Physiology of Peripheral Neurons Innervating Otolith Organs of the Squirrel Monkey. II. Directional Selectivity and Force-Response Relations

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SUMMARY AND CONCLUSIONS

1. The directional selectivity of peripheral otolith neurons was studied in the barbiturate-anesthetized squirrel monkey (Saimiri sciureus). Each unit's most sensitive axis was characterized by a functional polarization vector. The direction of a centrifugal force was varied with respect to the vector and to the macular plane. The neurons respond in an excitatory manner to shearing forces orthogonally disposed to the vector. The sensitivity to orthogonal shears was usually 10–15% of the sensitivity to parallel shearing forces. There was no significant response to orthogonal compressions, nor did compressions modify the response to shearing forces.

2. Force-response functions were obtained in the stimulus range of ±4.92 g. Forces were directed parallel to each unit's polarization vector. The functions are sigmoid shaped and possess both inhibitory and excitatory plateaus. The presumed physiological range of ±1 g is represented in the lower (concave upward) portion of the function and has a dynamic range, expressed in terms of response magnitude, amounting to 20–40% of the potential dynamic range of the neuron.

3. There was considerable variation among units in their ±4.92 g force-response curves. The salient features of the functions are described by three factors, tentatively identified as a transduction gain, a receptor bias, and a mechanical gain. Both the resting discharge (d₀) and the ±1 g sensitivity (s₀) vary in the same direction with changes in the factors related to transduction gain and receptor bias. It is shown that this covariation provides a quantitatively precise explanation for the positive relation between d₀ and s₀.

INTRODUCTION

Two complementary ideas have dominated thinking concerning the directional selectivity of hair-cell systems. The first, stemming from Breuer (3), is that hair cells respond to shearing displacements of the accessory structure, rather than to traction or compression. Evidence for this notion comes from studies of the effects of direct mechanical stimulation of the end organ (23, 25–27), from measurements of otolith displacements in response to shearing and compressional forces (4), and from a consideration of the functional polarization vectors characterizing otolith afferents (6, 7). The possibility that compressional forces could modify the response to shearing forces, though it has been suggested (2, 14, 28), has not been tested experimentally. The second idea, the so-called Lowenstein-Wersäll (22) hypothesis, is that there is a connection between the morphological and functional polarization of hair cells. Specifically, shearing displacements of the sensory hair bundle directed toward the kinocilium are presumed to be excitatory, oppositely directed displacements inhibitory. Support for the hypothesis comes from studies of the semicircular canals (11, 22), the otolith organs (6, 7), and lateral-line systems (8, 13). It is commonly assumed, as an extension of the hypothesis, that the effectiveness of a force is determined by its component acting along the polarization axis (6–8, 13, 20). Shearing forces directed orthogonal to this axis should then be ineffective. But in actual fact studies in lateral-line organs indicate that such forces have an excitatory effect (8, 13). One purpose of the present study was to investigate the directional selectivity of otolith neurons. We were particularly interested in determining the influence of orthogonal shears on afferent discharge and in ascertaining whether compressional forces, if ineffective in themselves, could modify the response to shearing forces.

Another purpose was to extend the analysis of force-response relations, previously restricted to stimuli in the ±1 g range (6, 7, 20), to forces of ±5 g. An extension of the input-output curve was considered of intrinsic interest.
motivation arose from a proposal, made in the preceding paper (6), concerning the positive relation observed in regular units between the resting discharge and the sensitivity to 1-g forces. It was suggested that two factors might be involved, a receptor bias and a transduction gain. The receptor bias, it was further hypothesized, was related to the position of the sensory-hair bundles under zero-force conditions, while the transduction gain was thought to determine the relation between the position of the hairs and the discharge of the afferent. The rationale for studying the extended force-response relation was as follows. Two units differing only in receptor bias might be supposed to have identical force-response relations except for a translation along the horizontal or stimulus axis. A difference in transduction gain would be reflected in the two units having force-response relations also differing by a vertical scaling factor. It was hoped that a multiple-regression analysis would provide a means of identifying the contributions made by each of the factors in determining the resting discharge, the sensitivity, and the relation between the two.

A preliminary report has been presented (12).

**METHODS**

**Directional selectivity**

Centrifugal-force trapezoids (cf. ref 6, Fig. 2) with peak forces of 1.23 g were used. Periods of force transition (T2 and T4) were 5 s. The other periods—T1, T3, and T5—were all either 5 or 20 s. Responses were measured as the difference between the average discharge rate occurring during the force plateau (T3) and the background discharge, the latter measured when the rotating device was motionless.

Three kinds of centrifugal force were studied. Parallel forces were in the same direction as the unit’s polarization vector \( f = (x,y,z) \) and resulted in either maximum excitation or maximum inhibition. Orthogonal-shear forces were directed at right angles to \( f \), but lay close to the plane of the corresponding macula.

![Directional selectivity for unit 213-27. Response to force trapezoids, T1 = T3 = T5 = 20 s. In this and subsequent figures, bars denote periods of force transition. A: Parallel excitatory (solid circle) and inhibitory (open circle) forces. Animal alignment: roll (R), 0°; pitch (P), 0°; yaw (Q) = 190° (excitation) or 10° (inhibition). B: Orthogonal-shear forces. R = 0°, P = 0°, Q = 100° (solid circles) or 280° (open circles). C: orthogonal-compression forces. \( R = 0°, P = 90° \) nose down, \( Q = 0° \) (solid circles) or 180° (open circles). D: shearing forces. \( R = 0°, P = 0°, Q \) as stated. E: force-response relations, animal in normal (open circle) or inverted (closed circle) positions.](http://jn.physiology.org/)

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**FIG. 1.** Directional selectivity for unit 213-27. Response to force trapezoids, T1 = T3 = T5 = 20 s. In this and subsequent figures, bars denote periods of force transition. A: Parallel excitatory (solid circle) and inhibitory (open circle) forces. Animal alignment: roll (R), 0°; pitch (P), 0°; yaw (Q) = 190° (excitation) or 10° (inhibition). B: Orthogonal-shear forces. R = 0°, P = 0°, Q = 100° (solid circles) or 280° (open circles). C: orthogonal-compression forces. \( R = 0°, P = 90° \) nose down, \( Q = 0° \) (solid circles) or 180° (open circles). D: shearing forces. \( R = 0°, P = 0°, Q \) as stated. E: force-response relations, animal in normal (open circle) or inverted (closed circle) positions.
Orthogonal-compression forces were directed at right angles to f and were also near perpendicular to the macula. Superior-nerve (SN) units were assumed to innervate the utricular macula; inferior-nerve (IN) units, the saccular macula.

The alignment procedures were as follows. The coordinate scheme may be found in Fig. 3 of the preceding paper (6). The roll angle $R_o$ was chosen by

$$\tan R_o = -xz/(y^2 + x^2) \quad (la)$$

or

$$\tan R_o = (y^2 + z^2)/xz \quad (lb)$$

Equation 1a was used for SN units, equation 1b for IN units. The pitch ($P_o$) and yaw ($Q_o$) angles for parallel forces were then determined by (see ref 6)

$$\tan P_o = (x \sin R_o - z \cos R_o)/y \quad (2)$$

and

$$\tan Q_o = [(x \cos R_o + z \sin R_o)/y] \cos P_o \quad (3)$$

Equations 1a and 1b assure that, during alignment, the corresponding macula is as close to a horizontal position as is consistent with equations 2 and 3. The values of $R_o$ and $P_o$ were chosen so that gravity acted in a downward direction on the macula. (For pitch, roll and yaw conventions, see ref 6.)

To obtain orthogonal-shear forces, $R$ and $P$ were kept constant and the yaw changed to one of two positions, $Q = Q_o + 90^\circ$ or $Q = Q_o - 90^\circ$. Responses were studied in both orthogonal positions. If the two responses were simply due to a misalignment of the animal—i.e., to an error in the original estimate of f—then they should cancel. A pure yaw will not affect the background discharge. Further, the macula should remain in a near-horizontal position and the shear component of the orthogonal force should predominate over compression.

In some units, other nonparallel shearing forces were studied. This was accomplished by varying $Q$, usually in steps of $30^\circ$.

Orthogonal-compression forces were obtained by keeping $R = R_o$, by setting $P = P_o \pm 90^\circ$ and $Q = 0^\circ$ or $180^\circ$. This maneuver brings the macula into a near-vertical position, almost perpendicular to the centrifugal-force axis. Of the two permissible values of $P$, that one was chosen which resulted in the higher background discharge. Responses were studied in the two orthogonal positions, corresponding to $Q = 0^\circ$ and $Q = 180^\circ$.

The effect of orthogonal-compression forces on the response to concomitant parallel forces was also studied. Here the response to parallel centrifugal forces was compared when $R_o$ (equations 1a and 1b) was set so the gravity first acted in a downward direction and then in an upward direction on the end organ. In the first position, the otolithic membrane should compress the macula; in the second position, traction should be exerted.

Extended force-response relations

Centrifugal-force trapezoids were used. The periods T1–T4 were all set to 5 s, T5 to 50 s. The animal was aligned so that the centrifugal-force and polarization vectors were either parallel (the excitatory position) or antiparallel (the inhibitory position). Discharge rates cited are the averages for the 5-s force plateau (T3). Inhibitory forces, ranging from 1.23–4.92 g in steps of 1.23 g, were presented in ascending order. This was followed by an identical sequence of excitatory forces. If the unit remained isolated, the excitatory sequence was filled in with forces which were odd multiples of 0.615 g and then the inhibitory sequence was filled in similarly. Resting (zero-force) discharge rates were determined by taking 10-s samples of activity with the rotating device motionless; typically four such samples were obtained, including one at the beginning and one at the end of the experiment.

RESULTS

All units included in this paper had regular discharge patterns. Directional selectivity was studied in 25 units, extended force-response relations in 17 units. Nine units contributed to both studies. The units were chosen because they showed minimal adaptation (cf. Fig. 7 A, B, ref 6).

Directional selectivity

Figure 1 presents results from an SN unit whose polarization vector consisted almost entirely of a $-Y$ component. (That is, the unit was excited by nose-down pitches, inhibited by nose-up pitches. Rolls were ineffective.) The animal was first aligned so that the polarization and centrifugal-force vectors were parallel (Fig. 1A). Maximum excitatory forces led to considerably larger responses than did maximum inhibitory forces. The effect of orthogonal shears was studied by yawing the animal $\pm 90^\circ$ from the maximum excitatory position (Fig. 1B). An average excitatory response (OR$_e$) of some 10 spikes/s was obtained; this amounted to 33% of the average response (PR) to parallel excitatory and inhibitory forces. The similarity of the responses in the two orthogonal positions precludes their arising from a misalignment error. In a more complete yaw series (Fig. 1D), excitatory responses were observed for shear forces subtending an angle of $225^\circ$, rather than the antici-
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Extended force-response relations

Figure 2 presents the responses of an SN unit to centrifugal forces in the extended range of \( \pm 4.92 \, g \). The discharge rate returns to background levels within a few seconds following termination of even intense stimuli. This, together with the reproducibility of the responses, indicates that the large forces used did not have a deleterious effect. The input-output function (Fig. 2E) is sigmoid shaped and is characterized by an inhibitory saturation. Intense inhibitory forces do not reduce firing below a minimum (or residual) discharge of 17 spikes/s. Evidence of saturation can also be seen in the individual responses to inhibitory forces (Fig. 2D). As the force increases, the peak of the inhibitory response moves earlier into the ascending portion of the force trapezoid. There is also a suggestion of an excitatory saturation near 300 spikes/s, though this feature was more clearly seen in other units (cf. Fig. 3). The inflection point of the function does not occur at zero force, but rather is displaced in an excitatory direction by some 2.5 g. As a result, the presumed physiological range of \( \pm 1 \, g \) is represented in the lower, or concave upward, portion of the function. This has two consequences. First, the sensitivity around zero force (\( s_0 \)) is only some 40% of the sensitivity around the inflection point (\( s_{\text{max}} \)). Second, there is a conspicuous response asymmetry. The excitatory responses continue to grow as force is increased (Fig. 2A), whereas relatively modest forces in the opposite direction lead to inhibitory saturation (Fig. 2C).

Table 1 summarizes data for all 17 units. The residual discharge (\( d_{\text{res}} \)) was typically 5–20 spikes/s; the values for individual units were uncorrelated with other aspects of their discharge. Other discharge rates, including the resting dis-
FIG. 3. Force-response relations for six units. Arrows mark inflection points. A: units 204-8 (solid circles) and 224-39 (open circles). The two curves are similar, except that the solid curve is shifted to the right by 1.0 g. B: units 226-23 (solid circles) and 213-27 (open circles). The two curves are similarly located along the horizontal axis and could be brought into concordance by first subtracting $d_{res}$ and then multiplying the lower curve by a vertical scaling factor of 2.0. C: units 226-71 (solid circles) and 226-79 (open circles). Here the two curves differ mainly in their steepness; they could be virtually superimposed, provided that the horizontal scale for the solid curve was expanded by a factor of 1.6.

charge ($d_0$) and the discharge rate at the inflection point ($d^*$), are expressed as differences from $d_{res}$. The location of the inflection point ($g^*$) was always to the excitatory side of zero force. The sensitivity ($s_0$) was usually 40–70% of $s_{max}$. The dynamic range for ± 1 g forces (DR = $2s_0$) was

TABLE 1. Force-response relations

<table>
<thead>
<tr>
<th>Unit</th>
<th>$d_{res}$, Spikes/s</th>
<th>$d_0 - d_{res}$, Spikes/s</th>
<th>$s_0$, Spikes/g · s</th>
<th>$s_0$/$s_{max}$</th>
<th>$\alpha$</th>
<th>$g^*-g$</th>
<th>DR/PDR</th>
<th>$X_1$, Spikes/s</th>
<th>$X_2$, $g^*$/$D&amp;G_{norm}$</th>
<th>$X_3$, $D&amp;G_{norm}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>204-8 (SN)</td>
<td>17.60</td>
<td>20.75</td>
<td>28.13</td>
<td>.398</td>
<td>.420</td>
<td>.212</td>
<td>148.2</td>
<td>2.70</td>
<td>0.876</td>
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<tr>
<td>204-25 (SN)</td>
<td>12.60</td>
<td>47.30</td>
<td>38.37</td>
<td>.241</td>
<td>.401</td>
<td>.250</td>
<td>185.8</td>
<td>2.13</td>
<td>0.977</td>
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<tr>
<td>213-11 (IN)</td>
<td>10.70</td>
<td>20.70</td>
<td>10.24</td>
<td>.192</td>
<td>.677</td>
<td>.262</td>
<td>355.5</td>
<td>0.83</td>
<td>1.408</td>
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<tr>
<td>213-27 (SN)</td>
<td>27.80</td>
<td>12.55</td>
<td>24.07</td>
<td>.489</td>
<td>.548</td>
<td>.305</td>
<td>72.8</td>
<td>2.43</td>
<td>0.644</td>
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<td>220-8 (IN)</td>
<td>5.80</td>
<td>34.15</td>
<td>40.81</td>
<td>.376</td>
<td>.606</td>
<td>.294</td>
<td>129.2</td>
<td>1.18</td>
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<td>221-17 (IN)</td>
<td>9.20</td>
<td>52.85</td>
<td>26.83</td>
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<td>.767</td>
<td>.283</td>
<td>90.5</td>
<td>1.00</td>
<td>1.12</td>
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<tr>
<td>222-35 (SN)</td>
<td>4.60</td>
<td>30.10</td>
<td>28.21</td>
<td>.347</td>
<td>.377</td>
<td>.220</td>
<td>146.1</td>
<td>2.36</td>
<td>0.936</td>
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<tr>
<td>224-33 (SN)</td>
<td>2.00</td>
<td>28.35</td>
<td>23.25</td>
<td>.241</td>
<td>.467</td>
<td>.217</td>
<td>139.2</td>
<td>2.36</td>
<td>1.28</td>
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<tr>
<td>274-30 (SN)</td>
<td>18.30</td>
<td>52.30</td>
<td>38.05</td>
<td>.348</td>
<td>.603</td>
<td>.344</td>
<td>127.8</td>
<td>1.28</td>
<td>1.036</td>
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<tr>
<td>226-23 (SN)</td>
<td>23.10</td>
<td>43.58</td>
<td>43.58</td>
<td>.345</td>
<td>.524</td>
<td>.298</td>
<td>170.6</td>
<td>1.97</td>
<td>0.907</td>
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</tr>
<tr>
<td>226-71 (IN)</td>
<td>7.20</td>
<td>19.27</td>
<td>39.19</td>
<td>.498</td>
<td>.519</td>
<td>.413</td>
<td>113.9</td>
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<tr>
<td>226-79 (IN)</td>
<td>7.40</td>
<td>44.95</td>
<td>30.81</td>
<td>.185</td>
<td>.589</td>
<td>.477</td>
<td>127.0</td>
<td>1.69</td>
<td>1.131</td>
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<tr>
<td>226-87 (IN)</td>
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<td>31.35</td>
<td>17.07</td>
<td>.108</td>
<td>.466</td>
<td>.225</td>
<td>89.2</td>
<td>1.76</td>
<td>1.386</td>
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</tr>
<tr>
<td>227-18 (SN)</td>
<td>25.80</td>
<td>39.85</td>
<td>31.38</td>
<td>.258</td>
<td>.453</td>
<td>.477</td>
<td>117.9</td>
<td>1.75</td>
<td>1.000</td>
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<tr>
<td>227-30 (IN)</td>
<td>24.90</td>
<td>12.93</td>
<td>17.48</td>
<td>.315</td>
<td>.805</td>
<td>.414</td>
<td>31.6</td>
<td>1.51</td>
<td>0.592</td>
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<tr>
<td>227-33 (IN)</td>
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<td>73.00</td>
<td>34.55</td>
<td>.089</td>
<td>.887</td>
<td>.378</td>
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<td>0.51</td>
<td>0.971</td>
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<td>230-9 (IN)</td>
<td>23.40</td>
<td>67.85</td>
<td>40.16</td>
<td>.213</td>
<td>.708</td>
<td>.322</td>
<td>141.8</td>
<td>1.33</td>
<td>1.090</td>
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<tr>
<td>SE</td>
<td>13.05</td>
<td>38.55</td>
<td>10.13</td>
<td>.282</td>
<td>.577</td>
<td>.296</td>
<td>117.9</td>
<td>1.75</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td>Mean ±</td>
<td>± 2.27</td>
<td>± 4.47</td>
<td>± 2.32</td>
<td>± 0.030</td>
<td>± 0.036</td>
<td>± 0.017</td>
<td>± 10.71</td>
<td>± 0.16</td>
<td>± 0.060</td>
<td></td>
</tr>
<tr>
<td>SD</td>
<td>9.37</td>
<td>18.44</td>
<td>9.55</td>
<td>.122</td>
<td>.149</td>
<td>.068</td>
<td>44.2</td>
<td>0.66</td>
<td>0.249</td>
<td></td>
</tr>
</tbody>
</table>

* Data unavailable at + 4.92 g.
on average 30% of the potential dynamic range (PDR), the latter defined as the difference in discharge rates obtained with forces of +4.92 and -4.92 g. The rates characterizing the excitatory saturation (see below and Fig. 4) can be estimated by the quantity \((2d^* + d_{res})\) and average 250 spikes/s with a range of 80–380 spikes/s.

There were considerable variations among units in their input-output functions. The differences can be described in terms of three factors (see legend to Fig. 3 for more details): a horizontal translation (Fig. 3A), a vertical scale (Fig. 3B), and a horizontal scale (Fig. 3C). The vertical scale can be measured by \(X_1 = d^* - d_{res}\); the horizontal scale by \(X_3 = \Delta g_{norm}\); and the horizontal translation by \(X_2 = g^*/\Delta g_{norm}\).

The value of \(g^*\) was determined by linear interpolation of second differences; linear interpolation was then used to obtain \(d^*\). \(d_{res}\) was defined as the discharge rate at \(-4.92\) g. \(\Delta g_{norm}\) was calculated as follows: the stimulus values \((g_k's)\) required to produce normalized discharge rates \([d - d_{res}]/\hat{d}\) of \(k = 0.50, 0.25, \) and \(0.10\) were tabulated for all units and the corresponding means \((g_k's)\) calculated. For each unit, \(\Delta g_{norm}\) was computed by linear regression to minimize differences between the \(g_k's\) and the \(g_k's\). The regression equation was \(g_k = (\Delta g_{norm}) \cdot g_k\). The smaller the value of \(\Delta g_{norm}\), the steeper the input-output function.

\(X_1\) and \(X_2\) may correspond, respectively, to the transduction gain and receptor bias discussed previously. \(X_3\) might possibly be thought of as a mechanical gain, relating effective force to displacement of the sensory-hair bundle.

The four variables \((X_1, X_2, X_3, \) and \(d_{res})\) can be used to normalize the functions obtained from different units (Fig. 4); here variations in \(d_{res}\) were accounted for by subtracting this value from all other discharge rates. To the extent that the normalization is successful, the variables may be said to summarize the salient features of the individual functions. The normalization is satisfactory, particularly in the region below the inflection point. The normalized points were found empirically to be approximated by a version of the normal distribution function, viz., \(2 \times N(\mu, \sigma)\) with \(\mu = g - g^* = 0\) and \(\sigma = 1.8 \times \Delta g_{norm}\) (see Fig. 4, curve).

Relations between extended and restricted force-response functions

In previous papers (6, 7) it was found that the discharge rate \((d)\) was related to the effective force \((F)\) in the restricted range of \(\pm 1\) g by the equation

\[ d - d_0 = s_0 (F + \alpha F^2) \]  

(4)

The three parameters \((d_0, s_0, \) and \(\alpha)\) bear simple relations to the variables governing the extended input-output function. Both the resting discharge \((d_0)\) and the sensitivity \((s_0)\) should increase as the vertical scaling factor \((X_1)\) increases (Fig. 3B) or when the function shifts to the left, i.e., as \(X_3\) decreases (Fig. 3A). The sensitivity should also increase with increasing steepness of the function, i.e., as \(X_3\) decreases (Fig. 3C). The asymmetry coefficient \((\alpha)\) should be influenced by both \(X_2\) and \(X_3\). Decreasing \(X_2\) should bring the zero-force point nearer the inflection point; hence, the curve in the \(\pm 1\) g range should become more symmetric and \(\alpha\) become smaller. Decreasing \(X_3 = \Delta g_{norm}\) should increase the effectiveness of a given \(F\); since the asymmetry grows as \(F^2\), \(\alpha\) and \(X_3\) should be negatively correlated. The last relation may be stated in another way. The portion of the extended function subtended by \(\pm 1\) g becomes more restricted, the larger the value of \(\Delta g_{norm}\); were \(\Delta g_{norm}\) allowed to approach infinity, the \(\pm 1\) g curve would approach a straight line.

To explore these relations, a multiple-regression analysis was performed. The dependent variables were \(Y_1 = d_0 - d_{res}\), \(Y_2 = s_0\), and \(Y_3 = \alpha\); the independent variables were \(X_1\), \(X_2\), and \(X_3\). The results, summarized in Table 2, confirm the qualitative reasoning in that the expected regression coefficients are of correct sign and are statistically significant. The multiple-correlation coefficients are high and indicate that the regression equations account for some 90% of the variances of \(Y_1\) and \(Y_2\) and for about 70% of the variance of \(Y_3\).

The resting discharge \((d_0)\) and the sensitivity \((s_0)\) both vary in the same direction with changes in either \(X_1\) or \(X_2\). This provides an explanation for the positive relation observed between \(s_0\) and \(d_0\). Figure 3A plots \(Y_1 = d_0 - d_{res}\) and \(Y_2 = s_0\) for the 17 units included here. The relation is similar to that seen in larger populations of otolith units (see ref 6) and can be fit by the empirical formula

\[ Y_2 = b_2 Y_1 + c \]  

(5)

The multiple-regression equations provide a means of estimating \(b_0\). The equations are of the form

\[ \hat{Y}_1 = b_{1i} X_i + b_{2i} Y_2 + b_{3i} Y_3 \]  

(6)

The hat over \(\hat{Y}_1\) is used to denote a multiple-regression estimate. The computation of \(b_0\) requires quantities of the form \(\Sigma \hat{Y}_1 \hat{Y}_i\) and these can be obtained from the available quantities \(\Sigma \hat{Y}_1 x_i\). As indicated in Fig. 5A, there is excellent agreement between the regression line computed by conventional means (solid line) and that derived from the multiple-regression equations (dashed line). The multiple-regression equations also provide accurate estimates of the deviations (\(\epsilon\)) of individual points from the
FIG. 4. Normalized force-response relation, 17 units. The four aberrant points at the top were all contributed by one unit. Curve is derived from normal distribution function (see text). Arrows below curve delimit average position of physiological (± 1 g) range.

straight-line fit of equation 5 (see Fig. 5D). The estimate is given by $e = Y_2 - b_0Y_1 - c$ and, from equation 6, can be expressed solely in terms of $X_1$, $X_2$, and $X_3$.

DISCUSSION
Directional selectivity

A common assumption is that there is a trigonometric relation between the direction of an applied force and afferent discharge. One exception to this notion is that excitatory responses are larger than inhibitory responses (6, 7, 20). A second exception is the demonstration that orthogonal shears have an excitatory effect. In these respects, the results obtained in the otolith organs are similar to those for lateral lines (8, 13). Three possible explanations may be offered for the orthogonal-shear effect.

The first, proposed by Flock (8), involves the
TABLE 2. Multiple-regression matrix

<table>
<thead>
<tr>
<th></th>
<th>$X_1$</th>
<th>$X_2$</th>
<th>$X_3$</th>
<th>Multiple Correl Coeff</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Y_1$</td>
<td>.355*</td>
<td>-28.8*</td>
<td>-10.3$</td>
<td>0.95*</td>
</tr>
<tr>
<td>$d_0 - d_{res}$</td>
<td>±.042</td>
<td>±3.1</td>
<td>±7.3</td>
<td></td>
</tr>
<tr>
<td>$Y_2$</td>
<td>.220*</td>
<td>-9.01*</td>
<td>-23.6*</td>
<td>0.94*</td>
</tr>
<tr>
<td>$s_0$</td>
<td>±.024</td>
<td>±1.75</td>
<td>±4.2</td>
<td></td>
</tr>
<tr>
<td>$Y_3$</td>
<td>-9.25$x 10^{-5}$$</td>
<td>.0772$</td>
<td>-.281$</td>
<td>0.83$</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>±4.97$x 10^{-4}$$</td>
<td>±.0361</td>
<td>±.086</td>
<td></td>
</tr>
</tbody>
</table>

Values are regression coefficients ± SE. Two-tailed $t$ tests: * $P < 0.001$; † $P < 0.01$; ‡ $P < 0.05$; § $P > 0.05$.

The fact that an afferent contacts several hair cells and these may be presumed to have somewhat different morphological polarization vectors. A force directed orthogonal to the afferent’s functional polarization vector will excite some of the hair cells and inhibit the others. Because of the asymmetries between excitatory and inhibitory responses, it may be supposed that excitation will predominate. The explanation, though plausible, can be dismissed on quantitative grounds. Suppose that the response contributed by a single hair cell is proportional to $F \cos \phi + \alpha (F \cos \phi)^2$. \( \phi \) is the angle between the applied force $F$ and the hair cell’s polarization vector. The quadratic term is used to represent the response asymmetry (6, 7). Let the afferent innervate a set of hair cells whose vectors are uniformly distributed over an innervation angle $\Delta \theta$. The expression for the afferent’s response $r(\theta)$, obtained on integration from $\phi = \theta - \Delta \theta/2$ to $\phi = \theta + \Delta \theta/2$, is

$$r(\theta) = \frac{F}{\Delta \theta} \left[ 2 \cos \theta \sin(\Delta \theta) + \frac{\Delta \theta}{2} (\Delta \theta + \cos 2 \theta \sin \Delta \theta) \right]$$

Equation 7 can be used to determine the relation between the afferent’s orthogonal response $r(90')$ and $\Delta \theta$.

By substitution, the ratio $OR/PR = \frac{\alpha}{\Delta \theta} (\Delta \theta - \sin \Delta \theta)/4 \sin (\Delta \theta/2)$, where $OR = r(90')$ and $PR$ is the average magnitude of $r(0')$ and $r(180')$. The afferent’s normalized asymmetry coefficient is, by definition, $\alpha = \frac{1}{(1/F)(r(0') + r(180'))/r(0') - r(180')}$. Substitution of $r(0')$ and $r(180')$ from equation 7 leads to $\alpha = 4 \alpha \sin (\Delta \theta/2)/r(90')$. Also in these experiments $F = 1.23 g$ and $\alpha$ is on the order of 0.25 (see ref 6).

For orthogonal shears, the ratio of the orthogonal to the parallel response (OR/PR) is typically 10–15% and this would require a $\Delta \theta$ of 120°–150°. Such a large innervation angle is inconsistent with anatomical observations of the branching patterns of the afferents (18, 21). Further, for the saccus, there is a restricted distribution of both morphological (18) and functional (6, 7) polarization vectors. The orthogonal-shear responses of saccular afferents, though smaller than those observed in utricular afferents, still amounted to 9%. A reasonable upper bound for the innervation angle would be $\Delta \theta = 30°$. The corresponding value of $r(90')$, predicted from equation 7, is less than 1% of PR. Such a response would make only a minor contribution to the observed orthogonal-shear responses.

A second mechanism involves consideration of the otolithic membrane as an elastic body. From classic elastic theory (16), local displacements of the membrane (and presumably the deflections of the underlying sensory hairs) need not parallel applied force. More importantly, orthogonal forces do not necessarily produce orthogonally related displacements. Stated more specifically, an orthogonal-shear force could result in a sensory-hair deflection with a component along the receptor’s polarization axis. This kind of explanation is not without difficulties. The fact that similar responses are produced by forces 180° apart (Fig. 1B) would require that the stress-strain relations of the membrane be nonlinear. The prevalence of excitatory orthogonal-shear responses would further require that

![Fig. 5](http://jn.physiology.org/10.1152/jn.00260.1995)

FIG. 5. Relation between $Y_1 = d_0 - d_{res}$ and $Y_2 = s_0$, the latter in spikes/sec. The regression of $Y_2$ on $Y_1$ (solid line, Fig. 5A) is statistically significant (two-tailed $t$ test, $P < 0.01$). Dashed lines and predicted deviation from regression line ($\epsilon$) derived from multiple-regression equations.
the nonlinearity of each local region of the membrane be closely related to the morphological polarization of the corresponding hair cells.

The third and simplest explanation assumes that orthogonal deflections of individual sensory hair bundles will lead to excitatory receptor potentials.

The lack of a significant response of otolith neurons to orthogonal compressions, though consistent with previous results (23, 25, 26), does raise problems. Here again the otolithic membrane may be considered as acting like an elastic body. Compression of such a body usually has two consequences: 1) pressure is communicated to underlying structures, and 2) there is an elongation of the body in a direction perpendicular to the applied force. Were the sensory hairs rigidly embedded in the otolithic membrane, either effect might be expected to result in a deflection of the hairs and a response of the corresponding afferents. The fact that this does not occur implies a special kind of mechanical linkage between the hair bundles and the otolithic membrane. The nature of the coupling is obscure. The hair bundles have been described as inserting into fluid-filled compartments separated by a meshwork located between the sensory epithelium and the membrane (5, 15, 17–19, 24). The sequestering of the hair bundles in compartments might prevent a response to compression forces. But it is not clear how such an arrangement could prevent compressional forces from influencing the response to shearing forces. Indeed, Benson and Barnes (2), in a theoretical investigation of an analogous situation, predict that compression of the otolithic membrane would increase the sensitivity of the end organ to shearing forces, whereas traction would decrease it. Despite the plausibility of the arguments offered, the conclusion is at variance with experimental results. Compressional forces affect neither the sensitivity of otolith afferents nor the shape of their force-response relations.

**Force-response relations**

The extended input-output functions are sigmoid shaped and possess both inhibitory and excitatory plateaus. Inhibitory saturation is reflected by the presence of a residual discharge of 5–20 spikes/s even when intense inhibitory forces are presented. The most obvious possibility, that the residual discharge is a consequence of injury, is deemed unlikely since none of the units in the present sample displayed any signs of injury, either during or after the presentation of large inhibitory forces.

Three mechanisms could be responsible for the existence of a residual discharge. 1) There may be a limit in the displacement of the otolithic membrane. This is considered an improbable explanation since it would then be expected that excitatory and inhibitory limbs of the force-response relation would saturate at similar force levels. Typically, though, inhibitory saturation was attained with forces of 2–3 g, whereas excitatory saturation was just barely reached, or not reached at all, with forces of 5 g. The difference in the force levels required for saturation provides a particularly compelling argument when, as our data permitted, comparisons can be made between units innervating the same end organ but having oppositely directed polarization vectors. In such a case, a given displacement of the otolithic membrane will excite one unit and inhibit the other. The fact that the excited unit does not saturate would seem to rule out a mechanical explanation for the saturation of the inhibited unit. 2) It is conceivable that the afferent would continue to fire in the absence of excitatory drive (presumably release of excitatory transmitter) from the associated hair cells. The possibility, though it cannot be dismissed, is at variance with current evidence concerning the etiology of activity in acousticolateralis afferents (1, 9, 10). 3) There could be a saturation in hair-cell mechanisms. The notion receives support from Trinkcr's (25) observation of both excitatory and inhibitory saturations in a receptorlike potential recorded from the cristae of the guinea pig.

Similar mechanisms may be responsible for the excitatory saturation. Our own data do not have a direct bearing on the question as to whether the displacement of the mammalian otolithic membrane becomes limited for shearing forces near 5 g. De Vries' (4) study of the mechanical displacement of the large saccular otolith of the ruff suggests such a saturation. The upper limit of firing of vestibular afferents is estimated to be 350–400 spikes/s (11) and may contribute to the saturation of units whose maximum response to linear forces approaches this value. Other units, though, exhibit maximum rates of under 200 spikes/s, and in these a saturation in otolith displacement or in hair-cell mechanisms may be more important.

**Relations between extended and restricted force-response relations**

The force-response relations in the presumed physiological range of ±1 g can be described by three parameters. These are a resting discharge ($d_0$), a sensitivity factor ($s_0$), and an asymmetry coefficient ($a$). In comparison, four variables ($X_1$, $X_2$, $X_3$, and $d_{res}$) are needed to specify the extended force-response curve, including the portion between ±1 g. Despite the complication
of an additional variable, the analysis based on the extended curve has advantages. The variables $X_1$, $X_2$, and $X_3$ admit of a plausible, if not unique, physiological interpretation. The same is not true for the three variable governing the $\pm 1 g$ relation. The reason (see Fig. 6) is that quite different extended curves can lead to virtually indistinguishable restricted curves. Regardless of the specific mechanisms determining the extended relations, these would obviously have to differ for the two examples included in the figure. Stated another way, a similarity in the restricted curve does not necessarily imply a similarity in underlying mechanisms. Further, if $d_o$ and $s_o$ are chosen as the primary variables of description, then the positive relation between them must be viewed as entirely empirical, and a unit which deviates from the relation can only be described as atypical. In contrast, the extended analysis provides a basis not only for interpreting the relation (Fig. 5A), but also accounts for seemingly aberrant units (Fig. 5B).

In a previous paper (6), the question was raised as to whether the positive relation between $d_o$ and $s_o$ seen in regular units was determined by variations in both the transduction gain and the receptor bias. To the extent that these factors can be identified, respectively, with $X_1$ and $X_2$, the multiple-regression analysis (see Table 2) provides an answer. Both $X_1$ and $X_2$ make significant contributions to the variances of $d_o$ and $s_o$ and, hence, they must also contribute to the relation observed between the latter two variables. The weaker relation observed among irregular units can, as previously suggested (6), be explained in terms of the lack of a consistent bias effect on the sensitivity of these afferents. Some insight into how this might influence the relation can be obtained by setting the appropriate regression coefficient (below) in equation 6 to zero. The result is that the theoretically computed correlation coefficient between $d_o$ and $s_o$ is reduced from 0.6 to 0.2.

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