The Otolithic Origin of the Vertical Vestibuloocular Reflex Following Bilateral Blockage of the Vertical Semicircular Canals in the Rabbit

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The influence of bilateral plugs of the anterior and posterior semicircular canals (ASCs, PSCs) on the vertical vestibuloocular reflex (VVOR-0) of the rabbit, oscillated about the longitudinal axis maintained in a horizontal orientation, was studied. Bilateral plugs of either the ASCs or PSCs reduced the gain of the VVOR-0 evoked by stimulus frequencies above 0.005 Hz, but left a residual gain of the VVOR at higher stimulus frequencies that could be attributed to the remaining vertical canals and utricular otoliths. Bilateral plugs of both the ASCs and PSCs totally eliminated the canal component of the VVOR-0, as determined from measurements made when the animal was oriented at 90° (“nose up”) with respect to the earth horizontal axis, eliminating changes in the gravitational vector acting on the utricular maculae (VVOR-90). Bilateral plugs of both the ASCs and PSCs also eliminated the nonlinear increase in gain observed at intermediate frequencies in intact rabbits when oscillated about a supine orientation (VVOR-180). The contribution of the utricular otolith to the VVOR-0 in rabbits with both the ASCs and PSCs plugged was compared with the predicted otolith contribution based on the assumption of linear summation of semicircular canal and utricular signals. The assumption of linear summation appears to be incorrect. Bilateral plugs of the ASCs and PSCs increased the latency and the time constant of vertical eye movements evoked by step-roll stimulation about the longitudinal axis maintained in a horizontal orientation.

In contrast to the horizontal vestibuloocular reflex (HVOR), the normal vertical vestibuloocular reflex (VVOR-0) of the rabbit, evoked by sinusoidal oscillation about the longitudinal axis, which is maintained in a horizontal orientation, has a higher gain (eye velocity/head velocity) and a smaller phase lead (eye position + 180° with respect to head position) at low frequencies of stimulation (Barmack, 1981). The low-frequency characteristics of the VVOR-0 can be attributed to a signal of utricular origin. This signal is modulated by changes in the mediolateral polarization vector of the majority of hair cells of the utricular maculae relative to the gravitational vector. This utricular otolith component of the VVOR-0 can be eliminated by turning

the rabbit 90° to a “nose-up” orientation, so that the longitudinal axis is coaxial with the earth vertical axis (VVOR-90). In this orientation, sinusoidal oscillation of the rabbit about the longitudinal axis does not change the polarization vector of otolith hair cells relative to the gravitational vector (Flock, 1964; Lindeman, 1969; Fernandez and Goldberg, 1976b). The gain and phase of the VVOR-90 are similar to those of the HVOR (Barmack, 1981).

If it is assumed that semicircular canal and utricular otolith signals combine linearly to evoke reflexive eye movements (VVOR-0), then it is possible to obtain an estimate of each of these input signals by vectorially subtracting the output signals under different conditions of vestibular stimulation. If the VVOR-90 (vertical semicircular canal signal) is subtracted from the VVOR-0 (vertical semicircular canal signal + utricular otolith signal), then a derived estimate of the utricular otolith to the VVOR-0 could be obtained. This derived estimate agrees with previous behavioral and electrophysiological experiments, which suggest that the utricular otoliths are sensitive to linear acceleration induced directly by linear translation or by low-frequency lateral tilt (Tait and McNally, 1934; Vidal et al., 1971; Loe et al., 1973; Baarsma and Collewyn, 1975a; Fernandez and Goldberg, 1976a, c).

Previously, the contribution of the utricular otoliths to eye movements has been evaluated by employing sinusoidally modulated linear accelerations (Baarsma and Collewyn, 1975a). However, it is technically difficult to test the effects of very low frequencies of linear acceleration (0.005–0.020 Hz) on eye movements, where the gain of the otoliths should be greatest (Barmack, 1981). Furthermore, this method of stimulation assumes that the semicircular canals would not be stimulated by linear accelerations, an assumption that may be questioned in view of the apparent sensitivity to linear accelerations of primary afferents that originate from the semicircular canals (Estes et al., 1975; Goldberg and Fernandez, 1975; Perachio and Correia, 1983).

The technique of canal plugging offers the possibility of studying the contribution of the utricular otolith to the VVOR-0 without the confounding influence of signals originating from the vertical semicircular canals. This technique also has an advantage over the techniques of sectioning branches of the vestibular nerve (Owada and Shiizu, 1960; Owada et al., 1960; Janeke et al., 1970; Fluor and Siegborn, 1974) or of making partial labyrinthectomies (Baarsma and Collewyn, 1975b; Igarashi et al., 1977) in that, at least in principle, the canal plugging operation should eliminate stimulus-modulated primary afferent signals, but should not change the spontaneous level of primary afferent discharge originating from the plugged canals.

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Previously it has been demonstrated that reflex responses to linear acceleration remain intact following plugging of all 3 pairs of semicircular canals (Money and Scott, 1962). Plugs of all 6 semicircular canals did not abolish nystagmus evoked by constant velocity rotation about an earth horizontal axis (Correia and Money, 1970), suggesting that this residual nystagmus was of otolith origin. Alternatively, it has been proposed that "barbeque nystagmus," evoked in human subjects by constant velocity rotation about an earth horizontal axis (Benson and Bodin, 1966), might be attributed, in part, to a sensitivity of the semicircular canals to linear acceleration (Steer, 1967; Young, 1967; Estes et al., 1975; Goldberg and Fernandez, 1975). Previously, we have demonstrated a low-frequency (0.01–0.10 Hz) gain enhancement of the VVOR-180 (supine orientation) (Barmack, 1981, 1987). It was suggested that this low-frequency enhancement might be attributable to a nonlinear central interaction between signals of semicircular canal and otolith origin. The technique of semicircular canal plugging offers an opportunity for studying the possible contribution of semicircular canal signals to the low-frequency gain enhancement of the VVOR-180.

In the present experiment we have used the technique of canal plugging to study the relative contributions of the anterior and posterior semicircular canals (ASCs and PSCs) to the VVOR-0. By plugging the vertical canals separately and together, it was possible to study the independent contributions of each of the canals and the utricular otoliths to the VVOR-0. More specifically, by plugging the ASCs and PSCs independently, we have studied the effects of removing a stimulus-modulated signal from each pair of vertical semicircular canals on the VVOR-0, VVOR-90, and VVOR-180. We have also compared the VVOR-0 in rabbits without vertical semicircular canal function with previous estimates of the utricular component of the VVOR-0 derived from separate measurements of the VVOR-0 and VVOR-90.

Materials and Methods

Preparatory surgical procedures. Thirty-six pigmented rabbits, weighing 1.0–2.0 kg, were the subjects in this experiment. In preparatory operations the rabbits were fitted with a dental acrylic head plug that permitted head restraint of the rabbits during vestibular stimulation and eye movement recording, as previously described (Barmack, 1988).

Plugging operations of the semicircular canals. Rabbits were anesthetized with halothane or ketamine hydrochloride (50 mg/kg), xylazine (6 mg/kg), and acepromazine maleate (1.2 mg/kg). The surgical approach to the middle ear and the plugging procedures were similar to those described previously (Barmack, 1988). For ASC plugs, exposure of the bony canal was achieved by removing the incus, which inserts on a bony fin separating the ampullae of the horizontal semicircular canal (HSC) and ASC. The opening was then enlarged anterodorsally. The PSC was exposed by enlarging the middle ear cavity posteroventrally. Because the PSC lies below the bony surface of the middle ear cavity, it was also necessary to open the facial canal and remove a segment of the facial nerve. A dental burr was used to make an opening about 1 mm posterior to and slightly above the bony promontory of the round window. The membranous portion of the posterior canal appeared as a distinctly darker outline after about 0.8 mm of the overlying bone had been removed by the dental burr. The vertical semicircular canals were plugged using small silver spindles (Barmack, 1988). The approximate locations of the plugs of the ASC and PSC are illustrated in Figure 1. Postoperatively, the rabbits were maintained for 1 week with daily intramuscular injections of penicillin G (50,000 U/kg) and prednisolone (6 mg/kg).

Post-mortem measurements of the circumferences and planes of orientation of each of the bony semicircular canals and otolith maculae were made in 3 rabbits. The planes of orientation were measured using available bony landmarks. The circumferences of the semicircular canals

were measured by inserting fine platinum–iridium wires (80 μ m in diameter) through openings in each of the bony semicircular canals and threading these wires around each of the semicircular canal "circuits," including the utricular segment. The wires were then withdrawn and their lengths measured. An x-ray photograph of a temporal bone of a rabbit shows such wires threaded into place in each of the canals (Fig. 1B). For purposes of illustration, small silver pellets were inserted into each of the ampullae to mark its relative location.

Eye position recording. Eye position was measured with an infrared light projection technique, as described previously (Barmack, 1988).

Vestibular stimulation. Rabbits were mounted with heads fixed at the center of rotation of a triaxial, servocontrolled rate table. The longitudinal axis of the table could be oriented horizontally (prone, VVOR-0), vertically ("nose-up," VVOR-90) or horizontally, but inverted ("supine," VVOR-180). During vestibular stimulation, the vision of both eyes of the rabbit was occluded by 3 layers of black cloth.

The gain (G) of the VVOR was measured as described previously from records of stimulus and eye velocity (Barmack, 1988). The phase of the VVOR-0, VVOR-90, or VVOR-180 was measured at each half-cycle of rotation (eye position + 180° with respect to head position). At stimulation frequencies below 0.02 Hz, 2 cycles of stimulation were usually measured. At frequencies above 0.04 Hz, 3 or more cycles were usually measured.

Results

Measurement of the planes and circumferences of the semicircular canals

The plane of the utricular macula lies approximately within the plane of the HSC. However, this gross anatomical description must be qualified by the microanatomical observation that the macular surface is curved, not planar (Flock, 1964; Lindeman, 1969). The saccular macula forms a dorsoventral angle of 12° and a posterior–anterior angle of 15° relative to the sagittal plane. Like the utricular macula, it also has a curved surface. The plane of the ASC forms an angle of 95° with respect to the plane of the HSC and an anterior–posterior angle of 50° with respect to the sagittal plane. The PSC forms a posterior–anterior angle of 42° relative to the sagittal plane. Of particular interest in these measurements were the length of the bony duct extending from the ampullae of the HSCs and ASCs to the utricular macula and the length of the common crus shared by the ASC and PSC. The funnel-shaped ampullo-utricular bony duct is about 2.2 mm long, and is illustrated in Figure 1A as a single membranous entity, although the exact location of the confluence of the membranous HSC and ASC has not been determined. The mean circumferences of the semicircular canals were as follows: HSC, 14.3 mm; ASC, 19.2 mm; and PSC, 14.7 mm. The relatively larger circumference of the ASC is consistent with indirect measurements of the semicircular canals of the cat and human, but not of the guinea pig (Curthoys et al., 1977).

Qualitative evaluation of bilateral plugs of the semicircular canals

There were no obvious postural disturbances or nystagmus following plugging of pairs of semicircular canals. However, following bilateral plugging operations, if the head of a rabbit was displaced by a transient external force, the head oscillated for a few seconds in a plane that was indicative of the deficit produced by the plugged semicircular canals. When the ASCs were plugged, external perturbations caused a rolling oscillation of the head. Following bilateral plugs of the PSCs, external perturbations caused more of a nodding movement of the head. These oscillations could be evoked only during the first 48 hr following the plugging operation.

Figure 1. Location of plugs of the semicircular canals relative to the membranous and bony labyrinths of the rabbit. *A*, Membranous labyrinth; the locations of the plugs of the ASCs and PSCs are indicated by arrows. *B*, X-ray photograph of a temporal bone of a rabbit taken from approximately the same perspective as in *A*. Fine wires were threaded into each of the semicircular canals and silver pellets were placed in the 3 ampullae. *ac*, *hc*, *pc*, Ampullae of anterior, horizontal, and posterior semicircular canals; *s*, saccule; *u*, utricle; *cc*, common crus; *rw*, round window.

Figure 2. VVOR-0 before and after bilateral anterior semicircular canal plugs. The VVOR-0 was evoked by oscillation of the rabbit about the longitudinal axis, which was maintained in a horizontal orientation. D_t , table onto right side; D_e , downward movement of the right eye.

Effects of bilateral plugs of either the ASCs or PSCs on the VVOR-0

Plugs of the ASCs and PSCs reduced the gain of the VVOR-0 at all frequencies tested, but this reduction was greatest at frequencies above 0.01 Hz (Fig. 2). The reduction in gain was accompanied by an increased phase lag in the VVOR-0 at 0.005–0.040 Hz (Fig. 3). At stimulus frequencies above 0.02 Hz, this relative phase lag of the VVOR-0 decreased, and at stimulation frequencies above 0.10 Hz, the phase lag of the VVOR-0 developed into a lead that exceeded the preplug values. The relative phase lead at frequencies above 0.10 Hz for rabbits with plugs of the PSCs was not significantly different from the phases recorded prior to the plugging operations. The residual low-frequency gain of the VVOR-0 following bilateral plugs of

either the ASCs or PSCs could undoubtedly be attributed to the otolith organs, which remained intact. At a stimulus frequency of 0.005 Hz, there was no reduction in the gain of the VVOR-0 caused by bilateral plugs of either the ASCs or PSCs. The peak acceleration at the stimulus frequency 0.01 deg/sec^2 was near the threshold for the semicircular canals (Barmack, 1981). The residual gain of the VVOR-0 at frequencies of stimulation above 0.10 Hz could be attributed primarily to the intact pair of vertical semicircular canals (ASC or PSC).

Effects of bilateral plugs of both the ASCs and PSCs on the VVOR-0

The VVOR-0 was measured in 5 rabbits in which both the ASCs and PSCs were plugged. These operations were performed in 2 stages. First, the ASCs were plugged, and subsequently the PSCs

Figure 3. Comparison of the effects of bilateral plugs of the ASCs and PSCs on the VVOR-0. The VVOR-0 was measured in 4 rabbits before (filled triangles) and after (open triangles) bilateral plugs were made in the PSCs, and before (filled circles) and after (open circles) bilateral plugs were made in the ASCs of nine rabbits. One standard deviation is illustrated for each data point, unless the SD was smaller than the range encompassed by the data point, in this and subsequent figures.

Figure 4. Comparison of the effects of bilateral plugs of the ASCs and bilateral plugs of the ASCs + PSCs on the VVOR-0. Bilateral ASC plugs were made in 7 rabbits. Preoperative and postoperative results are indicated by filled and open circles, respectively. After postplug measurements of the VVOR-0 were made, a second operation was performed in which the PSCs were also plugged bilaterally, and the VVOR-0 was measured again (filled triangles).

were plugged. After the ASCs were plugged, the gain and phase of the VVOR-0 were similar to the values previously measured (Figs. 3, 4). There was a residual gain of 0.20–0.30 at higher stimulus frequencies, accompanied by a decreased phase lag. When the ASCs and PSCs were plugged, the higher-frequency gain was attenuated and there was a larger phase lag (Fig. 4).

Effects of bilateral plugs of the ASCs and PSCs on the VVOR-90

The extent of the residual semicircular canal contribution to the VVOR-0 could be determined by measuring the VVOR-90, since the gravitational vector acts orthogonally to the polari-

Figure 5. Comparison of the effect of bilateral plugs of the ASCs and of the ASCs + PSCs on the VVOR-90. The VVOR-90 was evoked in 6 rabbits by oscillation about the longitudinal axis while the rabbits were maintained at 90° with respect to earth horizontal ("nose-up"). The VVOR-90 was measured before (filled circles) and after (open circles) bilateral plugs were placed in the ASCs. A second operation, in which the PSCs were also plugged bilaterally, was performed and the VVOR-90 was measured again (filled triangles). Plugs of the ASCs + PSCs completely abolished reflexive eye movements in the VVOR-90 orientation.

Figure 6. Comparison of the effects of bilateral plugs of the ASCs and of the ASCs + PSCs on the VVOR-180. The VVOR-180 was evoked in 6 rabbits by oscillation about the longitudinal axis while the rabbits were maintained in a supine orientation. The VVOR-180 was measured before (*filled circles*), and after (*open circles*) bilateral plugs were placed in the ASCs. A second operation, in which the PSCs were also plugged bilaterally, was performed and the VVOR-180 was measured again (*filled triangles*). Note that the gain of the VVOR-180 was similar to the gain of the VVOR-0 (Fig. 4) when both the ASCs and PSCs were plugged.

zation vector of hair cells of both the utricular and saccular maculae when the rabbits are oscillated about the longitudinal axis and maintained in the "nose-up" orientation. Consequently, rotation of the rabbit in the "nose-up" orientation does not change the gravito-inertial forces acting on otolith hair cells. The gain of the VVOR-90 of rabbits with plugged ASCs was reduced and the phase lead increased in comparison with the

VVOR-90 of normal rabbits (Fig. 5). However, when the ASCs and PSCs were plugged, the gain of the VVOR-90 was reduced to 0.00 at all frequencies tested (Fig. 5).

Effects of bilateral plugs of the ASCs and PSCs on the VVOR-180

The gain of the VVOR-180, evoked by sinusoidal rolls about the earth horizontal axis in the supine orientation, was enhanced in rabbits with unplugged semicircular canals over a range of frequencies (0.01–0.10 Hz) relative to the gain of the VVOR-0 evoked by the same sinusoidal rolls about the earth horizontal axis in the prone orientation (Barmack, 1981). Since the supine orientation alters the relative phase of signals originating from the utricular otoliths and the vertical semicircular canals, this gain enhancement was attributed to a nonlinear interaction between these signals. If this argument was correct, then plugs of the vertical semicircular canals should have eliminated the gain enhancement observed for oscillation about the supine orientation. The appearance of the gain enhancement was confirmed in the present experiment (Fig. 6). Bilateral plugs of the ASCs abolished the gain enhancement, but left a residual high-frequency response. Bilateral plugs of both the ASCs and the PSCs attenuated the residual high-frequency gain. The remaining gain of the VVOR-180 was similar to the gain of the VVOR-0. The phase of the VVOR-180 for rabbits with bilateral plugs of both the ASCs and PSCs was comparable to the phase measured for the same rabbits of the VVOR-0 if one subtracted 180° from each value of phase measured for the supine orientation.

Step-roll stimulation of rabbits with bilateral plugs of the ASCs and PSCs

The effect of combined plugs of the ASCs and PSCs on the latency and dynamics of the vertical eye movements evoked by step-roll stimulation about the longitudinal axis was studied in

Figure 7. Responses to step-rolls about the prone orientation before and after combined plugs of the ASCs and PSCs. *A*, Superimposed traces were obtained from R86 before and after plugs of the ASCs + PSCs were placed. *B*, Computer-averaged responses were obtained from R89 before and after plugs of the ASCs + PSCs were placed. Note the increased latencies and time constants of the responses of the plugged rabbits. The upper traces of each set are responses recorded from the right eye. The lower traces indicate the table position (inverted) relative to the right eye. The arrows indicate the onset of a small initial response in the same direction as the table movement.

Figure 8. Comparison of estimates of utricular otolith function with VVOR-0 evoked in rabbits with bilateral plugs of the ASCs and PSCs. Estimates of otolith function were obtained by vectorial subtraction of the VVOR-90 from the VVOR-0 in two separate groups of rabbits. The data from 9 rabbits (*dashed* and *dotted* lines) were obtained from Barmack (1981) (Fig. 7). Additional data from 6 rabbits (*dashed* lines) were obtained in the present experiment. These estimates of otolith function are compared with the VVOR-0 measured in 7 rabbits with bilateral plugs of the ASCs and PSCs.

3 rabbits. Using 20° steps with mechanical time constants of 70–100 msec, eye movements were evoked in normal rabbits at latencies of less than 20 msec. The time constant of these reflex responses could not be measured accurately because of the limitations of the frequency response of the rate table (Fig. 7, *A, B*). Following bilateral plugs of the ASCs and PSCs, the latencies of step-evoked vertical eye movements were increased to a mean of 143 msec ($n = 3$); the time constants of the responses were increased to a mean of 135 msec ($n = 3$), and the mean gains of the evoked eye movements were reduced by 45%. Curiously, the compensatory step-evoked vertical eye movements in the vertical canal-plugged rabbits were preceded by small (less than 1°), anticomensatory eye movements, which were completely masked in the normal rabbits by the short-latency responses that originated in the vertical semicircular canal. It is possible that these small, anticomensatory eye movements reflected inertial responses of the utricular otoliths (Appendix 1).

Discussion

Semicircular canal geometry in the rabbit

Plugs of either the ASCs or PSCs were equally effective in reducing the gain of the VVOR-0 over the range of frequencies tested in the present experiment. This might have been anticipated on the basis of the geometric measurements of the vertical semicircular canals. The anterior–posterior angle of the ASCs and the posterior–anterior angle of the PSCs were 50° and 42°, respectively, in relation to the sagittal plane. These measurements must be qualified by the fact that both the semicircular canals deviate from toroidal geometry. In particular, the PSC does not conform to a single plane. Furthermore, the diameter of the semicircular canals increases by at least 50% near the ampullae. Also, the exact conformations of the ampullo-utricular duct and the common crus are difficult to determine. This may be the reason that these components of the semicircular canals were excluded in previous attempts to measure the ori-

entation of the semicircular canals of rabbits (Ezure and Graf, 1984). It may also account for discrepancies of 5° for the sagittal orientation of the ASC and 16° for the sagittal orientation of the PSC between our results and previous measurements. Such deviations in geometry make it difficult to draw inferences concerning functional planes for semicircular canals based exclusively upon anatomical measurements. In fact, physiological estimates of functional planes of these semicircular canals deviate by as much as 10° from planes predicted by anatomical measurements in the cat (Estes et al., 1975). That both the ASCs and PSCs contribute equally to the VVOR-0 seems evident (Fig. 3). In the present experiment we did not determine the optimal plane of response for each of the vertical canals, primarily because of the technical limitations imposed by our methods of vestibular stimulation (only 2° of freedom) and of recording eye movements (horizontal and vertical, but not torsional).

Validity of the technique of semicircular canal plugging

There can be little doubt that the membranous semicircular canals were compressed by the plugs used in this experiment so as to totally impede the flow of endolymph. The correct location of each of the plugs was confirmed by postmortem visual inspection. Using a potentially more traumatic technique of canal plugging, in which both the bony and membranous semicircular canals were opened with a dental drill and subsequently filled with “bone dust,” other investigators have noted no significant decrease in the spontaneous activity of secondary vestibular neurons in animals that had received plugs of all 3 semicircular canals on one side (Abend, 1978). Previously, we have demonstrated that the changes in reflex function caused by the plugging procedure that we have used are reversible if the plugs are removed within 48 hr after their initial placement. Furthermore, we demonstrated that, at the light-microscopic level, there was no evident damage to the ampullae of the semicircular canals even if the plugs were left in place for 30 d (Barmack, 1988). In the present experiment, bilateral plugs of the ASCs and PSCs

appeared to have left otolith function intact. At the lowest stimulus frequency, 0.005 Hz, which is near threshold for the semicircular canals (Barmack, 1981), the gains of the VVOR-0 or VVOR-180 were within the range of the preplug gains (Figs. 3, 4, 6). If the labyrinth or vestibular nerve is damaged unilaterally, a spontaneous nystagmus, with the slow phase directed toward the side of the damage, is the immediate consequence (Baarsma and Collewijn, 1975b). This nystagmus is caused by a reduction of spontaneous primary afferent activity from the damaged side. If a semicircular canal plug caused damage to the ampulla of the plugged canal, then a similar nystagmus, with the slow phase toward the plugged side, should appear immediately upon recovery from anesthesia.

Interactions of signals of semicircular canal and otolithic origins

One of the principal reasons for conducting the present experiment was to examine the assumption that signals of otolithic and semicircular canal origin combine linearly to produce the VVOR-0. This assumption is clearly incorrect. Over the frequency range of 0.01–0.10 Hz, the measured gain of the otolith component of the VVOR-0 of rabbits with bilateral plugs of both the ASCs and PSCs was lower than predicted. The prediction was based on the assumption that the otolith component of the VVOR-0 could be obtained by subtracting the VVOR-90 (canal signal) from the VVOR-0 (semicircular canal + otolith signal) (Fig. 8). Although there is reasonable agreement between the predicted and measured phases of the otolith component of the VVOR-0, there is a big discrepancy between the predicted and measured gains, particularly in the frequency range over which both otolith and semicircular canal signals overlap. These data imply that there must be a significant central convergence and nonlinear interaction between vertical semicircular canal and otolith signals. This central nonlinear convergence leads to an overestimate of otolith gain in the normal rabbit (Fig. 8) and may also account for the nonlinear gain enhancement observed in normal rabbits during oscillation about the supine orientation (VVOR-180), which was eliminated by plugs of the ASCs and PSCs (Fig. 6).

Functional role for the utricular otoliths in the VVOR-0 compared with primary afferent physiology

The present experiment demonstrates that the otolith contribution to the VVOR-0 is largely restricted to a range of stimulus frequencies to which the semicircular canals are only marginally sensitive (0.005–0.100 Hz). The Bode plot for the VVOR-0 of rabbits with bilaterally plugged ASCs and PSCs had a peak gain of 0.38 at 0.005 Hz, and the gain decreased with increasing frequency to 0.08 at 0.100 Hz. This decrease in gain was accompanied by an increasing phase lag; from -3° at 0.005 Hz to -98° at 0.80 Hz. These dynamic characteristics would not be predicted from electrophysiological recordings from either primary or secondary otolith afferents. Primary otolith afferents have been divided into 2 categories, “regular” and “irregular,” based on the coefficient of variation of spontaneous discharge (Fernandez et al., 1972; Fernandez and Goldberg, 1976c). Both classes of primary otolith afferent have a relatively stable gain over a frequency range of DC–2.00 Hz. At higher stimulus frequencies, the “irregular” units evince a frequency-dependent gain enhancement. Although “regular” units

evince small frequency-dependent increases in phase lag, “irregular” units are characterized by frequency-dependent increases in phase lead (Fernandez and Goldberg, 1976c; Anderson et al., 1978). The dynamic gain characteristics of secondary vestibular neurons in cats with plugged semicircular canals are similar to “irregular” primary otolith afferents (Schor, 1974). The dynamic characteristics of otolith inputs to trochlear motoneurons have been inferred by vectorially subtracting the responses to sinusoidal rotation in yaw (stimulation of the HSCs) from the responses to roll (vertical semicircular canals and utricular otoliths) (Blanks et al., 1978). Although this analysis is subject to the same criticism—that it assumes a linear interaction of otolith and semicircular canal inputs—the dynamic characteristics ascribed to otolith inputs to trochlear motoneurons are similar to the dynamic characteristics of the VVOR-0 for rabbits with plugs of the ASCs and PSCs, described above. Thus, it appears that the dynamic characteristics of vestibuloocular reflexes that are dependent on otolith inputs reflect the central processing of otolith signals rather than the characteristics of primary vestibular afferents. Interestingly, in spite of the similarity of the dynamic characteristics of these 2 primary afferent populations, and in spite of the convergence of otolith and semicircular canal primary afferents at the level of the vestibular nuclei, the central processing of otolith and semicircular canal information must be sufficiently distinct and separate to account for the observed differences in the dynamic characteristics of the vestibuloocular reflexes driven by these inputs. This means that the otolith information that contributes to the VVOR-0 must undergo some “low-pass” filtering in the CNS, and that the information originating from the semicircular canals is not exposed to this process.

Appendix I

The inertial torque generated at the utricular maculae would be trivial relative to the sheer forces produced by gravity for most frequencies of head movement. However, for higher frequencies of stimulation, this might not be true. Gravitational forces can be described by

$$f = g \cdot v(d_u - d_c),$$

where g is gravitational acceleration (981 cm/sec^2), d_u the density of the utricular otoliths, d_c endolymph density, and v the volume of otoliths. The precise value of $g(d_u - d_c)$ is not known for the utricular otoliths of the rabbit (for estimates of d_u , d_c , and v for the cat, see Vidal et al., 1971), but it can be considered as its effective mass, m . The force created by gravity acting on this mass would be

$$f = g \cdot m.$$

For angular tilts from prone orientation, α , the sheer force F_s is

$$F_s = g \cdot m \sin \alpha.$$

The moment of inertia of the utricular otolith would be

$$I = m \cdot R^2.$$

R is the radius of gyration for the effective mass of the utricular otolith, m . Because, in the present experiment, the planes of the utricular otoliths could not be perfectly aligned with the axis of rotation, the radius of gyration was large, $R = 1.4 \text{ cm}$. The inertial torque T generated at the utricular otolith would be

$$T = m \cdot R^2 \cdot \omega,$$

where ω is the head angular acceleration in rad/sec. The total sheer force F_s acting at the utricular otolith would be

$$F_s = g \cdot m \sin \alpha - m \cdot R^2 \cdot \omega.$$

For the 20° symmetrical steps about the prone orientation, peak angular accelerations of 15 rad/sec were generated. These steps would generate inertial torques T that would amount to about 10% of the oppositely directed sheer force induced by gravity, F_s . At the onset of a step-roll, ω would be at a maximum and α at a minimum. It should be mentioned that comparably high inertial torques have not been studied in electrophysiological experiments in which the activities of primary or secondary otolith afferents were recorded (Vidal et al., 1971; Loe et al., 1973; Schor, 1974; Fernandez and Goldberg, 1976a–c).

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