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Unidirectional Amplification as a Mechanism for Low-Frequency Hearing in Mammals

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Abstract. Sound detection is achieved in the inner ear, or cochlea, which spatially separates frequencies. The highest frequencies are detected at the organ's base and successively lower frequencies at progressively more apical positions. Although a mechanism termed critical-layer absorption accounts for the spatial separation of frequencies above 1 kHz, hearing at lower frequencies appears to operate by a distinct mechanism that is poorly understood. We discuss a recently proposed ratchet mechanism for spatial separation of these low frequencies. This mechanism involves the synergistic interplay of two known active processes in the mechanoreceptive hair cells—active hair-bundle motility and membrane-based electromotility—to implement unidirectional amplification. It thus represents a mechanical analogue of the operational amplifier in electrical engineering. The mechanism provides a general design principle for unidirectional mechanical amplification that we have also employed to construct an active microphone.

Keywords: cochlear mechanics, hair-bundle motility, electromotility

PACS: 43.64.Bt, 43.64.Kc, 43.64.Yp

INTRODUCTION

The cochlea possesses an active process that provides tuned mechanical amplification of weak sounds [8, 9]. Loss of the active process greatly increases the hearing threshold and leads to severe hearing loss. The origin of the active process in the cochlea is highly debated, however, for cochlear outer hair cells exhibit two forms of mechanical activity. First, hair bundles provide active forces that can enhance their own deflection [7, 9, 13]. Second, the cell bodies of outer hair cells change their length upon changes in their membrane potential like piezoelectric elements, a phenomenon termed electromotility [1, 3, 21]. The relative contribution and importance of both processes to cochlear operation remain enigmatic.

We discuss recent theoretical work in which we have proposed a ratchet mechanism for spatial separation of low frequencies that employs a synergistic interplay between the two cellular processes [16]. The fundamental feature of this mechanism is unidirectional coupling, an important property of an ideal amplifier. Basilar-membrane vibration represents the system's input whereas hair-bundle deflection corresponds to the output. A simple amplifier operates reciprocally: a force applied to the input elicits a displacement at the output that equals the displacement at the input when the same force acts on the output [2, 14]. The action of electromotility breaks reciprocity and can lead to unidirectionality: sound-evoked forces on the basilar membrane elicit hair-bundle displacement, whereas internal hair-bundle forces do not feed back on the basilar membrane. Although amplification in the basal region of the cochlea is reciprocal, unidirectional amplification may underly cochlear mechanics near the apex.

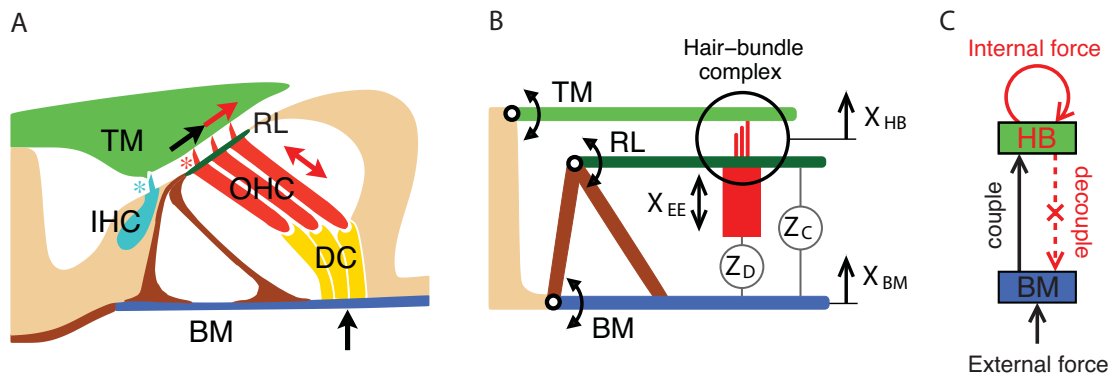


FIGURE 1. Micromechanics of the organ of Corti. (A) The mechanosensitive outer hair cells (OHC) together with Deiters' cells (DC) couple the basilar-membrane (BM) to the reticular lamina (RL) and tectorial membrane (TM). Upward displacement of the basilar membrane by sound (lower black arrow) deflects the hair bundles in the excitatory direction (upper black arrow). Active hair-bundle force increases the deflection (single-headed red arrow). Electromotility leads to a length change of the outer-hair cell bodies (double-headed red arrow). (B) Deflection X_{BM} of the basilar membrane is coupled to the deflection X_{HB} of the complex formed by the hair bundles, reticular lamina, and tectorial membrane through an impedance Z_C as well as an impedance Z_D that is in series with an element capable of an electrically controlled length change X_{EE} . (C) Unidirectional amplification emerges when an external sound force acting on the basilar membrane elicits hair-bundle motion whereas internal hair-bundle forces do not feed back on the basilar-membrane.

Unidirectional mechanical amplification can also be employed in engineering. Contemporary electronic amplifiers achieve unidirectionality by means of semiconductors. Our proposed mechanism constitutes the first scheme for implementing unidirectional amplification in a mechanical system. We have thus constructed an active microphone that implements this idea. Unidirectionality results from piezoelectric coupling between a dynamic microphone's diaphragm, representing the input, and its voice coil, corresponding to the output.

UNIDIRECTIONAL AMPLIFICATION IN THE COCHLEA

The micromechanics of the organ of Corti exhibits two fundamental degrees of freedom. Basilar-membrane vibration X_{BM} represents the system's input on which an external sound force F_{ext} acts (Fig 1A,B). A hair bundle's deflection X_{HB} denotes the system's mechanical output, which can be amplified through an internal hair-bundle force F_{int} . Because of geometrical constraints deflection of the hair bundles is proportional to displacement of the reticular lamina and tectorial membrane. Basilar-membrane and hair-bundle vibration are coupled viscoelastically through the cell bodies of outer hair cells and Deiters' cells as well as the surrounding fluid, which we describe through impedances Z_C and Z_D (Fig. 1B). Further, a change in the membrane potential of an outer hair cell induces an electrically evoked length change X_{EE} .

Consider a pure sound at angular frequency ω : $F_{ext} = \tilde{F}_{ext} e^{i\omega t} + c.c.$ in which the tilde indicates the Fourier transform and $c.c.$ denotes the complex conjugate. The vibration of the basilar membrane, the hair-bundle complex, and the electrically evoked length change of an outer hair cell then predominantly occur at the same frequency: $X_{BM} =$

$\tilde{X}_{\text{BM}}e^{i\omega t} + c.c.$, $X_{\text{HB}} = \tilde{X}_{\text{HB}}e^{i\omega t} + c.c.$, and $X_{\text{EE}} = \tilde{X}_{\text{EE}}e^{i\omega t} + c.c.$ For small physiological displacements the electrically evoked length change X_{EE} is proportional to the hair-bundle displacement X_{HB} : $\tilde{X}_{\text{EE}} = -\alpha\tilde{X}_{\text{HB}}$ with a complex mechanomotility coefficient α [6]. The basilar-membrane and hair-bundle displacements follow from

$$A \begin{pmatrix} \tilde{X}_{\text{HB}} \\ \tilde{X}_{\text{BM}} \end{pmatrix} = \frac{1}{i\omega} \begin{pmatrix} \tilde{F}_{\text{int}} \\ \tilde{F}_{\text{ext}} \end{pmatrix}. \quad (1)$$

The matrix A contains the impedances Z_{HB} and Z_{BM} of the hair-bundle complex and the basilar membrane as well as the coupling impedances Z_{D} and Z_{C} :

$$A = \begin{pmatrix} Z_{\text{HB}} + (1 + \alpha)Z_{\text{D}} + Z_{\text{C}} & -Z_{\text{D}} - Z_{\text{C}} \\ -(1 + \alpha)Z_{\text{D}} - Z_{\text{C}} & Z_{\text{BM}} + Z_{\text{D}} + Z_{\text{C}} \end{pmatrix}. \quad (2)$$

The key aspect of the above equation is the violation of reciprocity through electromotility. When $\alpha \neq 0$, the coupling from the basilar membrane to the hair bundles, represented by the matrix element A_{12} , differs from the coupling of the hair bundles back to the basilar membrane, given by the matrix element A_{21} , and reciprocity is broken. This behavior arises because electromotility breaks a symmetry: electromotility is controlled by hair-bundle displacement but not by basilar-membrane vibration. The violation of reciprocity reaches an extreme at a critical value $\alpha_* \equiv -1 - Z_{\text{C}}/Z_{\text{D}}$ at which the matrix element A_{21} , and with it the backward coupling from the hair bundles to the basilar membrane, vanishes whereas the forward coupling persists. The coupling between the basilar membrane and the hair bundles is then unidirectional (Fig. 1C). Because only hair-bundle motion is amplified in this case, it can exceed the passive, linear motion of the basilar membrane by orders of magnitude. This contrasts with reciprocal amplification in which hair-bundle and basilar-membrane displacements are both amplified and hence are nonlinear and of the same order of magnitude.

Measurements of basilar-membrane motion near the cochlear base show a strong compressive nonlinearity in the membrane's response to varying sound-pressure level indicative of amplification [4, 19, 22]. This accords with a presumed limitation of electromotility to frequencies below a few kilohertz, above which changes in the membrane potential are low-pass filtered by the membrane capacitance and hence small. Measurements from the cochlear apex, however, do not find a strong compressive nonlinearity in basilar-membrane motion [4, 10, 18]. One set of measurements reports tectorial-membrane vibrations that exceed basilar-membrane vibrations by orders of magnitude in agreement with unidirectional amplification [10]. Further evidence for unidirectional amplification in the apical but not the basal part of the cochlea comes from the tuning curves of auditory-nerve fibers, whose shapes differ between high-frequency and low-frequency fibers [11, 20]. We have thus proposed a model in which amplification near the base is reciprocal and frequency selectivity there emerges through tuning of the whole cochlear partition, yielding a mechanism termed critical-layer absorption [12]. Amplification in the apical region, however, is unidirectional. The basilar membrane is no longer tuned to the characteristic frequency but the hair-bundle complex exhibits an independent resonance enabled by unidirectional coupling ([16], Fig. 2). This model reproduces the observed shape changes in tuning curves from auditory-nerve fibers and hence provides their first conceptual explanation.

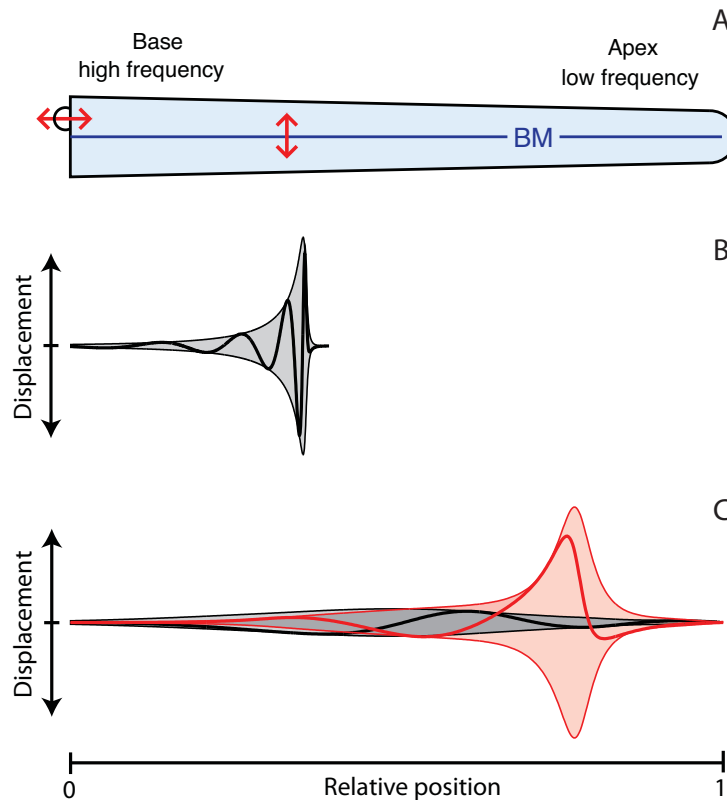


FIGURE 2. Cochlear mechanics. (A) Schematic diagram of the mammalian cochlea. (B) A high-frequency sound triggers a wave on the basilar membrane that peaks at a frequency-dependent place near the base and decays sharply beyond, a mechanism termed critical-layer absorption. (C) Unidirectional amplification in the apical region allows for a resonance in hair-bundle displacement (red) in the absence of a resonance in basilar-membrane motion (black). The wave can then travel across the characteristic place but elicits a maximal hair-bundle displacement at a characteristic position marked by an approximately symmetric tuning curve.

Unidirectional and reciprocal amplification differ fundamentally. In a theoretical study we have shown that cochlear amplification results in a large cumulative gain when amplification is reciprocal and acts on the basilar-membrane wave, whereas the gain does not accumulate when amplification does not feed back as a result of unidirectional coupling [15]. On the other hand, unidirectional coupling prevents distortion of the incoming signal whereas the signal becomes distorted when amplification is reciprocal [17].

UNIDIRECTIONAL AMPLIFICATION IN AN ACTIVE MICROPHONE

The above scheme represents a general mechanism for implementing unidirectional amplification in a mechanical system. As the ear exemplifies, mechanical amplification can be useful in detection of a mechanical signal because it can raise a particular

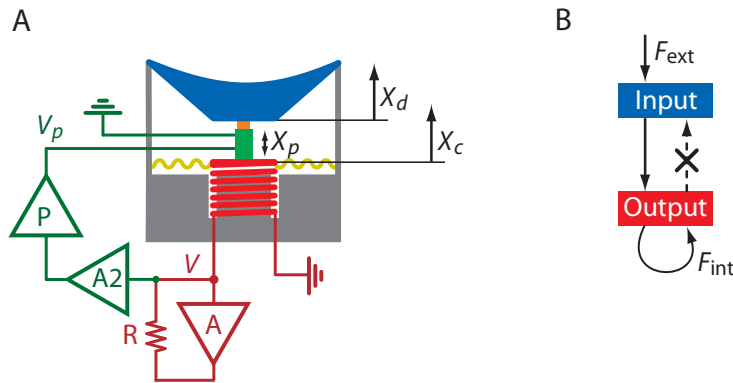


FIGURE 3. Unidirectional active microphone. (A) Sound vibrates the diaphragm (blue, displacement X_d) and hence the coil (red, displacement X_c). The induced voltage V is amplified and fed back into the coil through a resistor R . A piezoelectric element (green, length change X_p) is controlled by the coil voltage V that is tuned to the right amplitude and phase to eliminate the feedback of the internal Lorentz force on the diaphragm. (B) A schematic of unidirectional amplification.

signal above the noise level. Current microphones, however, are mechanically passive. One difficulty in implementing mechanical amplification in microphones is reciprocity that leads to undesired feedback. Because unidirectional amplification overcomes this difficulty, we have employed it to construct an active microphone [17].

A dynamic microphone functions by the same principle as a dynamic speaker [5]: a diaphragm is attached to a coil that moves in a magnetic field (Fig. 3A). Sound vibrates the diaphragm and thereby causes oscillations of the coil that electromagnetically induce a voltage. Such a system serves as a speaker when an oscillatory electrical signal is applied to the coil; the consequent Lorentz force vibrates the coil and hence the diaphragm, emitting sound. The system's dual function as microphone and speaker therefore results from two forces. An external sound force F_{ext} acts on the diaphragm, representing the microphone's input, and the internal Lorentz force F_{int} acts on the coil, corresponding to the output.

Because of the system's dual function as both speaker and microphone it can readily be converted into a mechanically active microphone (Fig. 3A). Indeed, positive feedback of the electrical signal in the coil can employ the internal Lorentz force to increase the coil's displacement resulting from an external sound force. Unidirectionality can be implemented through a piezoelectric element that is positioned between the diaphragm and the coil and that is controlled by the coil voltage, adjusted to the correct magnitude and phase. The device is closely analogous to the micromechanics of the organ of Corti: the diaphragm corresponds functionally to the basilar membrane, the coil to the hair bundle, and the piezoelectric element to the body of an outer hair cell. An active microphone constructed in this way functions as an ultra-sensitive, non-distorting sensor for mechanical signals such as sound, seismic vibrations, or even gravitational waves [17].

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