Mapping the cochlear partition's stiffness to its cellular architecture

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The mechanical properties of the cochlear partition are fundamental to auditory transduction. We measured the point stiffness of the partition, *in vivo*, at up to 17 radial positions spanning its width, in the basal turn of the gerbil cochlea. We found the linear stiffness at the position that is most likely under the outer pillar cells to be 1.5 times greater than adjacent positions toward the ligament, in the pectinate zone, and five times greater than adjacent positions toward the lamina, in the arcuate zone. This radial variation seems to reflect the cellular geometry of the partition: The pillar cell is positioned as a structural element, and the basilar membrane supports a rich cellular structure in the pectinate zone, whereas it borders a fluid-filled space in the arcuate zone. The radial variation in partition stiffness we find will influence passive cochlear mechanics, and also bears on active cochlear mechanics, since it supports the plausibility of cells as effective force generators. Our results from measurements made *in vivo* extend the findings of previous measurements made in excised cochleae, in which the cellular contribution to stiffness was less evident.

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INTRODUCTION

The cochlea's mechanical operation relies upon the stiffness of the cochlear partition. The cochlear traveling wave is thought to be produced by coupling between the stiffness of the partition and the inertia of the pressure-driven fluid, with the longitudinal position where the traveling wave reaches a peak attributed to a localized resonance within the partition (von Bekesy, 1960; Zwislocki, 1965; Peterson and Bogart, 1950). The complex structure of the cochlear partition makes its stiffness difficult to estimate. The present measurements of the radial variation in point stiffness were performed in order to better understand which components of the partition govern its stiffness.

Figure 1 is a cross section of the cochlear partition. It is composed of sensory and supporting cells resting upon the basilar membrane, and contacted from above by the tectorial membrane. The basilar and tectorial membranes are noncellular and fibrous. The basilar membrane is composed of filaments running radially between the spiral lamina and ligament, embedded within a ground substance. A layer of mesothelial cells borders the basilar membrane on the scala tympani side. Between the lamina and the outer pillar cell, the filaments lie side by side in one layer; between the outer pillar cell and the spiral ligament, the filaments group into bundles that form two or more layers. (Basilar membrane ultrastructure has been investigated in the guinea pig by Iurato, 1962, and in the cat by Cabezudo, 1978.) The pillar cells and attached reticular lamina have the microstructure and geometry of structural elements, and are likely to play a role in the partition's rigidity (Angelborg and Engstrom, 1972). In the pectinate zone the basilar membrane supports a diverse cellular mass, including the outer hair cells which are thought to operate as mechanical force generators. Above the arcuate zone is the fluid filled tunnel of Corti.

Stiffness was determined by measuring the force exerted by the partition when it was deflected at a point. The measurements were made in the base of the gerbil cochlea, at the basilar membrane side of the partition. A sinusoidal excursion was applied to a force transducer upon which a 20-μm-diam probe tip was mounted, and the ac force exerted by the partition on the tip was measured. Stiffness was calculated as the amplitude of the restoring force divided by the amplitude of the applied excursion. At each radial position, measurements were made over a 15-μm range of static deflections. This deflection sequence was repeated at different radial positions, to generate a set of stiffness-versus-deflection curves.

As a brief summary of our findings: In a region of the central pectinate zone with a radial width of 50 to 60 μm, the stiffness-versus-deflection curves displayed the shape that we have reported previously, characterized by an abrupt increase in stiffness from the contact level, followed by a plateau, and finally a quadratically increasing stiffness (Olson and Mountain, 1991). The elevated plateau stiffness, which seemed to represent the stiffness with the probe fully coupled to the partition, was present at a level of approximately 7 N/m. Just modiolar to the central pectinate region we found a narrow region, probably representing the outer pillar cells, in which the elevated plateau and overall stiffness were of greater magnitude. Further toward the modiolus, in the arcuate zone, the plateau was present at a level of only 1–2 N/m. This segmented radial stiffness variation seems to reflect the cellular structure of the cochlear partition.

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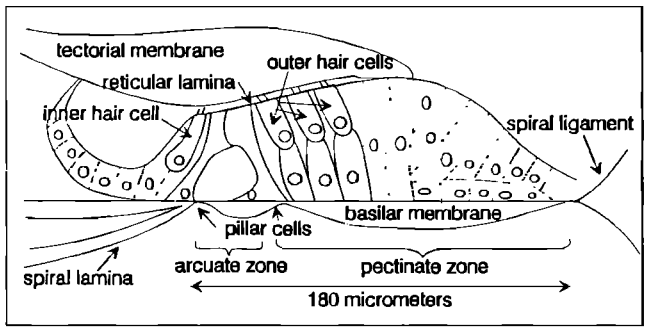

FIG. 1. Cross section of the cochlear partition in the base of the gerbil cochlea, based on a histological thin section. (Actually, the outer pillar cell tops are partly tucked beneath the inner pillar cell, which form a thin layer at their tops. However, this anatomical feature is not evident in the histological section that the figure is based on.)

In measurements made by others (Sellick *et al.*, 1983; Wilson and Bruns, 1983) details of the motion of the basilar membrane have been found to differ in the two radial zones of the partition. Several authors (Steele, 1977; Kolston *et al.*, 1989) have explicitly included a radially segmented partition stiffness, and have found that this class of models can be successful in reproducing experimental results, and reconciling seemingly contradictory results. The radial variation in stiffness that we find gives credence to these descriptions of cochlear mechanics.

I. METHODS

Experiments were performed in gerbils of the species *Meriones unguiculatus*. Animals were administered a 1-mg/kg dose of the tranquilizer acepromazine and an initial dose of 60 mg/kg of the anesthetic sodium pentobarbital, supplemented with 10-mg/kg doses at half-hour intervals. Following dissection to expose the cochlea, the round window membrane was removed, allowing perpendicular access to the basilar membrane side of the cochlear partition. The width of the basilar membrane at the measurement position was approximately 180 μm, as estimated both visually, and from the edges found in the stiffness measurements.

The experiments employed a piezoelectric force probe. The two major components of the probe are a voltage-to-displacement transducer and a force-to-voltage transducer. A needle with a 20-μm-diam fire polished glass tip was attached to the force transducer. The voltage-to-displacement transducer was used to vary the position of the force transducer in the range from 0.005 to 30 μm at frequencies from 0 to 100 Hz. The force transducer was capable of detecting ac forces on the order of 10 nN. Because physiological motions and forces in the cochlea are on the order of nanometers and nanonewtons, the probe operates over relevant ranges. The sensitivity and simplicity of the piezoelectric device make it a useful tool for measurements on a small, delicate object with limited accessibility. The probe has been described previously (Olson and Mountain, 1991).

After contacting the basilar membrane with the probe tip, an 80-Hz, 15-nm peak sinusoidal excursion was applied to the force transducer and the ac force exerted on the tip by the membrane was measured. Stiffness was calculated as the amplitude of the force at 80 Hz divided by the amplitude of the applied excursion. Stiffness was measured at each position as the probe was advanced in 1-μm steps to a maximum 10-μm deflection, and withdrawn in 1-μm steps to a minimum -4-μm retraction. Following such a set of measurements, the radial position of the probe was changed with a motorized micromanipulator. The order of radial measurements was random (i.e., it did not proceed sequentially from one radial boundary to the other) in order to reduce the likelihood of detecting an artifactual stiffness variation caused by damage or fatigue.

At each radial position, stiffness-versus-deflection measurements were initiated at a stiffness level of approximately 1 N/m. This starting level was chosen based on experience: In our previous measurements, initiated at the lowest detectable stiffness (roughly 0.3 N/m) the initial stiffness level was generally on the order of 0.5 N/m and almost always (18 out of 22 cases) less than 1 N/m (Olson and Mountain, 1991). In those measurements, the stiffness remained close to the initial level for up to 12 μm, and then suddenly increased. Based on its length and stiffness, we attributed this initial plateau to the underlying tympanic cells and ground substance of the basilar membrane, which probably have low resistance to the shearing force produced by point loading. Under the natural stimulus of pressure loading, the tympanic cells and ground substance would probably behave as fluid or gel layers, and not contribute significantly to the physiologically relevant stiffness of the partition. The protocol in the current study ignored stiffnesses of less than 1 N/m, and small initial stiffnesses that may have been present, were not recorded.

The absolute position along the axis of the probe needle at which a stiffness-versus-deflection measurement set was initiated, termed the start point, was not known precisely. This was due to variable drift in mechanical instruments that occurred at a maximal rate of approximately 5 μm per hour (which corresponds to 2 μm during one measurement set). In order to estimate the contour formed by the start points, in an additional experiment the start points at nine radial positions spaced by 20 μm were measured quickly. The start points close to the lamina and ligament were remeasured periodically to monitor drift, and all radial positions were mapped twice. Except for one point, the variation in start points was 5 μm. The variation was random, except for an overall slope of approximately 0.015 μm/μm, which was likely due to the error in perpendicular positioning of the probe.

Because the measurement was dynamic, the quantity we determine is strictly the mechanical impedance of the cochlear partition, which includes stiffness, viscous resistance, and inertia. At 80 Hz the mechanical impedance is expected to be dominated by stiffness, and our measurements, which included both the magnitude and phase of the force on the probe, and in previous experiments (Olson

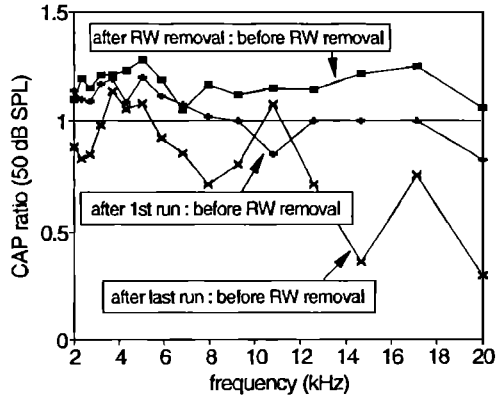

FIG. 2. Ratios of eighth nerve CAP responses at the indicated times to the first CAP responses, measured prior to removal of the round window. The stimuli were 50 dB SPL tone bursts spanning frequencies from 2 to 20 kHz.

and Mountain, 1991) were made at several frequencies, bore this out.

Mechanical disturbances were minimized by performing the experiments on a vibration isolation table in a sound chamber. Without signal averaging, the noise level at frequencies around 80 Hz corresponded to forces of approximately 4 nN(rms)/$\sqrt{\text{Hz}}$. 25 averages of data collection periods, 0.9 s in duration, were performed.

Cochlear integrity was monitored by the response of the eighth nerve to tone bursts spanning frequencies from 2 to 20 kHz and sound pressure levels (SPL) from 40 to 70 dB. The compound action potential (CAP) was measured with a silver wire electrode at the round window opening. In Figure 2 the ratio of the CAP responses to 50 dB SPL tone bursts at the indicated times, to the first CAP responses, measured prior to round window removal, are shown. The results shown are from the healthiest cochlea, no. 27, but are not outstanding relative to other animals. Just after round window removal, the CAP ratios were greater than one, probably because escaped cochlear fluid has improved the electrical contact of the electrode. After the first stiffness-versus-deflection run, the values of the CAP ratios were close to one across frequencies. At the end of the experiment, seven hours later, the CAP was reduced, especially at high frequencies. Because we did not measure the CAP threshold tuning curves, these data are not a precise indicator of damage. However, it is notable that the CAP was decreased much less than in our previous experiments, performed with a blunt stainless-steel probe tip, with a maximum 20-μm deflection (Olson and Mountain, 1991). The measured stiffness was not obviously correlated with this gauge of cochlear health.

Five experiments were performed, one with 40-μm radial spacing, three with 20-μm spacing, and one with 10-μm spacing. The results from the five experiments were similar.

II. RESULTS

Figure 3 shows the complete set of stiffness-versus-deflection curves from experiment no. 27. The arrows differentiate data taken when the probe was in the process of advancing from data taken retracting, and the quadratic function $k=k_0+A(x-x_0)^2$ has been fit to most of the curves. The fits were made by eye to the data points with stiffness greater than or equal to that of the plateau stiffness. The radial positions of the stiffness-versus-deflection curves were spaced by 20 μm, with position 1 close to the spiral lamina, and position 9 close to the spiral ligament. The cross-sectional sketch in Fig. 1 is from a longitudinal position which approximately corresponds to that of the measurements, and can be used to map the radial positions. The phase of the force on the probe relative to the probe's excursion is plotted beneath the stiffness curves. The phase of a restoring force due to stiffness is -180 deg, the phase of a force due to viscous resistance is -90 deg. A component of viscous resistance is present at small deflections, while for deflections greater than 2 μm, the force on the probe is predominantly a restoring force.

Notable features of many of the curves in Fig. 3 are (1) a plateau region, where stiffness is almost constant over two or more micrometers of deflection and, (2) a region of quadratically increasing stiffness at deflections beyond the plateau. Positions 4, 5, 6, and 7, comprising the central pectinate region, had a sharp rise to an elevated plateau of approximately 7 N/m, followed by a gradual, quadratic increase. At the pillar cell position (position 3) there is an elevated plateau with a value of 10.5 N/m, 1.5 times as large as the elevated plateau of the pectinate zone. Positions 7 and 8 show the stiffness increasing smoothly with proximity to the ligament. The elevated plateau is not evident at position 8, but an inflection in the stiffness-versus-deflection curve suggests that the structure responsible for the elevated plateau in the central pectinate region is also present at this more lateral position. In the arcuate zone, position 2, the quadratically increasing part of the curve is steeper than that of the central pectinate zone, but the plateau is present at a level, 1.5 N/m, which is not much greater than the stiffness upon contact. Close to the lamina and ligament, positions 1 and 9, the stiffness increased steeply with deflection, attaining values one to two orders of magnitude greater than those of adjacent positions.

In Fig. 4 three-dimensional plots of stiffness-versus-deflection-versus-radial position allow the results from positions spanning the width of the cochlear partition to be viewed together. Results from three experiments are plotted. (From Fig. 3 it is clear that at most deflections, stiffness is measured twice. The three-dimensional plots display the stiffness measured as the probe was in the process of advancing.) The overlying line drawing maps the radial position axis to the cochlear partition. The plots reflect the cellular anatomy of the cochlear partition, with a narrow pillar cell region flanked by two relatively compliant regions. While the plots emphasize the pillar cell, the differences between the arcuate and pectinate zone stiffnesses are also apparent. The stiffnesses of the arcuate zone positions increase smoothly from a low-level plateau, whereas the stiffnesses of the pectinate zone positions rise to an elevated plateau or inflection point from which they increase grad-

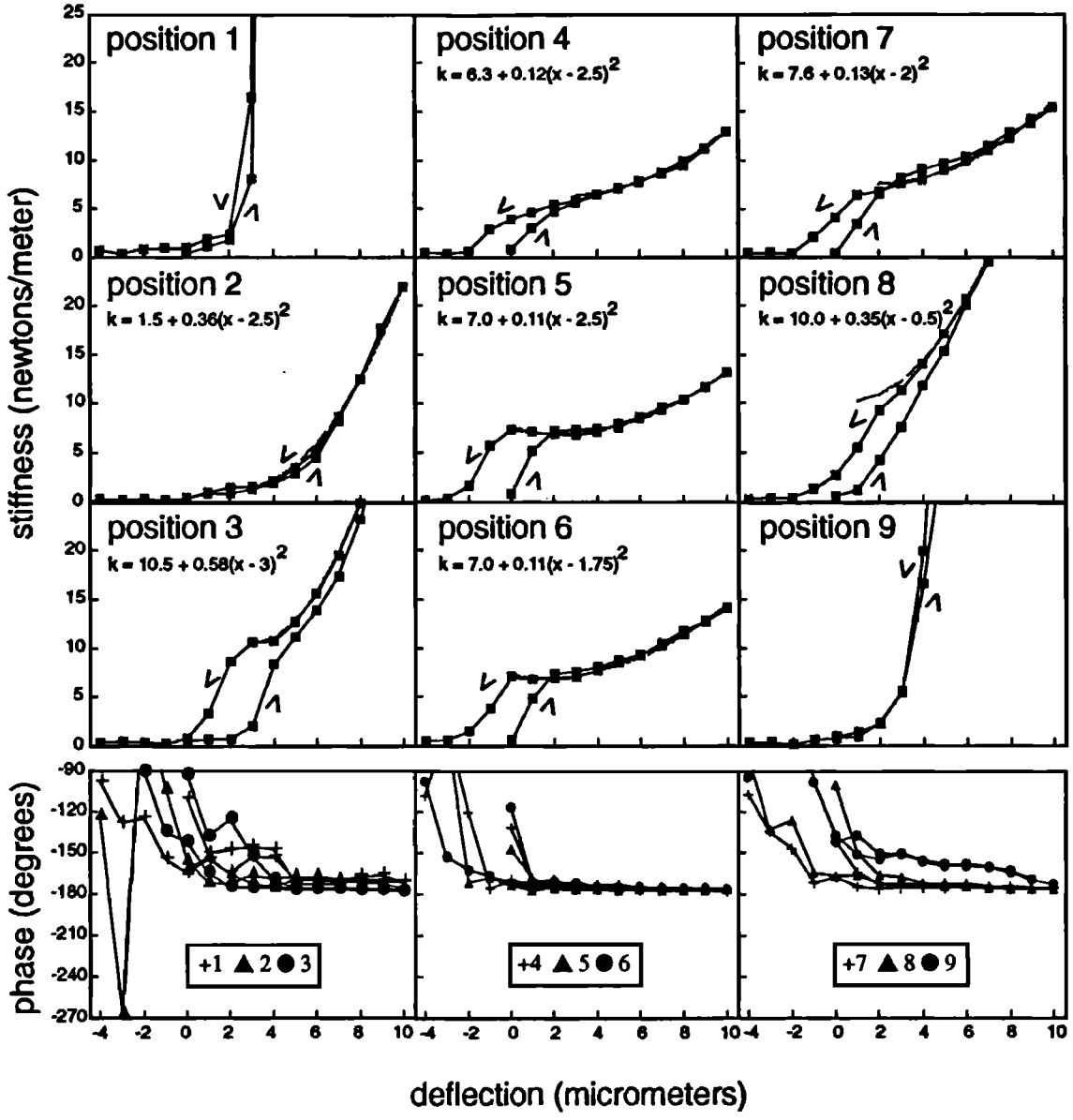

FIG. 3. Complete set of stiffness-versus-deflection curves, and phase-versus-deflection curves from experiment 27. The radial positions of the measurements were spaced by 20 μm. The position numbers refer to radial positions from close to the spiral lamina (position 1) to close to the spiral ligament (position 9). Stiffness is defined as the amplitude of the force on the probe divided by the amplitude of the probe's excursion. The phase is the phase of the force on the probe relative to the phase of the probe's excursion. The function $k=k_0+A(x-x_0)^2$ was fit to the data, with k_0 and A values as indicated in the lower right corner of each stiffness-versus-deflection plot.

ually at central positions, and more steeply at positions closer to the ligament. A contour is highlighted at a deflection of 4 μm, where the plateau stiffnesses are usually in evidence, to emphasize the plateaus. The relatively small arcuate zone stiffnesses, and large pillar cell stiffnesses were each present at one radial position in the experiments in which the spacing between positions was 20 μm [Fig. 4(b) and (c)]. When the spacing was 10 μm [Fig. 4(a)], the characteristic arcuate zone stiffness was found to extend over three radial positions, while the relatively large stiffness of the outer pillar cell location was still one position wide. This is consistent with the anatomy, since the arcuate zone is approximately 40 μm wide, and the filamentous structure that probably gives the pillar cell its rigidity is approximately 10 μm wide (Angelborg and Engstrom, 1972).

III. DISCUSSION

The quadratic function $k=k_0+A(x-x_0)^2$ provided a good fit to many of the stiffness-versus-deflection curves, as shown in Fig. 3. A constant, or plateau, stiffness (represented by k_0 in the fitted curve) is predicted for bending a structure with edge attachments or compressing simple elastic structures, and is known as a "linear stiffness." A quadratically increasing stiffness [represented by $A(x-x_0)^2$ in the fitted curve] is predicted for an edge-attached structure that is deflected to the point that

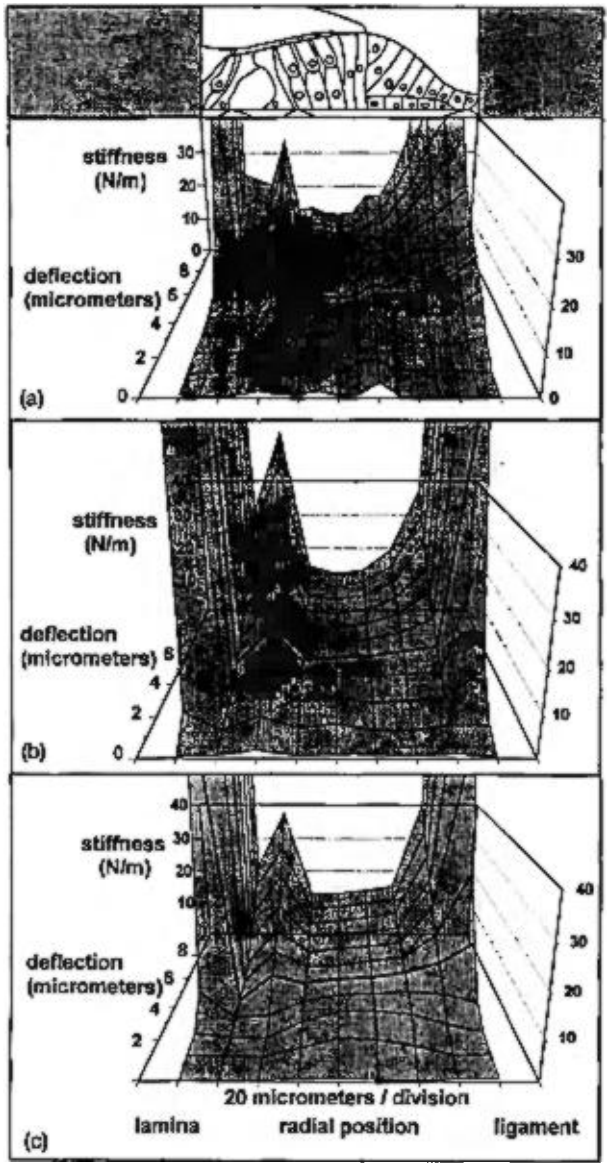

FIG. 4. Three-dimensional plots of stiffness-versus-deflection-versus-radial position from three experiments. The overlying line drawing maps the radial position axis to the cochlear partition. Experiments in 4a, b, and c corresponding to experiments 30, 28, and 27, were done with radial resolutions of 10, 20, and 20 μm, respectively. The stiffness at 4-μm deflection has been highlighted to emphasize the plateau stiffness.

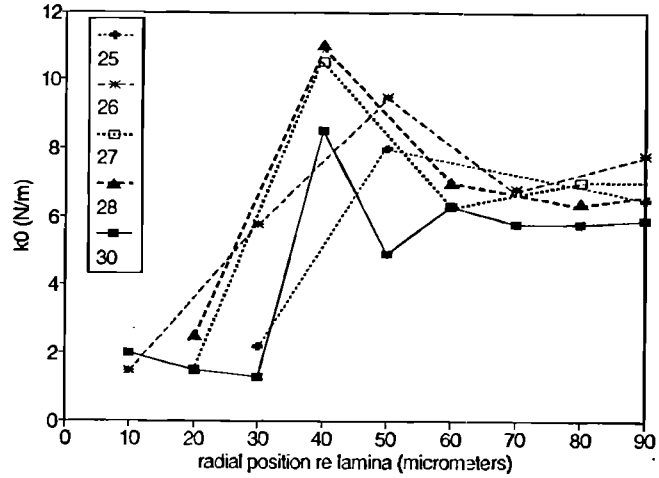

FIG. 5. When the function $k=k_0+A(x-x_0)^2$ is fit to the stiffness-versus-deflection data, k_0 gives the plateau stiffness value, and is taken to be the physiologically relevant stiffness. Here, k_0 is plotted against radial position. Each of the five symbols represents a different experiment. All five experiments showed an elevated plateau in the pectinate zone, but not in the arcuate zone. Three of the five experiments showed a clear "pillar cell" stiffness between the arcuate and pectinate zones. In the other two experiments, the pillar cell was less evident, likely due to the radial position resolution.

stretching becomes dominant, and the stiffness is then "nonlinear." Because of their transverse beamlike geometry, stretching of the basilar membrane filaments might be the dominant cause of the quadratically increasing stiffness. The plateau stiffness might be due to compressing cellular and extracellular elements within the partition, and to bending the basilar membrane filaments.

What part of the stiffness-versus-deflection curves, if any, should be considered to be a stiffness that is relevant to cochlear mechanics? Because passive cochlear motion is linear up to high sound pressure levels, the passive physiological stiffness is expected to be a stiffness that is linear, i.e., is constant with deflection, at least over the normal operating range. [We have not detected obvious differences in measurements made within an hour postmortem, as would be expected if aspects of the stiffness we measure depended on an active process (Olson and Mountain, 1991)]. The motion of the cochlear partition at the characteristic frequency place of a healthy cochlea due to a pure tone at 50 dB SPL is on the order of only 10 nm (Robles *et al.*, 1986). In contrast, we measure stiffness for deflections of the basilar membrane between 1 and 10 μm. However, we propose that the plateau stiffness, k_0, is the relevant physiological stiffness. The plateau region of the stiffness-versus-deflection curves likely represents the stiffness when the probe is fully coupled to the structure of the cochlear partition, and the partition is being pushed beyond its resting position, but is within its "linear" stiffness range. An extension of the plateau as the probe was retracted was commonly found, evidencing that the probe was fully coupled at this time. In some cases (see positions 5 and 6 in Fig. 3), the partition was apparently retracted even beyond its resting position, because the stiffness began to increase with retraction. Therefore, the elevated plateau *includes* the resting position of the cochlear partition, and so applies to the submicrometer motions that occur during normal cochlear function. [The plateau extension was even more apparent in previous measurements (Olson and Mountain, 1991), probably because (i) the probe tip was of buffed stainless steel, which might anchor itself to the partition, and (ii) the measurements were performed over 20 μm of static deflection, which would likely improve the probe/partition attachment.]

In Fig. 5 the plateau stiffness, k_0, is plotted against radial position for positions between the arcuate zone and the middle of the pectinate zone. The relative magnitudes of the plateau stiffnesses in the different regions seem to mirror the cellular geometry of the partition, indicating a substantial stiffening due to the pillar cell, and suggesting

that cellular elements, possibly in concert with the tectorial membrane, dominate the pectinate zone plateau stiffness.

It might be argued that the zonal differences in stiffness we find are due to the basilar membrane's anatomy. One anatomical difference in the two zones is the larger volume of ground substance in the pectinate zone. However, this substance seems to give little resistance to the advance of the probe (Olson and Mountain, 1991). A second difference is the configuration of the fiber bundles, which are in one layer in the arcuate zone, but separate into more than one layer in the pectinate zone (Iurato, 1962; Cabezudo, 1978). If the pectinate fiber layers are coupled, this structure would be stiffer than a single layered structure. However, the relative radial extents of the pectinate and arcuate zones (approximately 140 and 40 μm, respectively) predict a larger arcuate than pectinate zone stiffness, even when the separation of pectinate zone bundles is considered. (A model incorporating the separation of pectinate zone fibers, and a springlike contribution to stiffness from the outer pillar cells was explored by Miller, 1985.) Therefore, our results, which show an elevated plateau only in the pectinate zone, suggest that elements of the cochlear partition other than the basilar membrane contribute to, and even dominate, the stiffness of this zone. On the other hand, specialized basilar membrane anatomy, which could bear upon various mechanical properties (stiffness, mass, modes of motion) has been found in several species with specialized hearing requirements. For example, the greater horseshoe bat has a unique basilar membrane structure, which likely contributes to the expanded mapping of a narrow frequency band (Bruns, 1976), and most gerbil species have an excess of ground substance, especially in the middle turns, which might be involved in improved midfrequency sensitivity. (Plassmann *et al.*, 1987) In sum, it is likely that the species and place-specific stiffness of the cochlear partition is shaped by cellular elements of the partition in concert with extracellular structures.

Results from measurements of point stiffness made in excised cochleae of the guinea pig (Miller, 1985; Gummer *et al.*, 1981) were different from our *in vivo* results from the gerbil. Miller's stiffness measurements spanned the width of the cochlear partition. (Miller used a 10-μm-diam probe tip. To compare the stiffnesses she found with our results we multiplied her results by two, as for a beam model.) Miller found the arcuate zone stiffer than the pectinate zone, which had midzone stiffnesses of approximately 5 N/m (arcuate zone) and 1.5 N/m (pectinate zone). A cellular contribution to stiffness was apparent at the position of the outer pillar cells, where the stiffness was roughly equal to, or slightly greater than that of the midarcuate zone. Gummer *et al.* (1981) measured pectinate zone stiffness-versus-deflection at points radially centered on the basilar membrane and found an initial plateau stiffness with a magnitude of approximately 0.5 N/m, but did not detect an elevated plateau. The differing results from *in vivo* and excised cochlear measurements can probably be accounted for by differences in the cochlea due to the experimental conditions. Miller observed that in excised cochleae, while the basilar membrane and pillar cells remained, many of the cells were not intact. Therefore, the cellular contribution to stiffness indicated from measurements in excised cochleae is expected to be smaller than *in vivo*.

The radial variation in the stiffness of the cochlear partition in the basal turn of the gerbil cochlea is consistent with a stiffness that is substantially influenced by the cellular elements of the partition. In that case the barrier to a pressure difference across the partition would be dominated, not by the basilar membrane, but by many elements of the partition in the pectinate zone, and by the pillar cells in the arcuate zone. This segmented mechanical impedance will produce intrapartition pressure gradients, might support several different modes of motion, and will influence both passive and active cochlear mechanics.

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Angelborg, C., and Engstrom, H. (**1972**). "Supporting elements in the organ of Corti," Acta Otolaryngol. Suppl. **301**, 49–60.

von Bekesy, G. (**1960**). *Experiments in Hearing* (McGraw-Hill, New York), Chap. 12.

Bruns, V. (**1976**). "Peripheral auditory tuning for fine frequency analysis by the CM-FM bat, *Rhinolophus ferrumequinum*," J. Comp. Physiol. **106**, 77–86.

Cabezudo, L. M. (**1978**). "The ultrastructure of the basilar membrane in the cat," Acta Otolaryngol. **86**, 160–175.

Gummer, A. W., Johnstone, B. M., and Armstrong, N. J. (**1981**). "Direct measurements of basilar membrane stiffness in the guinea pig," J. Acoust. Soc. Am. **70**, 1298–1309.

Iurato, S. (**1962**). "Functional implications of the nature and submicroscopic structure of the tectorial and basilar membranes," J. Acoust. Soc. Am. **34**, 1386–1395.

Kolston, R. J., Viergever, M. A., deBoer, R., and Diependal, R. J. (**1989**). "Realistic mechanical tuning in a micromechanical cochlear model," J. Acoust. Soc. Am. **86**, 133–140.

Miller, C. E. (**1985**). "Structural implications of basilar membrane compliance measurements," J. Acoust. Soc. Am. **77**, 1465–1474.

Olson, E. S., and Mountain, D. C. (**1991**). "In vivo measurement of basilar membrane stiffness," J. Acoust. Soc. Am. **89**, 1262–1275.

Peterson, L. P., and Bogart, B. P. (**1950**). "A dynamical theory of the cochlea," J. Acoust. Soc. Am. **22**, 369–380.

Plassmann, W., Peetz, W., and Schmidt, M. (**1987**). "The cochlea in gerbilline rodents," Brain Behav. Evol. **30**, 82–101.

Robles, L., Ruggero, M. A., and Rich, N. C. (**1986**). "Basilar membrane mechanics at the base of the chinchilla cochlea. I. Input–output functions, tuning curves and response phases," J. Acoust. Soc. Am. **80**, 1364–1374.

Sellick, P. M., Patuzzi, R., and Johnstone, B. M. (**1983**). "Comparison between the tuning properties of inner hair cells and basilar membrane motion," Hear. Res. **10**, 93–100.

Steele, C. R. (**1974**). "Behavior of the basilar membrane with pure-tone excitation," J. Acoust. Soc. Am. **55**, 148–162.

Wilson, J. P., and Bruns, V. (**1983**). "Basilar membrane tuning properties in the specialized cochlea of the CF-bat, *Rhinolophus ferrumequinum*," Hear. Res. **10**, 15–35.

Zwislocki, J. J. (**1965**). "Analysis of some auditory characteristics," in *Handbook of Mathematical Psychology*, edited by R. Luce, R. Bush, and E. Galanter (Wiley, New York), Vol. 3.