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Spatial arrangement of the vestibular and the oculomotor system in the rat

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The treatment of the spatial aspects of vestibular sensation, ocular movement near primary position, and their neural processing requires numerical information about the directions of maximal sensitivity of the semicircular canals (SCC), the direction of gaze at primary position, and the directions of eye rotation generated by each individual extraocular muscle (EOM). A good approximation of this information can be gained from stereotaxic measurements of the geometrical arrangement of the canals' bony structure, from measurements of the pupil's orientation, and from measurements of the directions of muscle pull as well as of the center of eye rotation. The results of measurements in pigmented rats are given as unit sensitivity vectors and unit action vectors in head-fixed coordinate systems and compared with data from rabbit, cat, monkey, and human. The misalignment of 'coplanar' SCC with 2.5–15.6° is second only to humans, while the misalignment of the vectors of 'antagonistic' EOM with 27.2–39° is even more oblique than in humans and thereby even more so than in the other mammals. Misalignment of SCC and 'corresponding' EOM with 15.5–34.2° again is largest, followed by that in humans and then the other mammals. The rat may therefore be useful in studying those mechanisms by which the central nervous system deals with the obliqueness of systems that play such an important role in humans, too.

INTRODUCTION

When the head of an alert animal is rotated, the vestibulo-ocular reflex, mediated by a neural network, stabilizes the eyes to minimize slip velocity of retinal images. The reflexive eye movements compensate head movements in time as well as in space. In a similar manner as the transfer functions of the peripheral organs determine the transfer of a neural network in the frequency domain and hence the behavior in the time domain, the geometry of peripheral organs determines the geometrical function of the network in the space domain.

To treat the spatial properties of the systems involved, we chose a vectorial description for head and eye rotation, an approach also adopted in previous studies^{7,10,11,13}. The vectorial description allows to discuss directions of rotations separately, and the

magnitude of rotation may be introduced when needed simply by scalar multiplication. Also, with a vectorial description the components of the head rotation effective at each of the semicircular canals (SCC) can easily be obtained. It is only required to calculate the projection of the rotational vector onto the vector of maximal sensitivity of the particular canal. The effective component of rotation is related to the neural activity change elicited in the pertinent branch of the vestibular nerve. The problem of characterizing quantitatively the geometrical properties of the vestibular apparatus is thus reduced to the problem of describing numerically the unit directions of the vectors of maximal sensitivity.

Somewhat similar conditions hold for the extraocular muscle (EOM). Again, it seems appropriate to choose a vectorial representation of eye rotation and to reduce the problem of characterizing the geomet-

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rical properties of the EOM to the description of the unit directions of the action of the individual muscles. However, in contrast to the vestibular system the geometry is not constant, it rather changes, as the muscle insertion sites move, when the bulbus is rotated. As the measurements are usually confined to the primary position, the assumption of constant eye muscle geometry implies the restriction to (infinitesimal) small movements or to (instantaneous) differential quotients. In any case, the measurement of the geometry of the eye muscles in a single position should be complemented by a measurement of the gaze direction at primary position to indicate for which condition the measurements of eye muscle geometry is valid.

The geometrical arrangements of SCC and EOM at primary position have been determined quantitatively in a number of species, e.g. in humans^{2,17}, monkey^{3,15,16}, cat^{1,6}, and rabbit^{6,14}. In all these species, the unit vectors show a variable degree of obliqueness, and those vectors characterizing pairs of so-called 'antagonistic muscles' or 'coplanar canals' were found to deviate — in some instances considerably — from alignment.

Nevertheless, the relative alignment of these pairs encouraged some authors to contract a pair into one imaginary organ and to describe their push-pull action by a combination of the two^{6,7,13} in order to avoid the treatment of the overcompleteness of the systems by neglecting part of the obliqueness. However, a numerical evaluation of the unit vectors of EOM and SCC results in relative alignment and orthogonality only in rabbit, cat, and monkey, but it yields the largest obliqueness in humans: 35.7° on the average for the EOM 'pair' superior rectus-inferior rectus (SR-IR), and 23.3° for the SCC 'pair' ipsilateral anterior-contralateral posterior (iA-cP). It is obvious that it is the neural network which compensates for these non-negligible geometrical facts. In order to study the strategies and mechanisms by which the central nervous system (CNS) deals with obliqueness and overcompleteness of peripheral systems it seems appropriate to use an animal with particular oblique — and of course overcomplete — peripheral systems, as in such an animal the impact of obliqueness onto neural network functions can be expected to be more conspicuous. Therefore we chose to measure the spatial arrangement of the vestibular and of the oculo-

motor system of the rat, as this important laboratory animal is among those the neural gaze control of which is extensively studied¹², and to which a precise method of magnetic eye movement recording has been adapted⁹. The obliqueness of the geometrical arrangements of SCC and EOM and of their mutual relation will be compared to that of rabbit, cat, monkey and human, as in these mammals both SCC and EOM data are presently available.

In addition, the measurements presented here allow to specify quantitatively the geometrical task, that has to be carried out by the CNS to arrive at eye movements compensating spatially for head movements. In a forthcoming publication⁵ these data will serve as a basis for a quantitative analysis of the geometrical functions of the vestibular and oculomotor system as well as of the neural network mediating the vestibulo-ocular reflex in the rat.

Part of this work was presented in a preliminary form⁴.

MATERIALS AND METHODS

Anatomics

Semicircular canals. Pigmented rats (170–240 g) ($n = 3$) were anesthetized with Nembutal and perfused with 10% formalin. Before placing the head of the animal in a stereotaxic frame the tips of the ear bars and the contact point between incisor bar and mandibula were taken as points of reference to establish a fixed relation between measurements and the geometry of the head. Then the parietal, interparietal and occipital bone as well as the brain were removed to allow access to the right vestibular apparatus. The semicircular canals were dissected free using a fine drill and a dissecting microscope (10×). To determine the spatial position of the canals we used a mechanical probe out of a set; the cannula was fixed to an electrode manipulator with 3 orthogonal translatory degrees of freedom and an accuracy of 10 μm; the microscope was positioned in such a way as to provide a direction of view in the plane of the respective canal. The tip of the probe was calibrated at an auxiliary reference point and then placed at 10 arbitrary positions distributed along the course of the canal in the middle of the lumen and the 3-dimensional values were taken from the readings of the manipulator. Following other authors¹ data points from the

common crus and the ampullae were not used.

Extraocular muscles. Another set of pigmented rats (160–240 g) ($n = 3$) were injected with Nembutal and perfused with 10% formalin. Immediately after perfusion the skin and connective tissue around the right eye and on the zygomatic arch were removed. For determination of gaze direction 4 points on the cornea at the inner edge of the iris were measured.

Then the cornea was covered with cyanoacrylat, and the bulbus was connected to the zygomatic arch with dental cement to keep the bulbus firmly in primary position during the ensuing dissection; in addition, the surface of the bulbus was kept moist to prevent shrinkage. The skull was opened and the brain and frontal bone were removed to allow access to the EOM from above, and the jaw muscles and the mandible were removed to allow access to the EOM from below. Part of the maxillary bone was removed to facilitate access to the inferior oblique muscle. The Harderian gland, the lacrimal glands, and the adipose tissue were removed and the extraocular muscles were carefully dissected free as well as the sclera between the insertions of the muscles.

For measurement of coordinates again the probe method was used employing a stereotaxic frame and a dissecting microscope and referring to the tips of the ear bars and the contact between incisor bar and mandibula. To determine the position of muscle insertion the microscope was positioned in such a way as to provide a view orthogonal to the surface of the muscle; then the probe was positioned in the middle of the width of the muscle and the 3-dimensional values were taken from the readings of the manipulator. Apparently to determine the direction of pull of the individual EOM the line connecting the point of insertion and the origin of the muscles have to be measured. However, in rats the surface of the masseter muscle forces some of the EOM into a curved path. Therefore, the direction of pull is more accurately determined by the direction of the fibers in the distal part of the muscles; this also applies to the superior oblique muscle whose direction of pull is changed through the trochlea by approximately a right angle. In order to measure the superior and inferior muscles the head was turned upside down and positions of reference points were redetermined.

As the center of rotation of the bulbus is in effect

determined by the curvature of the sclera on the back of the bulbus gliding in a concave bolster formed by the Harderian gland, the lacrimal glands and adipose tissue we included up to 10 arbitrary spatial points on the sclera for calculation of the center of rotation in the measurements.

Mathematics

Semicircular canals. In a first step the vector orthogonal to the plane of the horizontal SCC was calculated using the method of principal components⁸. It is based on the calculation of a 3×3 covariance matrix of the data points and the determination of the eigenvectors of this matrix. The eigenvector corresponding to the smallest eigenvalue is orthogonal to the plane of the SCC. Vectors of all animals were normalized, added, and the vectorial sum was normalized again thus yielding an average unit sensitivity vector. Based on the direction of the unit vector of the horizontal canals a rotational transformation was established which abolished the roll component of the sensitivity vector of the horizontal SCC by pitching the frame of reference upward by 30.3° . This transformation was applied to all data thus changing in effect the external coordinate system as if the head was pitched downward by 30.3° so as to position the horizontal SCC horizontally.

In order to take advantage from the natural lateral symmetry of mammals, a pair of coordinate systems mirror-symmetrical to the mid-sagittal plane¹⁰ was used for the presentation of the anatomical data. The pair is made symmetrical by defining the positive x direction to be medial pitch, while y is upper yaw, and z is rostral roll; consequently, the coordinate system on the right side of the head is right-handed and the system of the left side is left-handed. It has the advantage to yield vectors identical in value and sign for both sides, while a graphic illustration of those vectors results in symmetrical figures.

This convention can be extended if it becomes necessary to describe unit vectors of both sides in a single coordinate system: then the vectors are denoted by ipsi- and contralateral rather than by left and right. For the conversion of a vector from ipsi- to contralateral, the vector has to be multiplied by -1 to take the opposite orientation of the frame of reference into account, and then the pitch component alone has to be multiplied by -1 to yield the mirror image of the

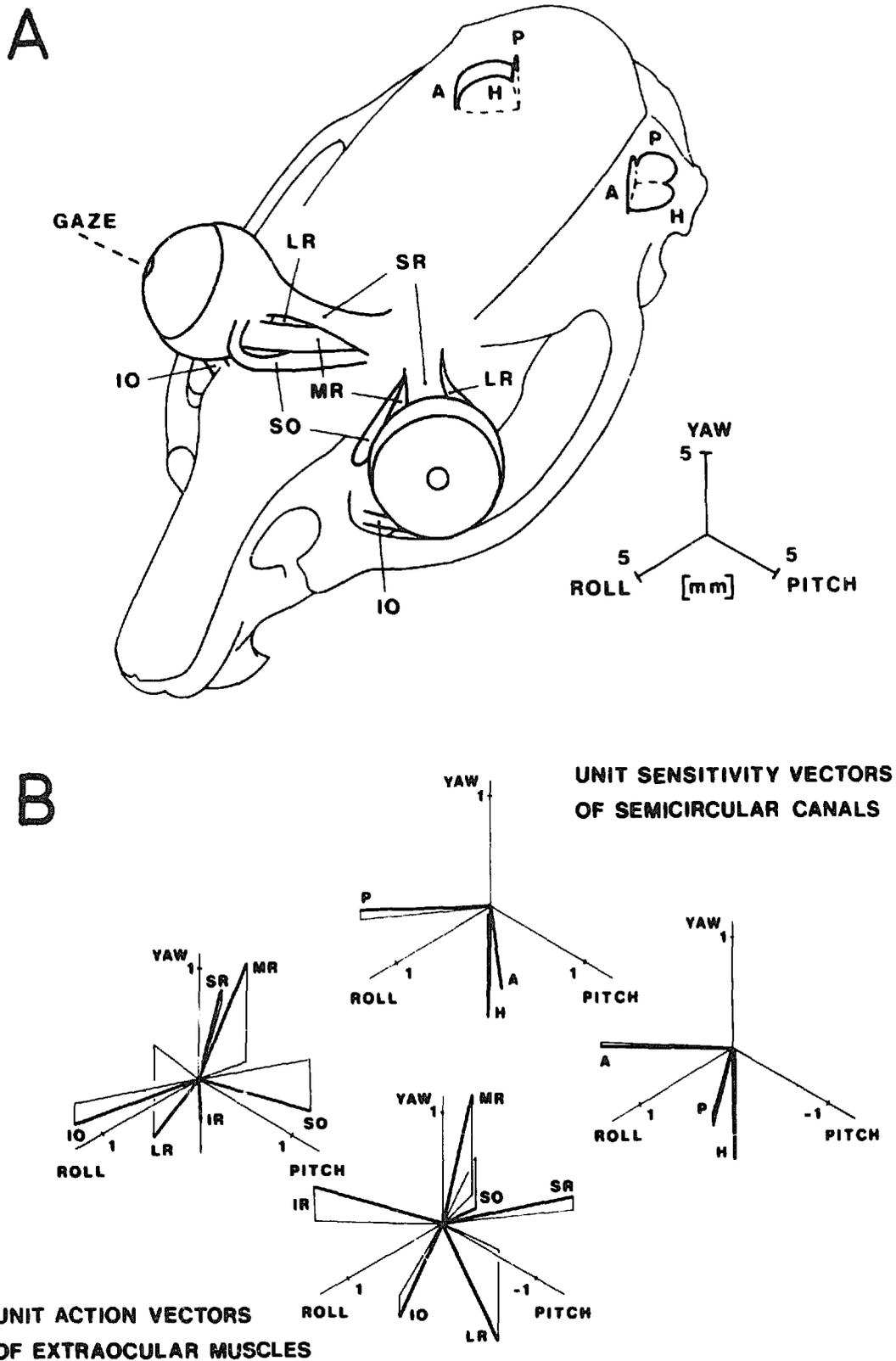


Fig. 1. A: scheme of the anatomical location of the rat's SCC and EOM based on a photograph. The head is pitched downward so that the roll component of the unit sensitivity vectors of the horizontal canals vanishes. The direction of view is symmetrical to all 3 axes of the coordinate system. B: scheme of the unit sensitivity vectors and the unit action vectors; the coordinate systems are Cartesian and right-handed on the right side of the head and left-handed on the left side, so that the unit sensitivity and action vectors are symmetrical to the mid-sagittal plane. To each vector (thick lines) a 'flag' (thin line) is attached, which shows the projection of the vector onto the horizontal plane to identify the spatial direction of the vector. See Tables I and II for abbreviations.

vector.

The directions of the unit sensitivity vectors of the vertical SCC were determined using again the principal component method with subsequent normalization. The sign of none of the vectors can be obtained from the calculation alone, therefore a convention has to be made. In accordance with previous studies here we refer to the physiological sensitivity of a given canal and define that sense of rotation positive, which yields an increase of neuronal activity. The sense of rotation is linked to the direction of the vector by a right-hand screw in a right-handed coordinate system and by a left-hand screw in a left-handed coordinate system.

Extraocular muscles and gaze direction. The axes of rotation produced by a single EOM near primary position can be assessed by the vector orthogonal to the plane which is spanned by the vector of the direction of the muscle fibers near the insertion point and the vector given by the insertion point and the center of rotation of the eye.

To determine the center of rotation, the surface of a sphere was fitted to the data points measured on the sclera and the center of this sphere was taken as the center of rotation. Then the outer product of the vector denoting the direction of pull and the vector pointing from the center of rotation to the insertion point yields a vector normal to the plane spanned by these vectors. Normalized averages of vectors were obtained in the same way as for the SCC.

One definition of the direction of gaze in an animal not having a fovea is the axis of circular symmetry of the optical apparatus. We determined the gaze direc-

tion by assuming that the pupil is symmetrical to this axis and that hence the gaze direction can be obtained by calculating the vector orthogonal to the regression plane of the pupil. This plane and the unit vector orthogonal to it were calculated using the same methods as for the determination of the vestibular unit vectors from a set of data points. It may be noted, that the gaze direction after formalin perfusion is only an approximation of the primary position of a living animal, but it is the main purpose of this measurement to define for which eye position the measurements of eye muscle geometry are valid.

RESULTS

A scheme of the anatomical location of SCC and EOM in relation to the skull is given in Fig. 1A. This scheme is based upon a photograph taken from the left side from such a viewpoint, that all 3 axes of the Cartesian coordinate system appear under the same angle¹⁰. In Fig. 1B the unit vectors characterizing the SCC and the EOM are shown in an equivalent perspective. A comparison between Fig. 1A and B helps to visualize their directions. For example, to visualize the direction of the unit action vector of the right SR, you hold your right hand in such a way that the palm shows to the eye ball while the fingers point in the direction of the muscle pull; then your extended thumb will point into the direction of the rotation exerted by the EOM. Likewise, if the fingers of your left hand follow the direction of head rotation which excites a left SCC maximally, your thumb will show the appropriate direction of the sensitivity unit vector.

TABLE I

Unit sensitivity vectors and angular orientations of semicircular canals in the rat

Unit sensitivity vectors of SCC are given in Cartesian pitch, yaw, and roll coordinates (medial, dorsal and anterior positive). As the symmetry of the Cartesian coordinate system pair used here matches the symmetry of the head, the coordinate values of the sensitivity unit vectors apply to either assignment as to which vestibular system is considered to be the ipsilateral and which the contralateral one. Angles between canal planes and reference planes in the coordinate system are given in degrees. iH and cH, ipsi- and contralateral horizontal; iA and cA, ipsi- and contralateral anterior; iP and cP, ipsi- and contralateral posterior.

| | <i>cH</i> | <i>iH</i> | <i>iA</i> | <i>cP</i> | <i>iP</i> | <i>cA</i> |
|------------|-----------|-----------|-----------|-----------|-----------|-----------|
| Pitch | - 0.022 | - 0.022 | 0.768 | - 0.589 | - 0.589 | 0.768 |
| Yaw | 1 | - 1 | - 0.031 | - 0.093 | 0.093 | 0.031 |
| Roll | 0 | 0 | 0.640 | - 0.802 | 0.802 | - 0.640 |
| Sag. pl. | 91.3 | 91.3 | 39.8 | 126.1 | 126.1 | 39.8 |
| Horiz. pl. | 1.3 | 178.7 | 91.8 | 95.3 | 84.7 | 88.2 |
| Front. pl. | 90.0 | 90.0 | 50.2 | 143.4 | 36.6 | 129.8 |

The numerical coordinates of the directions of the vestibular sensitivity vectors are summarized in Table I. Included are also the angles between the planes through the canals and the sagittal, horizontal, and frontal plane of the coordinate systems. The vanishing roll component of the horizontal canals (Fig. 1B, Table I) is a consequence of the choice of the coordinate system; however, in the rat the horizontal canals appear to be naturally rather insensitive to pitch rotations. A look at the vertical canals confirms the idea that the sensitivity vectors of both the posterior and the anterior canal have little yaw components, but, as can also be observed in Fig. 1B, pitch and roll components do not have equal values: the unit vectors of the posterior canals have larger roll sensitivity components, while the anterior canals have larger pitch components. Hence the idea that the vertical canals bisect the right angle are not confirmed in the rat.

The geometry of the extraocular muscles does depend upon the position and orientation of the eye. Therefore it seems useful to know at least the direction of gaze during the measurements in the same coordinate system that was used for the determination of the geometry. We obtained the following unit vector describing the (mean) gaze direction at primary position: pitch -0.772 , yaw 0.427 , and roll 0.470 .

The numerical coordinates of the axes of the natural oculomotor coordinate system with reference to the extrinsic coordinate system are given in Table II. The angles between the muscle planes, i.e. the planes through the direction of pull and the center of rota-

tion, and the planes of the coordinate system are also included. In contrast to the idea that the pulling direction of the lateral rectus (LR) and the medial rectus (MR) are essentially horizontal, these two muscles have considerable action components in roll and pitch direction, respectively. On the other hand, the so-called vertical eye muscles appear to generate more than negligible yaw components of bulb rotation. The particularly large yaw component of the superior obliquus (SO) may be due to the gaze direction at primary position: the optimal range for the insertion of the SO is taken by the cornea. The vertical muscles, especially the oblique muscles, also deviate from an idealized arrangement ruled by 45° with respect to the roll and pitch components. Again, this becomes also clear from Fig. 1B.

The angles between the vestibular unit sensitivity vectors given in Table III allow to consider the orthogonality and the alignment of the sensitivity unit vectors with respect to each other. From this table it is obvious, that the canals of one side are fairly orthogonal to each other with deviations from right angles of only 0.8 – 4.6° . In contrast to that, the obliqueness of vertical canals of opposite sides with deviations of 10.4 and 17.8 from right angles is quite large. The alignment of horizontal canals as a so-called coplanar pair is almost perfect with a deviation of only 2.5° , but the vertical pairs are misaligned by 15.6° .

The angles between the ocular unit action vectors as shown in Table IV reveal more prominent obliqueness of the oculomotor system than of the vestibular system. While the maximal non-orthogonality found between LR and IR with 42.4° is just about half

TABLE II

Unit action vectors and angular orientations of extraocular muscles in the rat

Unit action vectors of EOM are given in Cartesian pitch, yaw, and roll coordinates. As the symmetry of the Cartesian coordinate system pair used here matches the symmetry of the head, the coordinate values apply to either eye. Angles between muscle planes and reference planes in the coordinate system are given in degrees. LR, lateral rectus; MR, medial rectus; SR, superior rectus; IR, inferior rectus; SO, superior obliquus; IO, inferior obliquus.

| | LR | MR | SR | IR | SO | IO |
|------------|---------|---------|---------|-------|---------|---------|
| Pitch | - 0.540 | 0.098 | - 0.577 | 0.682 | 0.421 | - 0.423 |
| Yaw | - 0.839 | 0.905 | 0.121 | 0.313 | - 0.463 | - 0.196 |
| Roll | - 0.066 | - 0.415 | - 0.807 | 0.661 | - 0.779 | 0.885 |
| Sag. pl. | 122.7 | 84.4 | 125.2 | 47.0 | 65.1 | 115.0 |
| Horiz. pl. | 147.0 | 25.2 | 83.0 | 71.8 | 117.6 | 101.3 |
| Front. pl. | 93.8 | 114.5 | 143.9 | 48.7 | 141.2 | 27.8 |

TABLE III

Relative angles between canal planes in the rat

Relative angles between unit sensitivity vectors for 6 semicircular canals are given in degrees. The values are calculated from the data presented in Table I. See Table I for abbreviations.

| | <i>cH</i> | <i>iH</i> | <i>iA</i> | <i>cP</i> | <i>iP</i> | <i>cA</i> |
|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| <i>cH</i> | 0 | 177.5 | 92.7 | 94.6 | 83.9 | 89.2 |
| <i>iH</i> | 177.5 | 0 | 89.2 | 83.9 | 94.6 | 92.7 |
| <i>iA</i> | 92.7 | 89.2 | 0 | 164.4 | 86.7 | 79.6 |
| <i>cP</i> | 94.6 | 83.9 | 164.4 | 0 | 107.8 | 86.7 |
| <i>iP</i> | 83.9 | 94.6 | 86.7 | 107.8 | 0 | 164.4 |
| <i>cA</i> | 89.2 | 92.7 | 79.6 | 86.7 | 164.4 | 0 |

of a right angle, the misalignment of 'antagonistic' muscles ranges from 27.2° for SR and IR to 39° for SO and inferior obliquus (IO).

The relation between the vestibular and the oculomotor system is summarized in Table V giving the angles between sensitivity and action vectors. Of special interest are the spatial relations between those SCC and EOM that are linked by the strongest excitatory connection in the compensatory vestibulo-oc-

ular reflex; their unit vectors are approximately aligned while having opposite signs and may be called 'corresponding'. The spatial alignment between 'corresponding' SCC and EOM, given in the diagonal of Table V, is in almost all instances slightly closer than the alignment of 'antagonistic' EOM. Nevertheless, misalignment of muscles with one of its 'corresponding' canals is never smaller than 15.5° and reaches values of up to 35.2°.

TABLE IV

Relative angles between extraocular muscles in the rat

Relative angles between unit action vectors of the extraocular muscles of one eye. The values are calculated from the data presented in Table II. See Table II for abbreviations.

| | <i>LR</i> | <i>MR</i> | <i>SR</i> | <i>IR</i> | <i>SO</i> | <i>IO</i> |
|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| <i>LR</i> | 0 | 141.7 | 74.7 | 132.4 | 77.8 | 70.5 |
| <i>MR</i> | 141.7 | 0 | 67.1 | 85.6 | 93.1 | 125.8 |
| <i>SR</i> | 74.7 | 67.1 | 0 | 152.8 | 70.7 | 119.6 |
| <i>IR</i> | 132.4 | 85.6 | 152.8 | 0 | 111.9 | 76.4 |
| <i>SO</i> | 77.8 | 93.1 | 70.7 | 111.9 | 0 | 141.0 |
| <i>IO</i> | 70.5 | 125.8 | 119.6 | 76.4 | 141.0 | 0 |

TABLE V

Relative angles between extraocular muscles and semicircular canals in the rat

Relative angles between unit sensitivity vectors for semicircular canals and unit sensitivity vectors of extraocular muscles are given in degrees. The values are calculated from data presented in Tables I and II. See Tables I and II for abbreviations.

| | <i>cH</i> | <i>iH</i> | <i>iA</i> | <i>cP</i> | <i>iP</i> | <i>cA</i> |
|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| <i>LR</i> | 145.8 | 31.7 | 115.6 | 63.3 | 79.2 | 113.5 |
| <i>MR</i> | 25.6 | 155.0 | 102.6 | 79.0 | 107.9 | 68.4 |
| <i>SR</i> | 82.3 | 96.2 | 164.5 | 12.3 | 107.3 | 85.6 |
| <i>IR</i> | 72.7 | 109.2 | 20.5 | 164.0 | 81.0 | 83.6 |
| <i>SO</i> | 118.2 | 63.0 | 99.2 | 65.2 | 156.5 | 36.1 |
| <i>IO</i> | 100.7 | 78.2 | 75.7 | 116.3 | 19.7 | 153.7 |

DISCUSSION

The methods to determine the spatial orientation of SCC employed here followed the lines of previous authors^{1,6}, and hence the sources of errors are similar. We consider the method of measuring the anatomical locations to be precise enough not to introduce significant errors. The main source of systematic errors as it appears to us is the course of the endolymph fluid toroid ring inside the utricle, which is not accessible by the method employed. If the inertia distribution of the toroid is approximately symmetrical to the plane calculated from the bony structure of the SCC, then the potential systematic error arising from this uncertainty may be negligible.

It may be asked why we did not include measurements of origins and insertions of eye muscles, as these data might have allowed to calculate the geometry of the EOM in other positions than the primary one. We refrained from doing so, because already in primary position the eye muscles are forced into curved paths by bony and muscular surfaces. These constraints were taken into account in the present measurements, but they would result in unpredictable paths for other eye positions.

The calculation of the unit action vectors of the EOM is impaired by unavoidable uncertainties, too. As the EOM form a band, it may well be possible that asymmetries in the force distribution across the width of the muscle result in a deviating rotation axis; in addition the axis of rotation may be different, when a different number of motor units is activated. Another source of error and probably a more important one is the location of the center of rotation, which may even not be the same for all muscles. Here, direct measurements of rotations following electrophysiological stimulation may be helpful.

The data obtained from rats can be compared to equivalent data obtained from humans^{2,17}, cats and rabbits⁶, and rhesus monkey¹⁵. Thereby we take advantage of the fact, that in all species except in humans the geometries of both organs were determined by the same authors in the same coordinate system for either organ and that in all instances anatomical methods were employed. In this comparison we refer only to the angles equivalent to Tables III–V, hence for humans and monkeys part of the equivalent angles had to be calculated from the published vectorial

data, yet the monkey data were slightly corrected for the MR (Simpson, personal communication).

As the criterion of comparison we used the maximal angle of deviation from an idealized arrangement of SCC and EOM as mutually orthogonal or aligned. Then the deviations from alignment of 'coplanar' semicircular canals are least in monkeys and largest in humans, followed by rats, cats, and rabbits, while the deviations from orthogonality of 'non-coplanar' canals are again least in monkeys, largest in rabbits, followed by humans, rats and cats. It follows from these sequences, not only that obliqueness plays a most important role in humans, but also that rats rather than monkeys are suited to be a model for obliqueness in the vestibular system.

A similar comparison of the oculomotor systems results in the finding, that the deviations from alignment of EOM action vectors of 'antagonistic' pairs is least in cats and largest in rats, followed by humans, rabbits, and monkeys. Referring to the orthogonality the deviations are again largest in rats, here followed by monkeys, rabbits and humans. Again it can be concluded, that obliqueness is a very important feature of the human oculomotor system; but the rat has the most oblique oculomotor system of all species examined so far and may thus show the most conspicuous effects in the neural networks dealing with that obliqueness.

If the comparison is to be extended to the relation between vestibular and oculomotor apparatus, we have to refer to the same coordinate system for both organs. Unfortunately, the pitch angle of the extrinsic coordinate system of the human EOM data¹⁷ is not exactly known; we therefore established a kind of lower limit estimation for the purpose of this comparison by pitching the extrinsic coordinate systems in humans relative to each other in such a way as to minimize the average of the deviations of alignments of corresponding canals and eye muscles. The obliqueness of the systems as assessed by the maximal deviation from alignment is not less than 19.4° in any of the species; it is least in monkey, largest in rats, followed by humans, cats, and rabbits. Again, we end up with the finding that obliqueness is very important in humans and the best animal model to study this feature and also the strategies used by the CNS to deal with it seems to be the rat.

Particularly, at least as far as the vestibulo-ocular

reflex is concerned, the results quantitate the task to be met by the neural network mediating the vestibulo-ocular reflex to overcome the obliqueness of sensory and motor apparatuses and to arrive at perfect compensatory eye movements in space. Furthermore, the measurements provide a complete data base to establish a multidimensional model of the reflex near primary eye position, which would describe quantitatively the relative strength of the neural connectivities from all 6 SCC to all 12 EOM in the rat.

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