Physiology of Peripheral Neurons Innervating Otolith Organs of the Squirrel Monkey. I. Response to Static Tilts and to Long-Duration Centrifugal Force

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SUMMARY AND CONCLUSIONS

1. The response to static tilts was studied in peripheral otolith neurons in the barbiturate-anesthetized squirrel monkey (Saimiri sciureus). Each unit was characterized by a functional polarization vector, which defines the axis of greatest sensitivity. A circumstantial criterion was used to assign units to the inferior (IN) or superior (SN) vestibular nerves. The former neurons should innervate the saccus, the latter mainly the utriculus. Confirming past experiments, the polarization vectors for SN units lay near the plane of the utricular macula, those for IN units near the plane of the saccular macula. The polarization vectors for IN units were compared in two groups of animals. In one group, the vestibular nerve was intact; in the other, the superior nerve was sectioned. No differences were found and this, together with other observations, demonstrate that the saccus in mammals functions mainly (if not solely) as an equilibrium organ.

2. The resting discharge of otolith neurons averages some 60 spikes/s, the sensitivity some 30-40 spikes/s-g. IN units tend to have slightly lower sensitivities than do SN units. IN units with upwardly directed (+Z) vectors have substantially higher resting discharges than do units with downwardly directed (-Z) vectors. The +Z units are also characterized by more linear force-response relations.

3. There is a strong positive relation between the resting discharge and sensitivity of units characterized by regular steady-state discharge patterns. A weaker, but statistically significant, relation is demonstrable for irregular units. It is suggested that the relation seen in regular units is the result of the neurons differing from one another in terms of a receptor bias, a transduction gain, or both. Only the mechanism based on transduction gain is thought to be operative among the population of irregular units.

4. Centrifugal-force trapezoids were used to study the response adaptation to prolonged stimulation. Adaptation was more conspicuous in irregular units and was characterized by perstimulus response declines and poststimulus secondary responses. For regular units, adaptive properties were similar during excitatory and inhibitory responses. For irregular units, response declines were larger during excitatory stimuli, secondary responses larger following inhibitory stimuli. Typically, response declines were most rapid at the start of the force plateau. A few units, all of them irregular, exhibited a delayed adaptation with response declines beginning only after a constant force had been maintained for 10-20 s.

5. Excitatory responses of regular units are almost always larger than inhibitory responses. This is so during both the dynamic and static portions of force trapezoids. A similar asymmetry is seen in the dynamic response of irregular units; static response asymmetries of the latter units are more variable.

INTRODUCTION

Recent physiological studies of the peripheral vestibular system have been largely devoted to an investigation of the discharge characteristics of neurons related to the semicircular canals (4, 6, 14, 15, 26, 28). From these studies we now have a reasonably comprehensive picture of the kinds of information provided by canal afferents to central pathways. Much less is known concerning the physiology of otolith neurons. Work in mammals has, for example, been almost entirely concerned with the response to static tilts (3, 9, 13, 20, 35). Even here there are discrepancies. Fernández et al. (9), working in the squirrel monkey, were able to distinguish two classes of neurons. One group was assigned to the superior vestibular nerve and, hence, was considered as mainly innervating the utriculus. The other group was assigned to the inferior nerve and presumably was made up of saccular afferents. The two groups were found to differ in their...
functional polarization vectors and in their resting discharges and sensitivities. In contrast, Loc et al. (20) found only one class of neurons in a similar study in the cat.

The main purpose of the present experiments was to study the response of otolith neurons to precisely controlled centrifugal forces. The use of centrifugal force made it possible to vary both the magnitude and direction of the stimulus and also to investigate the time course of the response. In order to perform the experiments, though, it was first necessary to define the functional polarization vectors of individual units and, as in past experiments (9, 20), static tilts were used. The results of the static tilt tests confirmed the presence of two classes of neurons. To determine whether one of the groups indeed arose from the sacculus, unit activity was recorded in some animals after transection of the superior nerve. This paper will summarize these observations and will also describe the adaptive properties and response asymmetries of the neurons. A second paper (7) will consider their directional selectivity and force-response relations. A third paper (8) will describe the response of the afferents to sinusoidal forces and, on this basis, provide a quantitative formulation of the neurons' response dynamics.

METHODS

Eighty-six adult male squirrel monkeys (Saimiri sciureus), anesthetized with sodium pentobarbital (15 mg/kg), provided useful data. Body temperature was maintained at 36–38°C. Surgical and recording procedures have been previously described (14). The left vestibular nerve was exposed by removal of the posterior part of the cerebrum and a small portion of the cerebellum. In five animals, a sharpened hook was used to transect the superior vestibular nerve as it exits the internal auditory meatus; the completeness of the transection was assured by the visualization of the auditory and inferior vestibular nerves. The vestibular nerve was left intact in the remaining animals. The ncv was covered with a 3% solution of agar-agar dissolved in physiological saline and a chamber mounted over the exposure. The chamber was filled with mineral oil. The microelectrode—a glass micropipette filled with 3 M NaCl—was advanced by means of a screw micrometer mounted atop the chamber. The animal was placed in a superstructure mounted on guide rails which, in turn, were fixed to the horizontal platform of a rotating device (Fig. 1). The superstructure was positioned so that the animal's head was centered 1 ft off the rotation axis of the horizontal platform. The animal could be pivoted in the superstructure around pitch, roll, or yaw axes. The motion of the rotating device was controlled by a velocity servomechanism (Inland model 823). Linear forces were introduced by means of static tilts and centrifugal forces. In the centrifugal-force experiments, force trapezoids were used (Fig. 2). The five periods of the trapezoid (T1–T5) were characterized as follows. A background velocity $V_b = 90°/s (= 0.077 g)$ was maintained during T1 and T5. During T3, the velocity was held at a higher value $V_f$. During the transition periods T2 (and T4) the velocity increased (decreased) in such a way that the centrifugal force changed in a linear manner. Unless stated otherwise, T2 and T4 were 5 s and $V_f = 360°/s (= 1.23 g)$.

Single-unit signals were led from the electrode to a negative-capacitance preamplifier and then to an AC amplifier operated at a gain of 100 and a bandwidth of 100–3,000 Hz. The signals passed from the rotating device via slip rings to an additional filter and then to an oscilloscope. Action potentials were discriminated from background noise by the oscilloscope trigger circuit, the latter emitting a "unit" pulse during the rising phase of each action potential. The unit pulses and synchronizing marks were led on-line to a...
FIG. 2. Response of rotating device during force trapezoid. A: velocity (tachometer) profile. Bottom horizontal line, zero velocity. Background velocity (T1 and T5), 90°/s. Peak velocity (T3), 360°/s. Command signal to servomechanism obtained by adding constant voltage to trapezoidal waveform and then passing summed signal through an analog square-root device. B: force profile obtained by passing tachometer signal (A) through analog squaring device. Bottom line, zero force. Background force, 0.077 g. Peak force, 1.23 g. During force transitions (T2 and T4), force changes linearly. T2 = T3 = T4 = 5 s.

pulse-interval timer interfaced to a PDP-8 computer. Data were temporarily stored in computer memory and then transferred onto an IBM-compatible tape. The tape served as the input for off-line computations programmed on an IBM 370/168 computer.

As a preliminary step, the response of each unit to angular accelerations and to head tilts was examined. Neurons innervating any particular semicircular canal were easily identified because they responded to angular accelerations when the plane of the canal was brought into the plane of motion. Units were considered otolith neurons if they proved unresponsive to angular accelerations, but were sensitive to head tilt (see ref 16 for more details). Once an otolith neuron was identified, its response to pitches and rolls was studied. First, the animal was placed in the horizontal (prone) position and a 10-s sample of activity recorded. The animal was then manually tilted through successive increments around the roll axis until the horizontal position was regained. This was followed by a sequence of tilts about the pitch axis. Increments were either 45° or 90°. Each tilt required 5–15 s to complete. After a waiting period, a 10-s sample was recorded in the new position. The waiting period varied. In early experiments, it was always 30 s; in later experiments, the period was determined by the adaptive properties of the unit. If the unit showed little adaptation, only a 10-s wait was allowed. In units characterized by moderate adaptation, 30–60 s was permitted. Finally, in units exhibiting severe adaptation, the animal was returned to the horizontal position after each tilt; here waiting periods were 60 s. The adequacy of any particular procedure was assessed by comparing discharge rates obtained on successive returns to the horizontal position. Usually the rates agreed to within 5%.

The tilt data were used to compute a functional polarization vector and this vector, in turn, was used to align the animal during centrifugal force experiments. In a relatively few units (see Table I), dynamic responses were so large that reliable estimates of the polarization vectors could not be obtained; the alignment for these neurons was determined by noting the sign and magnitude of the dynamic responses to motions around the two tilt axes.

FORCE EQUATIONS AND ANIMAL ALIGNMENT

Here we review the equations needed to compute a functional polarization vector from static-tilt data (for more details, see ref 9) and also present those used in the alignment of the animal during centrifugal-force presentations.

Take the head-coordinate scheme of Fig. 3. The animal's horizontal (or xy-) plane coincides with the average plane of the two horizontal semicircular canals. By convention, the zero-tilt position is such that the animal is horizontal (prone) with its nose pointing towards the rota-
tion axis of the horizontal platform. Assume that each unit can be characterized by a polarization vector \( f = (x,y,z) \) of unit length. Let the animal be rotated in the superstructure from the zero-tilt position. The rotation can be described by a yaw angle \( Q \), a pitch angle \( P \), and a roll angle \( R \). Positive values of \( Q \) correspond to counterclockwise yaws (as viewed from above), positive values of \( P \) to forward pitches, and positive values of \( R \) to leftward (ipsilateral) rolls. By convention, yaws are performed first, rolls last.

The rotation will result in the transformation of a fixed-force vector in the head-coordinate system. The effective force \( F \) for the neuron may be taken as the scalar product of the transformed force vector and \( f \). The gravity vector \( g = (0,0,-1) \), after transformation, leads to

\[
F = x \sin R \cos P - y \sin P - z \cos R \cos P
\]

For the centrifugal-force vector \( c = (0,c,0) \), the effective force is

\[
F = c[x \cos R \sin Q + \sin R \sin P \cos Q] + y \cos P \cos Q + z \sin R \sin Q - \cos R \sin P \cos Q)
\]

If the response is a linear function of \( F \), then the discharge \( d \) will be given by

\[
d = sF + d_0
\]

where \( s \) is a sensitivity factor (the maximum response expected to a 1-g acceleration) and \( d_0 \) a resting (zero-force) discharge.

Equations 1 and 3 can, as shown in ref 9, be used to compute estimates of \( s \), \( d_0 \), and \( f \) from static-tilt data. Here it need only be mentioned that \( d_0 \) is obtained by averaging discharge rates for tilts 180° apart. Equation 2 can then be used to determine the values of \( Q \), \( P \), and \( R \) required to align \( f \) and \( e \), i.e., to maximize the effective centrifugal force. For fixed \( R \), the appropriate equations are

\[
\tan P = (x \sin R - z \cos R)/y
\]

and

\[
\tan Q = [(x \cos R + z \sin R)/y] \cos P
\]

If \( y \cos Q > 0 \), \( e \) and \( f \) should be parallel and a centrifugal force should result in a maximum excitatory response. The corresponding inhibitory position is obtained by yawing the animal 180°. Equations 4 and 5 can be solved for any value of \( R \). Hence, \( R \) is a free parameter and can be set to meet auxiliary conditions.

**Classification of Neurons**

Otolith neurons will be classified in terms of the presumed end organ each of them innervates and also on the basis of the regularity of their discharge patterns.

**Assignment of units to superior and inferior vestibular nerves**

Neurons in the posterior part of Scarpa’s ganglion contribute to the inferior vestibular nerve and innervate the posterior canal and the sacculus. Cells located more anteriorly give rise to the superior nerve and supply, besides the utriculus and anterior third of the sacculus, the horizontal and superior canals (12, 27). As in a previous paper (9), a circumstantial criterion was used in assigning otolith neurons to one or the other nerves. Units were assigned to the superior nerve if they were immediately preceded and/or followed in the same puncture by superior- or horizontal-oral canal units. Units preceded by posterior-canal neurons were assigned to the inferior nerve. Under the following conditions, no assignment was made: 1) no canal neurons were encountered in the puncture; 2) posterior-canal neurons followed, but did not precede, the otolith neuron; or 3) the puncture was anomalous in that superior- or horizontal-oral canal units were found after posterior-canal units had been encountered. Only 7 of 133 punctures were anomalous. As expected, only posterior-canal and otolith neurons were obtained after section of the superior nerve.

Table 1 summarizes the assignment of 335 otolith neurons on which the study is based. Included are 23 inferior-nerve units obtained in the cut-nerve preparation.

**Regularity of discharge patterns**

The simplest way to characterize the regularity of discharge in a population of units would be to compare their coefficients of variation (CVs)—the ratios of the standard deviation of intervals to the mean interval—at a single firing frequency. This is not possible because the discharge rates of different otolith neurons need not overlap. A more complicated procedure has to be adopted. Static-tilt data were used to construct CV distributions for six standard intervals, ranging from 7.5 to 32.5 ms in steps of 5 ms. One such distribution, that for 17.5 ms, is presented in Fig. 4. Every unit was assigned a per-

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**TABLE 1. Assignments of units**

<table>
<thead>
<tr>
<th>Class</th>
<th>Superior Nerve</th>
<th>Inferior Nerve</th>
<th>Unassigned</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regular</td>
<td>100</td>
<td>76</td>
<td>58</td>
<td>234</td>
</tr>
<tr>
<td>Intermediate</td>
<td>5</td>
<td>9</td>
<td>5</td>
<td>19</td>
</tr>
<tr>
<td>Irregular</td>
<td>38</td>
<td>32</td>
<td>12</td>
<td>82*</td>
</tr>
<tr>
<td>Total</td>
<td>143</td>
<td>117</td>
<td>75</td>
<td>335</td>
</tr>
</tbody>
</table>

* Includes three units for which formal static-tilt tests were not done.
The equations used in the treatment of static-tilt data minimize the asymmetry by overestimating the resting discharge. When the estimated resting discharge is suitably corrected, the force-response curves for static tilts and centrifugal force are brought into close agreement (Fig. 5C).

One of the force-response relations in Fig. 5C was obtained by varying the direction of a fixed force (gravity) relative to the head, the other by varying the magnitude of a centrifugal force acting along a single axis. The similarity of the two curves would imply, as has been assumed (equations 1 and 3 and ref 9), that the effectiveness of an arbitrarily directed force is given by its scalar product with the unit’s polarization vector. In a subsequent paper (7), an exception to this rule is described, viz., that forces directed perpendicular to the functional polarization vector may cause an excitatory response.

**RESULTS**

**Response to static tilts and centrifugal force**

The response of a regular otolith unit to static tilts is presented in Fig. 5A. Discharge rates obtained on pitching or rolling the animal are reasonably approximated by the trigonometric functions derived from equations 1 and 3. The one discrepancy is a response asymmetry. Excitatory responses are slightly larger than inhibitory responses. The asymmetry is more obvious in the response to force trapezoids (Fig. 5B). There are two reasons for this. First, the asymmetry becomes larger, the greater the effective force. For the static-tilt series, the maximum effective force was 0.71 g; that for force trapezoids, 1.23 g. Second, the equations used in the treatment of static-tilt data minimize the asymmetry by overestimating the resting discharge. When the estimated resting discharge is suitably corrected, the force-response curves for static tilts and centrifugal force are brought into close agreement (Fig. 5C).

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**Distribution of polarization vectors**

Most of the vectors for superior-nerve (SN) units lie near the horizontal plane (Fig. 6A, B). Inferior-nerve (IN) neurons have vectors located near the sagittal plane (Fig. 6E). This is so not only for IN units assigned to the inferior nerve on the basis of a circumstantial criterion, but also for units obtained after the superior nerve had been cut. The SN and IN vector populations are almost orthogonally related to one another. The SN vectors, when projected onto a coronal plane, form a median angle with the horizontal plane of 8.6° (Fig. 6B, arrows) and 76.1% of the vectors fall within ±30° of this angle. The corresponding values for the IN units are 10.8° (Fig. 6E, arrows) and 77.4%. The results suggest that the utricular macula is inclined in a dorsolateral-ventromedial direction by 5-10° from the horizontal plane and that the saccular macula is tipped dorsomedially-ventrolaterally by 15-20° from the sagittal plane. The saccular alignment was confirmed in dissected specimens.

Another difference between the two classes of units can be seen by comparing the distributions of their vectors within the corresponding macular planes. The SN vectors have a wide distribution within the plane of the utricular macula (Fig. 6C), whereas the IN units have a preferred dorsoventral orientation within the plane of the saccular macula (Fig. 6D). These observations are in concordance with the morphological polarization maps for the two maculae (Fig. 6, bottom left and right). One discrepancy between the morphological and physiological results concerns the proportion of SN units characterized by +X vectors. Such units, which are activated by ipsilateral tilts and should innervate the medial part of the utricular macula, occur with a
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FIG. 5. Response of unit 204-8, a regular SN unit, to static tilts (A) and to force trapezoids (B). A: solid circles and solid curve, rolls; open circles and dashed curve, pitches. Positive tilt angles, leftward (ipsilateral) rolls and forward pitches. Curves based on equations 1 and 3. B: solid and open points, respectively, excitatory and inhibitory force trapezoids. In this and subsequent figures, bars denote periods of force transition (T2 and T4). C: force-response relations. Solid points, force trapezoids; response based on difference between average rate during 5-s force plateau (T3) and resting discharge obtained with rotating device motionless. Open points, static tilts; resting discharge corrected for response asymmetry. Curve based on equation 7.

greater frequency than would be anticipated solely on the basis of an areal comparison of the two parts of the macula. The +X units comprise 75.5 ± 3.6% of the entire sample of SN units. In contrast, the medial part of the macula was estimated (9) to occupy 60.4 ± 1.3% of the end organ.

The vectors obtained from unassigned (UN) neurons (Fig. 6F) suggest that they represent an admixture of SN and IN units. Given the great differences in the vector distributions of SN and IN units, it seemed reasonable to reassign the UN units solely on the basis of their vectors. UN units with vectors lying within ± 30° of the horizontal plane were assigned to the SN class, those with vectors within ± 30° of the sagittal plane were placed with the IN units. Units not meeting either criterion remained unassigned.

Resting discharge and sensitivity

Table 2 summarizes data derived from static-tilt tests. For most groups, the resting discharge ($d_0$) is near 60 spikes/s and the sensitivity ($s$) is some 30–40 spikes/s-g. There is a small (approximately 10 spike/s) difference in the sensitivities of SN and IN units; the difference is statistically significant (two-tailed $t$ test modified for unequal variances, $P < 0.001$). A more striking difference concerns the resting discharge of regular IN units. Units characterized by +Z vectors have a higher resting discharge than do units with -Z vectors. There are two consequences of this difference. First, the two kinds of IN units have similar discharge rates in the zero-tilt position, even though this is near the position of maximum excitation for -Z units and of maximum inhibition for +Z units. Second, the differences in discharge rates at 180° are larger than would be anticipated solely on the basis of the two groups having oppositely directed vectors. The 0° mean rates (±SE) for the +Z and -Z units are, respectively, 51.9 ± 2.7 and 68.1 ± 3.7 spikes/s. The corresponding 180° figures are 98.5 ± 5.8 and 30.4 ± 2.1 spikes/s. No obvious differences in resting discharge were seen when irregular IN units with +Z and -Z vectors were compared.

There is a strong positive relation between the resting discharge and sensitivity of regular otolith neurons. Data are summarized in Table 2 by means of the regression equation

$$s = bd_0 + c$$ (6)
TABLE 2. *Resting discharge* \((d_0)\) and *sensitivity* \((s)\)

<table>
<thead>
<tr>
<th>Class</th>
<th>N</th>
<th>(d_0) Mean ± SE</th>
<th>SD</th>
<th>(s) Mean ± SE</th>
<th>SD</th>
<th>(s) vs. (d_0)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regular (all)</td>
<td>234</td>
<td>64.00 ± 1.77</td>
<td>27.07</td>
<td>33.29 ± 1.04</td>
<td>15.86</td>
<td>(r &lt; 0.005; \quad c = 0.54)</td>
</tr>
<tr>
<td>Superior nerve (all)</td>
<td>126</td>
<td>65.27 ± 2.42</td>
<td>27.19</td>
<td>37.22 ± 1.61</td>
<td>18.04</td>
<td>(r &lt; 0.005; \quad c = 0.54)</td>
</tr>
<tr>
<td>Superior nerve (+X, + Y)</td>
<td>58</td>
<td>69.86 ± 4.02</td>
<td>30.34</td>
<td>40.05 ± 2.42</td>
<td>18.24</td>
<td>(r &lt; 0.005; \quad c = 0.54)</td>
</tr>
<tr>
<td>Superior nerve (+X, - Y)</td>
<td>38</td>
<td>60.68 ± 4.65</td>
<td>28.68</td>
<td>37.01 ± 3.44</td>
<td>21.22</td>
<td>(r &lt; 0.005; \quad c = 0.54)</td>
</tr>
<tr>
<td>Superior nerve (-X, + Y)</td>
<td>31</td>
<td>62.43 ± 2.97</td>
<td>16.53</td>
<td>32.27 ± 2.12</td>
<td>11.82</td>
<td>(r &lt; 0.005; \quad c = 0.54)</td>
</tr>
<tr>
<td>Inferior nerve (all)</td>
<td>87</td>
<td>62.49 ± 2.94</td>
<td>27.46</td>
<td>28.61 ± 1.16</td>
<td>10.81</td>
<td>(r &lt; 0.005; \quad c = 0.54)</td>
</tr>
<tr>
<td>Inferior nerve (+Z)</td>
<td>46</td>
<td>75.72 ± 4.20</td>
<td>28.49</td>
<td>31.94 ± 1.77</td>
<td>12.02</td>
<td>(r &lt; 0.005; \quad c = 0.54)</td>
</tr>
<tr>
<td>Inferior nerve (-Z)</td>
<td>41</td>
<td>47.64 ± 2.61</td>
<td>16.74</td>
<td>24.87 ± 1.22</td>
<td>7.83</td>
<td>(r &lt; 0.005; \quad c = 0.54)</td>
</tr>
<tr>
<td>Intermediate (all)</td>
<td>19</td>
<td>57.17 ± 6.51</td>
<td>28.37</td>
<td>34.93 ± 4.03</td>
<td>17.57</td>
<td>(r &lt; 0.005; \quad c = 0.54)</td>
</tr>
<tr>
<td>Irregular (all)</td>
<td>79</td>
<td>58.66 ± 3.75</td>
<td>33.33</td>
<td>26.54 ± 2.20</td>
<td>19.59</td>
<td>(r &lt; 0.005; \quad c = 0.54)</td>
</tr>
</tbody>
</table>

\(a\) Includes 21 UN units. Two-tailed tests: \(b P < 0.005; \quad c P < 0.005; \quad d P < 0.01; \quad e P > 0.05\).

Also included are the product-moment correlation coefficients \((r)\). Highly significant relations are demonstrable for most groups of regular units. Presumably the individual groups represent afferents innervating selected portions of the corresponding maculae (cf. Fig. 6, bottom). A weak, but statistically significant, relation also exists for irregular units.

**Adaptation in response to centrifugal forces**

There was considerable variation among units in their adaptive properties. Some units (Fig. 7A, B) showed only minimal adaptation. In other units (Fig. 7C, D) adaptation was conspicuous and was reflected both by perstimulus response declines and by poststimulus secondary responses. Typically the response decline was rapid at the start of the force plateau and became more gradual as the force was prolonged. A few units, all of them irregular, exhibited a delayed adaptation. In these, response declines began only after the constant force had been maintained for 10–20 s. For the unit illustrated in Fig. 7E, \(F\) such a pattern was evident not only during the perstimulus excitatory response, but also during the secondary response following inhibitory forces.

The degree of adaptation shown by individual units can be related to the regularity of their discharge patterns. Normalized responses are presented in Fig. 8 for populations of regular and irregular units. Consider first the excitatory responses (Fig. 8A, C). Both response declines and secondary responses are larger for irregular units. Similar trends are seen in the inhibitory responses (Fig. 8B, D). The adaptive properties of regular units are similar during excitatory and inhibitory forces. Differences are seen in irregular units: response declines are larger during excitatory forces, secondary responses larger following inhibitory forces.

The adaptive properties of regular units are summarized in Fig. 9. There are strong positive relations between the excitatory and inhibitory response declines exhibited by individual units (Fig. 9A) and also between either excitatory or inhibitory response declines and the succeeding secondary responses (Fig. 9B, C). In all cases, statistically significant relations are obtained when all units are considered together or when the regular units are considered separately. Only in one case is the regression line for the regular units significantly different from that derived from the entire sample. For regular units (Fig. 9C) inhibitory response declines are almost always larger than the subsequent secondary responses. For irregular units, the reverse is true.

**Response asymmetries**

Table 3 compares excitatory and inhibitory responses for regular and irregular units. Force trapezoids were used. Dynamic responses were obtained from T2 = 4–5 s, static responses from

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**FIG. 6.** Functional polarization vectors in polar coordinates; concentric circles and radii, every 30°. Dots and crosses, respectively, vectors pointing toward and away from reader. A–C: vectors for 142 SN units viewed, respectively, from the +X axis (ipsilateral ear), +Y axis (back of head), and +Z axis (top of head). D–E: vectors for 115 IN units viewed, respectively, from +X and +Y axes. Circled points, units obtained after superior nerve sectioned. F: vectors for 75 UN units viewed from +Y axis. Arrows in B and E, respectively, denote median angles of SN and IN units. Bottom left and bottom right, respectively, morphological polarization maps for utricular and saccular maculae (from Lindeman, ref 19). Utricular map: anterior part of macula, upward; lateral part to left. Saccular map: anterior part of macula, upward; lateral part to left. Saccular map: anterior part to left; dorsal part, upward; map is tilted 23° forward from that shown by Lindeman (for discussion of this point, see ref 9).
FIG. 7. Force-trapezoid response histograms for three units. Excitatory responses to left, inhibitory responses to right. T₁ = 20 s, T₃ = 15 = 90 s; bins, 1 s. A, B: unit 208-7 (regular, SN) showing minimal adaptation. C, D: unit 213-28 (regular, UN), moderate adaptation. E, F: unit 206-18 (irregular, IN), delayed adaptation.

T₃ = 55–60 s. Responses were considered approximately equal (E ≈ I) if they did not differ by more than 20%. For most regular units, excitatory responses were larger than inhibitory responses (E > I) during both the dynamic and static portions of the stimulus. A similar situation held for the dynamic responses of irregular units. The static asymmetries for the latter units were more varied, the inhibitory responses being larger (I > E) in almost half the cases. The difference between the dynamic and static response asymmetries of irregular units is related to the fact that their response declines were typically more conspicuous during excitatory forces.

The response asymmetries for regular units can be described (see Fig. 5C) by the equation

\[ d - d_\text{a} = s (F + \alpha F^2) \]  

Here \( d \) is the discharge rate obtained with the force \( F \), \( d_\text{a} \) is the resting discharge, and \( s \) is the sensitivity. \( \alpha \) is a normalized asymmetry coefficient. Polynomial regression was used to

1 Loe et al. (20), working in the cat, described the asymmetries by a power law \( (d-d_\text{a}) = k (F-F_\text{min})^n \). Here \( d_\text{a} \) is the discharge rate in response to an inhibitory force \( F_\text{min} \) near 1 g. A graphical comparison of the power law and equation 7 indicates that the two formulations are virtually identical. The modal value of the exponent \( n \) was reported in the cat to be 1.3, which corresponds to an \( \alpha \) of 0.2–0.3.
FIG. 8. Normalized responses to force trapezoids. Points, means; shading, standard deviations. Normalization obtained by setting excitatory response during T2 = 4-5 s to 0.9. T3 = T5 = 90 s. A and B: excitatory and inhibitory responses, respectively, for 21 regular units. C and D: excitatory and inhibitory responses, respectively, for 14 irregular units.

derive values of $s$, $d_0$, and $\alpha$ from static-tilt data. (The estimates of $s$ are identical to those given by linear regression; those of $d_0$ are reduced by the product $\alpha \sigma$ multiplied by the mean square force.) The values of $\alpha$ for various groups of regular units are presented in Table 4. For most groups, $\alpha$ averages about 0.25, implying that the excitatory response to a 1-g force typically has a magnitude 1.67 times that of the comparable inhibitory response. Only 24 units (10.3%) were characterized by negative values of $\alpha$. The IN (+Z) units are distinctive in having more linear force-response relations than do other groups.

DISCUSSION

Distribution of functional polarization vectors

In a previous paper (9), we found that otolith units assigned to the superior (SN) and inferior (IN) vestibular nerves had quite different polari-
FIG. 9. Comparison between various aspects of adaptation for regular (solid circle) and irregular (open circle) units. Percent response declines measured during T3 = 85–90 s; percent secondary responses during T5 = 0–1 s. Percentages obtained by setting excitatory or inhibitory response during T2 = 4–5 s to 90%. Same neurons and stimuli as in Fig. 8. A: excitatory versus inhibitory perstimulus response declines. B and C: excitatory and inhibitory force trapezoids, respectively. Perstimulus response declines versus subsequent secondary responses. Significance (two-tailed t tests) of all regression lines, P < 0.001. Exception is regression for regular units in C, where P < 0.005.

TABLE 3. Response asymmetries, regular and irregular units

<table>
<thead>
<tr>
<th>Dynamic Responses</th>
<th>Static Responses</th>
</tr>
</thead>
<tbody>
<tr>
<td>E &gt; I</td>
<td>I &gt; E</td>
</tr>
<tr>
<td>(7)</td>
<td>(5)</td>
</tr>
<tr>
<td>(0)</td>
<td>(0)</td>
</tr>
<tr>
<td>(14)</td>
<td>(8)</td>
</tr>
<tr>
<td>E ≈ I</td>
<td></td>
</tr>
<tr>
<td>(3)</td>
<td>(5)</td>
</tr>
<tr>
<td>(0)</td>
<td>(0)</td>
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<tr>
<td>(8)</td>
<td>(8)</td>
</tr>
<tr>
<td>I &gt; E</td>
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<td>(0)</td>
<td>(0)</td>
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<td>*</td>
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<td>*</td>
<td>(2)</td>
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<tr>
<td>*</td>
<td>(2)</td>
</tr>
<tr>
<td>Totals</td>
<td>(2)</td>
</tr>
<tr>
<td>(12)</td>
<td>(13)</td>
</tr>
<tr>
<td>(12)</td>
<td>(12)</td>
</tr>
<tr>
<td>(27)</td>
<td>(29)</td>
</tr>
</tbody>
</table>

Numbers outside parentheses, regular units; numbers inside parentheses, irregular units. Row and column marked by asterisks include units silenced during inhibitory force.

TABLE 4. Response asymmetry coefficients (α), regular units

<table>
<thead>
<tr>
<th>Class</th>
<th>N</th>
<th>Mean ± SE</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regular (all)*</td>
<td>233</td>
<td>.223 ± .012</td>
<td>.189</td>
</tr>
<tr>
<td>SN (all)</td>
<td>126</td>
<td>.271 ± .015</td>
<td>.173</td>
</tr>
<tr>
<td>SN (+X, +Y)</td>
<td>38</td>
<td>.260 ± .018</td>
<td>.134</td>
</tr>
<tr>
<td>SN (+X, −Y)</td>
<td>38</td>
<td>.308 ± .028</td>
<td>.175</td>
</tr>
<tr>
<td>SN (−X, ±Y)</td>
<td>31</td>
<td>.247 ± .040</td>
<td>.225</td>
</tr>
<tr>
<td>IN (all)</td>
<td>86</td>
<td>.176 ± .018</td>
<td>.171</td>
</tr>
<tr>
<td>IN (+Z)</td>
<td>46</td>
<td>.093 ± .020</td>
<td>.135</td>
</tr>
<tr>
<td>IN (−Z)†</td>
<td>40</td>
<td>.272 ± .025</td>
<td>.157</td>
</tr>
</tbody>
</table>

* Includes 21 UN units. † Excludes 1 unit whose discharge was silenced during a portion of the tilt series.
and saccular macula are almost perpendicular to one another. Were the suggestion correct, the utricular macula of the cat would have to be sensitive to shearing forces, the saccular macula to compressional forces. Our results demand that both end organs in the monkey respond to shearing forces. It seems unlikely that the two maculae in a single species would differ so fundamentally in their receptor mechanisms. That the saccular macula in the two species would differ in this way appears an equally remote possibility. The second suggestion was that, in our study, too few data points were used in the vector calculations. Two comments are pertinent. First, since unbiased statistics were employed, the number of data points should influence the variance of the statistical estimates but not their central tendencies. Hence the use of too few data points could only serve to blur the distinction between the vectors derived from SN and IN units. Second, quite precise estimates can be obtained even with tilt increments of 45° or 90°. The expected error, expressed as the angle between the estimated and true vectors, can be shown theoretically to be on the order of 2–5°.

The problem was also explored empirically. Here we used units in which static-tilt data were obtained at 45° increments. Vectors were calculated from the original data set and from points 90° apart. The difference between the vectors obtained from the two calculations was typically 1.5° and never amounted to more than 5°. Little precision, it would appear, is purchased by increasing the number of data points. One suggestion not considered by Loe and his colleagues is that they failed to record from saccular afferents. These fibers occupy the ventroposterior margin of the vestibular nerve (12, 27) and, unless a special effort is made to record from them, they could easily be missed.

Some 75% of the SN units encountered were activated by ipsilateral tilts, 25% by contralateral tilts. The two groups of units are presumed to innervate, respectively, the medial and lateral parts of the utricular macula. The preponderance of ipsilaterally activated (+X) units can only be partly explained on morphological grounds. The pars medialis is estimated to comprise some 60% of the macula (9). The two parts of the macula have a similar density of hair cells (19). There is no evidence that the two regions differ in the density of their afferent innervation. Possibly our sampling methods were biased. But a similar preponderance of +X units has been seen in most microelectrode studies of the mammalian vestibular nerve (3, 9, 20) and vestibular nuclei (1, 11, 25). In any case, the preponderance is consistent with the oculomotor responses obtained upon stimulation of the entire utricular nerve (2, 30, 32) and with the postural and oculomotor asymmetries resulting from unilateral section of the nerve (5, 17, 18, 24, 31, 33, 34).

The present study demonstrates that the mammalian saccus is an equilibrium organ. Two other observations indicate that this is its main (if not sole) function. First, relatively few of the units encountered in the vestibular nerve are unresponsive to angular accelerations or head tilts. The proportion of unresponsive units is no larger in the inferior branch of the nerve, than it is in the superior branch. Second, we have studied the responsiveness of peripheral vestibular neurons to air-borne sound and to head vibrations (Young, Fernández, and Goldberg, unpublished observations). Some of the units respond to intense stimuli of this kind. However, the otolith (including saccular) afferents show no particular sensitivity in this regard when compared to fibers innervating the semicircular canals.

**Response adaptation**

Lowenstein and Roberts (21), in their study of otolith neurons in the isolated labyrinth of the ray, observed that units could show a response adaptation. Macadar et al. (22), using a similar preparation, divided utricular units into phasic, phasic-tonic, and tonic categories. Phasic units responded only during transitions from one tilt position to another; the discharge of tonic units was solely determined by instantaneous head position. Phasic responses and adaptation have also been described for neurons in the mammalian vestibular nerve (35) and vestibular nuclei (1, 23, 29). The great majority of units encountered in the present study can be considered phasic-tonic in the sense that they exhibited some adaptation but did respond in a sustained manner to maintained linear forces. In regular units, tonic response components dominated. Phasic responses were more conspicuous in irregular units. Even the latter units, though, were characterized by tonic responses. Indeed, the static sensitivities of regular and irregular units were similar (see Table 2). As will be shown in a later paper (8), the main difference between the two groups is the greater phasic sensitivity of the irregular units.

Similarities exist between the adaptation observed in mammalian otolith neurons and that previously described for semicircular-canal neurons (4, 14, 15). In both cases, adaptation is greater for irregular units and is characterized by perstimulus response declines and poststimulus secondary responses. One difference concerns a comparison between the adaptation obtained on excitatory and inhibitory stimulation. For canal neurons, inhibitory response declines and the
following secondary responses are larger than their excitatory counterparts. The results for otolith neurons are more complicated. Response declines are, particularly in irregular units, more conspicuous during excitatory forces, secondary responses larger following inhibitory forces.

**Resting discharge, sensitivity, and response asymmetries**

In a previous paper (9) we reported that SN units tended to have higher sensitivities and resting discharges than did IN units. The conclusion concerning sensitivities receives some support in the current study (Table 2). On the other hand, no differences in the mean resting discharges of SN and IN units were observed in the larger, and presumably more representative, sample presented here.

One finding, made possible by the larger sample, was that regular IN units with +Z vectors have higher resting discharges than do those with −Z vectors. The former units most likely innervate the superior part of the saccular macula, the latter the inferior part of the macula. The difference could be explained were the hair cells in the two parts of the macula in a similar excitatory state when the head was near the zero-tilt position. Introduction of a resting (or zero-force) condition will unload the saccular otolith and result in its moving upward with respect to the animal's z axis. The hair cells with +Z vectors will be biased in an excitatory direction, those with −Z vectors in an inhibitory direction. The discharge rates of the corresponding afferents, which are similar in a horizontal position, will diverge. A variation in the zero-force bias may also help to explain why the +Z units have more linear force-response relations.

In a later paper (7) evidence will be presented indicating an inverse correlation between the excitatory bias of an afferent and its response asymmetries.

The difference in the resting discharges of IN units may have functional consequences. The saccule is unique among vestibular end organs in being nearly maximally stimulated when the head is held motionless in an upright position. If the two populations of saccular afferents had the same resting discharge, their average background discharge in the zero-tilt position would differ by some 45 spikes/s. This conceivably could cause a tonic imbalance in motor systems which, like the oculomotor pathways (10), receive antagonistic influences from the two parts of the macula. The differences in resting discharge reduce the disparity in background activity to on the order of 15 spikes/s. The disparity is reduced to virtually negligible amounts in the normal head position, presumed to be 30° nose downward from zero-tilt.

The present study confirms past observations (9, 15) that there is a positive relation between resting discharge and sensitivity for regular units and demonstrates that a similar, though weaker, relation exists for irregular units. Two mechanisms may be responsible. The first involves the concept of a receptor bias. Consider the regular units. Their force-response relations almost always have a concave upward shape in the ± 1-g range (see Fig. 5C). As a result, excitatory responses are larger than inhibitory responses. Also, if the end organ is mechanically biased in an excitatory direction, there should be a simultaneous increase in the background discharge and sensitivity of the afferent. Such bias effects have been observed in both canal (36) and otolith units (8) in the squirrel monkey. A similar covariation in the resting discharge and sensitivity would be expected in a population of neurons if they had similar force-response curves but differed in their bias under zero-force conditions. The biasing of a particular afferent could conceivably be related to the zero-force deflection of the corresponding sensory-hair bundles.

A bias mechanism may be operative in regular units, but not in irregular units. Concerning the latter, detailed force-response relations are lacking. But, as the present study shows, static response asymmetries varied from unit to unit (Table 3). Biasing experiments in irregular units indicate that, in most cases, changing the background discharge has little effect on sensitivity (8, 36). In a few cases, reversed bias effects are seen (8). Here increasing background discharge is correlated with a decreased sensitivity. The lack of a consistent bias effect in irregular units may explain the weakness of the relation between resting discharge and sensitivity observed in these neurons.

The second mechanism involves the notion of a transduction gain. It may be imagined that two afferents would have the same zero-force receptor bias, yet differ in their sensitivities. The gain characterizing a particular unit might be related to several factors, e.g., the sensitivity of the receptor cells to a given degree of sensory-hair deflection, the amount of transmitter released at each synapse, the number and spacing of synapses contacted by the afferent, and the relation between postsynaptic depolarization and firing rate. Regardless of precise mechanisms, variations in transduction gain among a population of units should result in parallel changes in resting discharge and sensitivity and, hence, in a positive relation between the latter two variables. This explanation, unlike that involving a receptor bias, does not depend on the force-response curve being concave upward or having any other particular shape.

The relation between resting discharge and
sensitivity, as seen in regular neurons, may be due to variations among the population in a receptor bias and a transduction gain. For irregular units, it may be suggested that only the second mechanism is operative. Even among regular units, it is unclear as to what are the relative contributions of the two factors. This would depend on the variance of each of the factors within the population. To cite an extreme example, all units might have the same transduction gain. Then variations in resting discharge and sensitivity, as well as the relation between the two, would depend solely on differences in receptor bias. The problem is considered in the next paper (7).

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