The effect of gravity on the resting position of the cat's eye

Laurence R. Harris[1], **Herbert C. Goltz**[1], **Martin J. Steinbach**[1,2,3]

[1] Department of Psychology, York University, Toronto, Ontario, Canada M3J 1P3
[2] Department of Ophthalmology, Hospital for Sick Children, Toronto, Ontario, Canada M5G 1X8
[3] The Eye Research Institute of Canada, 399 Bathurst St, Ontario, Canada M5T 2S8

Abstract. We measured rotation (horizontal, vertical and torsional) and translation (horizontal and vertical) of the paralysed cat's eye in response to 45° steps of orientation presented in a pseudorandom order around the roll and pitch axes (with respect to the horizontal canals). During changes of position of the animal in the roll plane, the eyes rotated towards the lowest part of the orbit (left with left ear down; top when the cat was upside down, etc.) by an average of 0.55°. Changing orientation in the pitch plane evoked vertical rotations of $\pm 1.42°$ (upwards eye movement during forwards head pitch) and torsional rotations of $\pm 1.3°$. All these rotations taken together suggest that the centre of mass is in front of, below and temporal to the centre of rotation. The eyes translated temporally (thus separating by 0.72 mm) during forward pitching and there was a small vertical displacement (0.23 mm) when the animal was upside down. These findings are discussed with respect to a possible role of the extraocular proprioception system.

Key words: Gravity – Eye position – Extraocular muscles – Proprioception – Cat

Introduction

Any lack of correspondence between the centre of mass and centre of rotation of the eye presents a continuous threat to gaze stability since the eye would tend to rotate passively towards a mechanically stable position (where the centre of mass is directly below the centre of rotation). The eye would therefore be subject to slight horizontal, vertical and torsional torques (even if the eye itself was not moved by these presumably small forces) that depended on the position of the eye with respect to gravity.

The effective position of the centre of mass of the eye depends not just on intraocular structures but also on the

Correspondence to: L.R. Harris

various extraocular structures (muscles, nerves, blood vessels, etc.) attached to the outside. Indeed, it seems intrinsically unlikely that the functional centre of mass of the eye assembly and the centre of its rotation would correspond. Evidence from studies with paralysed humans has already suggested that indeed the centre of rotation and centre of mass of the human eye do not correspond and that passive drifts towards a mechanically stable position can be observed (Steinbach and Lerman 1990). Unfortunately it is hard to do more extensive studies of the eye position in paralysed humans.

This paper reports that the centre of mass of the cat's eye, like that of humans, does not correspond with its centre of rotation (although the relative positions are different in the two species). This misalignment leads to rotation in all three directions (horizontal, vertical and torsional) of the paralysed cat's eyes. We also noted some translation of the eye within the orbit under the influence of gravity. The location of the centre of mass may explain some curious spontaneous eye movements noticed when awake, unparalysed cats are held in unusual postures (Rude et al. 1991). These data have been briefly reported in abstract form (Harris et al. 1991; Goltz et al. 1992).

Materials and methods

Maintenance and preparation of the cats

Three adult female cats were used in this study. Anaesthesia was induced with a mixture of 25 mg ketamine hydrochloride, 2.5 mg acepromazine maleate and 0.1 mg atropine injected intramuscularly. Anaesthesia was then maintained by an intravenous infusion of sodium thiamylal (5 mg/kg/per hour). Animals were intubated and mounted in a stereotaxic instrument on a vestibular research table. They were held with atraumatic ear bars. The eye bars, after being used to align the head in stereotaxic coordinates initially, were replaced by a padded rod, applied to the top of the head, opposed to the mouth bar. The cats were then paralysed with a non-polarizing paralysing agent (Flaxedil, gallamine triethiodide 20 mg/kg per hour intravenously – this dosage was deliberately higher than that normally used; see Discussion). The expired carbon dioxide level was monitored and kept between 3 and 5%. Temperature was kept

between 38 and 40 °C by a homeothermic blanket. Heart rate was monitored; and anaesthesia was maintained throughout the experiment (sodium thiamylal, 5 mg/kg per hour intravenously). After the experiment, the animals recovered with no ill effects. One animal was measured twice, with experiments separated by several weeks.

The eyes were regularly irrigated with saline. In order to make the photographs of eye position easier to interpret, the pupil was constricted with a topical corneal instillation of 4% pilocarpine hydrochloride.

Orientation of the cats

The cat was held in a stereotaxic frame that was mounted on a table that could be oriented at any position in either the roll or pitch planes (see Harris 1987 for a technical description of the table). The stereotaxic holder was tilted 23° nose down, to position the horizontal canals orthogonal to gravity and coplanar with the roll and pitch axes (Blanks et al. 1972). This approximates the normal resting position of the cat's head (De Beer 1947; Wilson and Jones 1979) and will be referred to as the "zero position". Our convention with respect to this standard position is given in the legend to Fig. 1. Particular orientations of the cat were achieved by positioning the table by hand (using a protractor fixed to the frame; accuracy ±0.5°) and fixing the table at that orientation while the eye position measurements were taken. We normally waited about 30 s before taking a measurement, to allow for any possible dynamic effects. For some test positions, repeated measures were taken from a few seconds after arriving at a particular orientation to up to 5 min after arriving; no change was recorded. Many positions were tested more than once in each animal, but no consistent effect of the previous position (hysteresis) was noticed. Changes in position were performed about only one axis at a time.

Measurement of horizontal and vertical rotation of the eye

For two cats, rotations of the eye were measured by reflecting a table-mounted laser (Metrologic; neon; maximum power 1 mW; wavelength 632.8 nm; exit diameter <1.2 mm; divergence 1 mrad) off a tiny mirror (a back-surfaced cover-slip), mounted on the eye with gum tragacanth (weight of mirror plus gum 16 mg). The position of the reflected laser beam was recorded on a plastic hemisphere, radius 57 cm, centred on the cat's head. This method was not sensitive to torsion or to translation of the eye in the plane of the mirror. Control trials were performed with the mirror mounted on the stereotaxic frame. Unexpectedly, these control trials produced measurable deflections of the beam, presumably because the laser's neon tube was not rigidly mounted in its housing. These were minimized by selecting a laser which introduced a relatively small artefact and compensating for its movements in our measurements (see below).

Rotations of the eye could be easily calculated from the displacement of the laser beam since the sphere has a radius of 57 cm, at which distance 1 cm = 1°. Since the beam was reflected from a mirror, 1 cm of beam displacement corresponded to 0.5° of eye rotation. All measurements were made relative to the position of the beam with the table in the zero position. From these was then subtracted the artefactual movement of the beam that was found to occur when the mirror was rigidly attached to the frame. The accuracy of the laser measurements was ±0.33°, estimated as the mean standard deviation of the horizontal and vertical eye position for each orientation of the cat.

Measurement of translation of the eye

Also rigidly mounted on the table and facing towards the cat was a camera and ring flash. Its field of view included both eyes and a reference cross attached to the stereotaxic equipment. Photographs were prepared in the form of slides that could be projected as huge blow-ups (45:1 enlargement with respect to the actual size of the cat) on the wall of the laboratory. The horizontal and vertical position of the pupil was calculated by estimating the position of its centre from measurements of the position of the top, bottom, left and right edges of the pupil of each eye with respect to the reference mark attached to the stereotaxic frame.

The centre of the pupil could move in these photographs as a result of either rotation or translation of the eyeball in the skull, or both of these. The pupil displacement due to translation was obtained by vector-subtracting the displacement (in millimeters) expected from the rotation recorded with the laser technique, from the curve fitted through the photographed pupil displacement (in millimeters). Examples of these two curves are shown in Fig. 3. The difference between the curves was attributed to translation.

The accuracy of the photographic measures for horizontal and vertical pupil displacement was ±0.21 mm, estimated as the mean standard deviation of the horizontal and vertical eye position for each orientation of the cat. If the displacement was entirely due to rotation, this figure would correspond to ±1.15°.

Measurement of torsion of the eye

Torsion was also measured from the photographs. Taking advantage of the slit pupil of the cat, a line was drawn from the top corner of the pupil to the bottom corner and its angle measured with respect to the reference cross attached to the stereotaxic frame. The accuracy of the photographic measure of torsional pupil displacement was 1.6°, estimated as the mean standard deviation of the torsional eye position for each orientation of the cat.

Analysis of eye movements

Differences between the centres of mass and rotation would form a dipole. The torque exerted around the centre of rotation would be sinusoidally related to the tilt of this dipole. Such a torque would be exerted against the viscoelastic properties of the tissues that hold the eye in place. We would expect any displacement of the paralysed eye to be proportional to the force and thus proportional to the sine of the tilt. The following sine function was therefore fitted (using SigmaPlot; Jandel Scientific; see Figs. 1–4 for examples) to the static eye displacements measured in response to changes in orientation in 45° steps about each axis (roll and pitch). An estimate of the standard deviation of each parameter was provided by the curve-fitting programme. Initially, the data from each cat, and from the two separate experiments on the same cat, were analysed separately. Since there were no significant differences between the curves fitted through each cat's data, the data were subsequently pooled:

$$Eye = amp \times [\sin(\theta + \varphi)] + DC \tag{1}$$

where: Eye is eye displacement (in millimetres or degrees); θ is position of the table (in degrees); φ is phase advance of the response; amp is size of the variation; and DC is displacement of the variation from zero.

To estimate how good a fit this function was to the data, a linear regression ($y = amp \cdot x + DC$) was performed using:

$$x = \sin(\theta + \varphi). \tag{2}$$

The significance of the regression coefficient and hence the sine fit could be obtained by converted it to a Student t-score using:

$$t = \frac{r}{\sqrt{1 - r^2/n - 2}}. \tag{3}$$

Whether two sine fits had significantly different phases (φ_1 and φ_2) was ascertained from the Student t-score:

$$t = \frac{(\overline{\varphi_1} - \overline{\varphi_2})}{S_{\overline{\varphi_1} - \overline{\varphi_2}}}$$ (4)

where S is the pooled estimate of the standard error of the difference.

Results

Eye rotation

Many changes in orientation of the head produced significant angular eye deviations in the horizontal, vertical and torsional directions (although none that we used here produced significant deviations in all three directions at once). Horizontal and vertical deviations were recorded by the laser technique and torsional deviations were recorded photographically (see Materials and methods). The measured angular displacements for all animals are illustrated in Figs. 1 and 2. Table 1 summarizes the sine fits (see Materials and methods and Eq. 1) through these pooled data and also shows which conditions showed significant eye rotation (using Eq. 3).

During roll. As animals were tilted around the roll axis, a significant angular *horizontal* deviation of the eyes was noticed (see Table 1). The change in horizontal eye position with roll angle is shown in the top right panel of Fig. 1. The sine fit through these data shows that the maximum leftward rotation of the eyes ($\pm 0.47°$) oc-
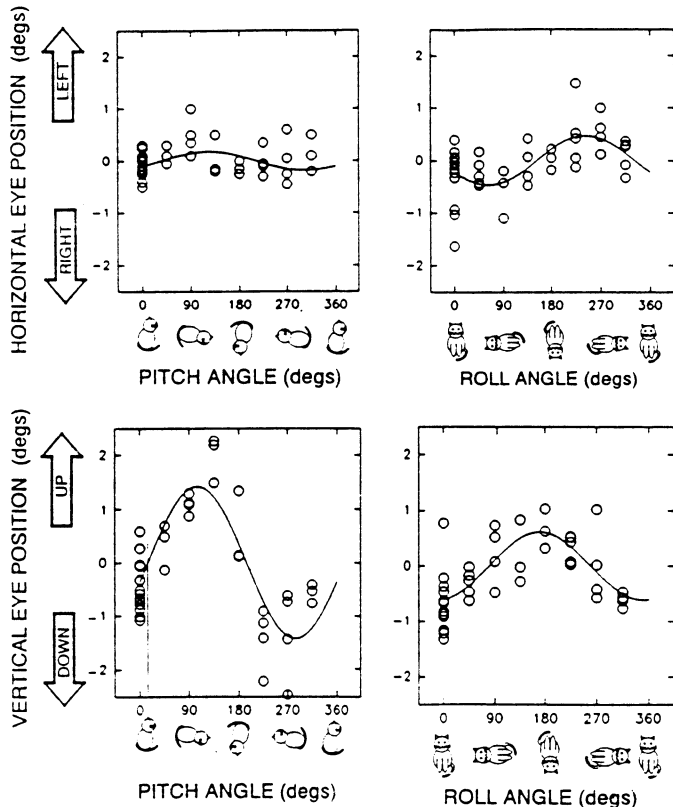

Fig. 1. The effect of pitch and roll on the horizontal and vertical angular position of the paralysed cat's eye measured by a laser technique. The *top two panels* represent the horizontal eye rotation and the *bottom two* represent the vertical eye rotation evoked by changes in orientation of the head about the pitch *(left-hand panels)* and roll *(right-hand panels)* axes. Zero degrees on the *abscissa* of all graphs corresponds to the zero position defined in Materials and methods (horizontal semicircular canals approximately horizontal). A roll of 90° corresponds to right ear down, 180° corresponds to upside down and 270° corresponds to left ear down. A pitch of 90° corresponds to nose down, 180° to upside down and 270° to nose up. The *ordinate* is in degrees of eye rotation (with respect to the head), with each animal's data adjusted to be centred around the mean for that animal. The data from both eyes of two cats are pooled and shown together with the best-fit sine. Details of the sine fits are given in Table 1. During pitch there was no significant horizontal rotation, but the eyes rotated upwards in the orbit when the head was pitched forwards, and downwards when the head was pitched back. During roll, the eyes rotated such that the front of the eye was towards the highest point in the orbit. *Vertical line, bottom left,* centre position of the eyes (see text)
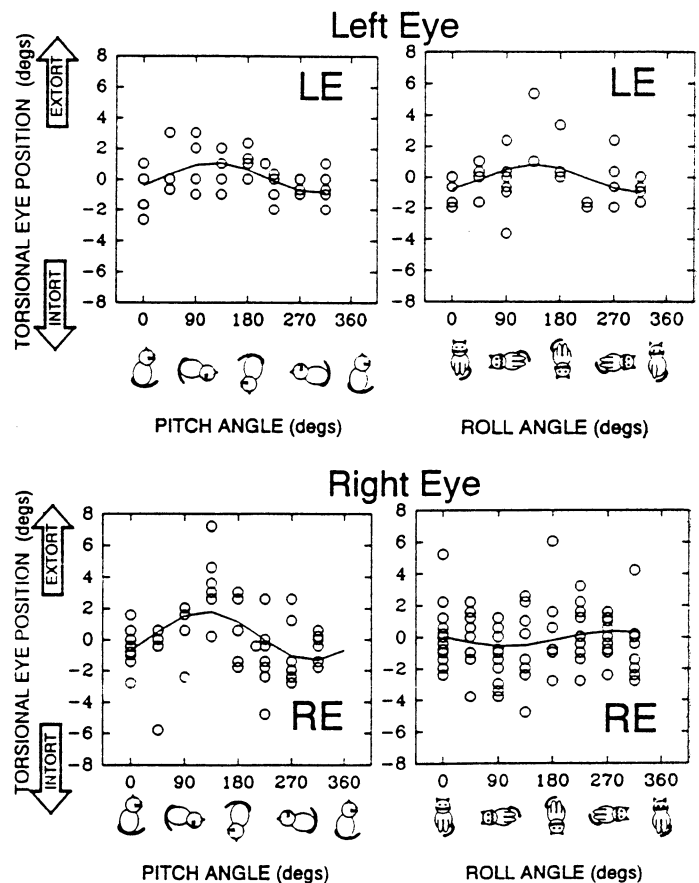

Fig. 2. The effect of pitch and roll on the torsional angular position of the paralysed cat's eye measured from photographs. The *top two panels* represent the torsion of the left eye (*LE*) and the *bottom two* represent the torsion of the right eye (*RE*) evoked by changes in orientation of the head about the pitch *(left-hand panels)* and roll *(right-hand panels)* axes. The *abscissa* is as for Fig. 1. The *ordinate* is degrees of eye torsion (*up, EXTORT,* extorsion: *down, INTORT,* intorsion) with each animal's data adjusted to be centred around the mean for that animal. The data from three animals are shown together with the best-fit sine (details in Table 1). During pitch both eyes underwent extorsion as the head was pitched forwards, reaching a maximum extorsion at approximately the same angle of pitch as the maximum upward eye rotation. There was no significant torsion during roll

Table 1. Rotation of the eye recorded during positioning of the cat about the roll and pitch axes: peak displacement for horizontal, vertical and torsional eye movements

	Eye rotation			
	Horizontal eye displacement	Vertical eye displacement	Torsion	
			Left eye	Right eye
Roll	±0.47° peak left at 242.2° ±11.0° roll	±0.62° peak up at 170.0° ±9.9° roll	No significant shift	No significant shift
r	0.58	0.70	0.3	0.17
t	4.75	7.00	1.86	1.59
n	46	46	36	84
P	<0.001	<0.001	NS	NS
Pitch	No significant shift	±1.42° peak up at 104.5° ±4.3° pitch	±0.97° max. extorsion at 122.3° ±15.5° pitch	±1.57° max. extorsion at 125.3° ±13.0° pitch
r	0.25	0.82	0.51	0.49
t	1.6	9.07	3.57	4.36
n	42	42	39	62
P	NS	<0.001	<0.001	<0.001

See legend to Fig. 1 for an explanation of the position convention. These values are from best-fit sine waves through the data, as illustrated in Figs. 1–4. Also shown are the regression coefficients of the fits and the statistical probability that these differ from straight lines. Data from left and right eyes have been pooled for the horizontal and vertical measurements

curred when the animal was tilted 242.2° (see Fig. 1 legend for our convention). This is close to the left-ear-down position of 270°. Although we only recorded the rotation of the left eye with the laser, the photographs of both eyes (see below, and Fig. 4, upper panel) indicate that both eyes rotated in the same direction (i.e. to the left) during left-ear-down roll.

As the animal was tilted around the roll axis, a significant *vertical* deviation of the eyes was also noticed. The change in position with roll angle is shown in Fig. 1 (lower right panel). The sine fit through the data shows that the maximum upward rotation of both eyes occurs at a tilt of 170°. The standard error of the angle was ±9.9°, so this is not significantly different from the upside-down position of 180° (t = 1.0, P = NS, n = 46).

The *torsional* displacements of the eye during roll are shown in Fig. 2 (right hand panels). Our photographic method of measuring torsion produced a great deal more variability than the laser technique (mean SD ±1.6° in contrast to a mean SD of ±0.33° for the laser: cf. Figs. 1 and 2 and notice the condensed ordinate scale for Fig. 2). No significant variation of torsional eye position with roll angle was found (see Table 1).

This is a significant finding because it helps to confirm paralysis in the animals. There is a large static torsional eye deviation induced in the unparalysed cat by reorientation about the roll axis (Anderson 1981; see below and Fig. 5).

During pitch. Table 1 and the upper left panel of Fig. 1 show that there was no significant variation in *horizontal* eye rotation during changes in position of the cats around the pitch axis.

A very significant *vertical* eye rotation was recorded in response to changes in orientation of the cat's head around the pitch axis. The eyes were displaced by up to 1.42° in either direction (see Table 1). The peak upward movement was found at 104.5° ±4.3° nose down. Since the variation is small, this is significantly different from 90° (t = 3.37 P < 0.01, n = 42), the position corresponding to the horizontal canals being vertical. This also implies that the centre position of the eyes (halfway between their maximum upward and downward excursion under the influence of gravity) is not at zero position, but instead at 14.5° nose tilted down from this position. This is indicated by a vertical line in Fig. 1 (lower left hand panel).

Significant *torsional* movements were found during pitch movements of the head. The peak extorsion was found at 123.2° ±15.5° and 125.3° ±13.0° for the left and right eyes, respectively (Fig. 2, left-hand panels; Table 1). As for all our torsional measures, the variation is relatively large and these points are not significantly different either from each other or from the point of maximal upwards eye rotation (104.5°; left eye: t = 1.12, n = 39, P = NS; right eye: t = 1.56, n = 62, P = NS).

Translation

Both eyes were photographed during the pitch and roll movements and the position of the pupil measured. The centre of the pupil could move in these photographs as a result of either rotation or translation of the eyeball or both. When the laser data (see above) indicated that there was no significant rotation, any variation could be safely attributed to translation. When the laser data adequately predicted the photographed movement, then there was no measurable translation of the eyeball. Only when the laser and photographed eye movements were each significant and significantly different from each other (which only happened for vertical movements recorded during

Table 2. Translations of the eye recorded during positioning of the cat about the roll and pitch axes: peak displacement for horizontal movements of the left eye and right eye and for vertical eye movements

	Eye translation		
	Horizontal eye displacement		Vertical eye displacement
	Left eye	Right eye	
Roll	NS laser – photo. amp 0.08 mm	NS	NS laser – photo. amp 0.07 mm
Pitch	± 0.37 mm peak left at 114.5° ± 4.5° pitch	± 0.35 mm peak left at 277.8° ± 9.4° pitch	peak up at 174.8° pitch laser – photo. amp 0.23 mm.
n	53	90	
r	0.86	0.71	
t	11.8	9.44	
P	<0.001	<0.001	

See legend to Fig. 1 for an explanation of the position convention. These values are from best-fit sine waves through the data in Figs. 1–4. Also shown are the regression coefficients of the fits and the statistical probability that these differ from straight lines. NS. all the displacements of the pupil noted in the photographs are accounted for by the rotation measured by the laser technique

pitch. see lower panel of Fig. 3) did the translation component need to be extracted from the ambiguous measure that the photographs provided. Under this circumstance the pupil displacement due to translation was obtained by vector-subtracting the displacement (in millimetres) expected from the rotation recorded with the laser technique from the curve fitted through the photographed pupil displacement (in millimetres). Examples of these two curves are shown in Fig. 3. The difference between the curves was attributed to translation. The eye translation data are summarized in Table 2. and the displacements measured are illustrated in Figs. 3 and 4.

During roll. There was no significant translation found in response to changes in orientation of the cat around the roll axis. Figure 3 shows the measured pupil displacements during roll rotation and the best sine fit (solid lines). The measured pupil displacements can be adequately accounted for by the eye rotation measured by the laser technique (dashed lines. taken from Fig. 1). The vectorial difference between the movement of the pupil due to rotation (dashed lines) and the actual movement of the pupil in the photographs (solid lines in Fig. 3) are sines of ± 0.08 mm (peak left at 335°) for the horizontal and ± 0.06 mm (peak up at 207.3°) for the vertical. These are well below the noise level of 0.21 mm.

During pitch. Since there was no significant *horizontal* rotation during changes in orientation around the pitch axis as measured by the laser (see Table 1). then any displacement of the pupils seen in the photographs must have been due to translation alone. The measured pupil displacements are shown in Fig. 4. Data from the two
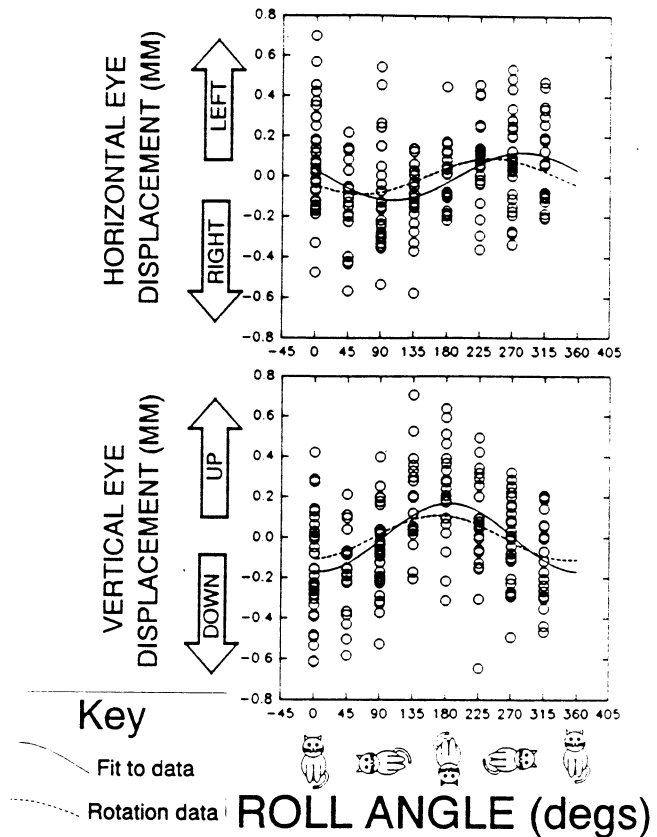

Key

Fit to data

Rotation data

ROLL ANGLE (degs)

Fig. 3. The effect of roll on the translation of the paralysed cat's eye. *Top panel*. horizontal positions, and *bottom panel*. vertical positions of the pupil measured from photographs. The measurements are from both eyes of three cats and each eye's data has been adjusted to be centred around the mean for that eye. The *abscissa* is as for Fig. 1. the *ordinate* is the displacement in millimetres. Also plotted is the best-fit sine through these data (*solid line*) and the displacement that would be expected owing to rotation (*dashed line*). For both horizontal and vertical measurements. there were no significant differences between the fit to these data (*solid line*) and the displacements expected owing to rotation (*dashed lines*)

eyes are plotted separately (top and middle panels). Also shown are the best sine fits (solid lines) and the insignificant variation due to rotation (dashed lines. taken from Fig. 1). There was a significant amount of lateral translation (see Table 1). and this translation was in the opposite direction in the two eyes. (The possibility that this observation might have indicated unintended movement of the entire animal towards or away from the camera. creating a looming effect. is considered in the Appendix.) That is. as the animal was moved towards nose down. the eyes moved apart (left eye moved left and the right eye moved right), reaching a maximum displacement of 0.37 mm at 114.5° for the left eye and 0.35 mm at 97.8° for the right eye (mean 106.5°). When the animal was oriented towards nose up. the eyes came together. reaching a minimum separation at a mean of 286.5°.

In response to pitch. the eye both translates and rotates in the *vertical* direction (bottom panel of Fig. 4). The rotation was ± 1.42° (peak upwards displacement at 104.5°: see Table 1. Fig. 1). which accounts for

Key

⎯⎯⎯⎯⎯ Fit to data
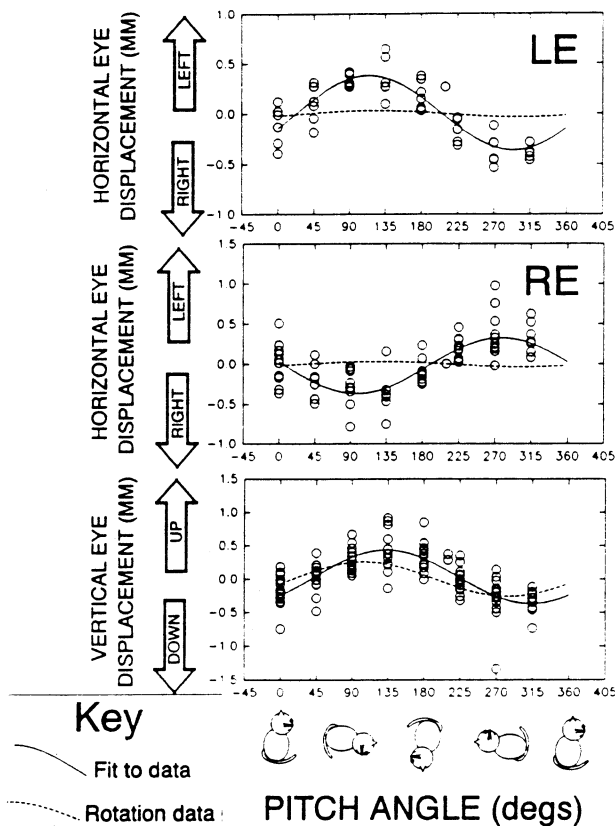
⎯⎯⎯⎯⎯ Rotation data

PITCH ANGLE (degs)

Fig. 4. The effect of pitch on the translation of the paralysed cat's eye. *Top panel,* horizontal position for left eye; *middle panel,* horizontal position for right eye; *bottom panel* vertical position of the pupils measured from photographs. The measurements are from three cats and each cat's data has been adjusted to be centred around the mean for that animal. The *abscissa* is as for Fig. 1, the *ordinate* is the displacement in millimetres. Notice that the ordinate is condensed compared with Fig. 3. *Solid line,* the best-fit sine through these data; *dashed line,* the displacement in the photographs that would be expected owing to rotation. Rotation was only measured for the left eye, so this curve has been used also on the right eye plot. The horizontal displacement seen in the photographs was due to translation, as there was no significant rotation in the horizontal direction (Fig. 1, top left panel). The left eye translated leftward and the right eye translated rightward during forward pitch as both eyes rotated upwards and outwards. Disentangling translation from the significant contribution of rotation in the vertical pupil displacement data of the *lower panel* (see text) revealed a significant upwards translation (difference between the two curves) when the head was close to being upside down

± 0.26 mm of pupil displacement (dashed line). The vectorial difference between the movement of the pupil due to rotation (dashed lines) and the measured movement of the pupil in the photographs (solid lines in Fig. 4, lower panel) is a sine describing ±0.23 mm of vertical translation of the eye with the peak upward translation at 174.8°, very close to the upside-down position.

Discussion

Our data have shown that there are significant passive movements of the paralysed cat's eye as the animal is

reoriented about the pitch or roll axes. As the animal is rolled, the eyes rotate towards the lowest part of the orbit (Fig. 1) with no measurable accompanying torsional (Fig. 2) or translational (Fig. 3) movement. As the animal is pitched nose down, the eyes rotate upwards in the orbit (Fig. 1), show extorsion (both left and right eyes, Fig. 2) and translate temporally (Fig. 4). As the animal is pitched nose up, the eyes rotate down (Fig. 1), show intorsion (Fig. 2) and translate nasally (Fig. 4). We interpret these passive, gravity-induced movements to be due to differences in the relative locations of the centres of mass and rotation of the cat's eye.

Confirmation of paralysis

The interpretation of our data as indicating passive movements requires that our animals were fully paralysed, so that we can be sure that all the movements we observed were indeed due to gravity and not muscle activity. Rodieck et al. (1967) have shown that small eye movements can still be found during systemic paralysis with gallamine triethiodide. These residual drift movements are probably due to sympathetic innervation of the eye but do not seem to be related to any sensory input. They could not therefore represent vestibular or visual responses to reorientation although they would contribute to the noise of our measurements.

To be sure that animals were completely paralysed we took the following measures:
1. We used a high dosage of the paralysing agent: twice the dose of Flaxedil routinely used to achieve paralysis [20 mg/kg per hour, compared with, for example, Barlow et al. (1977) who used 10 mg/kg per hour].
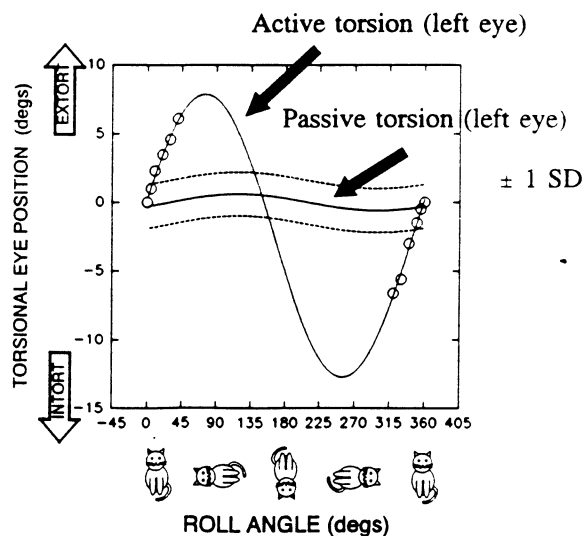

ROLL ANGLE (degs)

Fig. 5. A comparison between active torsional movements of the awake cat and insignificant passive torsional movements found in the paralysed cat in response to roll. The passive data curve is from the upper right panel of Fig. 2, with additional curves *(dashed lines)* to illustrate ± 1 SD. The active torsion data points are from Anderson 1981, with a sine fit superimposed. Anderson only measured the response over the range ±40°. Both sets of data are from the left eye *EXTORT,* extorsion; *INTORT,* intorsion

2. Reflex muscle activity was regularly looked for closely by regularly brushing the ears, or looking at the withdrawal reflex, etc.

3. Spontaneous eye movements were looked for by watching the laser beam reflected from the mirror on the eye.

4. Vestibular and optokinetic eye movements were looked for, using the reflected laser beam, and not observed.

Strong additional support for the paralysed condition of our animals comes from the lack of significant torsional movement we observed during roll. However, such movements might have been masked by the rather high noise level of our torsional measurements. Figure 5 compares the size of active torsional eye movements recorded during roll of alert cats by Anderson (1981) with our (insignificant) data from Fig. 2. Also shown is ± 1 SD of the passive data.

The meaning of eye rotations due to gravity

The eyes rotate towards the lowest point of the orbit during reorientations of the paralysed cat about the roll axis (left when the head is tilted left-ear down, up-when upside down and right when the head is tilted right-ear down; Fig. 1), which indicates that the centre of mass of the cat's eye is in front of the centre of rotation. The eyes rotate up when the head is pitched forwards and down when the head is pitched back (Fig. 1), indicating that the centre of mass is below the centre of rotation. The fact that the eyes rotate extorsionally when the head is nose down and intorsionally when the head is nose up (Fig. 2) indicates that the centre of mass is on the temporal and lower side of each eye.

Thus we can conclude that the centre of mass of the cat's eye is in front of, temporal to and below its centre of rotation (shown in cartoon form in Fig. 6.) The amplitudes of the various eye rotations we have recorded do not directly indicate where the centre of mass lies. They indicate the effect of the torque that the dipole, formed by the centres of mass and rotation, has when opposed to the viscoelastic forces of the tissues holding the eye in the orbit. Collins (1971) showed that the force required to move the cat's eye was 1.3 g/deg at the insertions of the muscles. Since the radius of the cat's eye is 1.05 cm (Tripathi 1974), this suggests that a torque of $1.3 \times 1.05 = 1.37$ g·cm is required to move the eye 1°. The average rotation of the eye during roll towards the lowest part of the orbit was 0.55°, suggesting an effective torque of $0.55 \times 1.37 = 0.75$ g·cm. Of course we do not know the mass of the eye assembly that is producing this torque, but if we take the mass of the eye (an approximate sphere of 1.05 cm radius and density close to 1 g/cm³, therefore a mass of approximately 4.85 g) as a minimum, then the centre of mass is a maximum of $0.75/4.85 = 0.15$ cm in front of the centre of rotation. The vertical rotation of 1.42° at a forwards pitch of 104.5° (see Fig. 1, Table 1) suggests a moment arm of length $1.42 \times 1.37 / 4.85 = 0.4$ cm (projecting down and 14.5° forwards when the cat is in the zero position): that is a centre of mass
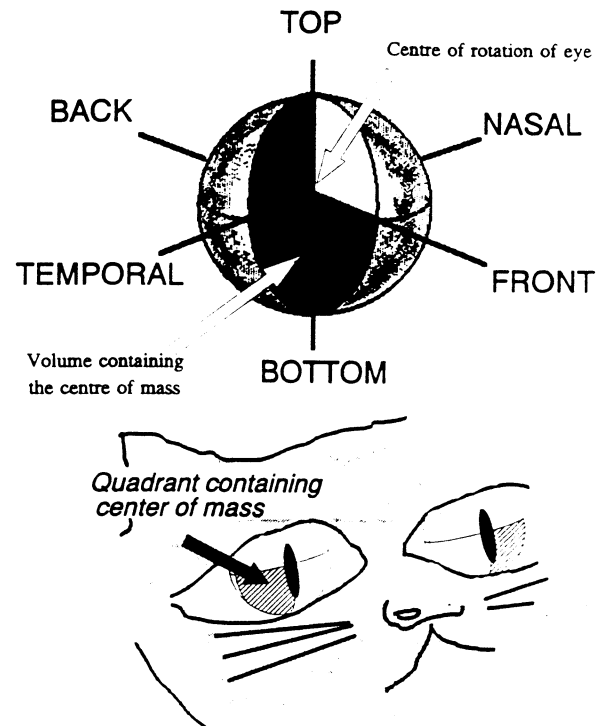

Fig. 6. The passive rotations of the paralysed cat's eye (right eye) are compatible with the centre of mass of the cat's eye being in the lower front temporal sector of the eye

0.1 cm in front and 0.39 cm below the centre of rotation. The forward displacement is in reasonable agreement with the estimate from the roll data, but the fact that the mass is *below* the centre of rotation leads us to expect torsional movements of about 1.4° during roll, whereas no significant torsion was found. The above calculations have been based on the measurements by Collins (1971) which were made on the lateral rectus muscle and refer to horizontal rotations of the eye. The lack of torsion in response to roll, despite vertical rotation in response to pitch, indicates that it takes more force to torsionally rotate the eye than it does to rotate it in the horizontal direction. The significant torsion recorded during pitch had an average of 1.3° (see Table 1), implying a torsional moment arm of at least length $1.3 \times 1.37/4.85 = 0.37$ cm in the temporal direction, but probably longer if the 1.3 g/cm is an underestimate for the force required to torsionally rotate the eye.

The position of the centre of mass was unexpected, since the optic nerve, which would seem to be the major mass attached to the eye, leaves from the *nasal* side of the *back* of the eye; and yet the movements we have seen indicate that the centre of mass is forward of and temporal to the centre of rotation. This suggests a significant role of the weight of the eye muscles and other anatomical features.

The meaning of eye translation due to gravity

The eyes move sideways in a separating motion when the head is tilted forwards and move together when the head

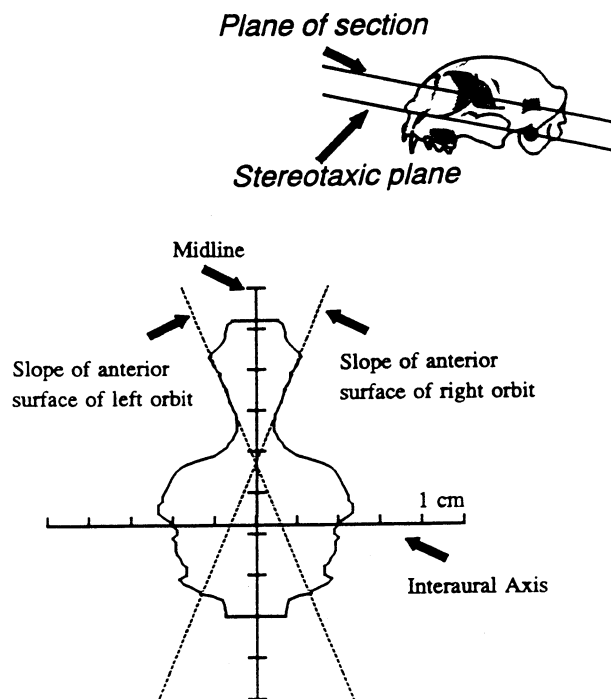**Plane of section**

Stereotaxic plane

Fig. 7. A cross section of a cat's skull parallel to and 6 mm above the stereotaxic plane corresponding to a section through the centre of the orbit (see *insert*). The diagram was obtained using measurements at 1-mm steps. Regression lines were fitted through the points describing the anterior walls of the orbits, showing that these walls diverge at the front with an angle of 45°. Both axes are marked in centimetres. The *horizontal axis* is positioned at the level of the ear bars and the *vertical axis* is in the midline

is tilted back (Fig. 4; Table 2). This seems puzzling, since there can be no direct sideways influence of gravity on the eyes when the animal is tilted around the pitch axis. However, careful measurements of a cross section through a cat's skull showed that nasal walls of the orbit tilt outwards towards the front with an angle of almost exactly 45°. This is shown in Fig. 7. Therefore, if the eyes moved forwards in the head as the animal was pitched nose down (i.e. towards the earth), they would also be forced to separate. They would have to move forwards 0.87 mm to be forced apart by the amount shown in Fig. 4 (0.72 mm).

During pitch, there was a small vertical displacement of the eyes towards the lower part of the orbit when the animal was upside down (Fig. 4). A similar effect could also be seen during roll to the upside-down position (Fig. 3) but was not significant there, owing to the noise inherent in our photographic method.

The significance of non-coincidence of the centres of mass and rotation

A central question is whether the force that the extraocular muscles need to exert to overcome the torque of the moment arm formed by the non-coincidence of the centres of mass and rotation is significant in the awake animal with a full complement of extraocular muscles. The above calculations suggest an effective moment arm

of around 0.4 cm (0.37 cm in the temporal direction and 0.1–0.15 cm forwards when the head is upright) with a torque of $4.85 \times 0.4 = 1.94$ g · cm. This would require a muscle tension (at a radius of 1.05 cm) of only $1.94/1.05 = 1.85$ g. This is less than the resting force of the unparalysed extraocular muscles (around 3 g; Collins 1971), but it still represents some 5% of the maximum tension that an extraocular muscle is capable of generating (about 35 g; Collins 1971). And it is a continuous influence – the muscles pulling against gravity have to add this percentage to their pull, whereas those pulling in the direction of gravity are assisted. When the animal's head is in an unusual posture (e.g. upside down), this relationship is altered.

Interestingly, the cat shows a spontaneous nystagmus in response just to being held at different orientations in the dark (Rude et al. 1991 and unpublished observations). When the animal is held upside down, spontaneous nystagmus is seen with slow phases up (in the orbit). That is just the direction expected if the elevators are chronically more active than the depressors in order to balance not only the antagonistic pull of the depressors but also the tendency of the eye to rotate downwards under the force of gravity. When this relationship with gravity is reversed, the elevators are suddenly not pulling against gravity, but are being aided by gravity and pull too hard. This is true for any orientation other than vertical. The quantitative characteristics of nystagmus (other than its direction) that this might result in are difficult to predict, owing to the nonlinear variation of the coefficients of viscosity and elasticity of the globe tissues and the unknown value of the force that the muscles actually generate under these conditions. Clearly more work is required to quantify the spontaneous eye movements and the torque generated by the eye muscles of cats held in various orientations with respect to gravity.

Non-coincidence as a challenge for proprioceptors

The extraocular muscles are unusual amongst voluntary, skeletal muscles in that proprioceptors, which play such a crucial role in the control of most of the voluntary musculature, are not involved in any simple way in the control of eye movements or in the maintenance of eye position (see Steinbach 1987 for a review). This might be because the eye musculature normally works with a constant load, unlike most other skeletal muscles (see Matthews 1972, 1982, 1988 for reviews of the role of muscle spindles).

The non-coincidence of the centres of rotation and mass described here represent a force on the eye that is difficult to predict. For different positions of the eye, a different amount of compensation is needed as the dipole connecting the centres is altered in orientation with respect to gravity. As the orientation of the head changes, then even for a given eye-in-orbit position, the effect of the dipole changes.

Steinbach (1992) suggested that one role of the extraocular proprioceptor system might be to detect the

effect of gravity on the eye, by reporting chronic, uncompensated pulls on some muscles exerted by gravity-induced torques such as we have described. This might then eventually result in a long-term compensation.

Comparison of cats and humans

Steinbach and Lerman (1990) showed, by photographing people who were anaesthetized and paralysed prior to having eye muscle surgery, that the eyes of paralysed humans rotated towards the highest side of the orbit when they were held on their sides. Steinbach and Lerman were able only to use roll stimuli and were unable to look at torsion. They concluded that the centre of mass is *behind* the centre of rotation in the human eye. If the centre of mass is behind, rather than in front as we have shown for cats, then, like cats, humans should show a spontaneous nystagmus when inverted in the dark. But this should be in the opposite direction to that predicted and found (Rude et al. 1991) in cats; that is humans should show a nystagmus with slow phases towards the inferior ridge of the orbit when inverted. Although we have been unable to locate reports of such eye movements in humans. Clement et al. (1989) have quantified a "general downward drive of the eyes" during exposure to micro-gravity. This would be expected if the eye muscles that pull the eyes downwards normally oppose a tendency of the eyes to drift upwards under gravity and are therefore unopposed under micro-gravity. Gnadt et al. (1991) demonstrated in humans that upward saccades made in the dark towards remembered target locations were hypermetropic, while downwards saccades made under the same conditions were hypometric. This finding suggests that a tendency of the eye to drift upwards is not correctly compensated for during saccadic movements. As well as being in the opposite direction, the effect of gravity on resting eye position in the cat is also rather smaller (less than 1.6°; see Table 1) than that found in most of the humans that Steinbach and Lerman (1990) reported (51% of whom showed movements of greater than 5° with a maximum of 15°). This suggests that the cat's eye is rather better balanced, and thus less vulnerable to changes with gravity, than that of humans.

If proprioception is involved, it is tempting to speculate that this inter-species difference may be connected to the differential occurrence of muscle spindles in the two species. There is enormous variation in the density and even the type of proprioceptors in the extraocular muscles of different species. Human eye muscles have an intermediate density of proprioceptors (Cooper et al. 1955; Spencer and Porter 1988). The greatest density is found in goat and sheep extraocular muscles (Harker 1972), whereas the smallest reported is from the cat (Cilimbaris 1910; Matthews 1972; Bach-y-Rita and Ito 1966; Alvarado-Mallart and Pinçon-Raymond 1976). However, palisade endings, which may represent a specialized type of extraocular proprioceptors are present in the cat extraocular muscles in abundance (Alvarado-Mallart and Pinçon-Raymond 1979; Porter and Spencer 1982). This variation suggests that whatever function these sensors are involved in is different in different species. Since goats and sheep have the largest number of spindles of any species so far examined (Harker 1972), then, if our speculation is founded, this might correspond to a relatively large dipole between their centres of mass and rotation, requiring extensive monitoring by the proprioceptive system. We therefore expect larger eye movements than seen in either the cat or human when goats are paralysed and rotated with respect to gravity. We are currently examining this possibility.

Appendix

The possible artefact of looming. Relative movement between the cat and the camera would have resulted in movement of the pupil in the photographs that might have been incorrectly attributed to rotation or sideways translation of the eyes. Care was taken to make the connection between the camera and the cat rigid, but small movements (< 1 mm) might have gone undetected. Therefore we calculated how much relative movement would be needed to account for the measurements we obtained:

$$\text{Disp} = \frac{(\text{IOD}/2) \times \text{Loom}}{\text{Cam} - \text{Loom}} \qquad (A1)$$

where Cam is the distance of the camera from the cat (25 cm), Loom is forward translation, IOD is the interocular distance (4 cm) and Disp is the measured sideways displacement of the pupil. Thus a loom of 4.9 mm is required to produce the measured displacement of 0.4 mm. It is not possible that the animal could have shifted by 0.5 cm in the apparatus unnoticed.

References

Alvarado-Mallart RM, Pinçon-Raymond M (1976) Nerve endings on the intramuscular tendons of cat extraocular muscles. Neurosci Lett 2:121–125

Alvarado-Mallart RM, Pinçon-Raymond M (1979) The palisade endings of cat extraocular muscles: a light and electron microscope study. Tissue Cell 11:567–584

Anderson JH (1981) Ocular torsion in the cat after lesions of the interstitial nucleus of Cajal. Ann NY Acad Sci 374:865–871

Bach-y-Rita P, Ito F (1966) Properties of stretch receptors in cat extraocular muscles. J Physiol (Lond) 186:663–688

Barlow HB, Derrington AM, Harris LR, Lennie P (1977) The effects of remote visual stimulation on the responses of cat retinal ganglion cells. J Physiol (Lond) 269:177–194

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

Cilimbaris PA (1910) Histologische Untersuchungen über die Muskelspindeln der Augenmuskeln. Arch Mikrosk Anat 75:692–747

Clément G, Andre-Deshays C, Lathan CE (1989) Effects of gravitoinertial force variations on vertical gaze direction during oculomotor reflexes and visual fixation. Aviat Space Environ Med 60: 1194–1198

Collins CC (1971) Orbital mechanics. In: Beach-y-Rita P, Collins CC, Hyde JE (eds) The control of eye movements. Academic, New York pp 285–325

Cooper S, Daniel PM, Whitteridge D (1955) Muscle spindles and other sensory endings in the extrinsic eye muscles: the physiology and anatomy of the receptors and of their connections with the brain stem. Brain 78: 564–583

De Beer GR (1947) How animals hold their heads. Proc Linnean Soc (London) 159: 125–139

Goltz HC, Harris LR, Steinbach MJ (1992) Gravity as a passive force on the cat's eye: implications for oculomotor control. Invest Ophthalmol Vis Sci [Suppl] 33: 1150

Gnadt JW, Bracewell RM, Andersen RA (1991) Sensorimotor transformation during eye movements to remembered visual targets. Vision Res 31: 693–715

Harker DW (1972) The structure and innervation of sheep superior rectus and levator palpebrae muscles. II. Muscle spindles. Invest Ophthalmol 11: 970–979

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

Harris LR, Steinbach MJ, Goltz HC (1991) Gravity affects the position of the paralysed cat's eye. Soc Neurosci Abstr 17: 337.4

Matthews PBC (1972) Mammalian muscle receptors and their central actions. Arnold, London

Matthews PBC (1982) Where does Sherrington's muscular sense originate? Muscles, joints, corollary discharges? Annu Rev Neurosci 5: 189–218

Matthews PBC (1988) Proprioceptors and their contribution to somatosensory mapping – complex messages require complex processing. C J Physiol Pharmacol 66: 430–438

Porter JD, Spencer RF (1982) Localization and morphology of cat extraocular muscle afferent neurones identified by retrograde transport of horseradish peroxidase. J Comp Neurol 204: 56–64

Rodieck RW, Pettigrew JD, Bishop PO, Nikara T (1967) Residual eye movements in receptive-field studies of paralyzed cats. Vision Res 7: 107–110

Rude SW, Powell KD, Baker JF (1991) Effects of roll tilt on pitch vertical vestibuloocular reflex. Soc Neurosci Abstr 17: 127.14

Spencer RF, Porter JD (1988) Structural organization of the extraocular muscles. In: Büttner-Ennever JA (ed), Neuroanatomy of the oculomotor system. Elsevier, Amsterdam, pp 33–79

Steinbach MJ (1987) Proprioceptive knowledge of eye position. Vision Res 27: 1737–1744

Steinbach MJ (1992) The need for eye muscle proprioception. In: Jami L, Pierrot-Deseilligny E, Zytnicki D (eds) Muscle afferents and spinal control of movement. Pergamon, London, pp 239–244

Steinbach MJ, Lerman J (1990) Gravity affects resting eye position in humans. Invest Ophthalmol Vis Sci [Suppl] 31: 533

Tripathi RC (1974) Comparative physiology and anatomy of the outflow pathway. In: Davson H, Graham LT (eds) The eye, vol 5. Academic, New York, pp 163–335

Wilson VJ, Jones GM (1979) Mammalian vestibular physiology. Plenum, New York