differences may be due to the following facts, which make a detailed comparison difficult. First, it is necessary to extrapolate our observation to 1 A.U. Second, our results correspond to averages taken over the dimension of the radio source region. Third, our observations apply to regions which may have a considerable extent out of the ecliptic plane and for which the solar wind may be substantially different. Fourth, we must assume that the conditions defining the storm region remain constant during 2 to 3 days when we measure the rate of the solar elongation of the radio sources. Such an assumption has already been verified during an earlier IP storm (*9*).

This new technique, which enables us to track for the first time the solar wind expansion by use of the ISEE-3 radio observations of IP storms, works because of the long duration of the IP storms (several days). By comparison with the earlier analysis of radio measurements from the IMP-6 (Interplanetary Monitoring Platform) satellite (*3*), our technique requires few ad hoc assumptions. We derive the movement of the solar wind plasma in the earth's direction without an assumption of an average interplanetary density model. Our first results show a slight acceleration from 50 to 150 $R_{\odot}$, consistent with the results predicted by theoretical models of the solar wind.

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References and Notes

1. E. N. Parker, *Astrophys. J.* **128**, 664 (1958).
2. ———, *Interplanetary Dynamical Processes* (Interscience, New York, 1963).
3. J. Fainberg, L. G. Evans, R. G. Stone, *Science* **178**, 743 (1972).
4. M. L. Goldstein, R. A. Smith, K. Papadopoulos, *Astrophys. J.* **234**, 683 (1979).
5. The International Sun-Earth Explorer spacecraft is a joint project of NASA and the European Space Agency.
6. R. Knoll *et al.*, *IEEE Trans. Geosci. Electron.* **GE-16**, 199 (1978).
7. J. Fainberg, *NASA Tech. Mem. 80598* (1979).
8. ——— and R. G. Stone, *Sol. Phys.* **15**, 222 (1970).
9. ———, *ibid.*, p. 433.
10. J.-L. Bougeret, J. Fainberg, R. G. Stone, *Astron. Astrophys.*, in press.
11. M. Dryer, *Space Sci. Rev.* **33**, 233 (1982), table I, p. 237.
12. L. F. Burlaga, *J. Geophys. Res.* **72**, 4449 (1967).
13. J. H. King, *Interplanetary Medium Data Book—Supplement 2* (Publication NSSDC 83-OX, National Space Science Data Center, NASA, Greenbelt, Md., 1983).
14. We acknowledge useful discussions with L. F. Burlaga and K. W. Ogilvie.
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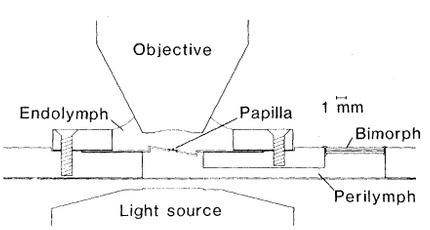
26 April 1983; accepted 6 July 1983

A Micromechanical Contribution to Cochlear Tuning and Tonotopic Organization

Abstract. *The response properties of hair cells and nerve fibers in the alligator lizard cochlea are frequency selective and tonotopically organized with longitudinal position in the organ. The lengths of the hair-cell hair bundles also vary monotonically with longitudinal position. In this study, quantitative measurements were made of the motion of individual hair bundles in an excised preparation of the cochlea stimulated at auditory frequencies. The angular displacement of hair bundles is frequency selective and tonotopically organized, demonstrating the existence of a micromechanical tuning mechanism.*

One of the persistent problems in auditory physiology has been to identify mechanisms responsible for sharp frequency selectivity (tuning) and tonotopic organization in the responses of cochlear hair cells and nerve fibers (*1*). Controversy exists concerning the nature of mechanisms that might supplement the tuning of basilar-membrane motion to provide sharper tuning of hair-cell and nerve-fiber responses (*2*). In light of recent measurements of basilar-membrane motion (*3*), it is unclear to what extent such additional tuning mechanisms are required in the mammalian cochlea; however, in the cochlea of one reptile, the alligator lizard (*Gerrnonotus multicarinatus*), there is a clear difference between basilar-membrane tuning and the tuning of both hair-cell receptor potential and nerve-fiber average discharge rate (*4–7*). Hair-cell and nerve-fiber responses are relatively sharply tuned and tonotopically organized with longitudinal position in the organ (*6, 7*), but the motion of the basilar membrane seems to be neither sharply tuned nor tonotopically organized (*8*). Therefore, this organ must contain an additional mechanism, between basilar-membrane motion and the generation of the hair-cell receptor potential, which produces both additional tuning and tonotopic organization. This mechanism has been proposed to reside in mechanically resonant properties of the hair-cell hair bundles (*4, 5, 9*). We now show that such a micromechanical mechanism exists, that tuning and tonotopic organization occur at the mechanical input to the hair cells.



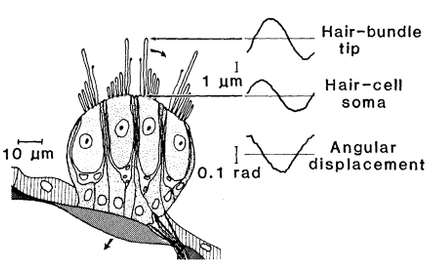


Fig. 1 (left). The experimental chamber. The dissected organ is cemented with Histoacryl adhesive across a hole in a partition separating two fluids. An artificial endolymph (2 m*M* Na^+, 169 m*M* K^+, 2 m*M* Ca^{2+}, 3 m*M* D-glucose, 5 m*M* Hepes buffer; *p*H 7.3) bathes the top (hair-bundle) surface of the organ; an artificial perilymph (168 m*M* Na^+, 2 m*M* K^+, 2 m*M* Ca^{2+}, 3 m*M* D-glucose, 5 m*M* Hepes buffer; *p*H 7.3) bathes the bottom (basilar membrane) surface. The organ is stimulated by driving the fluid in the bottom compartment at frequencies between 1 and 4 kHz with a piezoelectric bimorph element. The resulting motion of the organ is observed from above with differential interference contrast optics and recorded on videotape. Xenon-flash stroboscopic illumination is used to slow or stop the apparent motion of the organ. Fig. 2 (right). Method of quantitative measurement of hair-bundle motion. The schematic cross section of the organ [adapted from Mulroy (*10*)] shows four hair cells and the associated supporting cells resting on the basilar membrane (gray hatching). In response to stimulation, the basilar membrane appears to pivot (lower arrow), while the receptor organ rocks from side to side in the plane of the cross section. Motion of the receptor organ in this plane deflects hair bundles along their axes of morphological symmetry (upper arrow); such displacements produce maximal receptor potentials in hair cells (*11*). Stimulus-induced motions of the hair-bundle tips and hair-cell somata along the axis of symmetry were measured by processing video pictures of the moving organ with an electronic edge detector that tracked a contrast edge in the image (for example, the edge of a moving hair bundle) through a series of frames and produced an output proportional to the position of the edge. By focusing on the organ at different depths, the motion of the tip of a hair bundle (top waveform) and of the soma (middle waveform) were measured for an individual hair cell. The angular displacement of the hair bundle with respect to the soma (bottom waveform) was computed by subtracting waveforms of hair-bundle tip and somatic displacement and dividing the result by the height of the hair bundle, measured with the calibrated focusing knob of the microscope.

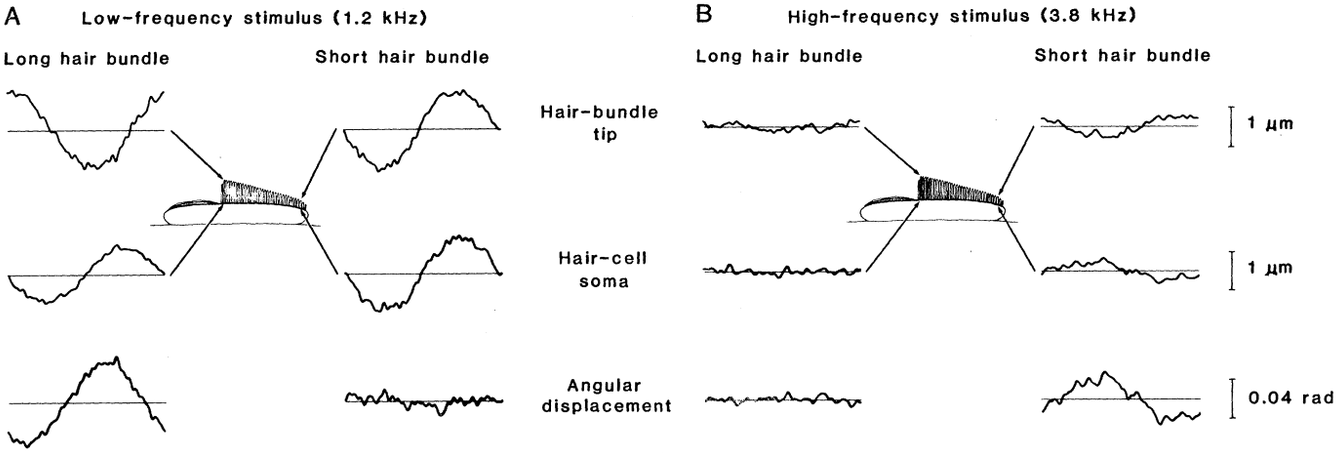


Fig. 3. (A) Waveforms of motion of the hair-bundle tip (top) and soma (middle) of two cells, one with a long and the other with a short hair bundle. At a low frequency of stimulation (1.2 kHz), the angular displacement of long hair bundles is greater than that of short hair bundles (bottom). The schematic longitudinal view of the organ shows roughly where the measurements were made. (B) Waveforms for the same cells as in (A) with 3.8-kHz stimulation. At this high frequency, the angular displacement of short hair bundles exceeds that of long hair bundles.

The auditory receptor organ of the lizard cochlea, the basilar papilla, comprises two morphologically distinct regions (*10*): a tectorial region in which hair bundles are covered with a tectorial membrane, and a freestanding region in which hair bundles project without encumbrance into endolymph. In the freestanding region, the heights of the hair bundles vary monotonically with position along the organ, from about 31 μm at the border of the tectorial region to about 12 μm at the basal end of the organ. This gradation of hair-bundle height correlates with the tuning properties of auditory nerve fibers innervating this region: the best frequency of neural response ranges from about 1 kHz for fibers entering the organ in the region of the long hair bundles, to near 4 kHz for fibers entering the organ in the region of the short hair bundles. We have excised the organ from the ear and placed it in an experimental chamber designed to simulate the fluid environment and the mode of stimulus of the cochlea (Fig. 1). To determine whether hair cells in different positions in the freestanding region of the organ are mechanically tuned to different frequencies, we measured the motions of hair bundles of individual cells with a video system during stimulation of the organ at frequencies between 1 and 4 kHz.

In response to stimulation, the lizard's basilar membrane appears to pivot about its attachment to the neural limbus, producing a side-to-side motion of the receptor organ (Fig. 2). As a result of the organ's motion, hair bundles pivot about their insertions at the top surface of the hair-cell somata (*11*). By measuring the motion of the tip of a hair bundle and that of the associated soma, we can compute the angular displacement of the hair bundle, which presumably constitutes the effective mechanical stimulus to the cell (*12*). We find that the motions of the tips of the hair bundles and of the somata are functions of frequency and longitudinal position along the organ (Fig. 3). At low frequencies (near 1 kHz) and moderate stimulus amplitudes (*13*), the motions of the somata are large and in phase with each other throughout the organ (Fig. 3A). However, the motions of the tips of the long and short hair bundles differ: short hair bundles move approximately in phase with the somata, whereas long hair bundles move out of phase. The angular displacement of long hair bundles is therefore larger than that of short hair bundles. At high frequencies (near 4 kHz), the amplitude of somatic motion is greater at the end of the organ with short hair bundles than in the region with long hair bundles (Fig. 3B). The motion of the tips of short hair bundles also exceeds that of the tips of long hair bundles and is out of phase with the somatic motion. As a consequence, the angular displacement of short hair bundles is greater than that of long hair bundles. In sum, the angular displacement of hair bundles is frequency-selective and tonotopically organized: long hair bundles move selectively at low frequencies, whereas short hair bundles move selectively at high frequencies (*14*).

These data suggest that in the lizard cochlea, mechanical properties of the hair bundles and the receptor-organ somata determine in part such neural and hair-cell response properties as frequency selectivity and tonotopic organization. The micromechanical contribution to peripheral frequency selectivity in the lizard can be estimated, from the difference between the tuning of basilar membrane motion (*8*) and hair-cell receptor potential (*7*), to be on the order of 0 dB per octave below the characteristic frequency and −12 dB per octave above. This estimate is consistent with theoretical predictions of a micromechanical model of the freestanding region (*4*).

Viewed in a narrow sense, micromechanical tuning is a method by which this primitive cochlea, apparently lacking a traveling wave of basilar membrane motion, provides tonotopic organization and additional tuning of hair-cell and nerve-fiber responses. However, because variations in receptor-organ structure are found generally in vertebrate hearing organs (*15*), receptor-organ micromechanics may contribute to peripheral frequency selectivity in other species as well (*16*).

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References and Notes

1. Responses of nerve fibers and hair cells are frequency-selective, that is, maximally sensitive to sound at one frequency, termed the characteristic frequency, and less sensitive at higher or lower frequencies. Response properties of cells, such as characteristic frequency, are tonotopically organized, that is, they are graded with position in the receptor organ.
2. Suggested sharpening mechanisms include micromechanical mechanisms within the organ of Corti, both passive [J. B. Allen, *J. Acoust. Soc. Am.* **59**, 930 (1977); J. J. Zwislocki and E. J. Kletsky, *Science* **204**, 639 (1979)] and active [S. T. Neely and D. O. Kim, *Hearing Res.* **9**, 123 (1983)], and electrical interactions between inner and outer hair cells [P. A. Lynn and B. McA. Sayers, *J. Acoust. Soc. Am.* **47**, 525 (1970)]. For a review, see P. Dallos [*Annu. Rev. Physiol.* **32**, 153 (1981)]. A. C. Crawford and R. Fettiplace [*J. Physiol. (London)* **306**, 79 (1980)]

have reported an electrical resonance in hair cells of the terrapin cochlea. Whether this mechanism exists in other cochleas is not yet known.
3. S. M. Khanna and D. G. B. Leonard, *Science* **215**, 305 (1982); P. M. Sellick, R. Patuzzi, B. M. Johnstone, *J. Acoust. Soc. Am.* **72**, 131 (1982).
4. T. F. Weiss *et al.*, *J. Acoust. Soc. Am.* **70**, S50 (1981).
5. T. F. Weiss, W. T. Peake, A. Ling, T. Holton, in *Evoked Electrical Activity in the Auditory Nervous System*, R. F. Naunton and C. Fernandez, Eds. (Academic Press, New York, 1978), p. 91.
6. T. F. Weiss, M. J. Mulroy, R. G. Turner, C. L. Pike, *Brain Res.* **115**, 71 (1976).
7. T. Holton and T. F. Weiss, *J. Physiol. (London)*, in press.
8. W. T. Peake and A. L. Ling, *J. Acoust. Soc. Am.* **67**, 1736 (1980).
9. L. S. Frishkopf, D. J. DeRosier, E. H. Egelman, *Soc. Neurosci. Abstr.* **8**, 40 (1982); T. Holton and A. J. Hudspeth, *ibid.*, p. 40; T. Holton, *Assoc. Res. Otolaryngol. Abstr.* **6**, 98 (1983).
10. M. J. Mulroy, *Brain Behav. Evol.* **10**, 69 (1974).
11. Pivoting of the stereocilia has been observed in hair cells of the frog crista in response to direct mechanical displacement [A. Flock, in *Psychophysics and Physiology of Hearing*, E. F. Evans and J. P. Wilson, Eds. (Academic Press, London, 1977), p. 15].
12. A. J. Hudspeth and D. P. Corey, *Proc. Natl. Acad. Sci. U.S.A.* **74**, 2407 (1977).
13. The amplitudes of angular displacement of the hair bundles shown in Fig. 3 do not exceed ±0.04 rad (±2.3°). From the geometry of the organ, the assumption that the organ pivots about the neural limbus, and the basilar-membrane data in the intact preparation (*8*), we estimate that sounds producing equivalent motions in the intact animal would not exceed 100-dB sound-pressure level at the eardrum.
14. There are at least two reasons somatic motion measured by the video technique demonstrates frequency-dependent place organization while basilar membrane motion measured by the Mössbauer technique in the intact preparation (*8*) does not. (i) The video measurements are made at the top (somatic) surface of the organ, whereas the Mössbauer measurements are made at the bottom (basilar-membrane) surface. Since these two surfaces are separated by the 50-μm thickness of the papilla, their motions need not necessarily show the same dependence on frequency and place. (ii) The two measurement techniques resolve motion along orthogonal axes. The video technique measures side-to-side motion of the organ, in a plane of focus parallel to the basilar membrane; the Mössbauer technique usually measures up-and-down motion of the basilar membrane, and thus will not resolve any side-to-side components of basilar membrane motion that result from the organ's pivoting about the limbus.
15. In fish [R. R. Fay and A. N. Popper, in *Comparative Studies of Hearing in Vertebrates*, A. N. Popper and R. R. Fay, Eds. (Springer-Verlag, New York, 1980), p. 3], amphibians [E. R. Lewis, *Neurosci. Lett.* **21**, 131 (1981)], reptiles [(*10*); R. G. Turner, A. A. Muraski, D. W. Nielsen, *Science* **213**, 1519 (1981)], birds [C. A. Smith, in *Progress in Sensory Physiology*, D. Ottoson, Ed. (Springer-Verlag, New York, 1981), vol. 2, p. 135], and mammals [D. J. Lim, *J. Acoust. Soc. Am.* **67**, 1686 (1980)].
16. Although micromechanical tuning has not been measured directly in any mammalian cochlea, recent measurements of a sharply selective, physiologically vulnerable component of basilar membrane motion (*3*) and of cochlear acoustic distortion products [D. T. Kemp, *J. Acoust. Soc. Am.* **64**, 1386 (1978); S. D. Anderson and D. T. Kemp, *Arch. Otorhinolaryngol.* **224**, 47 (1979); D. O. Kim, *Hearing Res.* **2**, 297 (1980)] have been interpreted as suggesting the existence of micromechanical processes coupled into the motion of the basilar membrane.
17. S. L. Shotwell, R. Jacobs, A. J. Hudspeth, *Ann. N.Y. Acad. Sci.* **374**, 1 (1981).
18. Supported by fellowships to T.H. from the Del E. Webb Foundation and the National Institutes of Health (GM07301) and grants to A.J.H. from NIH (NS13154) and the System Development Foundation. We thank J. N. Power for electronic design and construction, R. Jacobs for technical assistance, and H. Berg, R. A. Eatock, M. Konishi, R. S. Lewis, and D. C. Van Essen for comments on the manuscript.
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28 February 1983; accepted 25 July 1983

Alternating Current Delivered into the Scala Media Alters Sound Pressure at the Eardrum

Abstract. *Alternating current delivered into the scala media of the gerbil cochlea modulates the amplitude of a test tone measured near the eardrum. Variations in the electromechanical effect with acoustic stimulus parameters and observed physiological vulnerability suggest that cochlear hair cells are the biophysical origin of the process. Cochlear hair cells have traditionally been thought of as passive receptor cells, but they may play an active role in cochlear micromechanics.*

The cochlea functions as a mechanical frequency analyzer with a continuous distribution of resonant frequencies along its length. The frequency response of the vibration of the basilar membrane, upon which sensory cells (hair cells) are located, has been studied extensively (*1–3*). Recent measurements indicate that the frequency selectivity of the basilar membrane is sufficient to account for the sharp frequency tuning observed in cochlear inner hair cells and auditory nerve fibers (*2*).

Rhode demonstrated the physiological vulnerability of cochlear mechanics in the squirrel monkey and showed that the frequency selectivity and relative sensitivity decreased at high sound-pressure levels (SPL's) (*3*). His work has been extended to the cat and guinea pig (*2*). Cochlear mechanics can be modified by stimulation of efferent fibers that are thought to synapse primarily on outer hair cells (*4, 5*). The mechanics can also be modified by changes in the cochlear endolymphatic potential, which is the voltage gradient across the sensory epithelium (*4*).

Several proposed models assume an active mechanical role for the hair cells in the generation of the sharply tuned basilar membrane response (*6, 7*). Because the stereocilia of the outer hair cells are embedded in the tectorial membrane overhanging the basilar membrane (*8*), the models generally consist of a resonant basilar membrane coupled to the tectorial membrane by force-generating hair cells. The hair-cell stereocilia have been suggested to produce a force proportional to either displacement (*7*) or velocity (*6*). Both classes of models are prone to instability, which could account for a type of objective tinnitus in which sound is radiated out of the ear. If either class of models is valid, the hair cells must be able to undergo mechanical changes very rapidly.

We now report an electromechanical phenomenon in the cochlea, with characteristics consistent with the hypothesized hair-cell force-generating mechanism. By passing sinusoidal electrical currents into the scala media of the cochlea, we can induce rapid mechanical changes. The effect seems to be related to the hair-cell receptor potential, as reflected in the cochlear microphonic (CM).

Healthy gerbils weighing 60 to 90 g were anesthetized with sodium pentobarbital. A calibrated, closed acoustic system consisting of an earphone and probe-microphone was cemented into place at the meatal entrance to the bulla. A 0.16 or 1.0*M* KCl-filled glass pipette with a tip diameter of approximately 5 μm was inserted into the scala media of either the first or second cochlear turn, and sinusoidal currents of 1 to 50 μA peak-to-peak were delivered by an isolated current source. A subcutaneous, Ag-AgCl current return electrode was placed in the neck. The entire stimulus and data-collection system was controlled by computer.

Single tones were delivered to the earphone, and the resulting sound pressure near the tympanic membrane was measured with a probe-tube microphone. The amplified microphone output was sampled by an analog-to-digital converter at a rate of eight samples per period of the acoustic stimulus. Multiple data records of 1024 points were averaged and stored for subsequent Fourier analysis.

Figure 1A shows a typical spectrum obtained through the use of a 800-Hz tone at 65 dB SPL with a delivered current of 25 μA peak-to-peak at 150 Hz. The signal component at acoustic frequency F_a is the primary tone delivered to the earphone. The second and third acoustic harmonics are at multiples of F_a. There exist acoustic emissions at the frequency of the electrical stimulation (F_e) and its second harmonic. The spectral components of interest are those separated from the primary signal and its harmonics by a distance equal to F_e. We refer to these components as the upper