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Temperature-dependence of saccular nerve fiber response in the North American bullfrog

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Abstract

A clinical microwave device was used to heat the head and ear of the North American bullfrog in order to observe the temperature dependence of tuning in the sacculus, an organ known to possess the capability of electrical resonance in its hair cells. In tuning curves derived from reverse correlation analysis with noise stimuli, the temperature dependencies of the frequencies of tuning peaks and notches typically exhibited Q_{10}s less than 1.1; whereas the frequencies of electrical resonances are expected to have Q_{10}s of the order of 1.7. Therefore we conclude that electrical resonances are not significantly involved in tuning in the bullfrog sacculus.

Keywords: Frog; Sacculus; Temperature; Tuning; Auditory nerve

1. Introduction

Evidence from various investigators suggests that tuning even in a single acoustic sensor may arise from a variety of processes (Weiss et al., 1976; Crawford and Fettiplace, 1981; Manley, 1990). Because temperature dependence of dynamic properties varies from one process to another, studying the effects of temperature on tuning offers the possibility of noninvasively dissecting the tuning curve with respect to the processes contributing to it. Such studies have been conducted on amphibians (Moffat and Capranica, 1976; van Dijk et al., 1990; Stiebler and Narins, 1990), reptiles (Eatock and Manley, 1976, Eatock and Manley, 1981; Smolders and Klinke, 1984), birds (Schermuly and Klinke, 1985), mammals (Gummer and Klinke, 1983) and insects (Oldfield, 1988). Dynamics due to electrochemical mechanisms (i.e. channel kinetics) should be more highly sensitive to temperature changes than dynamics due to mechanical elements (e.g., masses, springs, and viscous resistances). Hodgkin et al. (1952), for example, found the rate constants associated with channel kinetics to have a $Q_{10} = f(T + 10°)/f(T)$ of three. Unless phase transitions occur, the values of Q_{10} for mechanical elements should be much lower, with typical values less than 1.3 (the Q_{10} for viscosity of water in the neighborhood of 20° C). By observing the effects of temperature on different components of tuning, and by noting the strength of their dependence, it may be possible to separate the contributions to tuning that arise from mechanical sources from the contributions that arise from channel kinetics.

The bullfrog sacculus, an organ of the anuran inner ear that responds primarily to substrate-borne vibration, has gained considerable attention due the electrical resonance found in hair cells that either have been isolated from the macula or remain embedded in the macula with the otoconial membrane removed. It has been shown that the resonance arises from channel kinetics and the associated ion flows, and it has been suggested that the tuning seen in saccular afferent axons arises (at least in part) from the resonance (Hudspeth and Lewis, 1988a, Hudspeth and Lewis, 1988b). Art and Fettiplace (1987) found that in hair cells of the turtle basilar papilla, the frequency of electrical resonance and the channel kinetics were strongly correlated; the resonant frequency increased approximately as the square root of the rate constant of closing of the potassium channel. They did not report the temperature dependence for that rate con-

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stant. If it behaves similarly to those of other potassium channels, with a Q_{10} of approximately 3 (Hodgkin et al., 1952; Frankenhaeuser and Moore, 1963), then the Q_{10} of the frequency of electrical resonance in the turtle papilla would be approximately the square root of 3, which is 1.7. The temperature dependence of saccular tuning therefore should bear implications regarding the relative importance of these electrical resonances in the overall tuning of saccular fibers. The frog sacculus also provides an opportunity to compare a seismic acoustic sensor, which it is, to auditory acoustic sensors, such as the frog amphibian papilla and the frog basilar papilla. Temperature shift experiments already have been carried out on those two organs (van Dijk et al., 1990; Stiebler and Narins, 1990).

An interesting feature found in a substantial fraction of the amplitude tuning curves of the bullfrog sacculus is a sharply tuned notch, usually accompanied by a positive jump in the phase tuning curve (Lewis, 1988; Yu, 1991; Yu et al., 1991). The notches usually accompany impulse responses with considerable ringing and therefore may reflect the action of an electrical resonance (e.g., in a feedback loop). If that were true, then we would expect the frequency of the notch to be strongly dependent on temperature.

2. Methods

2.1. Animal preparation

We used small to medium-sized North American bullfrogs (*Rana catesbeiana*, snout to vent length 3–5 inches) anesthetized with 80 μl of sodium pentobarbital (Nembutal®, 50 mg/ml) and 90 μl of ketamine hydrochloride (Vetalar®, 100 mg/ml) per 100 grams of body weight. Each drug was injected intramuscularly into opposite hind legs to avoid a precipitation. Supplemental doses were given if the animal failed to achieve a satisfactory level of anesthesia, and also as necessary during the course of the experiment if the frog showed signs of stirring. The VIIIth cranial nerve was exposed using a ventral approach (Capranica and Moffat, 1975) by drilling a small hole in the roof of the mouth. We made certain that the otic capsule was intact after the drilling, and that there was clear and healthy-looking circulation in the vicinity of the nerve.

2.2. Stimulus presentation

Following the surgery, the frog was mounted on its back on a lucite platform, its jaw held open with a restraint covered with moistened gauze, thereby exposing the hole and providing access to the VIIIth nerve. The animal was covered with moist gauze to prevent dehydration and facilitate cutaneous respiration. The lucite platform was bolted to a metal plate mounted on an electromagnetic vibrator (Bruel and Kjaer Minishaker, type 4810). The vibrator was driven by an electric signal produced by a random noise generator (General Radio Co., type 1390-B) and shaped by a graphic equalizer and a parametric equalizer to accommodate the dynamical properties of the loaded vibrator. The vibration stimulus was aligned dorsoventrally with respect to the frog and was monitored with a calibrated accelerometer (Bruel and Kjaer, type 4370) mounted on the platform next to the frog's head. A Hewlett-Packard (3561A) spectrum analyzer was employed to make sure that the spectral amplitude of the (random) dorsoventral vibration velocity was as uniform as possible. The velocity amplitude usually was constant to within ± 2 dB over the frequency range from 10 Hz to 300 Hz, when observed with 3.82-Hz frequency resolution. The total stimulus amplitude, taken over all frequencies, typically was in the range between 10^{-6} and 10^{-5} m/s. For acoustic isolation, the vibration setup was housed in a double-walled box, each wall being constructed from 1 inch plywood. The box in turn was isolated from ground-borne vibration by a low-pass filter constructed of layers of bricks and innertubes.

Yu et al. (1991) were concerned with the unnatural position of the frog (lying on its back) in the ventral approach to the nerve. They compared ventral and dorsal approaches in saccular and amphibian papillar electrophysiological experiments in the bullfrog. Their study showed no obvious differences in the responses from animals that were on their stomachs (dorsal approach) compared to animals that were on their backs (ventral approach).

2.3. Nerve fiber recording and characterization

The anterior branch of the VIIIth nerve was penetrated by a glass pipette microelectrode. The microelectrode signal was amplified by an A-M Systems Neuroprobe Amplifier (model 1600). The microelectrode trace and the seismic stimulus were recorded on a Tascam 4 track cassette tape recorder. The stimulus was encoded with an FM adapter (A.R. Vetter Co.) to preserve its low frequency components. An axon was identified as a saccular afferent by 1) its sensitivity to seismic stimuli (Koyama et al., 1982), 2) its tuning properties (Yu et al., 1991) and 3) its location in the VIIIth nerve (Boord et al., 1971; Lewis et al., 1985).

Tuning curves were generated from the recorded data and also in real time during the experiment by means of the reverse correlation (REVCOR) method (de Boer, 1967; de Boer and de Jongh, 1978; de Boer and Kuyper, 1968; Møller, 1977; Evans, 1977; for reviews see Eggermont et al., 1983; Eggermont, 1993). Using Gaussian white noise as a stimulus to the ani-

mal, the REVCOR function is often taken to be an estimate of the impulse response of the filter of the inner ear. A lab-built computer board was employed to generate the REVCOR function and its corresponding discrete Fourier transform. The board, triggered by spikes, averaged the stimulus noise in a fixed time window (usually 200 ms) immediately preceding each spike. The time axis of the resulting function was reversed, thereby yielding the REVCOR function. The averaging procedure was continued until a clear REVCOR function formed. Tuning curves were generated by applying a discrete Fourier transform (also in real-time) to the REVCOR function, yielding magnitude and phase as functions of frequency for the unit being studied. The phase function obtained using the Fourier transform only takes on values between plus and minus one-half cycle. Whenever the function exceeds either of these boundaries, it wraps to the opposite extreme. The phase function was unwrapped whenever there was an obvious, discontinuous, one cycle jump from one extreme to the other by adding one cycle of phase shift to all parts of the phase function downstream of where the wrap occurred. By this means we were able to generate phase functions spanning over more than one cycle.

2.4. Microwave heating

We required a heating method that would allow us to change the temperature of the ear quickly while maintaining electrode penetration of a single axon. Microwave heating met these criteria. The system we employed originally was used for hyperthermia treatment in cancer patients. It consisted of a 2450 MHz RF source (Cheung Associates, Inc. – Model CA2450-300CW) and a 9 cm diameter round applicator. Microwaves at this frequency deposit most of their energy in the first centimeter of tissue which corresponds well with the thickness of the frog's head. Because the frog was in an environment with metal structures that surely caused distortions and reflections of the microwave field, we carefully monitored local tissue temperatures with thermocouples.

With the applicator positioned about 15 cm from the frog, emitting 85 Watts of microwave energy for thirty seconds raised the frog's temperature by 0.5–1° C. For each temperature run, the frog was initially cooled to approximately 14° C with ice cubes placed on the abdomen, and then sequential thirty second exposures to the microwaves were used to warm the frog for each successive temperature data point.

The frog's temperature was monitored with four type-E thermocouples (50 gauge, Omega) placed at various points: 1) in the eustachian tube, against the skin on the side of the otic capsule, 2) under the skin on the roof of the mouth, 3) down the gullet, and 4) on the abdomen. The thermocouples were multiplexed through a switch box and monitored using an Omega 450 AET digital thermometer. Stiebler and Narins (1990) found that a thermocouple placed on the roof of the mouth showed the least deviation from the VIIIth nerve temperature. In control experiments where we actually breached the otic capsule and placed a thermocouple within the inner ear, the average of the mouth and eustachian tube thermocouples (taken 30 seconds after the cessation of the microwaves) was found to be within 0.1 to 0.2° C of the inner ear temperature.

While the physiological observations (of temperature and neural activity) were being made, the microwaves remained off. Metal thermocouples deform the microwave field, in fact even non-metal temperature probes cause distortions in the field (Chan et al., 1988a). The problem with thermocouples can be minimized, however, by aligning them perpendicular to the field (Chan et al., 1988b), and by waiting for localized heating near the thermocouples to dissipate before making the temperature measurement (Dunscombe et al., 1988). Therefore, we waited thirty seconds after the microwaves were turned off before taking the temperature reading. By that time, the temperature always was stabilized. Microwaves also produced large amplitude electrical noise in the microelectrode, precluding observation of spikes during active heating. For that reason, the microwave source remained off during the spike sampling time (up to 170 s) at each temperature, which led to temperature drift during the sampling in each case. Depending on the target temperature and the sampling time, the drift ranged from less than 0.1° C to almost 0.6° C.

To be certain that the microwave radiation was not permanently affecting the tuning, we used a frog with crushed ice on its abdomen and repeatedly heated the animal and allowed it to cool. Units that were characterized at the same temperature, but after the deposition of many cycles of microwave energy, showed no noticeable effects in either their tuning or their spike rate. This was consistent with studies that have shown that mild microwave irradiation had neither short term nor long term effects on electrophysiological and morphological properties in dorsal root ganglion cells from the rat (Wang et al., 1991).

The care and use of the animals reported on in this study were approved by the Animal Care and Use Committee of the University of California at Berkeley under Animal Use Protocol R087-1094.

3. Results

We were able to maintain penetration in eighteen axons (in ten frogs) over temperature ranges greater

than 2° C. For ten of those units, the ranges were greater than 5.0° C.

3.1. Spike rates

The spike rates observed in axons under constant-amplitude seismic stimulus showed clear dependence on temperature (Fig. 1). For temperatures ranging from 13° C to somewhat more than 20° C, the iso-intensity driven spike rate for 17 of 18 units increased with increasing temperature. The increase in spike rate ranged from 2.3 to 5 spikes/second per °C, corresponding to Q_{10} ranging from 2 to 7. Above approximately 22° C there was a tendency for the spike rate to reverse this trend and decline with further increases in temperature. One unit exhibited decreasing spike rates with increasing temperatures at lower temperatures.

3.2. Impulse responses

In 17 out of 18 units, the latency of the first peak of the REVCOR derived impulse response decreased at rates between 0.8 and 0.12 ms per °C (for constant-amplitude noise stimulus) as temperature increased. In this regard, the unit of Fig. 2 is representative. In one unit the latency of the first peak remained constant (over a temperature range of 4.8° C); but in all 18 units, subsequent peaks showed latency decreases that were disproportionately larger than that of the first peak - leading to slight time compression of the overall impulse response (e.g., see Fig. 2). In 14 out of 19 units, these temporal changes were sufficiently large to be reflected as conspicuous decreases in the mean slopes of the phase tuning curves (Fig. 3). The change in the damping of the impulse response was not consistent from unit to unit (see Figs. 2, 4 and 5). Five units displayed increased damping with temperature; six displayed decreased damping; and seven showed no obvious change. In five units, as the temperature rose, obvious fine structure (peak-splitting and trough-splitting) emerged in the impulse response (see Fig. 5).

3.3. Amplitude tuning curves

The varieties of amplitude tuning curves included those with broad (e.g., 2-octave) pass bands and no clear tuning peak, those with narrow pass bands (Qs as high as 10), and those with distinct notches. Representative examples are shown in Fig. 6. When these tuning curves were observed at 5 Hz resolution, the bin containing 120 Hz sometimes showed a small spike (as much as 4 dB). Subsequent spectral analysis of the stimulus noise with 0.4 Hz resolution showed a 120 Hz peak approximately 10 dB above the background noise (as expected from this amplitude ratio, the peak disappeared when the stimulus noise was observed with 4 Hz resolution). This weak 120 Hz contamination was traced to the random noise generator. For cosmetic purposes, the spike was removed from each of the tuning curves.

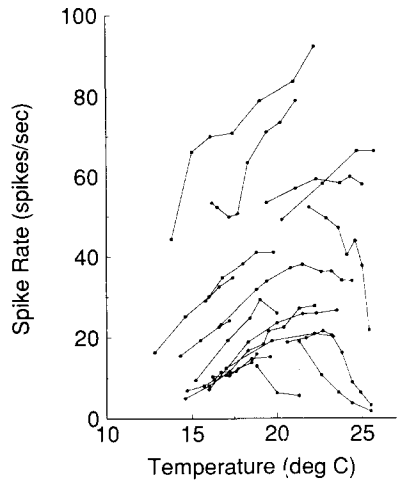

Fig. 1. Spike rate vs. temperature for 18 saccular axons. The stimulus was seismic noise (flat with respect to velocity between 10 and 300 Hz), with root-mean-square (rms) amplitude between 10^{-6} and 10^{-5} m/s. Each set of circles connected by a line indicates the spike rates from a single axon driven with a stimulus of fixed rms amplitude as the temperature of the frog varied. The dashed line connects data points from a single fiber at a point where the stimulus intensity was increased by 10 dB.

Changes in the broad-band tuning curves were difficult to quantify. In the 4 (out of 18) cases in which a single narrow pass band occurred and was maintained as temperature changed, the shifts in center frequency of the pass band were less than 1 % (0.014 octave) per °C, corresponding to Q_{10} less than 1.1. In 6 (out of 18) cases the notches were especially conspicuous, with depths greater than −10 dB. In all six cases, the maximum shift in the notch center frequency was approximately 0.3 to 0.4 % (0.004 to 0.006 octave) per °C, corresponding to Q_{10} approximately 1.04. As expected,

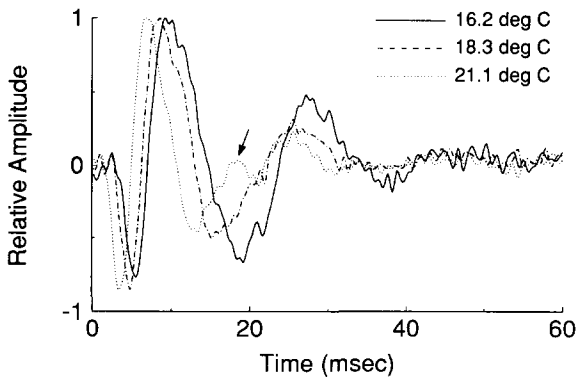

Fig. 2. Latency vs. temperature in REVCOR-derived impulse response. Arrow indicates presence of fine structure that arose as temperature was raised. The impulse responses correspond to the amplitude tuning curves in Fig. 6c.

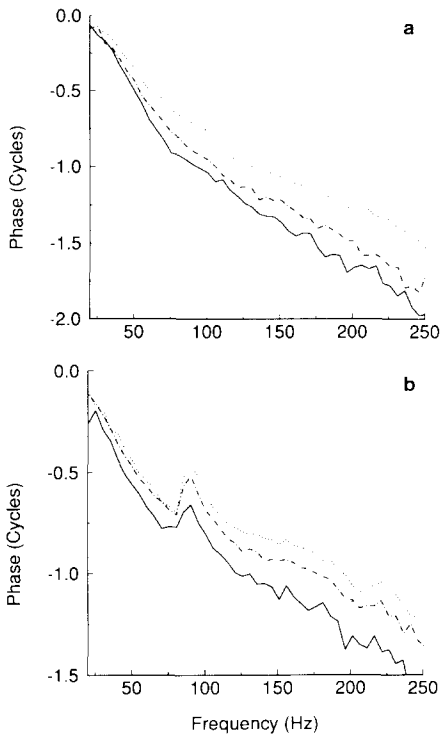

Fig. 3. Phase tuning curves. (a) corresponds to the amplitude tuning curves in 6c; (b) corresponds to the amplitude tuning curves in 6d. The positive jump in phase in (b) accompanies the notch in the corresponding amplitude tuning curve.

emergence of peak- and trough-splitting in the impulse response led to emergence of one or more high-frequency peaks in the amplitude tuning curve (Figs. 6c and f). This effect could be quantified as an increase in the ratio of the height of the amplitude tuning curve at the frequency of a high-frequency peak (see arrows in Fig. 6) to the height at the frequency of the low-frequency peak. The Q_{10}s for this increase ranged from 2.4 to 20.

4. Discussion

4.1. Spike rate

The temperature dependence of driven spike rates that we observed in saccular axons below 22° C (Q_{10} ranging from 2 to 7) was much the same as that seen by van Dijk et al. (1990) in amphibian and basilar-papillar fibers (their values of Q_{10} ranged from 5 to 10). In both studies, the affine natures of the temperature functions tended to give axons with low driven spike rates higher Q_{10}s than axons with higher driven spike rates. The observed increase in spike rate is consistent with work that shows that the rate at which quanta are released in synapses increases rapidly with increasing temperature (Parnas et al., 1989).

The decline in spike rate that we observed above 22° C may be related to the threshold shifts observed by Stiebler and Narins (1990). They found that threshold decreased reversibly with increasing temperature below approximately 22° C (in *Hyla regilla*) and 25° C (in *Eleutherodactylus coqui*), but then increased again at higher temperatures. Although work by Lillywhite

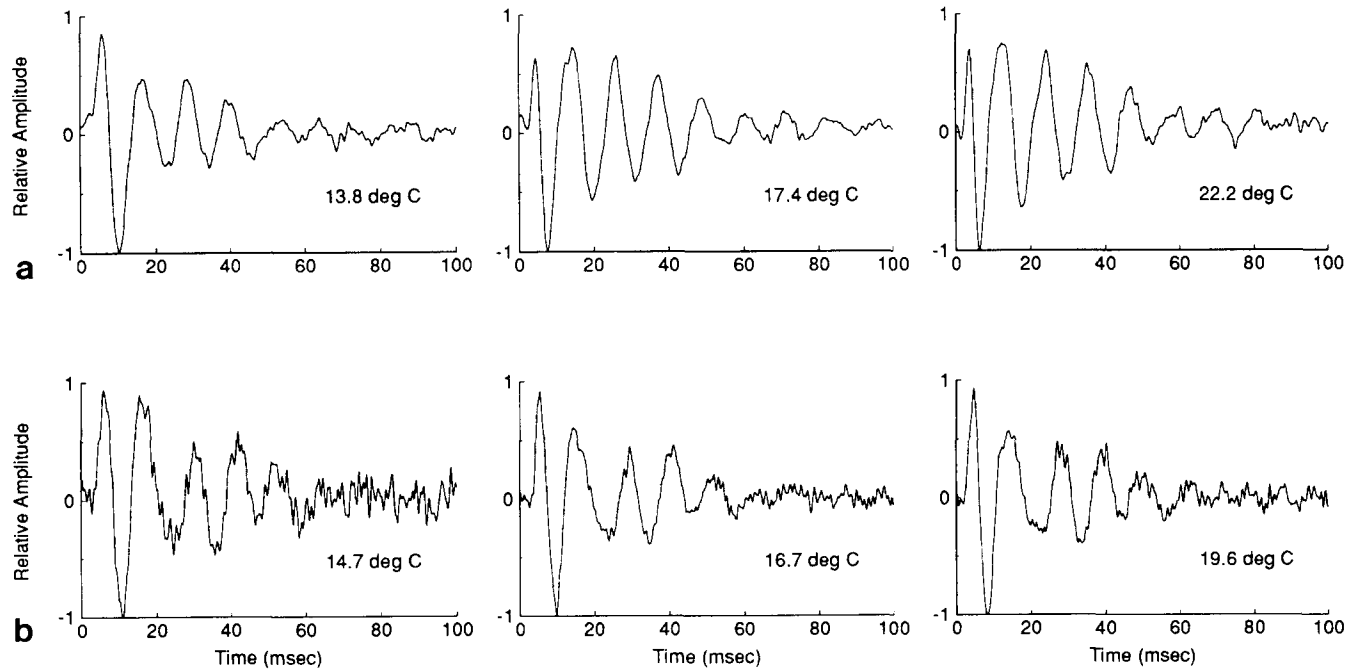

Fig. 4. REVCOR-derived impulse response vs. temperature. Impulse responses in the same row are from the same unit at different temperatures. The impulse responses in (a) correspond to the amplitude tuning curves in Fig. 6b; the impulse responses in (b) correspond to the amplitude tuning curves in Fig. 6e.

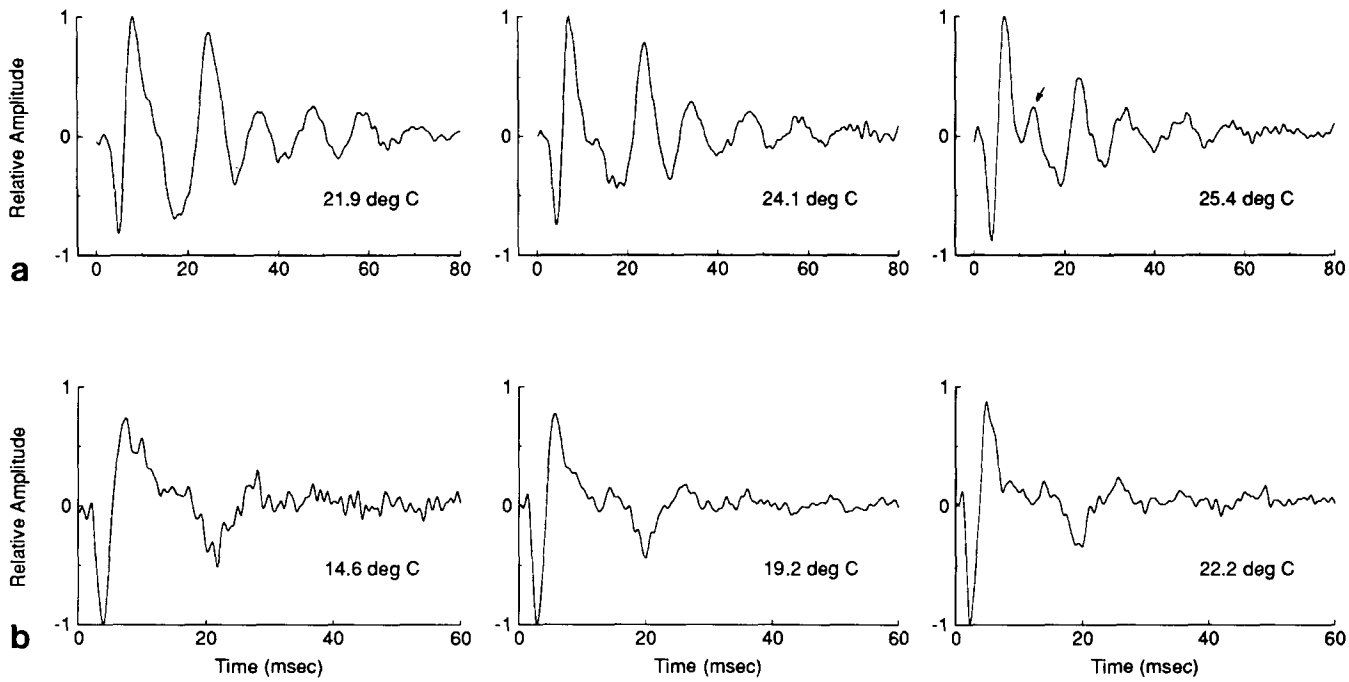

Fig. 5. REVCOR-derived impulse response vs. temperature. Impulse responses in the same row are from the same unit at different temperatures. The impulse responses in (a) correspond to the amplitude tuning curves in Fig. 6f; the impulse responses in (b) correspond to the amplitude tuning curves in Fig. 6d. Arrow in (a) indicates presence of fine structure that arose as temperature was raised.

(1971) showed that bullfrogs often prefer temperatures around 25° C when given a choice in an artificial thermal gradient, perhaps in its anesthetized state, these same temperatures cause thermal stress. Anesthesia suppresses lung respiration, and it has been suggested that if frogs are to depend on cutaneous respiration

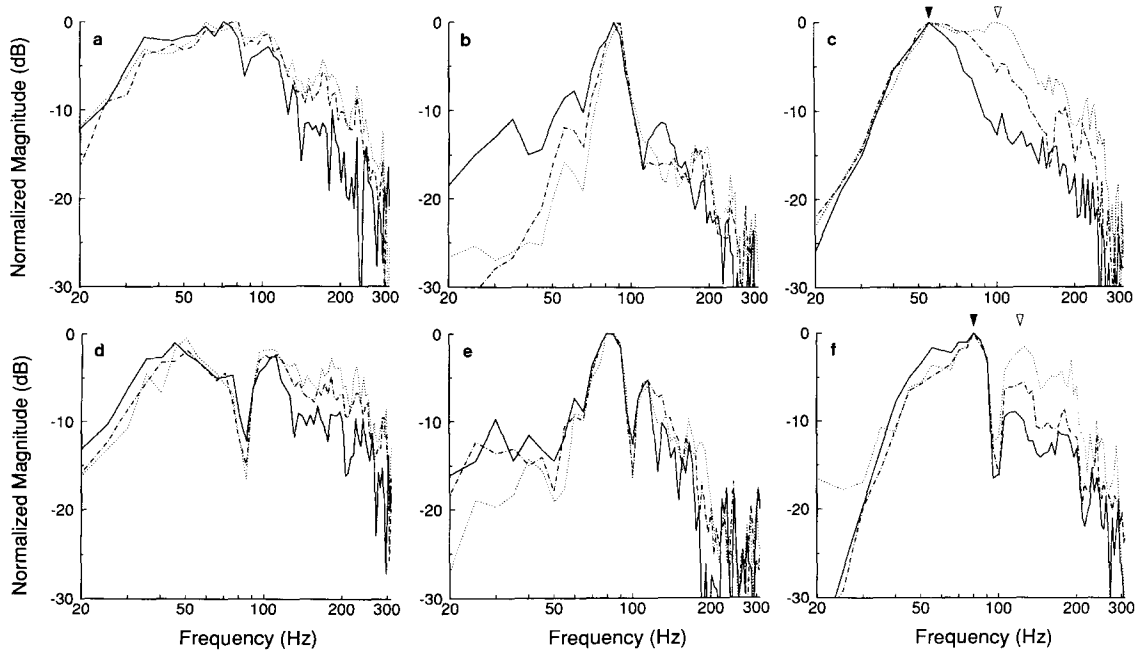

Fig. 6. Amplitude tuning curves vs. temperature. The temperature increases as the line style goes from solid to dot/dash to dotted. The temperatures for (a) were solid = 16.7° C, dot/dash = 20.8° C, and dotted = 24.4° C. The temperatures for (b) were: solid = 13.8° C, dot/dash = 17.4° C, and dotted = 22.2° C. The temperatures for (c) were: solid = 16.2° C, dot/dash = 18.3° C, and dotted = 21.1° C. The temperatures for (d) were: solid = 14.6° C, dot/dash = 19.2° C, and dotted = 22.2° C. The temperatures for (e) were: solid = 14.7° C, dot/dash = 16.7° C, and dotted = 19.6° C. The temperatures for (f) were: solid = 21.9° C, dot/dash = 24.1° C, and dotted = 25.4° C.

alone they be kept at temperatures below 18° C (Müller, 1976).

4.2. Impulse response

The latency decrease (up to 2 ms per 10° C) of the REVCOR derived impulse responses could be explained, in part, by temperature dependence of spike conduction velocity and temperature dependence of spike shape and, in part, by temperature dependence of synaptic delay. Spike conduction velocity in myelinated fibers in the frog increases up to 2 m/s per ° C (Engelhardt, 1951). Over the less than 1.0 cm of axon between the saccular macula and the recording site, the contribution to latency decrease from this source would be of the order of 0.5 ms per 10° C. Most of the temperature-dependent changes in spike shape (e.g., amplitude, time to inflection point) evidently occur over the temperature range below 12° C and above 35° C (Sjodin and Mullins, 1958; Hodgkin and Katz, 1949). Hodgkin and Katz found that the latency of the inflection point in the rising phase of the spike in squid giant axon decreased approximately 0.25 ms as the temperature was increased from 13.3° C to 33.5° C. Synaptic delay also decreases as temperature increases, with a Q_{10} between 1/3 and 1/4.5 (i.e., the speed of synaptic transmission increases with Q_{10} between 3 and 4.5) (Katz and Miledi, 1965; Parnas et al., 1989). In a neuromuscular junction, for example, the minimal synaptic delay is about 0.5 ms at 20° C and about 1.5 ms at 10° C (Katz and Miledi, 1965).

4.3. Amplitude tuning curves

The increased high frequency content that seems to appear in many broad-band units as temperature is increased could be the consequence of a low pass filter with a corner frequency that increases with temperature. The presence of a low-pass filter has been inferred from phase-locking in the frog amphibian papilla (Narins and Hillery, 1983) and the lizard basilar papilla (Weiss and Rose, 1988). Strong temperature dependence of the corner frequency is implied by comparative considerations (see Eggermont comment in Narins and Hillery, 1983), by observation of temperature dependence of phase locking (Stiebler and Narins, 1990), and by second-order Wiener-kernel analysis (van Dijk and Wit, 1995). The (−3 dB) corner frequencies inferred from these observations range from approximately 200 Hz at 16° C to 350 Hz at 23° C (van Dijk and Wit, 1995; Weiss and Rose, 1988). This is approximately the correct range to account for some of the shifts we observed (as in Figs. 6a and d). The range is too high, however to account for the shifts in other units (as in Figs. 6c and f).

The development of a higher-frequency peak in the tuning curve of Fig. 6f was associated with emergence of a distinct, higher-frequency component in the REVCOR-derived impulse response (evident as the conspicuous fine structure indicated by the arrow in the left panel of Fig. 5a). Similar emergence of fine structure in the impulse response (Fig. 2) is associated with the development of the high-frequency peak in the unit of Fig. 6c. We take the emerging fine structure to imply the presence of one or more distinct natural frequencies in the physical tuning structure. In that case, the shape changes in the tuning curves of Figs. 6c and f could be attributed to shifts (with changing temperature) in dominance of existing natural frequencies rather than to temperature dependence of the natural frequencies themselves.

In a short abstract, Moffat and Capranica (1976) reported that the best excitatory frequencies in fibers from amphibian papilla of the American toad (*Bufo americanus*) exhibited temperature dependence while those from the basilar papilla of the same animal did not. van Dijk et al. (1990) found that in bullfrog amphibian papilla fibers with amplitude tuning peaks at frequencies below 600 Hz, the frequencies of the peaks changed up to 4 % (0.065 octave) per ° C. In bullfrog amphibian papilla fibers tuned to higher frequencies, they found that frequencies of the peaks changed about half as much (up to 2 % or 0.03 octaves per ° C). They found no temperature dependence of tuning in the bullfrog basilar papilla. In two smaller frogs, *Eleutherodactylus coqui* and *Hyla regilla*, Stiebler and Narins (1990) obtained similar results. The tuning peaks of amphibian papillar fibers in those animals shifted from slightly less than 3 % (0.04 octave) to more than 8 % (0.12 octave) per ° C, with those tuned to frequencies below 500 Hz showing the greatest sensitivity. They found that the tuning peaks of basilar-papillar axons were much less dependent on temperature, with shifts up to approximately 1.4 % (0.02 octave) per ° C.

The Q_{10}s of the tuning-peak frequency of frog amphibian papillar axons thus appear to range from somewhat less than 1.5 (corresponding to 4 % per ° C) to somewhat more than 2 (corresponding to 8 % per ° C). This range spans the value 1.7 that we estimated (Introduction section) for hair-cell electrical resonance frequency. Thus one might conclude that tuning in the frog amphibian papilla (especially in the frequency range below 500 or 600 Hz) may involve hair-cell electrical resonances. The high dynamic order of the linear tuning curves from amphibian papillar axons, however, makes it clear that tuning cannot be achieved by single hair cell resonances acting alone (Lewis, 1988; Lewis et al., 1990).

The Q_{10}s of less than 1.1 that we observed both for the peak frequencies and for the notch frequencies of bullfrog saccular tuning curves, on the other hand, are very much lower than the 1.7 we estimated for hair-cell

electrical resonance frequency and suggest that such resonances are not significantly involved in tuning in that organ.

Yu et al. (1991) found that the notches in the tuning curves of saccular units often disappeared when the same units were responding to auditory stimuli rather than seismic stimuli. This suggests that perhaps the notch arises in the mechanical pathway by which seismic stimuli reach the saccular macula. Although this would be consistent with the low temperature dependence of the notch, if the notch arose in a pathway common to all saccular units one would expect it to be present in all saccular tuning curves and to exhibit the same center frequency in all units from the same sacculus. Neither of these expectations is true. Furthermore, in two successively penetrated axons from the same sacculus (excited by the same stimulus apparatus under essentially identical conditions), one often exhibits a notch while the other does not. Although the origin of the notch remains a mystery, we believe that our data eliminate the hypothesis stated in the introduction – the notch appears not to be a consequence of a hair-cell electrical resonance inserted in a feedback path in the physical tuning structure.

The presence of tuning curves as broad as two octaves brings into question the actual importance of tuning in the frog sacculus. That in turn brings into question the selective advantages that the sacculus provides to the frog. One might presume that the acute seismic sensitivity of the sacculus gives the animal an early-warning system for predators (e.g., by sensing predator footfalls). This presumption is supported by the 'cone of silence' that always seems to surround an observer walking in a field of calling frogs. The spectrum of the seismic surface waves generated by a footfall (or other impulsive stimulus) on moist soil exhibits most of its energy density between 20 and 150 Hz (Koyama et al., 1982; Lewis and Narins, 1985). The tuning bandwidths of saccular fibers match this spectrum well. Such a match will minimize the impact on detection of any noise sources peripheral to the tuned filter. In addition, the low-frequency roll-off of saccular filters must be very effective in eliminating the impact of seismic noise, which in most environments increases sharply at frequencies below approximately 3 Hz (Frantti et al., 1962). The seismic noise spectrum and the spectrum of seismic surface waves generated by footfalls both are essentially independent of temperature over the range (approximately 13° C to 26° C) that we used in this paper. Therefore, strong temperature dependence of tuning in the frog sacculus could be maladaptive. For example, if the band edges of the pass band shifted with a Q_{10} of 1.7, then over a temperature range of 13° C the pass band would shift by 1.0 octave and would no longer match the seismic spectra.

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