Electrical Tuning in the Ear

INTRODUCTION

Recently, there has been a growing tendency in the hearing research community to attribute tuning in the ears of lower vertebrates to the electrical resonances that have been observed in isolated receptor cells (hair cells). In this comment, I attempt to make two points: (1) that, on elementary theoretical grounds, tuning by resonances *per se* would have been maladaptive for the evolving vertebrate ear—allowing natural selection to achieve high resolution either in frequency or in time, but not both, and (2) that in two of the three lower-vertebrate acoustic sensors in which the situation has been studied carefully in the intact ear, the electrical resonances observed in isolated hair cells evidently are combined with other elements to form nonresonant tuning structures capable of high resolution in both frequency *and* time.

FUNCTIONAL AND SIGNAL CONTEXTS OF ACOUSTIC SENSORS

Among auditory scientists there is widespread belief that the quintessential function of the mammalian cochlea and of many of its homologs and analogs in the ears of nonmammalian vertebrates

is frequency sorting, setting the stage for pitch discrimination. Thus it would be argued that it is the frequency sorting of the cochlea that allows the human listener to discriminate notes in a Mozart piano concerto, and that it is the frequency sorting of the avian basilar papilla that allows a white-crowned sparrow on the Berkeley campus to differentiate the notes of its dialect from those of other, nearby white-crowned sparrow dialects. It has been known for several decades that the cochlea sorts frequencies in a graded (tonotopic) fashion along its length. Afferent axons from the region (basal end) of the cochlea closest to the tympanum and to the ossicular chain respond selectively to the highest audible frequencies; axons from the region (apical end) farthest from those structures respond selectively to the lowest audible frequencies; and the responsiveness of axons from the intervening regions gradually shifts from high to low frequencies as one progresses from basal to apical end. Thus, when a complex sound excites the mammalian ear, each place along the cochlea is believed to act as a different spectral filter—responsive to the spectral components of the sound that correspond to the tuning of that place, unresponsive to the other spectral components. Thus, each afferent axon might be considered to carry one element of a time-varying spectral image of the complex sound.

Although there is disagreement regarding the homologies among them, at least seven catalogued organs of the vertebrate inner ear in one animal or another are putative acoustic sensors:[1] the sacculus (in fish, amphibians and possibly reptiles), the utriculus (in some fish), the lagena (in fish, amphibians and possibly birds, reptiles, and monotremes), the papilla neglecta (in some fish and possibly some amphibians and birds), the amphibian papilla (in amphibians), the amphibian basilar papilla (in some amphibians), and the cochlea and its commonly recognized homologs (reptilian and avian basilar papillae). Spectral filtering of one sort or another has been found in all of these organs; and tonotopic organization has been observed so far in the reptilian and avian basilar papillae and the frog amphibian papilla as well as the mammalian cochlea.

At this time we can merely speculate about specific selective pressures that gave rise to each of these acoustic sensors and sculpted its signal-processing properties. For example, an acoustic sensor may have arisen in response to its adaptive value in remote de-

tection of predators or other dangers (*e.g.*, as an early warning system), its adaptive value in detection of prey or other resources, its adaptive value in interspecific or conspecific communication (*e.g.*, in identifying and locating offspring or prospective mates or prospective rivals), or some combination of these. The relevant signals would be the various acoustic cues to the presence of the event or animal to be detected. One can be certain about at least one aspect of the environmental context of the evolving acoustic sense: relevant signals undoubtedly were accompanied by noise and by interfering signals. At any point in space the acoustic signals, interference, and noise would be combined into one single-valued variable (*e.g.*, sound pressure as a function of time); and, under (common) adverse circumstances, only a tiny fraction of the amplitude of that variable would be determined by a particular relevant signal. Operating in a warm environment (*i.e.*, far from 0 deg K), the evolving acoustic sensory system inevitably also would face the problem of noise added by the thermal motion of its own elements.[2-4] It seems clear that the acoustic sensory system that could extract the relevant signal from all of this noise and interference would have had conspicuous selective advantage.[5]

In that regard, spectral filtering would be a powerful tool. Properly tuned (*e.g.*, to the spectral profile of the advertisement call of an animal of the same species), a spectral filter could respond to most of the energy of a particular relevant signal while remaining unresponsive to most of the energy in the noise and interfering signals. Thus, whereas the relevant signal might contribute only a tiny fraction of the amplitude of the single variable entering the filter, it could contribute a large fraction of what remained at the filter output. An array of filters—such as that in the mammalian cochlea, with each filter tuned to a different spectral range, would be especially effective. For example, the energy of noise generated by the wind or by thermal motion usually is distributed more or less uniformly over all frequencies. Relevant signals often have nonuniform spectral structures. Therefore, when a mixture of signal and noise energy passes into a filter array, in the spectral image that emerges at the output of the array the nonuniform spectral features of the signal should be discriminable from the uniformly distributed noise. This is the basis of operation of the spectrum analyzer, a tool commonly used by acoustic scientists and others

to discriminate signals from noise. The tuning and tonotopy observed in mammalian cochleae, in reptilian and avian basilar papillae, and in frog amphibian papillae, suggest that those hearing structures might be considered, in effect, spectrum analyzers.[6-11]

On the other hand, biologically relevant acoustic signals are not always discriminable simply on the basis of the spectral distribution of energy. For example, the spectral distribution of acoustic energy from predator's footfall will be very similar to that of the wind and that of the noise generated by thermal motion of the elements of the acoustic sensor (*i.e.*, an impulse has the same amplitude spectrum as white noise). Therefore, an acoustic sensory system that could separate signals on the basis of cues other than spectral energy distribution clearly would have been advantageous. One obvious family of such cues would be temporal events. Noise often is continuous in time, with indefinite duration. Signals, such as the call of a member of the listener's own species or the sound of the predator's footfall, typically start abruptly. Therefore, an acoustic sensory system that could analyze its inputs for discrete temporal events, such as signal onsets, would have provided conspicuous selective advantages. Temporal analysis is valuable for another strategy for separating relevant signals from noise and interference. The places in space where acoustic noise originates commonly are different from those at which signals originate, and different signals often arise from different places. These differences are reflected in binaural cues, including arrival-time differences between the two ears. Therefore analysis based on interaural time differences also would have provided conspicuous selective advantages.

In its role as a spectral analyzer, the acoustic sensory system presumably would have been selected for high resolution in frequency, which in turn would yield high resolution and consequent high discriminability of signals based on the spectral distribution of energy. In its role as a temporal analyzer, the acoustic sensory system presumably would have been selected for high resolution in time, which in turn would yield high discriminability of signals based on abrupt onset and on interaural time differences. Anyone familiar with spectral analysis would see a conflict here; when spectral resolution is determined by bandwidth, resolution in frequency is achieved at the cost of resolution in time, and vice versa.[12]

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SECOND-ORDER RESONANCE FILTERS

Recently, linear second-order resonances have been proposed as the spectral filters in the inner-ear acoustic sensors of several species of lower vertebrates. Such filters provide an instructive example of the conflict between temporal resolution and spectral resolution. The dynamic behavior of a second-order resonance in the absence of ongoing external influences is governed by

$$d^2X/dt^2 + 2a_r(dX/dt) + (w_o)^2 = 0 \tag{1}$$

where $X(t)$ is the dependent variable being considered (*e.g.*, the response variable of the spectral filter), and a_r and w_o are constants. The behavior of a second-order resonance (with residual excitation but in the absence of external inputs) is described by (the solution to Eq. 1)

$$X(t) = C_o\exp[-a_r t]\cos[w_r t + b_o] \tag{2}$$

where

$$(w_r)^2 = (w_o)^2 - (a_r)^2 \tag{3}$$

C_o and b_o are constants that depend on the initial conditions. The coefficients a_r and w_r both are independent of the initial conditions, and are the real and imaginary components of the natural frequencies of the system. When this second-order resonance is excited by an externally applied sinusoidal waveform, $A\{\cos[w_s t]\}$, of very long duration (a condition known as "sinusoidal steady state"), the response described by Eq. 2 will become negligible and the behavior of the system will be described by

$$X(t) = C_1 A\cos[w_s t + b_1] \tag{4}$$

where w_s is the frequency (rad/s) of the externally applied waveform and A is its amplitude. This behavior often is labeled the "sinusoidal steady-state response." For applied sinusoids of a particular amplitude, the constants C_1 and b_1 both depend on w_s, and

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the functions $C_1(w_s)$ and $b_1(w_s)$ describe the amplitude and phase properties of the resonance acting as a spectral filter. When w_s is equal to the filter's center frequency (w_c) given by

$$(w_c)^2 = (w_o)^2 - 2(a_r)^2 \tag{5}$$

then the function C_1 will be at its maximum value. The filter selectively responds to signal and noise components with frequencies in the neighborhood of w_c. For sinusoidal stimuli, other attributes of the filter include the range of frequencies over which the filter is selectively responsive (*i.e.*, the filter's "pass band"), the ability of the filter to discriminate signal and noise components within its pass band from those outside that band, and the time required for the filter to respond fully to a new sinusoidal component. For short-term acoustic events, the key attributes are the times required for sufficient energy to accumulate in the filter from the current event and for signal energy from past events to be cleared from the filter. Residual energy from past events interferes with the detection of current events.

If the center frequency of the second-order resonance filter is fixed, then the designer of the filter is left with just one degree of freedom—one parameter, that will determine all of the filter's other attributes. The parameter that is selected often is either the damping coefficient, δ,

$$\delta = a_r/w_o \tag{6}$$

or the quality factor, Q, often defined to be $1/2\delta$.

Interpreted physically, this value of Q gives the ratio of the energy stored in the filter to the mean energy lost per radian of oscillation under sinusoidal steady state conditions when the driving frequency is w_o (rad/s). One of the alternative definitions of Q is $w_r/2a_r$. For the undriven filter, still ringing with residual energy at the frequency w_r (rad/s), this value of Q equals the number of radians of oscillation required for the residual energy to diminish by a factor of $1/e$ (0.36788). Regardless of which definition is used, as Q increases, the residual energy in the filter (from past excitation) takes longer and longer to die away, so that the filter carries an increasingly large baggage of history. Thus, in a high-Q reso-

nance filter, a relevant signal would be contaminated not only with interference from concurrent external acoustic events, but also with internal residues from long-past events.

The sinusoidal steady state properties of a filter can be envisioned in a thought experiment in which the filter itself generates no noise, but white noise is applied to the input of the filter and the spectral distribution of the noise emerging at the output is analyzed. Noise is considered to be "white" if, on time average, its power is distributed uniformly over the spectrum, *i.e.*, over the duration of a given sample of the noise, the power density (power per unit frequency) is the same at all frequencies. From a second-order resonance filter, driven by white noise at its input, the power density of the noise emerging at the output is maximum at a center frequency (w_c) and declines monotonically as the frequency increases or decreases from that value. Above and below w_c are single frequencies (w_2 and w_1, respectively) at which the power density is one-half its value at w_c. Conventionally, the pass band of a filter is taken to be the range of frequencies lying between the half-power frequencies, so the width of the pass band is $w_2 - w_1$. The "relative band width," one conventional measure of the spectral resolution of a filter, is the ratio of the band width to the center frequency,

$$\text{Relative bandwidth} = (w_2 - w_1)/w_c \qquad (7)$$

Another measure of spectral resolution is the white-noise rejection ratio: the ratio of the output power falling within the pass band to that falling outside the pass band, given that the input to the filter was white noise. Spectral resolution increases as the relative bandwidth decreases and as the white-noise rejection ratio increases. For the second-order resonance filter, the relative bandwidth is approximately $1/Q$, and the white-noise rejection ratio is approximately Q. By both measures, the spectral resolution of such a filter increases with increasing Q. Recall, however, that increasing Q decreases the ability of the second-order resonance filter to sort current events from past events. Thus, in such a filter, natural selection would not have been able to manipulate spectral resolution and temporal resolution separately—improvement of

one always would have been accompanied by degradation of the other.

From the previous paragraph it is clear that there are two ways to achieve high resolution in frequency. One way is to reduce the filter's bandwidth—the narrower the bandwidth the greater the spectral resolution. The problem with this method is that no real filter can discriminate perfectly between signal (or noise) components that fall within the band from those that do not. The second method is to increase the ability of the filter to discriminate components within its band from those outside, independent of the width of the band. When spectral resolution is increased by bandwidth reduction, temporal resolution must decrease. When spectral resolution is achieved by improvement of a filter's ability to discriminate components within its band from those outside, on the other hand, time and frequency resolution can be manipulated independently. The width of the filter's band can be adjusted to give the desired temporal resolution, then the shape of the band edges can be adjusted to give the desired discrimination between spectral components within the band and those outside.

HIGHER-ORDER FILTERS

Perfect spectral discriminability would be achieved by a filter that passes all frequencies within its pass band and completely rejects all other frequencies. Although such a filter is impossible to realize, it provides us with a direction for design: as the stimulus frequency approaches the edge of the pass band from within it, the response amplitude should remain nearly constant (C_1 in Eq. 4 should be close to 1.0); as the frequency moves beyond the edge of the pass band, the amplitude should decline precipitously (C_1 should be 0). It already is clear that the band width and the steepness of the band edge cannot be manipulated independently in a second-order filter; both depend on the same parameter, Q. However, the two can be manipulated independently with filters of order greater than two. In fact, with the width of the pass band fixed, the way to increase the steepness of the band edge is to *increase* the order of the filter. The order of a linear system is the same as that of the differential equation describing its behavior in the absence of on-

going external excitation. Ordinarily, the order is equal to the number of interacting, discrete, dynamic elements (*e.g.*, discrete masses, discrete elastic elements, discrete chemical states, etc.) in the system.

Given the hypothetical functional and signal contexts outlined previously for acoustic sensors, one would expect natural selection to have favored high-order filters over second-order resonances. In this way, temporal resolution and spectral resolution could have been sculpted independently by natural selection, rather than reciprocally. In short, I have argued that second-order resonance filters are maladapted for service in vertebrate acoustic sensors. Nevertheless, from time to time, such filters have been proposed for the ear.

SECOND-ORDER RESONANCES IN VERTEBRATE ACOUSTIC FILTERS

Mammalian Cochlea

"In reality if we suppose the dampers of a pianoforte to be raised, and allow any musical tone to impinge powerfully on its sounding board, we bring a set of strings into sympathetic vibration, namely *all* those strings, and *only* those, which correspond with the simple tone contained in the given musical tone. Here, then, we have, by a purely mechanical process, a resolution of air waves precisely similar to that performed by the ear. . . . Now suppose we were able to connect every string of a piano with a nervous fiber in such a manner that this fiber would be excited and experience a sensation every time the string vibrated. . . . The sensations of simple tones of different pitch would under the supposed conditions fall to the lot of different nervous fibers, and hence be produced quite separately, and independently of each other."

This model, proposed by Herman Helmholtz in his celebrated work *On the Sensations of Tone* (as translated by A.J. Ellis),[13] is based on resonance and dominated the theory of hearing through the last half of the nineteenth century and the first third of the twentieth century. It also set the stage, I believe, for the present preoccupation of auditory scientists with frequency—often at the expense of temporal considerations.

In spite of the presence of the sounding board, the coupling from air to piano string is very weak; very little acoustic energy is transferred from air to the string during any given cycle of the acoustic stimulus. Owing to its very high Q, the string is able to accumulate incoming energy—in the displacement of the string against its elastic forces (potential energy) and in the velocity of the string's mass (kinetic energy). During each cycle of sympathetic vibration, the string dissipates a tiny fraction of its stored energy through viscous resistance. The string's acoustic energy reaches steady state when the rate at which it is dissipated becomes equal to the rate at which it is accumulated from the air. Under those conditions, the string will have accumulated $Q/2\pi$ times as much energy as it is able to collect over a single stimulus cycle. All resonance filters operate on essentially this same physical basis. In such filters, the "pass band" could be labeled more appropriately the "accumulation band."

The principal problem with this model was that it postulated a sluggish ear, one in which the response to a pure tone would grow in time and reach 63% $(1 - 1/e)$ of its full value only after $Q/2\pi$ stimulus cycles and one in which a huge amount of residual signal energy would make detection of current events extremely difficult. By application of something analogous to the piano's soft pedal, the value of Q would be reduced, but only at the expense of reduced frequency selectivity. Helmholtz pointed out that one of the conditions required to make his model applicable to the cochlea would be negligible coupling between neighboring sets of mechanical elements in the latter.

Owing to the work of Bekesy and many others that have followed, we now know that the condition of negligible coupling is not met in the actual *structural context* of the cochlea.[4] All of the mechanical elements of the cochlea are strongly bidirectionally coupled and individual mass and elastic elements therefore are prevented from pairing and forming resonances. Each mechanical element in the cochlea is shared by the filters associated with many frequencies, and each filter is a very high-order structure—well adapted for high resolution in both time and frequency. In spite of this demise of Helmholtz's mechanical resonance theory, there still is general agreement that mechanical elements, such as the elastic stiffnesses of the basilar membrane and hair bundles and

the masses of the cochlear fluids, play major roles in determining cochlear filter properties.

Turtle

Therefore, the hearing research community was especially excited when Crawford and Fettiplace showed that hair cells in the turtle (*Pseudemys scripta*) basilar papilla have *electrical* resonances and that these resonances play central roles in the spectral filters of that hearing organ.[14] Intracellular current steps applied to individual hair cells, *in situ*, produced a ringing response describable by Eq. 2. From that response, values of a_r and w_r could be deduced, and from them the filter properties (*i.e.*, the frequency dependence of C_1 and b_1 in Eq. 4) that the electrical resonance would impart to the hair cell. When sinusoidal acoustic stimuli were applied through the normal path—through the tympanum to the middle ear to the papilla to the hair cell, and the filter properties of the entire path were observed, the shapes and positions of the tuning peaks conformed very well to the properties deduced from the ringing responses. The behavior away from the peaks implied the presence of at least three additional natural frequencies in each filter. Two of these were almost the same for all of the hair cells and all of the animals observed, and they conformed well to the natural frequencies attributed by Moffat and Capranica to the middle ear of this turtle species.[15] The third natural frequency varied from animal to animal and, evidently, from hair cell to hair cell.[16] Crawford and Fettiplace concluded that of the five natural frequencies evident in the overall filter function associated with each hair cell, two were attributable to the electrical resonance of the hair cell itself, two were attributable to the middle ear, and one was a consequence of an unknown process. The center of the amplitude tuning curve, however, was dominated by the second-order resonance, with its characteristic concave flanks.

Subsequently, Crawford and Fettiplace found that electrical oscillations, elicited by electrical stimuli, were accompanied by vibrations of the hair cell's hair bundle.[17] In other words, the coupling between the mechanical elements of the papilla and the electrical resonance of the hair cell is *bidirectional*. Since the hair bundles are connected to a single (acellular) tectorial plate, and

thus can interact mechanically, this bidirectional coupling implies that the electrical elements of the various hair cells will interact with each other (through the mechanical linkage provided by the plate). Thus one would expect the natural frequencies observed in an individual hair cell to be determined to some extent by the dynamics in neighboring hair cells as well as those in the hair cell under observation. However, if the coupling between hair cells were strong, one would expect the electrical behavior of the individual hair cell to reflect high-order dynamics (many more than just five natural frequencies). The fact that it does not and the fact that the center of the observed tuning curve conforms as well as it does to that of a second-order resonance both imply that the coupling is weak.

On the other hand, the quality factor (Q) of the observed resonance should be very sensitive to bidirectional coupling.[18] When Art and Fettiplace examined papillar hair cells that were separated from the sensory epithelium and tectorial plate, and thus removed from their normal structural context, the Q values that they found were conspicuously higher than those for hair cells *in situ*.[19] Recalling that Q is the ratio of the magnitude of the imaginary part (w_i) of a natural frequency to twice the magnitude (a_i) of its real part, one sees that this result implies a conspicuous difference between the natural frequencies of the electrical resonance in isolation and *in situ*. Structural context did have an impact, but evidently not enough to rescue the turtle from a resonance-based auditory filter.

Frog

Electrical resonances have been found in isolated hair cells of the frog sacculus (a seismic sensor) and amphibian papilla (an auditory sensor).[4,20-22] In each of these sensors, when it is intact, the hair bundles are connected at their tips to a single, acellular gelatinous structure—the otoconial membrane or tectorial membrane.[23,24] During the observation of electrical resonances in each case, that structure was removed. Under those conditions, intracellular current steps applied to individual hair cells produced the same sort of second-order ringing responses that had already been seen in the turtle basilar papilla (*i.e.*, describable by Eq. 2).

Applying patch clamps to hair cells enzymatically separated from the sacculus of the bullfrog, R.S. Lewis identified the key underlying molecular elements (ion channels) and their dynamic properties (sensitivities and gating kinetics).[25-27] The resonance is largely a consequence of interaction between populations of voltage-sensitive calcium channels and calcium-sensitive potassium channels. Being aware of the potential effects of bidirectional coupling between the mechanical and electrical sides of the hair cell, Lewis pointed out that the operation of these resonances might be altered in the structural context of the intact preparation.[4]

His prediction was correct. The resonance frequencies observed in the isolated bullfrog saccular hair cells ranged from approximately 90 Hz to approximately 250 Hz. Frequency tuning curves for afferent axons from the intact sacculus of the bullfrog typically exhibit tuning peaks well below 100 Hz (the mode being approximately 50 Hz).[28,29] Thus, whereas the resonance frequencies in turtle hair cells match very well the tuning peaks in those cells, the same is not true for the bullfrog sacculus. Furthermore, whereas the peaks of the amplitude tuning curves from the intact turtle basilar papilla exhibit the concave flanks characteristic of second-order resonance, those of the bullfrog sacculus exhibit the convex flanks typical of higher-order dynamics (as described in the next section).

In hair cells of the frog amphibian papilla (with tectorial membrane removed), Pitchford and Ashmore observed electrical power spectra (tuning curves) with the concave flanks of a second-order resonance;[22] but, again, the tuning curves of axons from the intact amphibian papilla have conspicuously convex flanks and clearly reflect higher-order dynamics.

Evidence for Higher-Order Dynamics

Observing the response of a single acoustic axon to a one-dimensional stimulus (*e.g.*, sound pressure at the tympanum), the physiologist is treating the ear as a single-input single-output (SI/SO) system. There are two conventional ways to characterize the dynamic properties of a linearly-operating SI/SO system: the impulse response (a function of time) and the sinusoidal steady-state response (amplitude and phase as functions of frequency). Both characterizations bear clues to the order of the system. However,

when the characterizations are obtained from measurements on real systems, in the inevitable presence of noise, some of those clues will be obscured. Furthermore, even in the absence of noise they might be subtle. In the cases of the frog sacculus and amphibian papilla the clues are neither subtle nor obscure; they are conspicuous.[29-31]

The impulse response of a moderate to high-Q second-order system is a monotonically damped oscillation and, as such, is always maximally asymmetrical, with the largest amplitude occurring in the first cycle of oscillation (Fig. 1a). When plotted on a log-log scale (*i.e.*, as a conventional Bode diagram), the sinusoidal steady-state amplitude tuning curve of a moderate to high-Q second-order resonance exhibits a relatively sharp peak, with conspicuously concave flanks and asymptotic slopes (at high and low frequencies) whose magnitudes sum to two (Fig. 1c). The only convex portion of this amplitude tuning curve lies between the half-power frequencies (w_1 and w_2) and spans an amplitude range of only 3 dB. The range of phase shift of a second-order resonance is strictly limited to $\frac{1}{2}$ cycle. In the linear responses observed in single axons from the frog sacculus and amphibian papilla, the impulse responses approximate symmetry rather than maximal asymmetry; the largest amplitude occurs several half-cycles from the onset (Fig. 1b). The peaks of the sinusoidal steady-state (log-log) amplitude tuning curves are not sharp and their flanks are completely convex (over amplitude ranges of as much as 40 dB before they become obscured by noise) rather than concave (Figs. 1d,f). The magnitudes of the slopes (before they become obscured by noise) at high and low frequencies sum to numbers typically greater than ten, rather than two.[28,29] The range of phase shifts (as far as they can be followed before they are obscured by noise) varies from approximately $\frac{3}{2}$ cycles to 5 cycles, rather than $\frac{1}{2}$ cycle.[29,30] The dynamic order of a linearly-operating filter is greater than or equal to the sum of the magnitudes of the asymptotic slopes of the (log-log) amplitude tuning curve and greater than or equal to the range of phase shift measured in quarter cycles.[29]

Evidence for Involvement of Electrical Elements in Tuning
Given the mismatch between the observed tuning properties of the intact frog ear and those expected from resonances, the presence of electrical resonances in isolated acoustic hair cells does

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not necessarily imply that the elements of those resonances are even involved in tuning. Probably the strongest evidence for the actual involvement of electrical elements in the high-order tuning of the intact frog ear is found in the temperature dependence of tuning curves. The elements (mass and stiffness) involved in purely mechanical tuning typically are only weakly dependent on temperature. Channel dynamics, on the other hand, typically are strongly dependent on temperature. Therefore, one expects tuning curves involving hair-cell ion channels to be strongly temperature dependent and tuning curves involving only mechanical elements to be weakly temperature dependent. In 1976, Moffat and Capranica reported strong temperature dependence in the threshold tuning curves of the intact amphibian papilla of the toad *Bufo americanus*, and weak temperature dependence of those of the basilar papilla from the same species.[32] Recently, P. van Dijk extended these studies by examining the temperature dependence of amplitude and phase tuning curves from the bullfrog amphibian papilla and sacculus and amplitude tuning curves from the bullfrog basilar papilla.[33] He found strong temperature dependence in lower-frequency (100 to 500 Hz) axons of the amphibian papilla (approximately the range of frequencies over which Pitchford and Ashmore observed electrical resonances), weak temperature dependence in basilar papillar axons, and intermediate temperature dependence in higher-frequency (> 500 Hz) axons of the amphibian papilla. Of two saccular axons observed in this study, one exhibited strong temperature dependence and the other intermediate.

High-Order Filters from Electrical Elements?
In isolated acoustic hair cells, the interaction of voltage-sensitive calcium channels and calcium-sensitive potassium channels produces a second-order electrical resonance. That resonance does not appear in the (high-order) tuning of the intact ear, yet the temperature dependence of that tuning suggests that the channels themselves are involved in it. This strongly suggests that when the ear is intact, the channels are part of a higher-order dynamic system, and that the system is reduced to second order (and allowed to resonate) by isolation of the channel populations in the single cell. There are at least two differences between the experimental situation with isolated hair cells and that with the intact ear: (1) the otoconial or tectorial membrane (which mechanically links the
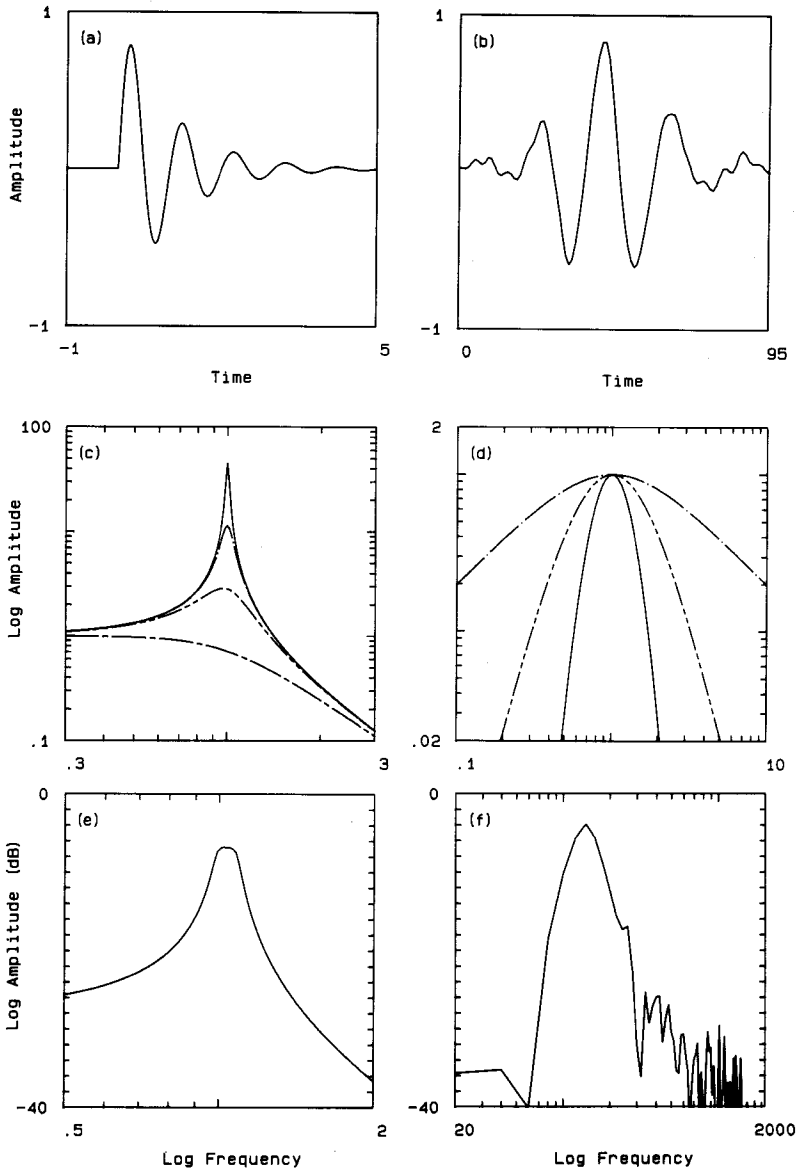
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FIGURE 1 Impulse and sinusoidal steady state responses of second-order reso-
nance filters and high-order filters. (a) Impulse response of a second-order reso-
nance filter with Q of 3. (b) Linear impulse response of the auditory filter associated
with a single axon from the amphibian papilla of the American bullfrog (courtesy

hair bundles to one another) is present in the latter, absent in the former; (2) the response is observed in primary afferent axons in the latter, in single hair cells in the former. If the coupling between the mechanical and electrical sides of the frog acoustic hair cell were bidirectional, as it is in the turtle, then the first difference would be enough to account for the reduction in dynamic order in the isolated hair cell. There now is direct evidence of bidirectional coupling in the frog saccule[34,35] and compelling indirect evidence of it in the frog amphibian papilla.[36,37]

The individual afferent axon of the bullfrog sacculus or amphibian papilla typically innervates several hair cells.[38] Thus, the filter properties of those hair cells might be expected to combine in parallel, converging on the single axon. If the resonant frequencies of the various hair cells were different, a parallel combination of them would yield high-order linear tuning curves. If the responses of second-order resonances simply were added, the summed resonances would lead to multiple peaks, with an antiresonant trough between each pair of adjacent peaks. If the resonant peaks were spaced approximately one-half bandwidth apart, then the peaks and troughs would nearly cancel, leading to a nearly

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of X. Yu, obtained by the reverse correlation method[51,52]). Small noise fluctuations occur on the right and left of the response. Symmetry is especially pronounced in this example; but among the dozens of axons observed so far we have not found any with asymmetry even approaching that characteristic of second-order resonances. For a given shape of amplitude tuning curve, a filter designer can improve the faithfulness of reproduction of temporal waveforms passed through the filter by making the impulse response more symmetrical (which makes the phase shift more closely approximate a linear function of frequency). Perfect symmetry is impossible with analog filters, but it can be achieved in modern digital filters and is a common design goal in finite impulse response (FIR) filters. (c) Amplitude tuning curves of second-order resonance filters with Q's of 1, 4, 16 and 64. (d) Amplitude tuning curves generated by non-resonant, band pass filters. From the top to the bottom curve the dynamic order of the filter was 2, 4 and 16, respectively. (e) Amplitude tuning curve of a filter derived from summing the outputs of four second-order resonances ($Q = 20$), all with the same input. The concave band edges are consequences of the transitions from the steep slopes derived from the resonant peaks to the asymptotic slopes (the magnitudes of which sum to two). (f) Linear amplitude tuning curve of the auditory filter associated with a single axon from the bullfrog amphibian papilla (courtesy of X. Yu, obtained by reverse correlation). The effects of noise (owing to limited experimental sampling time) are seen on the right and left of the tuning peak. The Convex band edges are typical; so far, in dozens of frog amphibian papillar and saccular axons, we have not seen any tuning curves with the concave edges characteristic of resonances. Frequency in Hz.

flat top across the pass band of the resultant amplitude tuning curve (Fig. 1e); and the width of the band would be limited only by number of summed resonances. Whether or not notches are present, convexity in the (log-log) amplitude tuning curve generated by summed parallel resonances still is limited approximately to the upper 3 dB, and the total phase shift is limited to $\frac{1}{2}$ cycle. Approximately 20% of the afferent axons from the bullfrog sacculus exhibit single antiresonances of very high Q, suggesting the possibility of simple parallel summation. Arguing against this interpretation, however, are the facts that the phase shift in these axons ranges over several half-cycles, not just one, and the slopes of the flanks of their (log-log) amplitude tuning curves are convex (over several tens of dB, until they disappear into the noise floor). The amplitude tuning curves for the remaining 80 percent of axons from the intact bullfrog saccule and all axons from the intact frog amphibian papilla exhibit single peaks and no antiresonances. They too exhibit phase shifts that range over several half cycles and amplitude tuning curves with convex flanks. In order to achieve such phase and amplitude tuning curves, the responses of some resonances would have to be added and the responses of others subtracted (leading to what is known in electrical network theory as a "partial-fraction expansion realization" of the filter).[39] There are at least two ways that the paths through some hair cells might be additive while those through others are subtractive: (1) the afferent axon might receive excitatory synapses from some hair cells and inhibitory synapses from others; or (2) the afferent axon might be connected to hair cells of opposite mechanical orientation. There presently is no evidence that any hair cell makes an inhibitory synapse on an afferent axon, making possibility (1) very unlikely. Possibility (2) exists for some hair cells of the frog amphibian papilla, but not for those in the (low frequency) regions where Pitchford and Ashmore found resonances, and not for the bullfrog sacculus at all.[11,38] Even if possibilities (1) or (2) were available, partial-fraction expansion realizations of filter properties are extremely sensitive to the gains of the individual paths and therefore seem to be a poor basis for reliable filter design by natural selection.

Thus the evidence strongly suggests that the bidirectional coupling between the electrical and mechanical sides of the hair cell

must play an important role in organizing the voltage-sensitive calcium channels and calcium sensitive potassium channels from several or many hair cells into a filter with high dynamic order. In this way, structural context evidently translates would-be maladaptive, resonant filters into filters that are selectively advantageous indeed.

OTHER VERTEBRATES AND OTHER SENSORS

Strong temperature dependence of tuning curves also has been observed in the basilar papillae of gecko,[40] caiman,[41] and pigeon,[42] suggesting the involvement of electrical elements in each case. Direct observations of electrical resonances recently have been extended to isolated hair cells of the basilar papillae of alligator and chick.[43,44] Thus it appears that electrical elements (ion channels) are involved in the filters of acoustic sensors in amphibians, reptiles, and birds. In the guinea pig cochlea, on the other hand, the temperature dependence of tuning is very weak,[45] suggesting that electrical elements are not conspicuously involved in tuning in the mammalian cochlea. Electrical resonances have been sought directly in mammalian hair cells, but none has been found so far.[46,47]

The extent to which structural context has prevented ion channels populations from forming (maladaptive) resonances in acoustic hair cells *in situ* in the more derived reptiles (*e.g.*, crocodilians) and birds, and forced them instead to participate in high-order filters, remains to be seen. The nonlinear (threshold) tuning curves published for those animals definitely suggest high dynamic order in the underlying linear filters.[48,49]

Recently, Housley et al.[50] found electrical resonance and evidence of voltage-sensitive calcium channels and calcium-sensitive potassium channels in isolated hair cells from the frog (*Rana pipiens*) semicircular canal crista. However, under normal conditions, the resonance in those hair cells evidently is suppressed by A-type currents; and the spectral filters of semicircular canals are extremely broadly tuned (bandwidths of several decades) and very low order. The authors conclude that the elements necessary for electrical resonance may be present in the generalized lower-ver-

tebrate hair cell (vestibular and acoustic), but that selection may have incorporated those elements into the tuning process only in acoustic sensors. I would amend that conclusion by suggesting that selection could take good advantage of those elements only after sufficient bidirectional coupling were present to insure that they formed high-order filter structures rather than resonances.

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