cat. Am J Physiol 223: 55–62

Correia MJ, Guedry FE (1966) Modification of vestibular responses as a function of rate of rotation about an earth-horizontal axis. Acta Otolaryngol 62: 297–308

Correia MJ, Money KE (1970) The effect of blockage of all six semicircular canals ducts on nystagmus produced by linear acceleration in the cat. Acta Otolaryngol 69: 7–16

Demer JL (1981) The variable gain element of the vestibulo-ocular reflex is common to the optokinetic system of the cat. Brain Res 229: 1–13

Goldberg JM, Fernandez C (1971) Physiology of peripheral neurons innervating semicircular canals of the squirrel monkey. I. Resting discharge and response to constant angular accelerations. J Neurophysiol 34: 635–660

Hain TC, Maria BL, Zee DS (1987) Modification of the dynamics of post-rotatory nystagmus by lesions of the cerebellum. In: Graham M (ed) The vestibular system: neurophysiologic and clinical research. Raven Press, New York (in press)

Harris LR (1985) The effect of opposing canal and otolith signals during off-vertical-axis rotation in the cat. J Physiol (Lond) 371: 30P

Harris LR (1986) Adaptation of the vestibulo-ocular reflex does not affect the response to off-vertical axis rotation in the cat. J Physiol (Lond) 382: 78P

Harris LR (1987a) Vestibular and optokinetic eye movements evoked in the cat by rotation about a tilted axis. Exp Brain Res 66: 522–532

Harris LR (1987b) Vertical canal stimulation abolishes horizontal velocity storage: effects on optokinetic nystagmus and eye movements evoked by a rotating linear acceleration. Int Meeting of the Barany Society (in press)

Harris LR (1987c) The eye movements evoked by a rotating linear acceleration vector depend on a central velocity storage mechanism. Brain Res 437: 393–396

Harris LR, Cynader M (1981a) The eye movements of the dark reared cat. Exp Brain Res 44: 41–56

Harris LR, Cynader M (1981b) Modification of the balance and gain of the vestibulo-ocular reflex in the cat. Exp Brain Res 44: 57–70

Judge SJ, Richmond BJ, Chu FC (1980) Implantation of magnetic search coils for measurement of eye position: an improved method. Vision Res 20: 535–538

McKinley PA, Peterson BW (1985) Velocity modulation of the vestibuloocular reflex in humans and its relation to smooth pursuit. Exp Brain Res 60: 454–464

Raphan T, Cohen B (1985) Velocity storage and the ocular response to multidimensional vestibular stimuli. In: Berthoz A, Melvill Jones G (eds) Adaptive mechanisms in gaze control. Facts and theories. Elsevier Science Publishers, North Holland

Raphan T, Cohen B, Henn V (1981) Effects of gravity on rotary nystagmus in monkeys. In: Cohen B (ed) Vestibular and oculomotor physiology. Ann N Y Acad Sci 374: 337–346

Raphan T, Matsuo V, Cohen B (1979) Velocity storage in the vestibulo-ocular reflex arc (VOR). Exp Brain Res 35: 229–248

Waespe W, Buettner U, Henn V (1981) Visual-vestibular interactions in the flocculus of the alert monkey. I. Input activity. Exp Brain Res 43: 337–348

Waespe W, Cohen B, Raphan T (1983) Role of the flocculus and paraflocculus in optokinetic nystagmus and visual-vestibular interactions: effects of lesions. Exp Brain Res 50: 9–33

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