The initial conditions for solving the coupled differential equations are $P_{E\text{-}FAD}(0) = 1$, $P_{E\text{-}FAD\bullet S}(0) = 0$, $P_{E\text{-}FADH_2}(0) = 0$ at $t = 0$. We evaluate the probability distribution of on-times, $p_{on}(t)$. The probability for an on-time between t and $t + \Delta t$ is $p_{on}(t)\Delta t$, which is the same as the probability of having the emission switched off between t and $t + \Delta t$, $\Delta P_{E\text{-}FADH_2}(t) = k_2 P_{E\text{-}FAD\bullet S}(t)\Delta t$. Explicitly, $p_{on}(t) = dP_{E\text{-}FADH_2}(t)/dt = k_2 P_{E\text{-}FAD\bullet S}(t)$. Solving Eqs. (9) and (10) for $P_{E\text{-}FAD\bullet S}(t)$ by Laplace transform yields

$$p_{on}(t) = k_1 k_2 / 2a\{\exp[(a + b)t] - \exp[(b - a)t]\} \quad (12)$$

where $a = \sqrt{[¼(k_1 + k_{-1} + k_2)^2 - k_1 k_2]}$ and $b = -½(k_1 + k_{-1} + k_2)$.

32. In contrast, we found there is no static disorder in k_1, because k_1 are the same among individual molecules measured at low concentration of the cholesterol substrate (k_1 being rate limiting). Similarly, the off-time distributions for individual molecules are found to be identical to each other. Therefore, there is no static disorder for the $FADH_2$ oxidation half-reaction (Eq. 3).
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41. The covariance parameter for x and y is

$$\frac{n\sum_i^n x_i y_i - \left(\sum_i^n x_i\right)\left(\sum_i^n y_i\right)}{\sqrt{\left[n\sum_i^n x_i^2 - \left(\sum_i^n x_i\right)^2\right]\left[n\sum_i^n y_i^2 - \left(\sum_i^n y_i\right)^2\right]}} \quad (13)$$

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Frequency Tuning of Basilar Membrane and Auditory Nerve Fibers in the Same Cochleae

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Responses to tones of a basilar membrane site and of auditory nerve fibers innervating neighboring inner hair cells were recorded in the same cochleae in chinchillas. At near-threshold stimulus levels, the frequency tuning of auditory nerve fibers closely paralleled that of basilar membrane displacement modified by high-pass filtering, indicating that only relatively minor signal transformations intervene between mechanical vibration and auditory nerve excitation. This finding establishes that cochlear frequency selectivity in chinchillas (and probably in mammals in general) is fully expressed in the vibrations of the basilar membrane and renders unnecessary additional ("second") filters, such as those present in the hair cells of the cochleae of reptiles.

In mammalian cochleae, the bulk of auditory information is transmitted to the brain via the inner hair cells, which provide the sole synaptic inputs to 90% to 95% of the afferent fibers of the auditory nerve (*1*). Auditory nerve excitation is triggered by depolarization of inner hair cells upon deflection of their "hair" bundles toward the taller stereocilia (*2, 3*). Presumably, the forces that deflect the stereocilia bundles are derived from the vibrations of the basilar membrane (BM), but it is not known how these vibrations are transmitted to the inner hair cells (*4*). Although the BM and auditory nerve fibers are similarly tuned at frequencies close to the characteristic frequency (CF) (*5–9*), there is no consensus about whether neural threshold corresponds to a constant magnitude of BM displacement, velocity, or some function of these variables.

Until now, comparisons of the response properties of auditory nerve fibers or inner hair cells and the BM have been indirect, involving data from different subjects [with one exception (*10*)]. For example, a frequency-threshold tuning curve recorded from a single auditory nerve fiber in one subject was compared with BM data from another individual of the same species (*5–7*). Alternatively, comparisons have been based on averaged data obtained from two different groups of subjects (*8*). Considering the variability of both neural [for example, see (*11*)] and mechanical responses [for example, see (*5, 9*)], and also the different measurement conditions, such comparisons are bound to lead to imprecise conclusions. To clarify how mechanical vibrations are translated into neural spike trains, we conducted experiments that previously were not successful. We recorded sequentially, under identical conditions, the responses to tones of a BM site and of auditory nerve fibers innervating neighboring inner hair cells in the nearly normal ears of two anesthetized chinchillas (*12*).

The magnitudes of mechanical and neural responses as a function of stimulus frequency were compared by using tuning curves, which plot the stimulus levels at which a fixed response criterion is reached. In one cochlea, four fibers were encountered with CFs (9.5, 9.3, 8.0, and 7.8 kHz) comparable to the CF of the BM recording site (9.5 kHz). The fiber CFs indicate that they terminated very near the BM recording site or about 0.08, 0.64, and 0.72 mm away, respectively (*13*). Figure 1A shows tuning curves for the BM and one fiber, selected because its CF coincided with that of the BM site and could be compared with the BM tuning curve directly. At the fiber's CF threshold [13-dB sound pressure level (SPL)], BM vibrations had a peak displacement of 2.7 nm or, equivalently, a peak velocity of 164 μm/s. These values were used to plot isodisplacement and isovelocity tuning curves. At frequencies between CF and 1 kHz, there was a good match between neural thresholds and a constant BM velocity. When the entire frequency range of measurements was considered, however, neural thresholds were better fit by mechanical displacements subjected to high-pass filtering at a rate of 3.8 dB per octave. The other three fibers had similar tuning curves, which were well fit (after normalization to the BM CF) by BM displacement high-pass filtered at rates of 4.0, 3.9, and 4.1 dB per octave (*14*).

In another cochlea, the BM recording site had a CF of 9 kHz and four fibers were found with comparable CFs (9.25, 8.7, 8.1, and 8.0 kHz) and probable terminations 0.10, 0.14,

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0.38, and 0.47 mm, respectively, from the BM site. The fiber with CF closest to that of the BM site had a CF threshold of 0.5-dB SPL, at which BM peak vibration was 0.26 nm or 14.6 μm/s (Fig. 1B). As in Fig. 1A, this fiber's thresholds did not correspond to a constant BM displacement. Rather, neural thresholds were well matched by BM displacement high-pass filtered at a rate of 4.8 dB per octave (approaching a constant velocity of 14.6 μm/s) over almost the entire frequency range of measurements. (Note that velocity curves are shaped like displacement curves high-pass filtered at a rate of 6 dB per octave.) The tuning curves of the three other fibers also were well matched by high-pass filtered BM displacement (at rates of 4.1, 4.3, and 2.7 dB per octave) (*14*).

Thus, at near-threshold stimulus levels, the frequency tuning of auditory nerve fibers in both cochleae closely resembled that of BM displacement modified by high-pass filtering. However, neural tuning curves lacked the high-frequency plateaus (Fig. 1, arrows) often demonstrable in BM responses (*7–9, 15–17*).

The question of how BM mechanics determines auditory nerve excitation has often been posed in terms of the existence of a "second filter," which receives its input from (but does not feed back on) the BM (the "first filter") and transforms poorly tuned and insensitive vibrations into well-tuned and sensitive responses of hair cells and auditory nerve fibers (*10, 18, 19*). Indeed, electrical second filters (resonances due to interactions of ionic channels in the basolateral membranes of hair cells) exist in the cochleae of turtles (*20*). In the case of mammals, however, the discovery that BM responses are, in fact, well tuned and sensitive (*5, 6, 8*) has convinced many that a second filter is unnecessary (*21*). The common current view is that the vibrations of the BM are boosted by a mechanical feedback from the organ of Corti (*22*), perhaps involving somatic electromotility of the outer hair cells (*23*). However, the lack of consensus regarding the correspondence between BM vibration and auditory nerve excitation has permitted a lingering defense (*24*) of second filter models or even denials that BM vibrations participate in stimulation of the auditory nerve (*25*). The present results show that the tuning of auditory nerve fibers closely approximates that of BM vibrations (Fig. 1) and thus demonstrate that there is no need for a second filter.

Only one previous investigation studied auditory nerve fibers and the BM in the same cochleae (*10*). That investigation yielded results strikingly different from the present ones: sharply tuned and sensitive responses of auditory nerve fibers were obtained from cochleae in which BM vibrations were insensitive and poorly tuned. In retrospect, it seems apparent that the method used to measure BM vibrations induced severe but localized cochlear damage and that the neural recordings came from fibers connected to sites other than those where vibrations were measured.

Other comparisons of frequency tuning in auditory nerve fibers and at the BM have been indirect. Those involving BM recordings from reasonably healthy cochleae have yielded diverse results, some indicating that neural thresholds correspond to a constant BM displacement (*7, 26*) and others favoring a sensitivity to velocity (*5*) or a combination of displacement and velocity (*8*). The present findings are consistent with the latter study (*8*) and with another that noted that the "tails" of tuning curves of inner hair cells are less sensitive than those of outer hair cells or BM displacement (*27*).

In conclusion, although the BM and auditory nerve fibers are similarly tuned at threshold levels, certain transformations do intervene between BM vibration and auditory nerve excitation. These transformations (high-pass filtering and removal or attenuation of the high-frequency magnitude plateau) may arise from micromechanical interactions of the organ of Corti, the tectorial membrane, and the endolymph in the subtectorial space (*28*) or from electrical processes in the inner hair cells, including filtering by the basolateral membrane and synaptic effects of extracellular potentials (*29*).

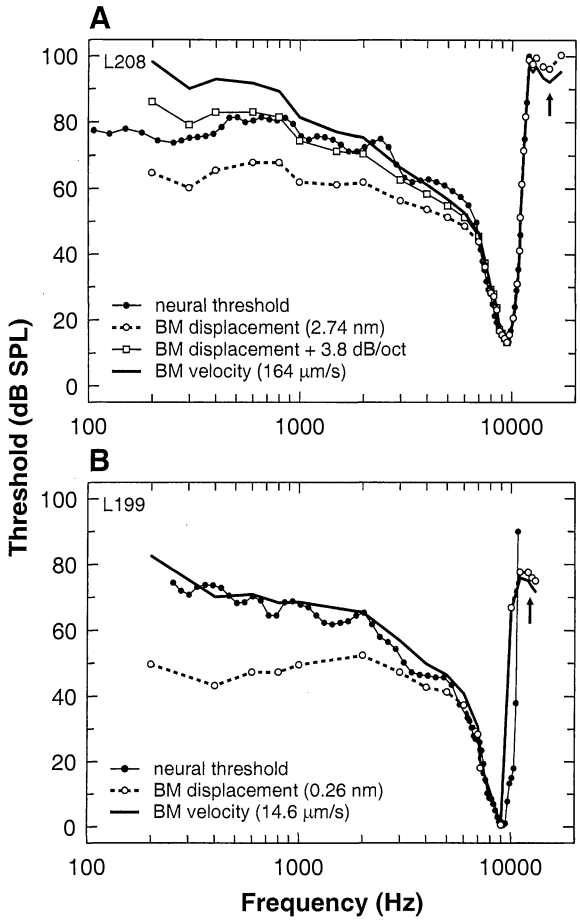

Fig. 1. Frequency tuning of responses to tones of BM sites and auditory nerve fibers with similar CF. (**A** and **B**) Comparison of the frequency-threshold tuning curve for one fiber (filled symbols connected by thin solid line) with isodisplacement and isovelocity mechanical tuning curves (open circles connected by dashed line and thick solid line, respectively). In (A) another curve (open squares connected by solid lines) indicates the result of high-pass filtering the displacement curve at a rate of 3.8 dB per octave. The tip of the BM tuning-curve in (B) appears spuriously narrow because of the low-frequency resolution of data sampling [1000 Hz, versus 250 Hz in (A)]. The fibers had spontaneous activity of 11.2 (A) and 76.3 (B) spikes per second (*33*).

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33. All animal procedures were approved by Northwestern University's Animal Care and Use Committee. Each chinchilla was deeply anesthetized with diallyl barbituric acid in urethane. The left pinna was resected and the head was attached to a metallic holder. A calibrated miniature microphone, with its tip placed within 2 mm of the eardrum, was used for in situ determination of SPLs (expressed relative to 20 μPa). The auditory bulla was opened widely and a gross electrode, which recorded compound action potential thresholds of responses to tone pips, was placed on the round window. Both middle-ear muscles (cochlea L208) or only the tensor tympani (L199) was detached. Then the surgical preparations necessary for microelectrode recording from auditory nerve fibers (31) and for measuring BM vibrations with a laser velocimeter (32) were made consecutively. After the otic capsule was opened and reflective microbeads were dropped onto the BM, the otic capsule hole was covered with a window (made from slide coverslip glass) to minimize motion of the perilymph (7). Stimuli for BM recordings were 128 to 512 repetitions of gated tones (5 to 100 ms in duration, presented every 53 to 500 ms). BM tuning curves were computed from velocity-intensity functions (resolution: 5 or 10 dB, 100 to 1000 Hz) by interpolating at each frequency the response magnitude corresponding to neural threshold at CF. Frequency-threshold tuning curves of auditory nerve fibers were measured with 50-ms tone pips, presented every 100 ms, by an automated procedure (11). They had a resolution of 32 frequency steps per octave near CF and 8 steps per octave at lower frequencies.
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Linking Winter and Summer Events in a Migratory Bird by Using Stable-Carbon Isotopes

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For migratory birds, early arrival and physical condition on the breeding grounds are important determinants of reproductive success and fitness. Differences in arrival times often exceed a month, and later arriving individuals are often in poorer condition. Habitat-specific isotopic signatures indicate that the quality of winter habitats occupied by American redstarts (*Setophaga ruticilla*) determines their physical condition and spring departure dates, which in turn result in variable arrival schedules and condition on temperate breeding grounds. These findings link events in tropical winter grounds with those in temperate breeding areas for a migratory songbird and provide evidence that winter habitats may be limiting.

Natural selection acts on individuals throughout the annual cycle. For migratory animals, understanding these selection processes has been limited by our inability to follow individuals yearround, yet events during each phase of the annual cycle are likely to influence those in subsequent phases. Many long-distance migratory birds, such as the American redstart, spend 3 to 5 months on their temperate breeding grounds, 1 to 2 months on autumn migration, 6 to 7 months on tropical wintering areas, and another month on spring migration (*1*).

For many migratory species, males arrive at breeding habitats before females (*2*), and breeding success and physical condition decline with arrival date (*3, 4*). Early arrival appears to be advantageous because it gives access to the best breeding sites and mates, as well as additional time to replace lost clutches (*5*). Declining reproductive success for late arriving birds is also attributed to poor physical condition of these individuals (*4*). Factors that determine arrival time and physical condition of birds in breeding areas are poorly understood.

To test the hypothesis that winter events influence arrival dynamics on the breeding grounds, we studied American redstarts in two habitats in southwestern Jamaica: a black mangrove (*Avicennia germinans*) forest in which males predominated (65% male and 35% female) and a drier, second-growth scrub habitat in which females were more abundant (30% male and 70% female). Sexual habitat segregation is common in redstarts during the winter period (*6*) and is produced by the dominance behavior of older males forcing most females and young males into habitats of poorer quality (*7–9*). In autumn 1995 and 1996, redstarts were captured with mist nets, measured, bled for hormone and stable-isotope assays, color-banded, and released. In late March and early April, those individuals that remained on territory over the winter were recaptured for remeasurement. We found that individuals wintering in the forest habitat, regardless of sex, maintained or gained body mass, whereas individuals in scrub habitat lost up to 11% of their body mass [0.06 ± 0.05 g (mean ± SE) compared with -0.24 ± 0.07 g; two-way analysis of variance: sex $F = 0.09$, $P = 0.77$; habitat $F = 15.1$, $P = 0.0004$; sex by habitat $F = 2.56$, $P = 0.12$]. Individuals in scrub habitats showed other signs of deteriorated physical condition, including elevated plasma corticosterone concentration (*9*).

The poor physical condition of redstarts in scrub habitat did not lead to lower overwinter survival (*8*), but it did result in a delay in departure schedules (*10*). Both males and females departed significantly later from scrub habitat in both years (Fig. 1). Furthermore, departure time was inversely correlated with change in body mass (Fig. 2), implying that redstarts in better physical condition were able to leave sooner.

To determine if habitat segregation during winter influences the arrival schedules of birds

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