When an organism hears, sounds appear as fluctuations in the rate of action potentials occurring across a tonotopic array of axons within the auditory nerve. These action potentials are initiated at the hair cell/afferent fiber synapse, where the hair cell converts the energy of impinging sound waves into neurotransmitter release. The constantly changing sounds of the environment are encoded in the auditory nerve by temporal fluctuations in the spike rate of each axon. Electrophysiologists typically characterize an auditory afferent axon in terms of its spontaneous spike rate, sensitivity, capacity to adapt, suppressibility and tuning properties. Changes in axonal spike rates reflect directly the events at the hair cell synapse and indirectly the changes in the receptor potential, capacity to adapt, suppressibility and tuning properties. Changes in axonal spike rates reflect directly the events at the hair cell synapse and indirectly the changes in the receptor potential, the extent to which the intrinsic properties of hair cells influence sensitivity, adaptation, tuning and spontaneous spike rate in the auditory nerve is not clear. How hair cells contribute to peripheral signal processing varies among the vertebrates. Many features of the response characteristics of the auditory nerve are largely determined prior to hair cell stimulation and reflect the specialized anatomy and mechanical operation of outer, middle and inner ear structures. The vertebrate ear relies heavily upon an elaborate extracellular and acellular infrastructure, which in most cases includes an ear drum, middle ear bone(s) and many membranes and fluid-filled ducts, all of which serve to conduct, focus, filter and transduce auditory stimuli. As a result, auditory neuroscience has had to step lightly when assigning functional significance to the biophysical properties of sensory hair cells.

The gross anatomy of the inner ear of terrestrial vertebrates varies enormously among taxa, and discovering consistent correlations between hair cell biophysics and auditory nerve physiology across taxonomic lines has been a challenging exercise. The frog auditory system becomes particularly useful in this regard because, unlike that of reptiles, birds and mammals, it contains three (instead of the usual one) endorgans committed to the encoding of auditory information. The frog auditory system includes a low-frequency vibration/sound detector (the sacculus), a low- to mid-frequency sound detector and discriminator (the amphibian papilla) and a high-frequency sound detector (the basilar papilla). Differences exist in the response properties of afferent nerve fibers emerging from these endorgans that may be attributed to the intrinsic properties of these organs and of their sensory hair cells. Below, we attempt to uncover the major contributions of hair cells to the response properties of the fibers in the frog auditory nerve.

**Tuning of auditory nerve fibers and hair cells**

Beginning at the body surface (the tympanic membrane in...
most cases), the sound waveform is processed in several stages (Fig. 1), resulting in a unique end-product being delivered to each hair cell. One of the most significant transformations occurring is spectral filtering, which is performed at several sequential points along the pathway of sound conduction, ultimately leading to many finely tuned single nerve fibers. Incoming sounds are first filtered, or tuned, by specialized properties of the frog’s tympanum, and its single middle ear bone, the columella. Next, the shapes of the perilymphatic and endolymphatic ducts through which the sound must pass serve to direct different broad bandwidths of sound to different auditory organs (Purgue and Narins, 2000). Further tuning occurs within each organ on the basis of its unique architecture (Fig. 2) and physiology.

A single auditory nerve axon usually exhibits a preference for a narrow band of frequencies, within which a single stimulus frequency to which the axon is most sensitive, the characteristic frequency, may be identified. Bullfrog (*Rana catesbeiana*) and leopard frog (*Rana pipiens*) auditory nerve fibers exhibit characteristic frequencies over a continuous range of frequencies between 20 and 2000 Hz (Capranica and Moffat, 1975; Feng et al., 1975; Frishkopf and Geisler, 1966; Frishkopf and Goldstein, 1963; Lewis et al., 1982a). True treefrogs (family Hylidae) exhibit a discontinuous range of auditory nerve fiber characteristic frequencies up to approximately 4 kHz, in some cases with a gap between the lower and upper ranges exceeding 2 kHz (Capranica and Moffat, 1983). This gap corresponds to frequencies falling above the upper limit of the amphibian papilla but below the lower limit of the basilar papilla, thus providing the first clues to the origins of tuning (Boord et al., 1970; Feng et al., 1975; Frishkopf and Geisler, 1966; Frishkopf and Goldstein, 1963; Liff, 1969; Sachs, 1964). For most frogs studied, the bandwidth of the sacculus, typically 20–120 Hz (Christensen-Dalsgaard

Fig. 1. Energy transfer in and the anatomy of the frog inner ear. Incoming sounds are filtered extensively prior to reaching the hair cell. This figure identifies sites at which the anatomy or physiology of the inner ear is known to affect the passage of sound energies into the auditory nerve. Not shown are the tectorial structures present within each endorgan and the contact membranes marking the boundaries between endolymph and perilymph. The periotic canal is thought to shunt energy away from the amphibian papilla and basilar papilla during the low-frequency pressure changes that occur during respiration and vocalization (Purgue and Narins, 2000). 1, tympanic membrane; 2, columella; 3, periotic canal; 4, endolympathic space; 5, sacculus; 6, amphibian papilla; 7, basilar papilla; 8, stereociliary architecture and physiology; 9, membrane electrical properties and ionic currents; 10, synaptic architecture and physiology; 11, innervation patterns.

Fig. 2. The hearing organs of the frog. The frog inner ear contains three organs that contribute to the hearing of airborne sounds. The sacculus contributes to hearing, vibration detection and the gravitational sense. (A) The approximately flat and circular sensory macula lies beneath a thin tectorial membrane attached to the hair cell stereociliary tips and the large otoconial mass. (B) The amphibian papilla is a hollow chamber containing an ‘S’-shaped sensory epithelium in the chamber roof with a thick tectorial membrane hanging beneath the epithelium. (C) The sensory epithelium of the basilar papilla lies along part of the inner wall of this circular organ, which rests in the frog ear at the convergence of the endolymphatic and periotic canals. The basilar papilla tectorial membrane resembles a thin curtain occluding approximately half of the endolymphatic duct as it enters the organ. Arrows indicate the direction in which the hair bundles protrude *in situ*. N, nerve.
and Jørgensen, 1988; Christensen-Dalsgaard and Narins, 1993; Egert and Lewis, 1995; Koyama et al., 1982; Lewis, 1986 1988; Moffat and Capranica, 1976; Yu et al., 1991), narrowly overlaps the bandwidth of the amphibian papilla, typically 100–1250 Hz (Capranica and Moffat, 1975; Feng et al., 1975; Lewis et al., 1982a; Narins and Wagner, 1989; Ronken, 1991; Stiebler and Narins, 1990; Zelick and Narins, 1985). In adult bullfrogs and leopard frogs, the basilar papilla is most sensitive to frequencies at approximately 1.4 kHz, but responds well to approximately an octave band of frequencies centered around this (Feng et al., 1975; Ronken, 1990, 1991). For the arboreal frogs Eleutherodactylus coqui and Hyla (Pseudacris) regilla, basilar papilla best frequencies range from 2 to 4.5 kHz (Narins, 1987; Narins and Wagner, 1989; Stiebler and Narins, 1990; Zelick and Narins, 1985).

Features other than the characteristic frequency are useful for discriminating saccular, amphibian papilla and basilar papilla afferent fibers. Auditory afferent fibers typically respond well to a narrow range of frequencies surrounding the characteristic frequency. A careful mapping of the response thresholds (in dB) of a fiber to a broad range of frequencies around the characteristic frequency produces what is known as a tuning curve. The shape of a tuning curve can reveal much about the underlying mechanisms of frequency tuning. W10dB (the tuning curve bandwidth 10 dB above the characteristic frequency threshold) and Q10dB (the characteristic frequency divided by W10dB) are both indices of tuning sharpness, and in the frog both vary with characteristic frequency (Ronken, 1990, 1991). Saccular afferent fibers are broadly tuned, with pass bands for a single fiber typically encompassing most of the saccular range (i.e. 50–100 Hz) and exhibiting Q10dB values of 0.5–1.0 (Egert and Lewis, 1995; Lewis, 1988; Lewis et al., 1982a). In contrast, amphibian papilla afferent fibers with characteristic frequencies in the range of saccular fiber characteristic frequencies exhibit sharper tuning curve peaks and have Q10dB values as high as 4–5 (Ehret and Capranica, 1980; Liff, 1969; Ronken, 1991; Stiebler and Narins, 1990). Q10dB values are lower for fibers from the high-frequency (caudal) region of the amphibian papilla, where they rarely exceed 2 (Ronken, 1991). In the basilar papilla, tuning curves lack a sharp characteristic frequency peak, instead exhibiting a more blunted, or rounded-out, characteristic frequency region. Basilar papilla Q10dB values rarely exceed 2 (Ronken, 1990, 1991; Stiebler and Narins, 1990). Ronken (1990) demonstrated that Q10dB is a reliable parameter for identifying low-frequency amphibian papilla neurons, but W10dB was the only reliable parameter for separating amphibian papilla and basilar papilla neurons with similar characteristic frequencies.

In mammals, in which the mechanisms of tuning have been extensively studied, the initial stage of frequency resolution is achieved through the specialized mechanical properties of a cochlear basilar membrane (von Bekesy, 1960). The basilar papillae of both birds and reptiles contain structures analogous to those in the mammalian cochlea. In frogs, a growing body of evidence suggests that mechanical tuning in the ear is probably less dissimilar to mechanical tuning in mammalian ears than previously imagined (Hillery and Narins, 1984; Lewis and Narins, 1999; Purgue and Narins, 2000). However, in addition to any mechanical tuning, a small number of hair-cell-based tuning mechanisms have been proposed for non-mammalian vertebrates. Electrical tuning is a phenomenon whereby the electrical properties of the hair cell’s basolateral membrane exhibit band-pass filtering capabilities (for a review, see Fettiplace and Fuchs, 1999). Electrical resonances observed in isolated saccular and amphibian papilla hair cells (Holt and Eatock, 1995; Hudspeth and Lewis, 1988; Lewis and Hudspeth, 1983; Roberts et al., 1986; Smotherman and Narins, 1998, 1999a) occur at frequencies that match within approximately 100 Hz the characteristic frequencies of afferent fibers exiting these organs, and electrical tuning is well supported in the rostral half of the amphibian papilla (Pitchford and Ashmore, 1987; Smotherman and Narins, 1999a). Hair cells from the caudal, upper-frequency region of the amphibian papilla do not appear to be electrically tuned (Smotherman and Narins, 1999a).

Saccular and low-frequency amphibian papilla hair cells exhibit many similarities in their electrical properties. In both organs, whole-cell capacitances, which vary predictably with cell body size (principally cell length) vary from 8 to 18 pF. Considering the two endorgans together, resonant frequency is generally inversely proportional to cell size (Smotherman and Narins, 1998, 1999a). The time constant of the cell membrane, τm, will largely determine how quickly the receptor potential can fluctuate, thereby defining the maximum frequencies that can be faithfully encoded by the hair cell. τm depends upon the whole-cell capacitance and the membrane’s resistance, Rm, which is inversely proportional to the number of open ion channels in the membrane. We have found that both Ca2+ and K+ channel (K(Ca)) numbers increase in proportion to resonant frequency in the frog amphibian papilla (Smotherman and Narins, 1999a). Thus, a concurrent decline in cell capacitance and membrane resistance provides for a sequential reduction in τm for hair cells encoding progressively higher acoustic frequencies. Perhaps the strongest support for electrical tuning in the frog comes from the tonotopic mapping of ion channel kinetics onto the sensory epithelium of the amphibian papilla (Smotherman and Narins, 1999a). The lowest-frequency hair cells, located in the saccular and the rostral-most region of the amphibian papilla, possess a very slow Ca2+-dependent K+ channel (the maxi- or BK-type K(Ca) channel) which conducts the whole-cell current I(K(Ca)). The rate of activation of I(K(Ca)) systematically changes by an order of magnitude along the tonotopic axis of the amphibian papilla. Variations in the kinetic properties of the K(Ca) channels reflect differences in single-channel mean open times for neighboring hair cells (Art et al., 1995; Wu et al., 1995), which appear to arise from post-translational variations in channel assembly (Jones et al., 1998).

If the sacculus and amphibian papilla both rely upon electrically tuned hair cells for spectral resolution, why then should tuning curve Q10dB values from these organs be different? The answer to this question may come in several
parts. First, the amphibian papilla tectorial membrane may be adding significant band-pass spectral filtering not available in the sacculus (Shofner and Feng, 1983; Lewis and Leverenz, 1983; A. P. Purgue and P. M. Narins, unpublished data). Second, differences in innervation patterns may be contributing to differences in the responses observed between these two organs. While both saccular and low-frequency amphibian papilla hair cells exhibit type II innervation patterns (many synaptic boutons per cell, with many cells being innervated by a single afferent), saccular afferents appear to contact many more hair cells than amphibian papilla afferents (Lewis et al., 1982a; Simmons et al., 1992). In fact, Lewis et al. (1982a) found that one saccular afferent in the North American bullfrog may contact as many as 200 hair cells. In contrast, an amphibian papilla afferent fiber typically contacts fewer hair cells, all of which may be tuned to a narrower range of resonance frequencies because of the tonotopic arrangement of hair cell frequencies of the amphibian papilla (Lewis et al., 1982b; Smotherman and Narins, 1999a). Similar to the sacculus, basilar papilla innervation patterns are also more consistent with improving sensitivity rather than acute frequency resolution, since each of the approximately 200 afferent fibers innervates approximately 10% of the 50 or so hair cells in the basilar papilla epithelium (Simmons et al., 1992).

Ion channel kinetics are known to be highly temperature-sensitive. As a result, clear temperature sensitivity is also seen in the electrical resonances of electrically tuned saccular hair cells (Smotherman and Narins, 1998), which exhibit Q10 values of 2.0. It has been postulated that, if electrical processes contribute significantly to the tuning seen in auditory nerve fibers, then an auditory fiber’s characteristic frequency should exhibit similar temperature-dependence. This was shown to be true for the turtle (Trachemys scripta elegans) basilar papilla (Vu et al., 1995) and for the auditory afferents of the pigeon Columba livia (Schermuly and Klinke, 1985) and cayman Caiman crocodilus (Smolders and Klinke, 1984), in which electrical tuning is also suspected. In the frog, only the low-frequency amphibian papilla fibers exhibit strong characteristic frequency temperature-dependence (van Dijk et al., 1990; Stiebler and Narins, 1990): characteristic frequencies were observed to increase with temperature with a Q10 of approximately 1.7. In contrast, saccular, upper-frequency amphibian papilla and basilar papilla auditory nerve characteristic frequencies are temperature-insensitive (van Dijk et al., 1990; Egert and Lewis, 1995; Stiebler and Narins, 1990), arguing for a predominantly mechanical source for tuning in these organs.

**Adaptation and suppression**

Post-stimulus time histograms are commonly used to plot the time course of a nerve fiber’s activity after stimulus onset. Assuming that the fiber responds to a stimulus, the evoked spike rate may, over the duration of the stimulus, increase, stay the same or decline. Post-stimulus time histograms are therefore useful for characterizing the adaptation profile of an auditory nerve fiber. In mammals, auditory nerve fibers exhibit a stereotyped decline in neural discharge rate over the duration of a tonal stimulus (Kiang et al., 1965; Smith, 1977). This pattern of adaptation has also been observed in many non-mammalian vertebrates (Eatock et al., 1981; Fay, 1978; Furukawa and Ishii, 1967; Johnstone and Johnstone, 1969; Sachs et al., 1974) including frogs (Lewis, 1986; Megela, 1984; Megela and Capranica, 1981, 1982). Unlike mammals, however, adaptation patterns observed in fish, amphibians and reptiles show considerable diversity, with some fibers exhibiting little or no changes in firing rate during long-duration tone bursts, and other fibers firing action potentials only at stimulus onset. In the frog auditory nerve, adaptation patterns are different for each endorgan: saccular fibers do not adapt (Lewis, 1986); amphibian papilla fibers range from non-adapting to rapidly adapting, depending on fiber characteristic frequency (Megela and Capranica, 1981); and basilar papilla fibers were reported to exhibit intermediate adaptation patterns similar to the typical mammalian profile (Megela and Capranica, 1981; Megela, 1984; Ronken, 1990).

Upon mechanical deflection of a hair cell’s stereociliary bundle, a positive current rushes into the stereocilia through mechanically gated ion channels (Hudspeth and Corey, 1977), initiating a depolarization of the hair cell’s membrane potential and subsequent release of neurotransmitter. In some vertebrate hair cells, the hair bundle will adapt to either sustained or repeated deflections (Eatock et al., 1987), leading to a reduction in the size of the depolarizing current. Adaptation of the transducer current is a Ca2+-dependent process (Lumpkin and Hudspeth, 1998; Ricci and Fettiplace, 1997, 1998; Ricci et al., 1998) that relies upon a collection of myosin proteins present in the stereocilia to reset the sensitivity of the mechanotransducing ion channels during sustained stimulation (Burlacu et al., 1997; Gillespie et al., 1993; Hasson et al., 1997). Different hair cells may exhibit different adaptation properties based upon differences in stereociliary physiology, which include differences in Ca2+ influx as part of the transducing current, Ca2+ buffering and different myosin motors driving adaptation. In the frog, six different hair bundle architectures (types A–F) have been recognized within the auditory system (Lewis and Li, 1975; see Fig. 3), and each architectural subtype exhibits a unique set of transduction and adaptation properties, including sensitivity, range and rate of adaptation (Baird, 1994a,b; Baird and Lewis, 1986). Baird (1994a,b), working in the frog utriculus, found that the tallest hair bundle types adapted more quickly and more completely than shorter hair bundles, although a range of adaptation speeds was observed for each bundle type, depending on location within the sensory macula. However, neither hair bundle height nor architecture co-varies with characteristic frequency in any of the frog auditory organs. In the amphibian papilla, adaptation rate and characteristic frequency co-vary in nerve fiber recordings, suggesting a relationship between the physiology of frequency selectivity and adaptation. However, the three principal hair bundle architectures of the amphibian papilla
(types A, D and E; Fig. 3) are distributed perpendicular to the tonotopic axis of the organ. Therefore, in the frog auditory system, differences in the adaptation parameters of neighboring nerve fibers cannot yet be assigned directly to properties of the underlying hair cells.

Hair cells isolated from the frog sacculus have been a model preparation for the study of hair bundle adaptation physiology (Assad and Corey, 1992; Corey and Assad, 1992; Eatock et al., 1987; Howard and Hudspeth, 1987), yet saccular nerve fibers do not exhibit signs of adaptation in post-stimulus time histograms. The saccular epithelium is predominantly composed of one hair bundle type (type D; see Lewis and Li, 1975), which is a short, symmetrical bundle of stereocilia with a true, bulbed kinocilium slightly longer than the stereocilia. The contributions of hair bundle adaptation, as observed in the in vitro hair cell preparations, may not be recognizable in the temporal patterns of spike discharge, but rather appear in the tuning curve of the nerve fiber. It has been shown that short-term adaptation occurring at the site of transduction may contribute to the spectral filtering properties of turtle basilar papilla hair cells (Fettiplace and Fuchs, 1999; Ricci et al., 1998). Adaptation of the transducer current, occurring within milliseconds during slow sinusoidal deflections of the stereociliary bundle, may add an additional level of spectral filtering into the sound-transducing pathway, defining another way in which hair cells contribute to the spectral resolution of the afferent fiber.

Ricci et al. (1998) found shorter adaptation time constants in hair cells taken from the high-frequency (approximately 600 Hz) end of the turtle basilar papilla. This phenomenon has yet to be demonstrated in the frog, although the basic components have been described for saccular hair cells (Choe et al., 1998; Lumpkin and Hudspeth, 1998). This line of inquiry may offer some explanation for why eighth nerve fiber adaptation profiles (in post-stimulus time histograms) become progressively more peaked with increasing characteristic frequency (Megela and Capranica, 1981; and see Megela, 1984). Furthermore, amphibian papilla auditory nerve fibers exhibited less peaked adaptation profiles at lower stimulus frequencies, suggesting that hair bundle adaptation was acting as a low-pass filter, which (for a pure tone stimulus) translates into greater temporal adaptation at higher frequencies. The distribution of adaptation properties in amphibian papilla and basilar papilla hair cells remains to be investigated, but certainly offers promising advances.

A phenomenon similar, and possibly related, to adaptation is one- or two-tone suppression. In some cases, the presentation of a single tone can cause a reduction in an auditory fiber’s spontaneous activity (one-tone suppression; Christensen-Dalsgaard and Jørgensen, 1996). This phenomenon has also been reported in mammals (Lewis and Henry, 1995). Two-tone suppression occurs when the addition of a second tone of appropriate frequency above or below the fiber’s characteristic frequency causes a reduction in that fiber’s response to a characteristic frequency tone (Benedix et al., 1994; Frishkopf and Goldstein, 1963). Both one- and two-tone suppression appear to be restricted to the low- to mid-frequency portion of the amphibian papilla (Feng et al., 1975; Christensen-Dalsgaard and Jørgensen, 1996).

When seen in amphibian papilla nerve fibers, suppression and adaptation occur with similar time courses and in some ways are experimentally indistinguishable from each other (Lewis, 1986). It is natural to suspect similar origins, which leads to the assumption that the phenomenon of suppression has its roots in the transducing current. However, it seems highly unlikely that a suppressor tone could modulate the underlying mechanisms of adaptation (i.e. stereocilial Ca2+ concentrations), but the suppressor tone could manipulate the transducer current directly by mechanically shifting the angle of deflection of the hair bundle. Two-tone suppression occurring in mammals derives from mechanical interactions between the tones within the cochlea (Legoux et al., 1973; Westerman and Smith, 1984). A similar mechanical basis for suppression is suspected in the frog amphibian papilla, where the complex vibration patterns of the tectorial membrane are implicated (Hillery and Narins, 1987; Lewis and Leverenz, 1983; A. P. Purgue and P. M. Narins, unpublished data).

In each of the frog auditory organs, sound energy is transmitted to the hair cells through the movements of a tectorial membrane. Preliminary work in the amphibian papilla suggests that the tectorial membrane may move maximally at a different angle when responding to different stimulus frequencies, thereby contributing an additional level of bandpass filtering prior to hair cell stimulation. If so, then the combination of two simultaneous tones would probably produce a different mean vector of membrane motion from that produced by any one tone and would change the resulting pattern of hair cell stimulation. Hair bundles are polarized, being maximally stimulated when the hair bundle is deflected towards the kinocilium and maximally suppressed when it is deflected away from the kinocilium, which means that the angle at which the hair bundle is deflected by the tectorial membrane will determine the size of the transducer current. We suspect that two-tone suppression in the amphibian papilla may occur when a second (suppressor) tone causes a shift in the angle of hair bundle deflection away from the kinocilium by altering the mean vector of motion in the overlying tectorial membrane, resulting in an attenuation of the hair cell’s alternating current response to its characteristic frequency tone (Lewis, 1986). In the case of one-tone suppression, in which spontaneous activity is measured in the absence of a primary tone, the suppressor tone might induce a movement of the tectorial membrane that drives the hair bundle away from the kinocilium and thus dampens the resting current passing through the transducer channels. Within the frog ear, only the amphibian papilla has an intricate, frequency-related distribution of hair bundle vectors (Lewis, 1976, 1977), which is consistent with the suppression phenomenon being restricted to this organ. Adaptation and suppression appear to be similar in nature because they both probably involve a reduction in the amplitude of the transduction current; but while suppression comes about via mechanical interference prior to hair cell stimulation, adaptation is based upon the molecular physiology of the stereocilia.
Spontaneous activity

By mammalian standards, all frog auditory nerve fibers have low rates of spontaneous activity (Ronken, 1990). The spontaneous firing rate varies from 0 to approximately 50 spikes s\(^{-1}\) for each of the amphibian auditory endorgans. The highest spike rates were reported for the saccus (Christensen-Dalsgaard and Jørgensen, 1988), while the lowest spike rates were found in the upper frequency region of the amphibian papilla (Lewis, 1986; Ronken, 1990, 1991; Yu et al., 1991; Zelick and Narins, 1985). While there are many potential sources for spontaneous activity in the auditory system, Megela and Capranica (1981) uncovered what may be the most revealing clue about its origins in the frog. They found a strong correlation between an eighth nerve fiber’s adaptation profile and its spontaneous spike rate; generally, they reported that non-adapting or slowly adapting fibers had high spike rates, while more rapidly or fully adapting fibers had lower spike rates or did not spike. This relationship appears to be maintained throughout the frog’s auditory system: non-adapting saccular nerve fibers have high spike rates, amphibian papilla fibers exhibit a range of adaptation time constants and spike rates, and moderately adapting basilar papilla fibers have intermediate spike rates.

The link between adaptation and spontaneous spike rate is likely to be found in the adaptation properties of the transducer apparatus. Since slowly and rapidly adapting hair bundles have been shown to differ in the ways in which they regulate and respond to Ca\(^{2+}\) influx (Lumpkin and Hudspeth, 1998; Ricci and Fettiplace, 1997, 1998; Ricci et al., 1998), it may be true generally that non-adapting hair bundles possess a transduction apparatus more tolerant of Ca\(^{2+}\) influx and, consequently, these cells maintain larger resting transducer currents. A more rapidly adapting hair bundle would be one that is more sensitive to the accumulation of Ca\(^{2+}\) in the stereocilia, with reductions in the transducer current occurring at lower concentrations of stereociliary Ca\(^{2+}\).

It has yet to be shown whether the amplitude of the resting transducing current is indeed different for hair cells that adapt differently, but the correlation between adaptation and spontaneous spike rate in the frog supports the conclusion that the spontaneous activity observed in auditory nerve fibers has its roots in the adaptation characteristics of the underlying hair cells. It has been speculated that auditory system background noise levels play a role in acoustic signal processing by enhancing the sensitivity of the system through stochastic resonance (Jaramillo and Wiesenfeld, 1998; Narins et al., 1991; Zelick and Narins, 1985). While there are many potential sources for spontaneous activity in the auditory nerve, the frog sacculus (Christensen-Dalsgaard and Jørgensen, 1988) has been described as the most sensitive vertebrate mechanosensor studied to date (Narins and Lewis, 1984). Most of this sensitivity appears to...
be dedicated to vibration detection, since saccular afferents have been reported to be less sensitive to sound than either amphibian papilla or basilar papilla fibers (Christensen-Dalsgaard and Jørgensen, 1988; Christensen-Dalsgaard and Narins, 1993; Moffat and Capranica, 1976; Yu et al., 1991). Responding to sound under closed-field conditions, saccular afferents exhibit a broad range of thresholds, with most falling between 60 and 90 dB sound pressure level (SPL) (Christensen-Dalsgaard and Narins, 1993; Yu et al., 1991). Low-frequency (characteristic frequencies approximately 100–600 Hz) afferents exiting the rostral and medial portions of the amphibian papilla include the frog’s most sensitive auditory nerve fibers (Narins, 1987; Ronken, 1991; Stiebler and Narins, 1990; Zelick and Narins, 1985), in which thresholds generally range between 40 and 90 dB SPL. Moving caudally in the amphibian papilla, and up in frequency to approximately 1200 Hz, amphibian papilla afferents become slightly less sensitive overall, with thresholds typically approximately 10–20 dB higher than those of their rostral counterparts (Ronken, 1991; Stiebler and Narins, 1990; Zelick and Narins, 1985), although not all studies have found caudal amphibian papilla afferents to be significantly different from their rostral counterparts (Feng et al., 1975; Narins, 1987; Narins and Wagner, 1989; Yu et al., 1991). Basilar papilla afferents consistently exhibit minimum thresholds that are 10 to 20 dB higher than those of most amphibian papilla fibers. Basilar papilla fiber thresholds vary upwards from 50 or 60 dB SPL (Megela, 1984; Narins, 1987; Narins and Wagner, 1989; Ronken, 1990; Stiebler and Narins, 1990; Zelick and Narins, 1985). Only one study found some basilar papilla afferents with thresholds as low as 40 dB SPL (Ronken, 1991). Overall, the broad range of nerve fiber thresholds in the frog probably represents the inner ear’s sound-processing strategy for extending the range of stimulus amplitudes it is capable of encoding.

There are many features of the frog auditory system that may influence its sensitivity. Within the hair cell, three of these stand out: stereociliary bundle stiffness, the resting membrane potential and the input resistance of the basolateral membrane. Beyond the hair cell, the number of synapses per hair cell, the total synaptic area per hair cell, the number of hair cells innervated by a single afferent fiber and the diameter of the afferent fiber are all post-transductional morphological features of the innervation strategy suspected of contributing to auditory nerve thresholds (Boyle et al., 1991; Boyle and Highstein, 1990; Edds-Walton et al., 1999; Liberman, 1980, 1982). We would like to know the relative contributions of each of these factors to auditory nerve fiber thresholds. Frog auditory nerve fiber response thresholds are not easily broken down into discrete categories; rather, they generally vary along a continuum. Nonetheless, the response properties of saccular, amphibian papilla and basilar papilla fibers have some common features, with some useful patterns emerging.

From the above information, there are two trends that offer clues for a better understanding of threshold in auditory fibers: (i) a wide range of thresholds exists for each endorgan and (ii) the low-frequency region of the amphibian papilla is more sensitive than the rest of the auditory system. Since the low-frequency amphibian papilla also exhibits a wide range of thresholds, these two trends may not be causally related. Specifically regarding the wide range of thresholds observed, we can add the following information. First, although the sensitivity of the transducing apparatus may depend upon the height and stiffness of the hair bundle, the distribution of hair bundle architectures seems to be neither sufficient nor consistent with this being the source of variations in threshold. Second, thresholds do not vary systematically with characteristic frequency (Megela and Capranica, 1981; Ronken, 1990, 1991) and, since basolateral membrane ionic currents do vary with characteristic frequency (Smotherman and Narins, 1999a,b), it becomes less likely that the ionic currents driving the receptor potential contribute significantly to threshold. Third, in each endorgan, there is substantial diversity in the number of hair cells innervated by a single afferent fiber, and there is equal diversity in the number of synapses per hair cell (Lewis et al., 1982a,b; Simmons et al., 1992). Each of these studies reported a difference in the innervation patterns of the rostral and caudal regions of the amphibian papilla, where a significant reduction in innervation density and afferent fiber diameters occurs rostro-caudally. Simmons et al. (1992) found that this pattern continued into the basilar papilla. Thus, hair cell innervation density and/or fiber diameter appear to be the most likely candidates for the physiological basis of threshold variations. However, there are a few points worth mentioning with regard to the enhanced sensitivity of the low-frequency region of the amphibian papilla. Fourth, the sacculus and rostral amphibian papilla have similar innervation patterns, yet the sacculus maintains higher auditory thresholds than the rostral amphibian papilla for overlapping frequencies. Nevertheless, the sacculus does exhibit lower thresholds than the amphibian papilla for substratum-borne vibrations (Christensen-Dalsgaard and Jørgensen, 1988; Christensen-Dalsgaard and Narins, 1993), suggesting that the threshold differences for the sacculus and rostral amphibian papilla originate in the mechanics of these organs. Fifth, the hair cells of the rostral amphibian papilla are the only homogeneous population of hair cells in the frog auditory system that do not possess an inward rectifying K⁺ current (I_K1 in Fig. 3) (Holt and Eatoock, 1995; Smotherman and Narins, 1999a,b). This type of K⁺ channel is presumed to be open at the hair cell’s resting potential, resulting in lower membrane input resistances. Lower input resistances at the basolateral membrane make it less likely that small transduction currents would result in the release of neurotransmitter, so that hair cells possessing this channel should have higher thresholds than those devoid of this channel, and vice-versa. Whether this pertains in vivo is not yet known. The unique absence of these channels in the rostral amphibian papilla hair cells is consistent with the role of this ionic current in elevating auditory nerve thresholds.
Concluding remarks

As a result of over 40 years of eighth nerve afferent recordings in the frog, there are ample data available on the response properties of the frog auditory system. Information about the physiology of frog auditory hair cells has been much slower in coming, but has benefited greatly by the overall advances made in the field of vertebrate hair cell physiology. The frog auditory periphery continues to be an exceptional preparation for the investigation of vertebrate hearing, and many of its features described here are consistent with the roles hair cells play in sound detection in other vertebrates, including mammals. At present, the frog ear is being used as a model system to investigate several key properties of hair cell physiology, including the contribution of the hair bundle to signal processing, the role of reverse properties of hair cell physiology, including the contribution of the hair bundle to signal processing, the role of reverse properties of hair cell physiology, including the contribution of the hair bundle to signal processing, the role of reverse properties of hair cell physiology, including the contribution of the hair bundle to signal processing, the role of reverse properties of hair cell physiology, including the contribution of the hair bundle to signal processing, the role of reverse properties of hair cell physiology, including the contribution of the hair bundle to signal processing, the role of reverse properties of hair cell physiology, including the contribution of the hair bundle to signal processing, the role of reverse properties of hair cell physiology, including the contribution of the hair bundle to signal processing, the role of reverse properties of hair cell physiology, including the contribution of the hair bundle to signal processing, the role of reverse properties of hair cell physiology, including the contribution of the hair bundle to signal processing, the role of reverse properties of hair cell physiology, including the contribution of the hair bundle to signal processing.

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