

## Vestibular and optokinetic eye movements evoked in the cat by rotation about a tilted axis

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**Summary.** Horizontal and vertical eye movements were recorded from cats in response to either a) off-vertical axis rotation (OVAR) at a range of velocities (5–72 deg/s) and a range of tilts (0–60 deg) or b) horizontal (with respect to the cat) optokinetic stimulation (10–80 deg/s), also around a range of tilted axes (0–60 deg). The responses to stopping either of these stimuli were also measured: post-rotatory nystagmus (PRN) following actual rotation, and optokinetic after nystagmus (OKAN) following optokinetic stimulation. The response found during OVAR was a nystagmus with a bias slow-phase velocity that was sinusoidally modulated. The bias was dependent on the tilt and reached 50% of its maximum velocity (maximum was  $73 \pm 23\%$  of the table velocity) at a tilt of 16 deg. The phase of modulation in horizontal eye velocity bore no consistent relation to the angular rotation. The amplitude of this modulation was roughly correlated with the bias with a slope of 0.13 (deg/s) modulation/ (deg/s) bias velocity. There was also a low-velocity vertical bias with the slow-phases upwardly directed. The vertical bias was also modulated and the amplitude depended on the bias velocity (0.27 (deg/s) modulation/ (deg/s) bias velocity). When separated from the canal dependent response, the build up of the OVAR response had a time constant of  $5.0 \pm 0.8$  s. Following OVAR there was no decline in the time constant of PRN which remained at the value measured during earth-vertical axis rotation (EVAR) ( $6.3 \pm 2$  s). The peak amplitude of PRN was reduced, dependent on the tilt, reaching only 20% of its EVAR value for a tilt of 20 deg. When a measurable PRN was found, it was accompanied by a slowly-emerging vertical component (time constant  $5.4 \pm 2$  s) the effect of which was to vector the PRN accurately onto the earth horizontal. OKN measured about a tilted axis showed no differences in magnitude or direction from EVAR OKN even for tilts as large as 60 deg. OKAN

following optokinetic stimulation around a tilted axis appeared normal in the horizontal plane (with respect to the animal) but was accompanied by a slowly emerging (time constant  $4.1 \pm 2$  s) vertical component, the effect of which was to vector the overall OKAN response onto the earth horizontal for tilts less than 20 deg. These results are compared with data from monkey and man and discussed in terms of the involvement of the velocity storage mechanism.

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

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### Introduction

When a cat is subjected to a step change in velocity of rotation about an earth-vertical axis (EVA), the horizontal semicircular canals are stimulated by the angular acceleration. The signal from the canals drives the eyes at a roughly equal but opposite velocity to the movement of the head. This compensatory movement is interrupted, if necessitated by the restricted oculomotor range, by fast resetting movements. The overall saw-tooth pattern of response is called nystagmus. Nystagmus rapidly declines after a step change in velocity in the dark. If the lights are on during such a step change in velocity, then a second reflex comes into play: optokinetic nystagmus (OKN). OKN complements vestibular nystagmus and produces a nystagmus that doesn't decline at all during constant velocity rotation.

During off-vertical axis rotation (OVAR), even in the dark, there is also a continuous nystagmus (Raphan et al. 1981 monkey; Benson and Bodin

1966a man). The response has two components: a bias velocity and a sinusoidal modulation of that bias. In man the sinusoidal component dominates, but in the monkey and, as I now demonstrate, in the cat there is a large bias component. In the cat the phenomenon has only so far been comprehensively studied in the rather extreme case of barbeque-spit rotation (Correia and Money 1970) although there has been a preliminary report by Denise and Darlot (1985).

During OVAR there are two forces applied to the cat: angular acceleration (as during EVA rotation), and also a rotating vector of gravity (see Fig. 1c). The otoliths are sensitive to linear accelerations (e.g. gravity) and it is now generally accepted that it is their stimulation that largely underlies the nystagmus produced in response to a rotating gravity vector. This was confirmed by studies in canal-plugged animals which continued to demonstrate a nystagmus similar (but not identical) to that of the intact animal during OVAR despite a complete lack of nystagmus when the axis of rotation was earth vertical (Correia and Money 1970 cat; Cohen et al. 1983 monkey). The initial stimulation of the canals does contribute slightly to the overall OVAR response (Harris 1986a).

The cat has proved an excellent model in the study of the control of eye movement in frontally-eyed animals. I therefore wanted to quantify the pattern of nystagmus produced by OVAR and how the components of the response might vary with the angle of tilt of the axis.

When OVAR suddenly stops, the otoliths produce an after-effect that largely cancels the post-rotatory nystagmus of canal origin. The otolith response can be demonstrated in isolation by simply returning the axis to the earth vertical during rotation (Raphan et al. 1981). The response, like the contribution of the otoliths during rotation, shows characteristics broadly similar to optokinetic after nystagmus (OKAN). The cat has been widely used as a model for the OKN system (see Maioli and Precht 1984) and therefore represents a useful animal with which to quantify this parallel.

Indeed the similarity of the response to OVAR and the optokinetic response are so striking that both may bring about their effects by way of a common velocity storage mechanism (Raphan et al. 1979; Hain 1986). There must be three velocity stores to account for compensatory eye movements in different planes (Cohen et al. 1983; Raphan and Cohen 1985) and cross-coupling between these (Robinson 1982) predicts the appearance of vertical components in the OVAR response. Preliminary reports suggest that OVAR post-rotatory nystagmus in man (Harris

and Barnes 1985) and OKAN in monkey (Raphan and Cohen 1983) are accompanied by such cross-coupling effects. These predictions are here systematically investigated in the cat.

## Methods

### *Preparation and maintenance of the cats*

Three adult, female cats (Scruff, Gloria and Minstrel) were used in this study. They were selected for their docility. Under sterile operating conditions and Saffan anaesthetic (alfaxalone iv. induction dose: 18 mg/kg supplemented as required) they were implanted with a preformed scleral search coil (A5632 Cooner Wire Company, after Judge et al. 1980) and head-restraining tubes (Kopf). The wire from the eye coil was fed under the skin to a small connector imbedded in dental acrylic that also held the head-restraining tubes. A good grip of the acrylic on the skull was ensured by six 2 mm self-tapping stainless-steel screws with their heads carefully left about 2 mm above the skull's surface. The method is described in detail in Harris and Cynader (1981a).

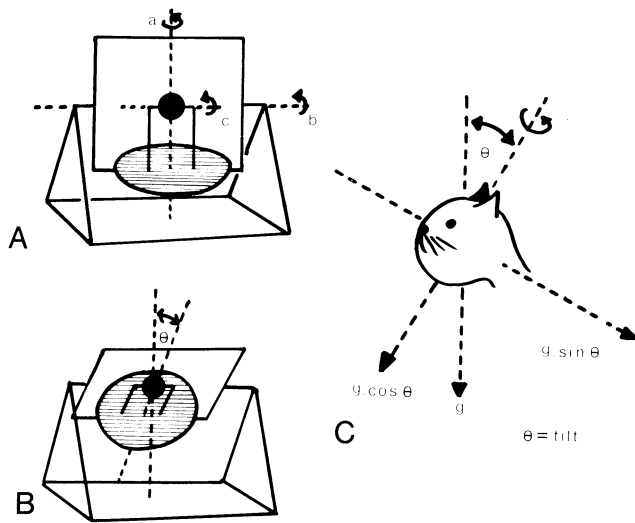
### *Stimulation procedure*

Cats were mounted on a platform held in the centre of a two-axis servo-controlled rate table under the control of a PDP 11/23 computer. This is shown as a cartoon in Fig. 1.

The two axes were nested such that the inner motor always rotated the cat about his yaw axis and the outer motor moved not only the cat but also the yaw-axis motor. The outer motor was used to position the axis of rotation of the inner motor with respect to gravity. A further degree of freedom was allowed by being able to tilt by hand the platform on which the cat sat with respect to the axis of the inner motor. This meant that cats could be accurately positioned with the plane of their horizontal canals perpendicular to the axis of rotation (23 deg/nose down: Blanks et al. 1972). The cat could be accelerated at 100 deg/s up to the velocity of rotation. Constant velocity rotation was obtained with less than 7% fluctuation even when rotation was about an axis tilted by 60 deg.

They were restrained in a snug-fitting bag (Feline Restraint Inc, Chicago) and their heads were attached to the stereotaxic frame by means of bolts that fitted in the implanted tubes (Kopf Animal Restraint System). There was no reward given for good behaviour although cats were immediately released if they showed signs of discomfort. Alertness was maintained by making a variety of noises around the animals and by keeping recording sessions as short as possible. After a couple of days to get used to the apparatus, runs of up to two hours were tolerated without signs of distress. No cat was ever sick in the apparatus or showed any signs of nausea.

Visual stimulation was provided by reflecting the beams of two projectors that were attached to the frame off a 12 cm diameter cylinder of 1 by 5 cm mirrors positioned 15 cm above the animal. These projected an array of vertical stripes (contrast 80%) onto a cylindrical screen that surrounded the animal at a distance of 0.5 m attached to the frame. Movement of the mirrors and hence the stripes (10–80 deg/s) was under control of the computer which also turned the projectors on and off. Because the mirrors, projectors and screen were all attached to the frame, the whole assembly could be tilted together. Thus optokinetic nystagmus could be evoked with no visual cues about the tilt available to the animal.



**Fig. 1A–C.** Cartoon showing the capability of the equipment. Rotation at constant velocity was around axis 'a', tilt was produced by a displacement around axis 'b'. The angle of the cat with respect to the axis of rotation could be varied around axis 'c' to position the horizontal canals in the plane of optimum stimulation. Notice that when the axis of rotation was tilted (B), the whole frame containing the cat was tilted: this included the magnetic fields for measuring eye movements, the motor that rotated the animal and all the equipment for stimulating optokinetic nystagmus (see text) as well as the animal itself. The axis of rotation *with respect to the cat* always remained constant i.e. perpendicular to the plane of the horizontal canals. C shows the directions of action of the gravity vectors. The vector at 90 deg to the axis of rotation (of amplitude  $g \sin \theta$ ) swung around the cat as he rotated

#### *Measurement, calibration and analysis of eye movements*

The cats were held at the centre of two sets of Helmholtz field coils that induced currents of two different frequencies in the implanted scleral eye coil (Robinson 1963). The position of the eye coil was then extracted from the induced currents (EMCO eye position apparatus). The DC voltages thus obtained (corresponding to horizontal and vertical eye position) were low-pass filtered (DC–40 Hz), sampled at 12 ms intervals by an A-to-D converter (Cambridge Electronic Design) and stored on disc by the PDP 11/23 computer.

Eye movements were calibrated by rotation about an earth vertical axis in the light at 25 deg/s (when the gain of the cat's vestibular plus optokinetic system is unity: Maioli et al. 1983). The vertical calibration was then calculated from the relationship between vertical and horizontal ascertained from a dummy search coil mounted on protractors. These calibration figures were subsequently confirmed by measurements on dead animals by moving the field coils in 10 deg steps over the range  $\pm 90$  deg around the now-stationary search coil. The direction of eye movement is always specified with respect to the cat: that is, horizontal eye movements are always from the cat's left/right, even if he is lying on his side.

In order to analyse the slow phase eye movements, fast phases were removed by positioning cursors by eye around the differentiated record (i.e. eye velocity) displayed on a graphics terminal. Periods with velocities outside these limits were then removed as well as  $\pm 24$  ms from when they passed criteria. No attempt was

made to fill in the gaps which were ignored by subsequent curve fitting programmes. Sine waves were fitted by least-squares linear regression to:

$$y = A \sin(x + \text{phase}) + \text{SSEV}$$

where  $y$  = slow-phase eye velocity;  $A$  = amplitude of sinusoidal component and SSEV = average steady-state eye velocity. 'Phase' was varied in a staircase fashion until the best fit with a positive slope was identified from the regression coefficient. Phase = 0 corresponds to the data being in exact synchrony with the stimulus trace which defined the sample period.

Time constants referred to in the results section were defined as the time taken to reach  $1/e$  of the maximum. They were obtained from the best fit exponential fitted by least squares regression. For the purposes of this paper deviations from simple exponentials were ignored.

## **Results**

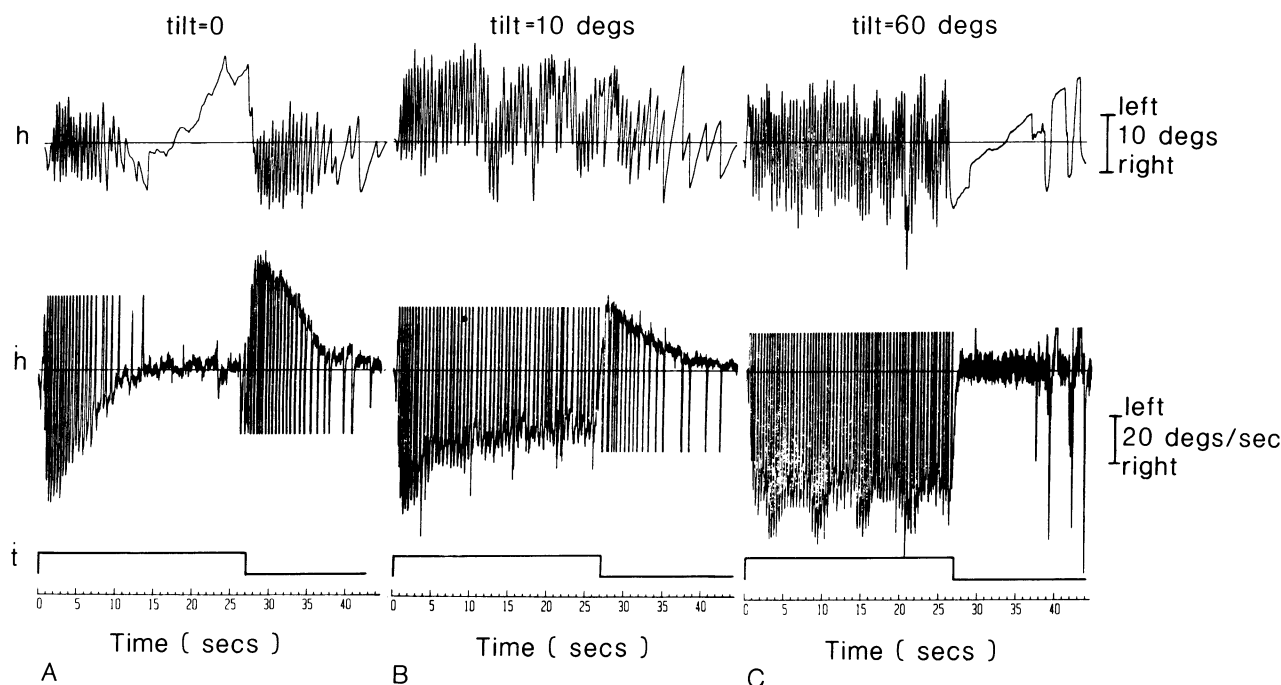
### *1. Eye movements during rotation around an off-vertical axis (vestibular alone)*

Figure 2 shows the typical pattern of eye movements evoked from a cat in total darkness by rotation about a tilted axis. When the axis is vertical (Fig. 2a) the response decays with a time constant of  $6.3 \pm 2$  s such that after about 15 s there is no further nystagmus. When rotation is about a tilted axis, the initial response decays to a continuous nystagmus that is maintained indefinitely. The average horizontal eye velocity of the maintained response approaches that of the rotation. Superimposed on this is a characteristic sinusoidal modulation in velocity with a period of one per revolution. There is also a vertical component (not shown in Fig. 2) which has a very slow constant upward velocity component ( $0.32 \text{ deg/s} \pm 0.15 \text{ deg/s}$  over all cats for all tilts above 16 deg; see below) but an appreciable tilt-dependent sinusoidal component.

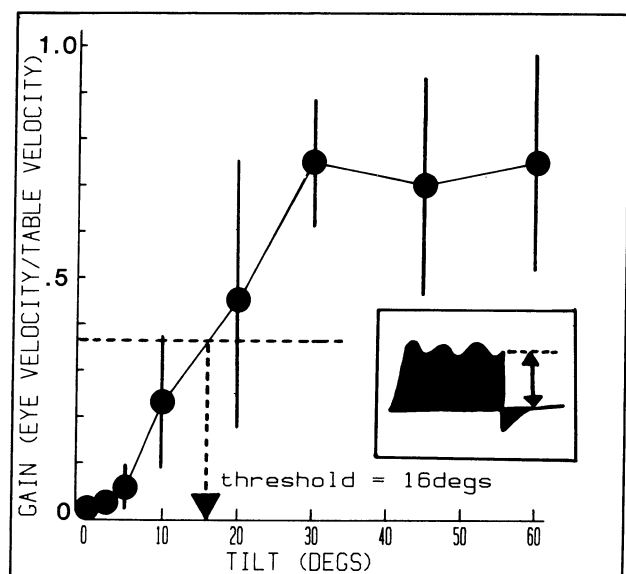
Figure 3 shows the effect of tilt on the average steady-state horizontal slow-phase eye velocity (SSEV: as defined in Methods). All the velocities used (5–72 deg/s) have been normalized by plotting the *gain* (slow-phase eye velocity/table velocity) against the tilt. At angles of tilt above 30 deg, the gain of the SSEV is  $0.73 (\pm 0.23)$ . At smaller angles of tilts there is a regular decrease in the SSEV. The threshold for the effect of a tilt (the point when the SSEV is 50% of its maximum velocity) is 16 deg.

To measure the build up of the otolithic component of the SSEV alone, animals were suddenly tilted 15 s after rotation about an EVA had commenced, by which time the initial response had disappeared. The time constant of the build up which followed the head tilt was  $5.0 \pm 0.8$  s.

The phase of the peak of the horizontal modulation in velocity is completely random with respect to



**Fig. 2A–C.** The effect of tilt on horizontal nystagmus. For each set of traces the table rotated (lower trace 't') at constant velocity of 60 deg/s for 27 s when it came to an abrupt halt and remained stationary for the remainder of the trace. For each panel the upper trace is horizontal eye position, 'h' and the centre trace ('h') is horizontal eye velocity with the fast phases clipped for clarity. Calibration scales are given on the right hand side. All records were obtained during rotation in complete darkness. **A** shows the effect of rotating about an earth-vertical axis (EVA), the axis was tilted by 10 deg in **B** and by 60 deg in **C**



**Fig. 3.** The relationship between tilt and the steady state eye velocity (measured as described in the text: see insert). The data points show the averages for three cats for table velocities over the range 5–72 deg/s. The vertical bars represent standard deviations. Defining threshold as 50% of the maximum response produces a value of 16 deg of tilt

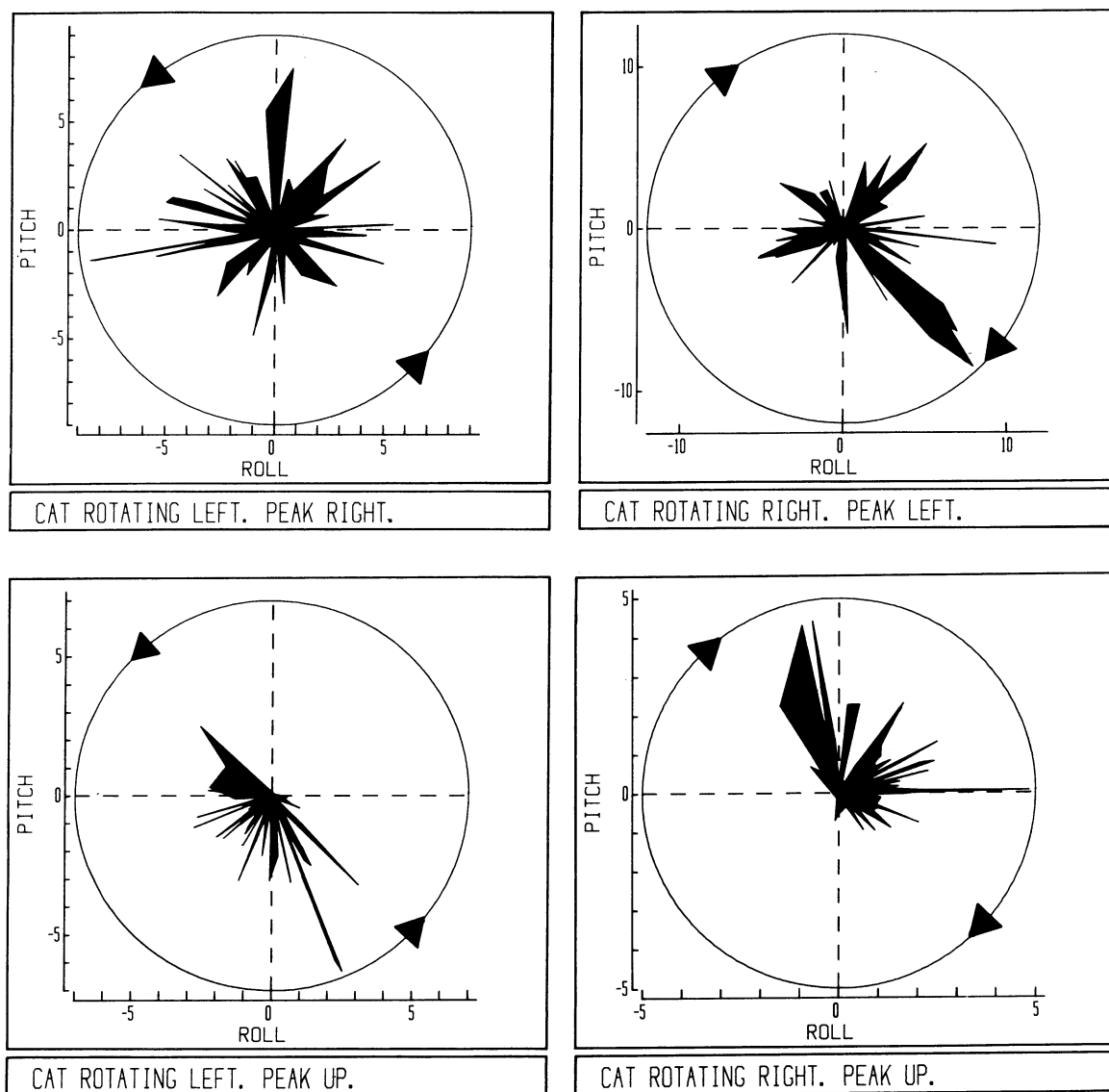
the position of the table. This can be seen by the star-like patterns of Fig. 4. The extremely jagged appearance of the phase plots shows that the amplitude of the sinusoidal component also bears no relationship to the rotation.

Although there is also a lot of scatter in the position of the peak of the vertical sinusoidal component, the phase of the peak-upwards velocity is more related to the direction of tilt (Fig. 4). The average phase of the peak-upward vertical sine component leads the nose-down position by 62 ( $\pm 38$ ) and 98 ( $\pm 33$ ) deg rotating left and right respectively. These are not significantly different.

The amplitude of the sinusoidal components is only roughly correlated to the corresponding SSEV (regression coefficients 0.62 and 0.43 and slopes of 0.13 and 0.27 (deg/s) peak modulation/(deg/s) SSEV for horizontal and vertical sinusoidal modulation respectively).

## 2. Eye movements following rotation around off-vertical axis (vestibular alone)

Returning to Fig. 2, the post-rotational nystagmus following OVAR (Fig. 2b, c) can be seen to be very



**Fig. 4.** The solid circle in each panel plots the roll and tilt of the animal with respect to gravity. The direction of rotation is shown by the solid arrows. The top of each circle represents 'nose up' and the bottom 'nose down'. The left hand edge represents 'left ear down' and the right, 'right ear down'. The angle of the radiating lines corresponds to the phase of the peak of the eye movement velocity modulation in the compensatory direction. The length of the vectors represents the amplitude of the sinusoidal component according to the scales given on the axes in deg/s. The data have been divided into four sections corresponding to left/right rotation and up/down eye movements. There was no systematic variation with tilt or velocity of rotation and so all the data have been plotted on the same diagrams

much attenuated compared to that following EVA rotation (Fig. 2a). The maximum velocity of post-rotational nystagmus depends on the tilt of the axis as shown in Fig. 5. In Fig. 5, as for Fig. 3, the eye velocities have been normalized by plotting gain (eye velocity/table velocity). Above threshold (16 deg) there is less than 20% of the response found after EVA rotation. There is however, no reduction of the time constant of decay of post-rotatory nystagmus, which remains at  $6.3 \pm 2$  s over the range of tilts from which it is measurable (0–20 deg).

There is also a vertical nystagmus evoked when OVAR suddenly stops. This is despite the fact that the vertical canals were only minimally stimulated by the preceding rotation (see methods). As for the horizontal post-rotational nystagmus, this vertical post-rotational effect is only appreciable for tilts less than 16 deg. For tilts above this there is no appreciable horizontal or vertical after-effect. There are no such vertical eye movements when rotation about an EVA is suddenly stopped. The direction and extent of the vertical component further depends on the

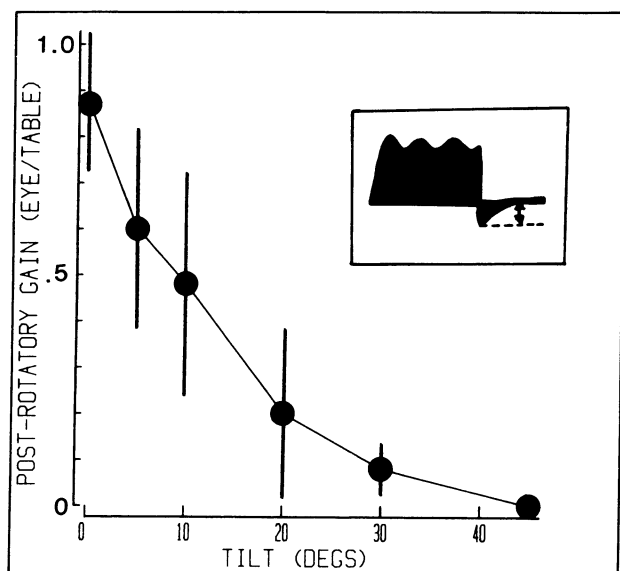


Fig. 5. The peak amplitude of the post-rotatory response measured as shown in the inset. The vertical bars represent standard deviations. By threshold tilt (16 deg; see Fig. 3) the maximum amplitude was only 20% of the rotation speed

exact position (i.e. tilt) of the cat when rotation is stopped. If the cat is, for example, stopped in the left-ear-down position after rotation to the right around an axis tilted by 10 deg (i.e. still with an appreciable horizontal post-rotatory nystagmus: see Fig. 5) then the horizontal slow phase is to the right with a peak velocity of about 40% of the velocity of the previous rotation (Figs. 2b, 5). This is accompanied by a small but significant vertical component with the slow phases directed downwards. The overall nystagmus is therefore oblique and with the slow phases directed down and to the right. If the animal is stopped nose up or nose down, there is no vertical nystagmus.

What this means for the direction of the overall nystagmus is shown in Fig. 6. If horizontal nystagmus (with respect to the cat) is tilted down from earth horizontal by virtue of the head tilt, it is accompanied by a vertical nystagmus with upward directed slow phases. If the horizontal nystagmus is tilted up from earth horizontal it is accompanied by a vertical nystagmus with downward directed slow phases. The solid line in Fig. 6 shows 100% compensation for the head tilt. The nystagmus is indeed vectored in such a way as to bring the nystagmus onto the earth horizontal. It is not possible to extend this plot beyond tilts of 20 deg because there is no appreciable horizontal post-rotational nystagmus to vector beyond this amount of tilt (see Fig. 5).

The vectoring effect takes time to build up. The time constant (see methods) is  $5.4 \pm 2.0$  s. This is

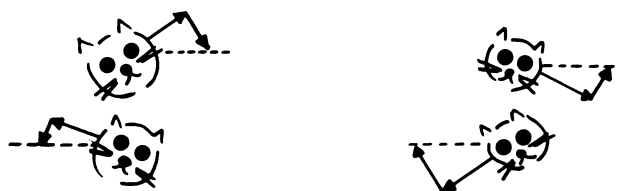
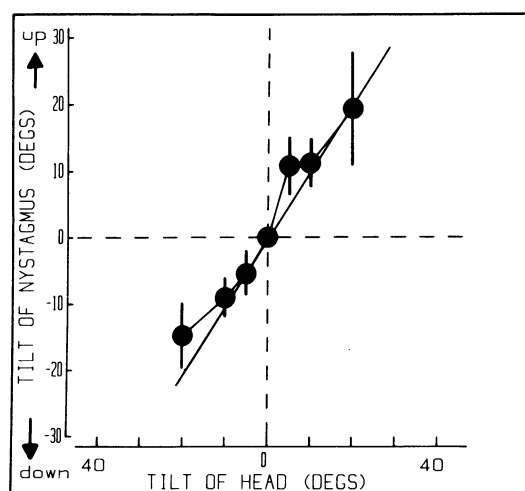
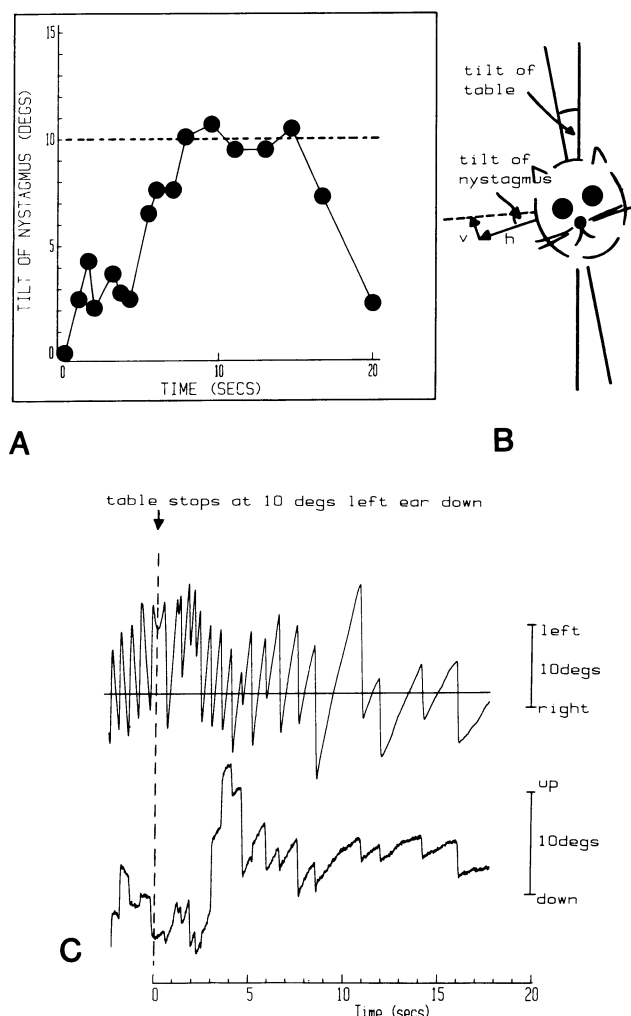


Fig. 6. The tilt of post-rotatory nystagmus as a function of head tilt. The vertical axis plots the tilt of nystagmus. 'UP' and 'DOWN' refer to the direction of the slow phases of the vertical nystagmus. The right-hand side of the 'TILT OF HEAD' axis combines head tilts which would result in the horizontal (with respect to the cat) nystagmus being tilted downwards with respect to earth horizontal. The left-hand side of this axis combines head tilts which would result in the horizontal (with respect to the cat) nystagmus being tilted upwards with respect to earth horizontal. These conditions are illustrated in the cartoons below the diagram. The solid line plots 100% compensation for the head tilt i.e. a nystagmus accurately aligned with earth horizontal

shown in a typical example plotted in Fig. 7. From about 9 s the nystagmus is accurately vectored onto the earth horizontal. All the data that are shown in Fig. 6 were taken from the nystagmus measured about 10 s after the rotation stopped. Notice that the fast phases are not always in the same direction. Whilst most of those in the example presented in Fig. 7 are rightward and down, there are some rightwards and up (at 3, 3.7 and 5.1 s after the table stopped in this figure). Occasionally horizontal fast phases are seen with no accompanying vertical fast phases at all.

### 3. Eye movements during and following off-vertical axis (optokinetic stimulation)

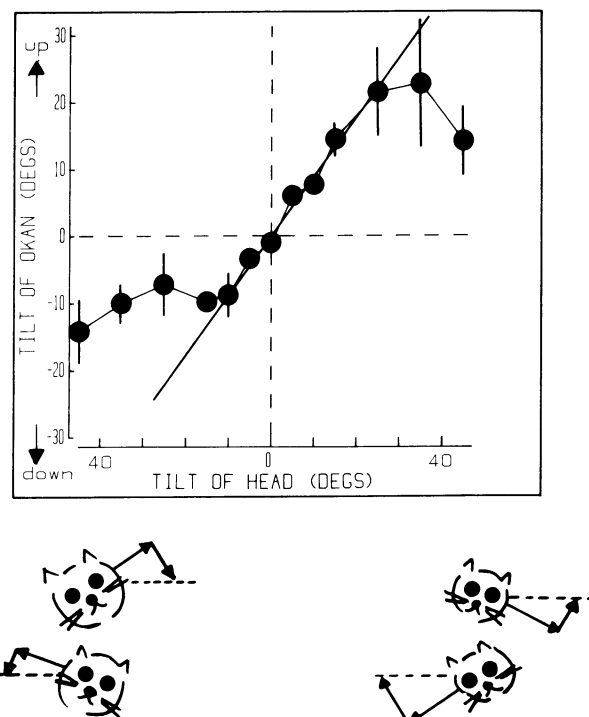
Optokinetic nystagmus (OKN) and its after effect (OKAN) were also measured while the animal was



**Fig. 7A–C.** The time course of the development of tilt in post-rotatory nystagmus. **A** The tilt of nystagmus measured from each of the slow phases shown in the original data traces shown in **C** below. **B** Shows how the tilt of nystagmus is defined

tilted over the range 10–80 deg/s. The arrangement of the apparatus is shown in Fig. 1 which makes it clear that the drum was tilted along with the animal – there were no visual cues by which the animal could detect the tilt. The OKN appears entirely normal and has the normal time constant of build up (about 7 s). Horizontal OKAN also appears normal with a time constant of  $7.43 \pm 2.8$  s. The OKAN, however, like the post-rotatory nystagmus described in Sect. 2, is distinguished by the presence of a vertical component not seen after OKN when the drum was rotated about an EVA.

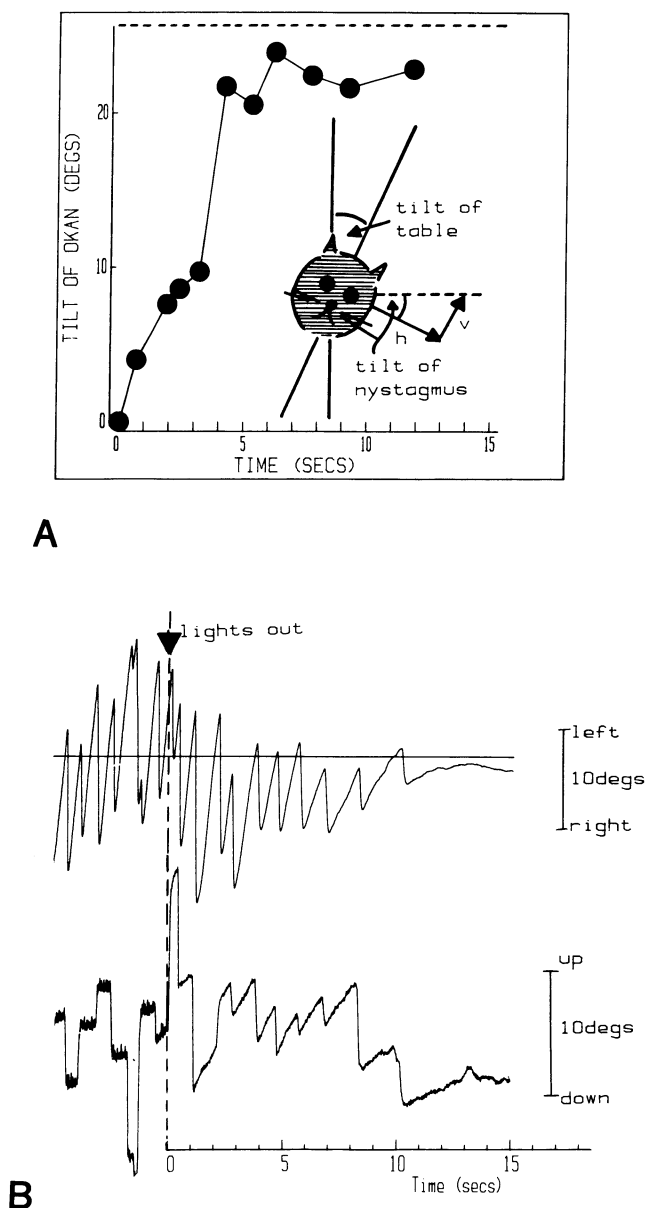
The vertical component, as in the case of post-rotational nystagmus, is a function of the direction and degree of tilt and the amplitude and direction of the on-going horizontal component. As for post-



**Fig. 8.** The tilt of OKAN as a function of head tilt. The format is exactly the same as for Fig. 6

rotatory nystagmus (Fig. 6) the tilt-dependent emergence of a vertical component produces an oblique nystagmus that aligns approximately with the earth-horizontal. This is illustrated in Fig. 8.

Unlike post-rotatory nystagmus there is no reduction in the peak velocity of horizontal OKAN with tilt (cf. Figs. 2, 5). This means that Fig. 8 can be extended beyond the  $\pm 20$  deg of Fig. 6. The solid line shows complete compensation for tilt in which the nystagmus is vectored accurately onto the earth horizontal. For tilts between 15 deg requiring downward slow phases and 25 deg requiring upward slow phases, the nystagmus is indeed, as for post-rotatory nystagmus, vectored onto the earth horizontal. For tilts beyond this, however, the direction of nystagmus is not tilted further but appears to plateau at 10–15 deg for conditions requiring downward slow phases and 15–30 deg for those requiring upwards slow phases. There is an asymmetry here in which vertical OKAN with upward-directed slow phases is evoked by a larger range of tilts than oppositely directed OKAN. Over the range of tilts in which post-rotatory nystagmus is present ( $\pm 20$  deg, see Fig. 5), however, there is adequate vectoring to bring both the post-rotational nystagmus and the oppositely directed OKAN into the same plane, i.e. that of the earth horizontal.



**Fig. 9 A,B.** The time course of the development of tilt in OKAN. Format as for Fig. 7. The cat was tilted 25 deg left ear down

Figure 9 shows the time course of this vectoring effect. As for post-rotational nystagmus, it takes time for the OKAN to be vectored towards the earth horizontal. The time constant is  $4.1 \pm 2$  s. This is not significantly different from the time constant of build up of the vectoring effect for post-rotatory nystagmus (5.4 s cf. Fig. 7). Notice again that occasionally the vertical fast phases are in the same direction as the vertical slow phases (at 2 s after 'lights out': upwards in the example shown).

These data were obtained from OKN induced while the animal was held with a *static* tilt. This is

therefore not directly comparable to the *dynamic* change of the direction of tilt which occurs during OVAR. Such movement would induce a compensatory vestibular response (see Sect. 1) and thus reduce the retinal slip. Clearly open-loop studies are needed to take this point further.

## Discussion

### *Eye movements during off-vertical axis rotation*

These data have shown that when a cat is subjected to off earth-vertical axis rotation (OVAR) there is a continuous nystagmus that does not decline after a tilt-dependent level has been reached. In the cat, as in the monkey (Raphan et al. 1981; Young and Henn 1975), a continuous nystagmus is the dominant feature of the response to OVAR as opposed to the sinusoidal modulation in velocity which dominates the human response (Benson and Bodin 1966a; Correia and Guedry 1966; Harris and Barnes 1985). Since retinal slip is much reduced by this compensatory nystagmus of otolithic origin, optokinetic nystagmus (OKN) can no longer be regarded as the only complement to the vestibular system during prolonged rotation in the cat.

However, Fig. 3 shows that in the light OKN will still account for some 25% of the maintained response to rotation even about an axis tilted by more than 20 deg. And OKN, when looked at on its own, is unaffected by concomitant tilt (results, Sect 3). The independence of horizontal OKN from stimulation of the otoliths is also suggested by the lack of any effect on horizontal OKN of bilateral ablation of the otolithic end organ (Takahashi et al. 1977).

*a) Function.* Clearly extending the duration of a functionally compensatory nystagmus is useful. However, it must be appreciated that the forces applied by OVAR are ambiguous. OVAR cannot be distinguished from counter-rotation at the end of a revolving centrifuge arm by the pattern of forces associated with these procedures in the steady state. The only difference between them is that, for OVAR the only linear acceleration is gravity, whereas during counter rotation an extra linear acceleration is added so that the vector sum exceeds 1 g.

During counter-rotation an ongoing unidirectional horizontal nystagmus, useful only to correct for rotation, would be maladaptive. Instead, the movement required to fixate earth-stationary objects would be sinusoidal corresponding to the linear displacement of the subject and further dependent on



fixation distance. The dominance in man of the sinusoidal component may thus reflect this alternative interpretation of the ambiguous forces produced by OVAR. In fact Darlot et al. (1986) have demonstrated that the feeling of counter-rotation is experienced when a person is actually subjected to OVAR.

The cat appears to interpret the rotating linear acceleration vector as indeed being produced by OVAR: hence the dominance of the compensatory nystagmus and the extreme variability of the small sinusoidal modulation (Fig. 4). Perhaps the differences between the response to OVAR in cat and man reflect adaptation to the expected associations between head movements and changes in orientation with respect to gravity.

*b) Mechanism.* A model of the mechanism for the phenomena reported here has to account for the bias and sinusoidal modulation of both the horizontal and vertical nystagmus seen during OVAR. It also has to be flexible enough to account for the different emphasis between species, particularly between man and cat or monkeys, placed on the modulation and bias components.

There is no signal in the otolithic nerve that could generate the effects of OVAR directly (Goldberg and Fernandez 1982; Raphan et al. 1983). The necessary directional signal must be constructed centrally. The otoliths may generate their effect by a process of mathematical correlation operating through the velocity storage mechanism (Hain 1986). The large bias shown here (Fig. 3) probably requires a greater degree of non-linearity in the interactions between linear accelerations and the velocity storage element in the cat than in man.

#### *Eye movements following off-vertical axis rotation*

Following OVAR, post rotatory nystagmus (PRN) is attenuated (Fig. 5) and accompanied by the gradual emergence of a vertical component which vectors any residual nystagmus onto the earth horizontal (Fig. 7). If the cat is held at a tilt and subjected to an OKN stimulus, the subsequent horizontal OKAN is also accompanied by a vertical component that vectors the response likewise onto the earth horizontal (Fig. 9). The time constants of neither horizontal PRN ( $6.3 \pm 2$  s) nor horizontal OKAN ( $7.43 \pm 2.8$  s) are reduced in the cat by tilt. In the squirrel monkey it has been suggested that the properties of OKAN are not affected by otolith organ ablation either (Takahashi et al. 1977). The time constants of PRN reported here in three cats are not different from each other or from the decline of peri-rotatory

EVA nystagmus. However, they are significantly less than usually reported (cf. for example Robinson 1976; Harris and Cynader 1981b). This may be attributable to repeated exposure to rotation, albeit over an extended period, which is known to reduce the time constant (Jäger and Henn 1981).

The emerging vertical component depends on the amplitude of the horizontal component and on the tilt. There is never a vertical component alone after either OVAR or OKN about a tilted axis, even for very large tilts (60 deg). The amplitude of the vertical component is limited (see Fig. 8) but within the range in which an appreciable post-rotatory effect is seen (16 deg left ear or right ear down), it is adequate to vector either PRN or OKAN onto the earth horizontal. The appearance of a vertical component in PRN with concomitant tilt has been observed in man (Harris and Barnes 1985) and has also been shown to accompany OKAN induced in tilted monkeys (Raphan and Cohen 1983).

*a) Function.* An effect of tilting the axis of rotation is effectively to abolish PRN. The PRN is maladaptive since it is a compensation for an illusion of movement: it is therefore efficient that it is abolished by a system that is able to contribute more information about the true nature of the stimulus. Vision may effectively provide such information and cancel PRN with OKAN. But following OVAR, vision is once again replaced by the otolithic system which cancels PRN.

For tilts less than 16 degs, the otolithic cancelling of PRN is, however, incomplete (as is its peri-rotational contribution). Under these circumstances the remaining retinal slip can, if the lights are on, generate an OKAN which completes the job of cancelling the PRN. This is true despite the vectoring of the PRN described above: the vertical component induced in the PRN by tilt is effectively cancelled by an oppositely-directed vertical component of OKAN which emerges with approximately the same time course.

What could be the ecological validity of the vectoring effects described? PRN following rotation about an EVA represents appropriate compensation for the system's best guess about what might be happening, i.e. that the subject is now rotating in the opposite direction. Sudden tilting during such PRN provides information that the subject is not in fact rotating (since rotation about such a tilted axis would be accompanied by the forces discussed above) and is in fact duly accompanied by a sudden reduction in PRN or OKAN (Benson and Bodin 1966b; Raphan et al. 1981). But when there is no sudden tilt and no rotating gravity vector to suggest a tilted axis of

rotation, the system's best guess has to be that rotation is about an EVA and that the head tilt is with respect to this axis. Such a real stimulus would require a compensatory response with horizontal and vertical components (see Raphan et al. 1981, Fig. 5b). The time constant of vectoring (5.4 s, see Fig. 7) matches very well with the build up of the otolithic system during rotation (5.0 s, see results Sect. 1). So the system is responding as fast as it can in what it must take to be the most adaptive way.

*b) Mechanism.* A model of the mechanism to explain the post-rotatory effects of OVAR has to account for the interactions of otoliths, canals and preferably the OKAN system that produce tilt-dependent changes in the amplitude and direction of the after effects of OVAR. The model introduced by Hain (1986) to explain peri-rotational responses proposing convergence through the velocity storage mechanism can also go some way towards explaining these after-effects.

Hain's model predicts a reduction in the time constant of PRN during tilt. This was not found in these studies but two factors need to be taken into account. The time constant of PRN firstly was already rather short (6.3 s) and secondly, more importantly, was unmeasurable for tilts above 20 deg because of the extreme reduction in the amplitude of PRN (Fig. 5). However, since OKAN is postulated to share the velocity storage elements with the VOR (Raphan et al. 1979) and since the magnitude of OKAN was not found to be reduced here, it is perhaps more puzzling that the dominant time constant of horizontal OKAN was not reduced by tilt either here in the cat or in the monkey (Raphan and Cohen 1983).

The appearance of a vertical component accompanying PRN (Figs. 6, 7) and OKAN (Figs. 8, 9) also follows from coupling linear acceleration detection through the velocity storage elements if there are three: one for each of the canal planes (Cohen et al. 1983; Hain 1986; Raphan and Cohen 1985; Robinson 1982, 1985). However, again there are differences between the prediction (Hain 1986 Fig. 7) and what was found. A vertical component to OKN was not found *during* OKN obtained on a tilt. Instead, the vertical component emerges only slowly and only during OKAN (Fig. 9). Since the cat's pursuit system is functional only at very low velocities (Evinger and Fuchs 1978) it is probably not strong enough to explain this lack of vertical OKN by pursuit correction. Also the vertical component appears to be limited not by velocity but by the size of the tilt, reaching a maximum at around 20 deg, independent of the velocity of the horizontal OKAN that is being

vectored. Thus, following OKN at 60 deg/s around an axis tilted by 20 deg the peak velocity of the emergent vertical component to OKAN is adequate for vectoring. Subsequent to OKN around a greater tilt, even at a much lower velocity, only an inadequate vertical component emerges (Fig. 8).

During OVAR in the dark, the vertical component both for cat (see above) and man (Harris and Barnes 1985) has a bias with upward-directed slow phases independent of the direction of rotation. Yet the accompanying vertical PRN is in the appropriate direction for vectoring and again emerges slowly (Fig. 7 and Harris and Barnes 1985, Figs. 4, 5). Thus for neither OKAN or PRN does the vertical response during the preceding rotation predict the subsequent appearance of the vectoring vertical component.

It seems that the basic principles of mathematical correlation of linear acceleration signals connected to velocity storage mechanisms will qualitatively explain the response of the cat to OVAR. However, the cat seems to show several non-linear effects in the coupling to the velocity storage system. Finally it should be noted that torsional responses are by no means large enough (Andersen, 1981) to contribute significantly to the almost complete vectoring reported here (Figs. 6, 8).

If the otolith system indeed operates through the velocity storage mechanism then other manipulations that affect the store should also affect the OVAR response (cf. Demer 1981). Some preliminary studies involving opposing the canals and otoliths (by sudden deceleration to a slower rotation velocity, Harris 1986a) or modification of the gain of the VOR (Harris 1986b) indicate that the use of the velocity store in the cat may be very non-linear indeed.

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