Functions of separate sensory receptors of nonauditory labyrinth of the cat

KENNETH E. MONEY AND JOHN W. SCOTT
Department of Physiology, University of Toronto, Toronto, Canada

Money, Kenneth E., and John W. Scott. Functions of separate sensory receptors of nonauditory labyrinth of the cat. Am. J. Physiol. 202(5): 1211-1220. 1962.—A technique for plugging individual semicircular canals of cats was developed, and it was established that the plugging of a semicircular canal completely blocked its receptivity without influencing the functions of the other vestibular receptors. It was found that cats with all six semicircular canals plugged were lacking all sensitivity to angular acceleration, but they retained normal responses to linear acceleration. Results of several vestibular tests led to the conclusion that the vertical semicircular canals initiate corrections for fast angular displacements from the normal orientation when the displacements are about horizontal axes and that the otoliths initiate corrections for slow angular displacements about horizontal axes. In tests of single horizontal canals, the durations of postrotatory nystagmus were the same after rotations in opposite directions. It was concluded that in the intact animal both horizontal semicircular canals contribute equally to reception of angular acceleration in both directions.

Although labyrinthectomy has been performed on many species, the discrete removal of parts of the labyrinth has been largely confined to fish, frogs, and pigeons. In mammals, the situation of the labyrinth in hard bone and the nature of the nerve supply have discouraged such procedures. For this reason it was of interest to develop a technique of functional removal of individual semicircular canals in the cat (Felis domestica). The object was to determine the basic functions of the semicircular canals in the cat, and also to investigate directional sensitivity in the horizontal semicircular canals.

Agreement is quite general that a semicircular canal is the sensory receptor of angular acceleration in its own plane, but whether a single canal is sensitive to accelerations in one direction only or in both directions (clockwise and counterclockwise) has been a matter of controversy for more than 70 years. Since the ampulla of each semicircular canal is found adjacent to the utricle and is considered the “end” of the canal, the terms “ampulla-leading acceleration” and “ampulla-trailing acceleration” are used to describe the two directions of rotation. Similarly, the terms “ampullofugal” and “ampullopetal” are used to describe the direction of endolymph movements relative to the walls of the canal. These terms are illustrated in Fig. 1.

METHODS

Normal cats were given a series of vestibular tests and then subjected to the functional removal of various combinations of semicircular canals. The tests were repeated 10 days after the operation and again 10 weeks after the operation. A total of 42 cats was studied, of which four were controls not subjected to an operation.

Operative Technique

By relating the positions of the semicircular canals to external bony landmarks and to the vertical portion of the seventh cranial nerve it was found that any one of the semicircular canals could be approached selectively with a dental drill without encroaching on any other part of the labyrinth, without intracranial penetration, and without violating the middle ear (Fig. 2). By drilling quickly across a canal, bone chips were packed into the two open ends produced by the transection, and very little perilymph was lost. A gap of 2 or 3 mm was left between the two ends.

The animal was anesthetized with pentobarbital. Antiseptic precautions were observed, and a Zeiss operating microscope was used in guiding the drill.

Vestibular Tests

Rotatory tests. In order to hold the cat securely for the rotatory tests, it was first placed in a wooden box with the head protruding. Sponge rubber was packed around the cat and secured under gentle pressure with a roller bandage. The head was secured by applying a “bivalve plaster cast” similar to that described by Crampton, Schwan, and Warburton (1) except that in this case the cast covered only the head and consisted of top and bottom halves. The two halves were held together with adhesive tape. The casts were made with flat bases...
parallel to the hard palate. It was found that four casts of different sizes were sufficient to fit any of the cats encountered.

The cat, in the box and plaster cast, was placed in the position selector (Fig. 3). The box was held in place by canvas straps, and the head in its cast was anchored with a wooden block and rope. The position selector was mounted on an electrically driven turntable and held the animal so that the selected semicircular canal could be maintained in the plane of rotation.

On each occasion of testing, one series of rotatory tests was made at 12 rev/min and another at 30 rev/min. At each speed of rotation, rotatory tests were made clockwise and counterclockwise in each of three orientations: 1) Horizontal orientation: the horizontal canals in the plane of rotation; 2) vertical orientation: the hard palate parallel to the axis of rotation and the rostrocaudal axis of the skull parallel to the plane of rotation; 3) rotary orientation: the hard palate parallel to the axis of rotation and the rostrocaudal axis of the skull also parallel to the axis of rotation (Fig. 4).

The animal was accelerated quickly to a constant angular velocity which was maintained for 60 sec, at which time the rotation was stopped abruptly. The duration of the postrotatory nystagmus was measured with a stop watch, using direct visual observation.

Nonrotatory tests with cat not blindfolded. For the first 4 days after the operation the animal was observed daily in its cage; its posture and any resting nystagmus were noted. At the preoperative and postoperative occasions of testing, the reactions of the animal when placed on the floor (gait, circling movements, etc.) were also recorded.

Nonrotatory tests with cat blindfolded. Slow angular displacements. The reactions to slow angular displacements (1–3°/sec) through 45° in four different directions were observed. The four directions were: to the left, to the right, head up, and head down. The displacement was achieved by a tilting table driven by a lead weight acting on a piston in oil. The speed of the angular displacement varied somewhat throughout the arc and varied with the weight of the cat and its position on the table. The table had a surface of sandpaper which allowed the animal to be tilted through 45° without sliding off.

Linear accelerations. The cat was held by the trunk and manually accelerated downward in three different orientations: head first, hind limbs first, and the long axis of the animal horizontal. An additional downward acceleration was carried out holding the cat by the scruff of the neck. The reactions of the head and limbs were observed.

"Drop" tests. a) The animal was held by the trunk in the normal orientation 3 ft above a rubber mat and suddenly released. b) The animal was held by its four limbs upside down 3 ft above the rubber mat and suddenly released. c) The animal was placed on a rubber mat on a platform 4 ft above the ground. The platform was suddenly released and allowed to fall to the ground.

Fast angular displacements. The animal was placed on a platform which was given an abrupt angular displacement of 35° at a rate of approximately 45°/sec (Fig. 5). The displacements were given in each of four directions: to the left, to the right, head up, and head down.

RESULTS

Rotatory Tests

Some of the results of the rotatory tests are presented in Table 1. Not recorded in Table 1 are the results of tests on three cats subjected to bilateral labyrinthectomy, six cats in which all six semicircular canals were plugged, and one cat in which labyrinthectomy was performed on one side and all three semicircular canals were plugged on the other side. In all of these animals there was no postrotatory nystagmus in any of the postoperative tests.

Two additional animals lost all semicircular canal function postoperatively, one after unilateral labyrinthectomy. The other had all canals plugged, except one horizontal; this animal developed distemper postoperatively.

Nonrotatory tests with cat blindfolded. SLOW ANGULAR DISPLACEMENTS. The reactions to slow angular displacements (1–3°/sec) through 45° in four different directions were observed. The four directions were: to the left, to the right, head up, and head down. The displacement was achieved by a tilting table driven by a lead weight acting on a piston in oil. The speed of the angular displacement varied somewhat throughout the arc and varied with the weight of the cat and its position on the table. The table had a surface of sandpaper which allowed the animal to be tilted through 45° without sliding off.

Nonrotatory tests with cat blindfolded. SLOW ANGULAR DISPLACEMENTS. The reactions to slow angular displacements (1–3°/sec) through 45° in four different directions were observed. The four directions were: to the left, to the right, head up, and head down. The displacement was achieved by a tilting table driven by a lead weight acting on a piston in oil. The speed of the angular displacement varied somewhat throughout the arc and varied with the weight of the cat and its position on the table. The table had a surface of sandpaper which allowed the animal to be tilted through 45° without sliding off.

Linear accelerations. The cat was held by the trunk and manually accelerated downward in three different orientations: head first, hind limbs first, and the long axis of the animal horizontal. An additional downward acceleration was carried out holding the cat by the scruff of the neck. The reactions of the head and limbs were observed.

"Drop" tests. a) The animal was held by the trunk in the normal orientation 3 ft above a rubber mat and suddenly released. b) The animal was held by its four limbs upside down 3 ft above the rubber mat and suddenly released. c) The animal was placed on a rubber mat on a platform 4 ft above the ground. The platform was suddenly released and allowed to fall to the ground.

Fast angular displacements. The animal was placed on a platform which was given an abrupt angular displacement of 35° at a rate of approximately 45°/sec (Fig. 5). The displacements were given in each of four directions: to the left, to the right, head up, and head down.

RESULTS

Rotatory Tests

Some of the results of the rotatory tests are presented in Table 1. Not recorded in Table 1 are the results of tests on three cats subjected to bilateral labyrinthectomy, six cats in which all six semicircular canals were plugged, and one cat in which labyrinthectomy was performed on one side and all three semicircular canals were plugged on the other side. In all of these animals there was no postrotatory nystagmus in any of the postoperative tests.

Two additional animals lost all semicircular canal function postoperatively, one after unilateral labyrinthectomy. The other had all canals plugged, except one horizontal; this animal developed distemper postoperatively.

Nonrotatory tests with cat blindfolded. SLOW ANGULAR DISPLACEMENTS. The reactions to slow angular displacements (1–3°/sec) through 45° in four different directions were observed. The four directions were: to the left, to the right, head up, and head down. The displacement was achieved by a tilting table driven by a lead weight acting on a piston in oil. The speed of the angular displacement varied somewhat throughout the arc and varied with the weight of the cat and its position on the table. The table had a surface of sandpaper which allowed the animal to be tilted through 45° without sliding off.

Nonrotatory tests with cat blindfolded. SLOW ANGULAR DISPLACEMENTS. The reactions to slow angular displacements (1–3°/sec) through 45° in four different directions were observed. The four directions were: to the left, to the right, head up, and head down. The displacement was achieved by a tilting table driven by a lead weight acting on a piston in oil. The speed of the angular displacement varied somewhat throughout the arc and varied with the weight of the cat and its position on the table. The table had a surface of sandpaper which allowed the animal to be tilted through 45° without sliding off.

Nonrotatory tests with cat blindfolded. SLOW ANGULAR DISPLACEMENTS. The reactions to slow angular displacements (1–3°/sec) through 45° in four different directions were observed. The four directions were: to the left, to the right, head up, and head down. The displacement was achieved by a tilting table driven by a lead weight acting on a piston in oil. The speed of the angular displacement varied somewhat throughout the arc and varied with the weight of the cat and its position on the table. The table had a surface of sandpaper which allowed the animal to be tilted through 45° without sliding off.

Nonrotatory tests with cat blindfolded. SLOW ANGULAR DISPLACEMENTS. The reactions to slow angular displacements (1–3°/sec) through 45° in four different directions were observed. The four directions were: to the left, to the right, head up, and head down. The displacement was achieved by a tilting table driven by a lead weight acting on a piston in oil. The speed of the angular displacement varied somewhat throughout the arc and varied with the weight of the cat and its position on the table. The table had a surface of sandpaper which allowed the animal to be tilted through 45° without sliding off.

Nonrotatory tests with cat blindfolded. SLOW ANGULAR DISPLACEMENTS. The reactions to slow angular displacements (1–3°/sec) through 45° in four different directions were observed. The four directions were: to the left, to the right, head up, and head down. The displacement was achieved by a tilting table driven by a lead weight acting on a piston in oil. The speed of the angular displacement varied somewhat throughout the arc and varied with the weight of the cat and its position on the table. The table had a surface of sandpaper which allowed the animal to be tilted through 45° without sliding off.
In addition to those recorded in Table 1, six cats were subjected to bilateral plugging of the horizontal canals with plasticine and bone wax. These six were not tested preoperatively; three of them underwent operations with ether anesthesia and were tested 2 hr after withdrawal of the ether. Postoperatively, in all six, there was no postrotatory horizontal nystagmus but there was rotary and vertical nystagmus of durations within the normal range following the appropriate rotation.

There was some indication of a response decline in the three tests of the control animals. The intervals between the tests on these animals were the same as in the experimental series.

Nonrotatory Tests With Cat Not Blindfolded

**Bilateral labyrinthectomy.** During the first 4 days following bilateral labyrinthectomy the animals usually were found lying with the head level and resting between the forepaws. They refused to stand, and, when provoked, exhibited gross instability of the head. While eating, these animals would throw the head up and down violently in the pitching (sagittal) plane, often through more than 90°; oscillations of the head in the rolling (frontal) plane often accompanied the pitching movements and would frequently precipitate a rolling of the animal to one side or the other. No resting or positional nystagmus was ever observed in these animals.

Eight weeks after the operation, when placed on the floor, the animals walked in a crouching position without fully extending the hind limbs. The head oscillated in the rolling and pitching planes and the animals frequently fell to one side or the other. Four months after the operation the animals still walked in a crouching position but seldom fell over, and the oscillations of the head were no longer apparent. The pitching movements of the head while eating were still evident but greatly reduced.

**Unilateral labyrinthectomy.** During the first 2 days after the operation the animals lay with the head between the forepaws and the operated side of the head held lower than the intact side. There was in every case a resting horizontal nystagmus with the fast component directed away from the operated ear. A rotary component of nystagmus was also present, with the fast component turning the dorsal edge of the eyeball away from the operated ear. On the 3rd postoperative day the resting nystagmus was no longer apparent, but in two of the four preparations of this kind the rotary component reappeared when the animal was held in certain positions. This positional nystagmus was observed on the 10th postoperative day, but it was not present at the tests 10 weeks after the operation.

When placed on the floor on the 10th postoperative day, these animals walked holding the operated side of the head lower than the other side, and they frequently fell to the operated side. They did not fully extend the hind limbs.

In one animal labyrinthectomy was performed on one side and all three canals were plugged on the other side. This animal also exhibited positional nystagmus, as well as the other signs described above for animals with unilateral labyrinthectomy only. Ten weeks after the operation this animal still held the head, when standing, with the labyrinthectomized side lower, and when placed on the floor it frequently ran in circles toward the labyrinthectomized side. There was no positional nystagmus at this time.

The animals with simple unilateral labyrinthectomy did not exhibit any running in circles, but they still held the operated side of the head lower than the intact side 10 weeks after the operation, and, indeed, this tilt of the head never disappeared completely in any of these animals even though one was kept for 10 months after its operation. After 10 weeks these animals rarely fell when walking.

**Canal-plugging operation only.** No animal after only a canal-plugging operation ever exhibited a resting or positional nystagmus or a tilted posture of the head. In all animals in which there were canals plugged on one side only (cats 41, 58, 61, 42, 47, B100), including those in which all three canals on one side were plugged, the
TABLE I. Durations of postrotatory nystagmus in seconds

<table>
<thead>
<tr>
<th>Cat number, and type of operation</th>
<th>Pre-op 16 RPM</th>
<th>Post-op 10 weeks</th>
<th>Pre-op 30 RPM</th>
<th>Post-op 10 weeks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>#12. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>-</td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#13. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>4</td>
<td>12</td>
<td>4</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#14. all canals except one posterior plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>-</td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#15. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>4</td>
<td>12</td>
<td>4</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#16. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>-</td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#17. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>-</td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#18. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>-</td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#19. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>-</td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#20. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>-</td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#21. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>-</td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#22. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>-</td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#23. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>-</td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#24. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>-</td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#25. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>-</td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#26. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>-</td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td><strong>#27. all canals except both horizontal canals plugged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HORIZ.</td>
<td>4</td>
<td>-</td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td>VERT. 6</td>
<td>4</td>
<td>4</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>ROT. 26</td>
<td>15</td>
<td>11</td>
<td>18</td>
<td>18</td>
</tr>
</tbody>
</table>

**NOTE:** All animals were operated on by 10.220.33.2 on July 14, 2017. http://ajplegacy.physiology.org/ Downloaded from

K. E. MONEY AND J. W. SCOTT

nonrotatory tests without blindfolds revealed little evidence of vestibular abnormality even on the 1st day after the operation. At this time the animals were found standing normally with the head level. When placed on the floor they held the head level and walked normally except for an occasional jerky movement of the limbs; they did not fall. Some of the animals ran quickly in a straight line immediately after being placed on the floor. Ten days and also 10 weeks after the operation, all of these animals walked in a manner indistinguishable from that of normal cats.

Animals which underwent canal-plugging procedures involving both ears exhibited vestibular abnormalities depending on which canals had been plugged. Animals with only the two horizontal canals plugged frequently exhibited a slow swayng of the head and neck in the yawing (horizontal) plane 10 days and also 10 weeks after the operation. The swayng movements usually consisted of turning the head and shoulders around in the yawing plane up to 180° from its normal orientation and then moving it back through the normal orientation, continuing 360° until it stopped again 180° from the normal orientation on the other side. This cycle was usually repeated two or three times immediately after the animal was placed on the floor, and it was followed by normal walking or running.

Animals with all six canals plugged exhibited less often the swayng of the head in the yawing plane, which was a prominent characteristic of the animals which had only the two horizontal canals plugged. For the first few days after the operation these animals frequently exhibited other oscillations of the head, often through more than 90°. The oscillations were most marked in the rolling plane, sometimes lasting for 5 or 10 sec at a time, and oscillations were also observed in the pitching plane, especially when the animals were eating. These animals often fell to the side, sometimes an animal would fall to one side and immediately leap to its feet and fall promptly to the other side, giving the impression that the animal was bouncing from side to side. Ten days after the operation these animals exhibited jerky limb movements but usually could walk a few yards before falling. At this stage it was observed that the hind limbs were consistently more prone to inappropriate movements than were the forelimbs. Often the hind limbs would collapse or fall to one side or the other while the head and forelimbs retained
nonauditory labyrinth of the cat

normal orientation. At this stage, the hind limbs usually were not fully extended in walking. Ten weeks after the operation these animals walked almost normally, fully extending all the limbs. The only abnormality in the gait at this time was an occasional jerky movement of the head or limbs; occasionally when running they fell to the side for no apparent reason.

In these tests the animals with only the four vertical canals plugged or all canals except one horizontal plugged were found to be very similar to the animals with all six canals plugged, except that they were never seen exhibiting oscillations of the head in the yawing plane.

Nonrotatory Tests With Cat Blindfolded

Normal cats (including preoperative tests). There is considerable variation among individual cats in their responses to the following tests; the responses described below are the most usual ones.

SLOW ANGULAR DISPLACEMENTS. When slowly tilted through 45°, regardless of the direction of the tilt, normal cats crouch appropriately and do not fall off the tilting surface. In some cases they walk to one of the edges of the surface and curl the forepaws over the edge.

LINEAR ACCELERATIONS. When a normal blindfolded cat is held by the trunk and accelerated downward, head first, the forelimbs extend and the toes of the forelimbs move up and forward and spread widely. When accelerated toward the floor, hind limbs first, the hind limbs extend, and the toes spread. When held by the scruff of the neck and accelerated downward, all four limbs extend and the toes spread and the head is moved quickly upwards.

DROP TESTS. A normal cat when dropped in the normal upright orientation from 3 ft above a rubber mat extends the limbs slightly, spreads the toes, and lands gracefully without the head or the trunk coming into contact with the mat. When dropped upside down the animal quickly rotates the appropriate amount in the air and lands gracefully in the normal upright position. When the platform on which a cat is resting is suddenly dropped, all four limbs are extended and the toes are spread widely; the head is held high (Fig. 7).

FAST ANGULAR DISPLACEMENTS. When quickly tilted through 35°, regardless of the direction of the tilt, normal cats hop, run, or crouch in such a way that they do not fall, i.e., the sides of the limbs or trunk never come into contact with the supporting surface (Fig. 5).

Bilateral labyrinthectomy. The bilaterally labyrinthectomized cats always fell when subjected to either fast or slow angular displacements (Figs. 5 and 6). They always failed to respond to all of the linear accelerations applied and they gave no response in any of the drop tests. When dropped upside down no limb or head movement would occur until the animal had landed on its back on the soft rubber mat. When blindfolded and placed on the soft rubber mat of the dropping platform these cats would lie quietly on the back or side for long periods of time, and when the platform was dropped with the animal in one of these unusual orientations it made no head or limb movements until after the platform hit the floor mat. If the cat were placed in the normal orientation and the platform was dropped, again the cat would not react until after the platform hit the floor mat (Fig. 8).

Unilateral labyrinthectomy. SLOW ANGULAR DISPLACEMENTS. In four of the five cats tested 10 days after unilateral labyrinthectomy, all animals showed normal reactions to at least some of the linear accelerations, but in every case there was a marked lack of response relative to the preoperative performance. Ten weeks after unilateral labyrinthectomy the responses to linear accelerations were greater than after 10 days, but still not as great as preoperatively.

DROP TESTS. Ten days after unilateral labyrinthectomy, when the animals were dropped in the normal upright orientation, they retained the upright posture while falling but after touching the mat they fell onto the operated side. Only one animal showed this tendency in the tests 10 weeks after the operation; the others remained upright, although they still landed less gracefully than normal cats.

When on the platform and dropped, all the animals in the first postoperative tests showed a lesser response than preoperatively. Responses in the second postoperative tests were greater than in the first postoperative tests, but they were still not as great as preoperatively.

In the first postoperative tests only two of the five animals rotated the appropriate amount and landed on their feet when dropped upside down; the other three showed some reactions of the head and limbs but they failed to rotate the appropriate amount in the air. Of these three, one rotated the appropriate amount in the air in the second postoperative tests; the other surviving animals reacted in much the same way as they had in the first postoperative tests. Postoperatively, even when these animals rotated the appropriate amount in the air, they landed less gracefully than normal cats.

FAST ANGULAR DISPLACEMENTS. In the first postoperative tests all the unilaterally labyrinthectomized animals fell when quickly tilted toward the side of the operation; often they rolled 360° before stopping in the normal upright posture. In three of these animals, this was the only direction of fast tilting which resulted in a fall. The other two animals fell after a head-upwards tilt
as well, and one of them fell also after a tilt toward the intact ear.

Each of the animals reacted in the same way on the second postoperative occasion of testing as it had on the first, except that two of the animals which formerly fell only after a fast tilt toward the operated ear did not fall after any of the fast tilts.

The cat in which labyrinthectomy was performed on one side and all three canals were plugged on the other side, in the first postoperative tests fell after all the slow angular displacements except the one toward the ear with the canals plugged, and fell after all the fast angular displacements except the one head down. Its responses to linear acceleration and to dropping on the platform were similar to those of the animals with simple unilateral labyrinthectomy. When dropped in the normal upright orientation onto a mat 3 ft below, the animal landed heavily and its head struck the mat. When dropped upside down the animal failed to rotate at all and landed on its back. In the second postoperative tests this animal fell after slow tilting toward the side of the labyrinthectomy and in the head-up direction. Its reactions to fast tilting were similar to those in the first postoperative tests. The reactions to linear accelerations were more vigorous than in the first postoperative tests, but the reactions to the drop tests were the same as in the first postoperative tests.

Canal-plugging operations only. (Animals with all six canals plugged, or all canals plugged except one horizontal, or all canals plugged except both horizontals.) There were no apparent differences between the responses of these three groups to the tests with the animals blindfolded.

Slow angular displacements. Ten days after the operation, 7 of these 11 cats fell after at least one of the slow tilts. These animals invariably made compensatory movements before some sudden jerky movement resulted in their falling off the tilting surface. The other four cats did not fall after any of the slow tilts. Ten weeks after the operation, only 3 of the 11 cats fell after any of the slow tilts, and these 3 reacted normally to slow tilting in all four directions in most of the trials; they fell off only occasionally.

Linear accelerations. In both the first and the second postoperative tests these animals gave responses to linear accelerations which were essentially the same as their preoperative responses, except that two of the animals did not respond postoperatively to linear accelerations when held by the scruff of the neck.

Drop tests. When dropped in the normal upright orientation these animals exhibited a remarkable tendency to extend their forelimbs anteriorly and their hind limbs posteriorly so that the limbs were parallel to the floor; the back was arched with the dorsal surface concave, and the animals landed on their chests. This tendency was less marked but still apparent, especially in the forelimbs, in the second postoperative tests.

In both the first and the second postoperative tests when dropped upside down, these animals reacted quickly with head and limb movements and some rotation of the trunk, but only 3 of the 11 animals ever rotated the appropriate amount in the air, and these 3 did so in only some of the trials.

When on the platform and dropped, there was some indication that the responses postoperatively were somewhat less vigorous than preoperatively, especially the responses of the hind limbs in the first postoperative tests. In the second postoperative tests the responses were the same as in the preoperative tests (Fig. 7), and differ from the responses seen in the labyrinthectomized animal (Fig. 8).

Fast angular displacements. In all these animals there were obvious defects in the responses to all the postoperative fast tilting tests. All the animals fell when tilted to the left or to the right, and often they would roll 360° before stopping in the upright position. Nine of the eleven animals fell onto the back when tilted head up. When tilted head down four of the animals rotated 180°, in some of the trials, so that the hind limbs moved up and forward in a semicircle and the animals landed on their backs; the other seven rotated in the same manner but not as far, and then fell either to the

\[ \text{FIG. 5. Diagrammatic representation of results of rapid tilt (45°/sec) tests.} \]

\[ \text{FIG. 6. Diagrammatic representation of results of slow tilt (1°/sec) tests.} \]
side or back again to the upright orientation. There was little difference between the responses at the first and the second postoperative tests.

Canal-plugging operations only. (Animals in which only one ear was operated upon.) In all these animals the postoperative tests with the cat blindfolded revealed no differences whatever between the preoperative and postoperative behavior, excepting the test in which the animals were dropped upside down. In this test all animals rotated in the air, the appropriate amount, and landed gracefully in half, or more than half, of the trials; in the other trials the animals rotated, but not the correct amount, and they did not land gracefully on their feet. There were few differences between the results of the first and the second postoperative tests.

Canal-plugging operations only. (Animals in which only the two horizontal canals were plugged, cats 62, 8117, and 68.) In the first postoperative tests two of these three cats occasionally fell after some of the slow or fast tilts. It was observed in most of these instances that a yawing movement of the head through approximately 90° preceded the fall. These instances in the first postoperative test were the only ones in all the “blindfold” tests in which these cats showed postoperative responses differing from their preoperative responses, again excepting the test in which the animal was dropped upside down. In this test two of the animals never rotated the correct amount postoperatively, and the third rotated the correct amount three times in nine postoperative trials.

DISCUSSION

Directional Sensitivity of Single Horizontal Semicircular Canals: Previous Work

There is considerable controversy as to whether a single semicircular canal is sensitive to accelerations in both directions or only in one direction. The relevant evidence can be classified conveniently according to the techniques employed.

Caloric tests. In several species caloric tests have produced evidence supporting the theory of equal sensitivity in the two directions (2–5). As McNally (6) suggested, “...the hot or cold caloric test elicits in each case its own form of nystagmus, presumably from stimulating the same canal in opposite directions.” Similarly, Cawthorne, Fitzgerald, and Hallpike (7) argued that if ampullopetal endolymph flow produces the greater response in the human, then hot caloric stimulation should produce a greater response than cold stimulation. This was found to be the case in only 10% of a group of 50 normal subjects, and, indeed, in 80% of the subjects the cold caloric test produced nystagmus lasting longer than in the hot caloric test (4).

Electrophysiological techniques. It has been found that there is a resting discharge along most single nerve fibers from the ampullae and that rotation in one direction causes an increase in the frequencies of the discharges, whereas rotation in the opposite direction causes a decrease in the frequencies. This general picture is widely accepted, having been demonstrated by Lowenstein and Sand (8, 9) in the dogfish and the ray, by Adrian (10) and by Gernandt (11) and by Gernandt and Thulin (12) in the cat, by Eckel (13) in the rabbit, and by Ledoux (14, 15) in the frog. This evidence indicates sensitivity in both directions. Even though it is usually found that the magnitude of the frequency increases is greater than the magnitude of the frequency decreases, the conclusion from this, that the increases produce more vigorous responses than the decreases, is not justified because little is known about how the central mechanism handles the information communicated to it.

Some workers have reported electrophysiological
fish, Steinhausen (22) in the pike, Vilstrup (23) in the circular canals. This has been shown by Breuer (19) dominately unidirectional, sensitivity in single semicircular canals. These procedures have consistently produced evidence observations which are not in agreement with the accepted general picture (16-18).

Stimulation of individual receptors in exposed labyrinths. These procedures have consistently produced evidence favoring the theory of unidirectional, or at least predominately unidirectional, sensitivity in single semicircular canals. This has been shown by Breuer (19) and Ewald (20) in the pigeon, Maxwell (21) in the dogfish, Steinhausen (22) in the pike, Vilstrup (23) in the shark, Szentagothai (24) in the cat and the dog, and Fluur (25) in the cat.

The theory of predominately unidirectional sensitivity is commonly called “Ewald’s second law,” having regard to Ewald’s experiments published in 1892 (20), although the theory of completely unidirectional sensitivity was formulated by Brown in 1874 (26).

Unilateral labyrinthectomy or cutting the eighth nerve. These procedures have been carried out in humans (7, 27-31), cats (32, 33), dogs (3, 34), albino rats (35), guinea pigs (36), pigeons (20, 37), frogs (20, 30), salamanders (39), fish (21, 40), and many other species. When caloric or rotatory tests of the horizontal canal of the intact ear have been made a week or two after the operation they have uniformly indicated defective responses to angular acceleration toward the operated side, and in many cases they have indicated a complete lack of response to acceleration in this direction. Tests performed a longer time after the operation have indi-
the intact ear, but postrotatory nystagmus after a rotation toward the operated ear is readily elicited; this has been interpreted to support the theory of unidirectional sensitivity in the intact animal (37), but in these animals the vestibular nuclei were lacking the normal resting bombardment from the operated side. In Ewald's "pneumatic hammer" experiment the horizontal canal was shown to produce more vigorous responses to ampullopetal endolymph displacement than to ampullofugal endolymph displacement (20); in this experiment the labyrinth being tested had been violated and was exposed to the hammer during testing. Caloric stimulation of the labyrinths of pigeons indicated that the canals receive in both directions with no reported inequality (45), and Dohlman (46) showed, in pigeons, that when the reception of a single horizontal semicircular canal was blocked by deformation of the ampulla the other horizontal canal produced rotatory and postrotatory nystagmus "uniform in both directions." In these last two experiments the labyrinth producing the responses was intact and the vestibular centers were not disturbed.

**Directional Sensitivity of Single Horizontal Semicircular Canals: Present Work**

The sensitivity of a semicircular canal is commonly determined indirectly by measuring the duration of the nystagmus produced by a standard stimulus; the longer the duration the more sensitive the canal. A canal equally sensitive to acceleration in both directions is one which provokes nystagmus of equal duration after equal stimuli in opposite directions.

The animals in which all six canals were plugged had no postrotatory nystagmus after rotation in any plane. Those in which only the horizontal canals were plugged had no postrotatory nystagmus after rotation in the plane of the horizontal canals, but the durations of postrotatory nystagmus after rotary and vertical spins were only slightly different from the preoperative values. Similarly, those animals in which all the canals were plugged, except the two horizontal, had no rotary or vertical nystagmus, but the durations of nystagmus after rotations in the plane of the horizontal canals were essentially the same as preoperatively. This indicates that only the horizontal canals contribute to horizontal nystagmus and that horizontal nystagmus can be taken as a response to stimulation of the horizontal canals.

In the nine cats in which only one of the two horizontal canals was plugged, the remaining horizontal canal in both the first and the second postoperative tests was found to be equally sensitive to angular impulses in the two directions (Fig. 9). This finding was the same regardless of whether the canals plugged included all three of one ear, only the horizontal canal of one ear, or all the semicircular canals except the horizontal canal of one ear. On the other hand, after unilateral labyrinthectomy the duration of nystagmus produced by ampullopetal movement in the remaining horizontal canal was greater than the duration of nystagmus produced by ampullofugal movement, especially in the first postoperative tests (Fig. 9), and an analysis of variance showed that this difference was highly significant. In the single horizontal canals tested after plugging operations, an analysis of variance showed that there was no significant difference between the durations of nystagmus in the two directions; this was obvious from simple inspection of the data. Here, too, the animals with undisturbed vestibular centers exhibited equal sensitivity in the two directions.

**Vertical Semicircular Canals**

It was a remarkable finding that in normal cats the duration of the vertical, ventrally beating nystagmus was consistently greater than the duration of dorsally beating nystagmus after angular impulses equal in magnitude but opposite in direction. After rotation at 12 rev/min this was so in every one of the 30 preoperative tests performed; the mean duration of ventrally beating nystagmus was 13 sec whereas that of dorsally beating nystagmus was only 6 sec. At 30 rev/min the mean durations were 18 and 10 sec, respectively, and the relationship was maintained in 20 of the 30 preoperative tests. In one of the tests the durations were equal and in one other the duration of the dorsally beating nystagmus was the greater.

Mygind (47) mentioned in a paper in 1925 that "...the vertical downwards pointing nystagmus after acceleration upwards lasts about twice as long as the opposite reaction." Our findings confirm Mygind's statement and they also suggest that central factors rather than cupular position determine the duration of postrotatory nystagmus. It is further suggested that single vertical semicircular canals do not produce vertical nystagmus of equal durations after equal but opposite angular impulses. This is in contrast with the findings in the horizontal canals.

The results of the fast tilt tests indicate that the vertical canals normally initiate corrections for fast angular displacements about horizontal axes. The oscillations of the head following plugging of all vertical canals support this contention.

**Otoliths**

The reactions to linear acceleration and to slow angular displacement in the animals which had all six semicircular canals plugged indicates an independence of the receptors of linear acceleration and the receptors of angular acceleration. It has been shown in lower forms of life that reactions to gravity and to linear acceleration are initiated by the otoliths.

**Validity of Surgical Procedures**

It is important to ensure that the surgical procedures accomplish their objectives and nothing more. In this connection the following points should be considered.

1) The operation encroached only upon the canals
themselves, not the ampullae nor the vestibule. It is entirely feasible to plug one canal without approaching within 5 mm of another canal or the vestibule (Fig. a).

2) Plugging the canals does not obstruct the blood vessels to any of the sensory receptors of the labyrinth.

3) No resting or positional nystagmus or tilted posture of the head was ever found after canal-plugging operations; resting nystagmus and a tilted posture of the head were found after every unilateral labyrinthectomy.

4) It was a consistent finding that a plugged canal lost its function permanently and that the other canals were unaffected. Similarly, when all six canals were plugged the function of the otoliths was left intact.

5) Examination of six of the ears, post mortem with the dissecting microscope, revealed in every case that the parts of the labyrinth not directly encroached upon in the operation were of normal appearance. The positions of the lesions were confirmed; holes left by the drill were plugged with calcifying scar tissue having the appearance of bony callus.

Much of the laboratory work in this study was done at the Defence Research Medical Laboratories, Toronto, Canada, under the supervision of Dr. W. H. Johnson.

REFERENCES


5. LEDOUDX, A. C. Oto-Laryngol. 46: 290, 1940.


34. DREYFUS, R. Arch. ges. Physiol., Pflüger's 32: 312, 1893.


42. DREYFUS, R. Arch. ges. Physiol., Pflüger's 32: 312, 1893.