Review

Experiments in comparative hearing: Georg von Békésy and beyond

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ABSTRACT

Georg von Békésy was one of the first comparative auditory researchers. He not only studied basilar membrane (BM) movements in a range of mammals of widely different sizes, he also worked on the chicken basilar papilla and the frog middle ear. We show that, in mammals, at least, his data do not differ from those that could be collected using modern techniques but with the same, very loud sounds. There is in all cases a major difference to frequency maps collected using low-level sounds. In contrast, the same cannot be said of his chicken data, perhaps due to the different roles played by the BM in mammals and birds. In lizards, the BM is not tuned and it is perhaps good that Békésy did not begin with those species and get discouraged in his seminal comparative work.

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1. Introduction

The historical context of the initiation of a field of science often plays a decisive role, at least for a period of time, on the experimental framework used in that field. Georg von Békésy dominated the field of experimental auditory mechanics for the first half of the 20th century and undeniably played a critical role in establishing the conceptual and experimental approaches used. This proved, however, to be hardly constrictive, since Békésy's approaches were so comprehensive as to offer an enormous variety of challenges to (later) specialists of fields ranging from psychology through physiology to engineering. The foremost challenge was to explain the origin of the sharp tuning evident in human auditory perception, which required detailed studies of how the brain's auditory pathway processes frequency, but also the development of much more sensitive methods to measure both the mechanics of the basilar and tectorial membranes. As it turned out, the first much improved measurements of basilar membrane frequency selectivity were published more than ten years after Békésy's measurements had been made (Johnstone and Boyle, 1967) and it still took a further fifteen years before it was possible to measure cochlear tuning that was as sharp as single auditory nerve-fiber tuning (Sellick et al., 1982). While Békésy's self-confidence in

undertaking such an enormous variety of experiments strikes the modern reader as almost immodest, it should be remembered that he was essentially working in an experimental vacuum, supported only by a reasonable base of anatomical knowledge and by a few highly speculative theories of the past — going back to early Greek times. In that context, it is refreshing to see how Békésy grasped the opportunities to attack a wide range of issues in hearing using mostly homemade equipment (as necessary in all experimental laboratories of the time), but generally with an acute sense of the issues at stake in each area. We note especially Békésy's wide range of precise micromanipulators and optical equipment that made the surgery and his mechanical measurements possible.

It is thus hardly unexpected that Békésy studied non-human animal hearing with an openness that surprises those of us who feel an ever-increasing need to explain why such studies are at all relevant to understanding human hearing. It is such comparative studies that are the subject of this exegesis and our reflections on what has been achieved in this field since Békésy's times. For this, we shall assume the broadest possible use of the term "comparative", as to include all animals other than humans.

2. Békésy's animal studies

2.1. Basilar membrane measurements then and now

Békésy had various animals easily available to him, such as guinea pigs and chickens, but a number of studies seem to have been the result of "lucky coincidences", such as his study of the basilar membrane (BM) responses of an elephant. Békésy writes, in

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memorable understatement, "By good fortune, the head of an adult elephant became available for study" (von Békésy, 1960a, p. 508). This attitude, when added to his use of the cow as an experimental subject, illustrates Békésy's (correct) expectation — as a physicist—engineer — that size would be correlated with some systematic trends in middle- and inner-ear structure and physiology. In the elephant, he noted. "Because the brain …is small relative to the head, the auditory meatus has a length of 18 to 20 cm" (von Békésy, 1960a, p. 508). This fact had no doubt indelibly established itself in his mind, as he recalled to one of us (GAM) on a visit to his laboratory in Hawaii in 1970, that he had been called to the zoo because of the dead elephant. With some effort, an assistant had removed a very large block of tissue from one side of the head, only to discover on his return to the laboratory that the block only contained external meatus!

That particular experimental series on cochlear mechanics (von Békésy, 1960a, pp. 500–510) included his famous stroboscopic observations on the motion of the basilar membrane when activated by sounds of different frequencies and his description of the traveling wave that showed localized maxima in all species. This he carried out in the guinea pig, chicken, mouse, rat, cow and elephant to compare all these to data from human cochleae (Fig. 1). The value of these data has, of course, over the long time of subsequent studies with successive technical refinements, been placed in doubt. Békésy's technique required the use of very loud sounds (>120 dB SPL) and it has since been clearly shown that not only are such sounds damaging, but even normal cochlear tuning is much poorer at higher sound intensities (>60 dB SPL). Not only that, many of Békésy's measurements (but not all) were carried out on cadaver material (it was probably his assumption that it didn't matter for his measurements whether the animal was alive or recently dead), so that the active, sharply-tuned components of cochlear frequency analysis that were discovered many years later could not have been seen.

Of course the broadness of tuning found by Békésy was not lost on him. He clearly recognized that there was a major discrepancy between these measurements and e.g., psychophysical data from humans and quite a number of his later experiments aimed to explain this discrepancy. He settled on lateral inhibitory mechanisms as a likely explanation, probably in part because he had observed such effects himself using his cochlear model "with nerve supply" (the skin of his forearm — von Békésy, 1960b). At the time, virtually no recordings of the tuning properties of auditory-nerve fibers were available, and those that were (Galambos and Davis, 1943; Tasaki, 1954) revealed a tuning that was not that much better than Békésy had measured. We now know that lateral

inhibition was not the correct hypothesis to explain the tuning discrepancy, and, even early on, the hearing research field never took the lateral inhibition hypothesis very seriously. It has been argued that Békésy did this research field a disservice by studying cadaver material, thereby ruling out any possibility of finding an active mechanism.

Gold (1988) had, of course, developed his theory of an active feedback mechanism in the cochlea in 1948 and had visited Békésy in that year to discuss it with him. Gold (1988) reported finding Békésy uninterested and convinced that some sort of lateral inhibition in the cochlea or in the brain would explain the differences between his (Békésy's) mechanical measurements and human perception. It is interesting to speculate the extent to which the field of hearing research would have evolved differently had Békésy's reception been enthusiastically positive, considering the fact that Gold also had great problems obtaining support from the entire hearing research community (including Hallowel Davis, who later recanted, Gold, 1988). Gold (1988) complained about the impossibility of communicating with the "otologists and neurologists" of his day. While Békésy's support would undoubtedly have led to Gold's ideas being taken more seriously, the great limitations in equipment (which Gold himself acknowledges "But whatever we did we couldn't measure it", 1988, p. 302) would, in any case, have greatly delayed any potential advances. In one way, Békésy's lack of acceptance had a positive effect on Gold: "So I returned from my meeting with Békésy *even more convinced* that I was correct…" (Gold, 1988, our emphasis).

We would suggest that considering the context of the times in which Békésy worked and the fact that until the discovery of otoacoustic emissions in 1978 (when suitable equipment first became available), almost no-one took the involvement of active mechanisms seriously, the net effect of Békésy's work on future research was positive. We consider Békésy's cochlear mechanics data as the major stimulus for an enormous amount of research in the following decades to explain the "major discrepancy" in tuning described above.

It was not until decades after Békésy and Gold's major contributions and many stages of improvements in surgical and experimental techniques that the sharp tuning of the intact cochlea could be measured and the hypothesis was made that in fact, cochlear and neural tuning are the same (e.g., Sellick et al., 1982). Thus comparisons of more recent frequency maps of mammalian cochleae with those measured by Békésy reveal that his measurements show systematic — and sometimes dramatic — differences from the neural maps. In the guinea pig, for example, Békésy's map is shifted down in frequency to about 60% of the values published for neural data (Tsuji and Liberman, 1997) (Fig. 2A). Békésy's results for the mouse, however, are dramatically different from those of Müller et al. (2005) for the CBA/J mouse; Békésy's frequencies are at best only 15% of those found for mouse neural data (Fig. 2B). In the chicken, on the other hand, Békésy's data at the higher frequencies represent double the frequency found in the neural map (Fig. 2C; Manley et al., 1987). A smaller difference (and in the other direction!) exists between BM and neural measurements in the pigeon cochlea (Fig. 2D; Gummer et al., 1987; Smolders et al., 1995). We now know that when measured under very loud or hypoxic conditions or before the active process has developed during ontogeny, the best response frequency of any given cochlear location in mammals is shifted toward lower frequencies (e.g., Arjmand et al., 1988). These shifted maps correspond better to the maps measured by Békésy, except for the mouse, where no known effects can explain the huge differences.

These comparisons show that Békésy's measurements were made under relatively poor conditions in comparison with what could be done today using much more sophisticated measurement
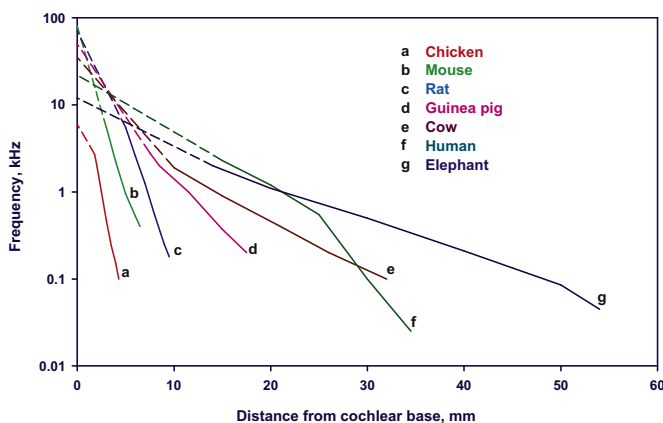
Fig. 1. Frequency-place maps for all 7 species that Békésy measured using stroboscopic illumination. The dashed lines have been added to connect the last data point to the putative upper frequency limit in each species.
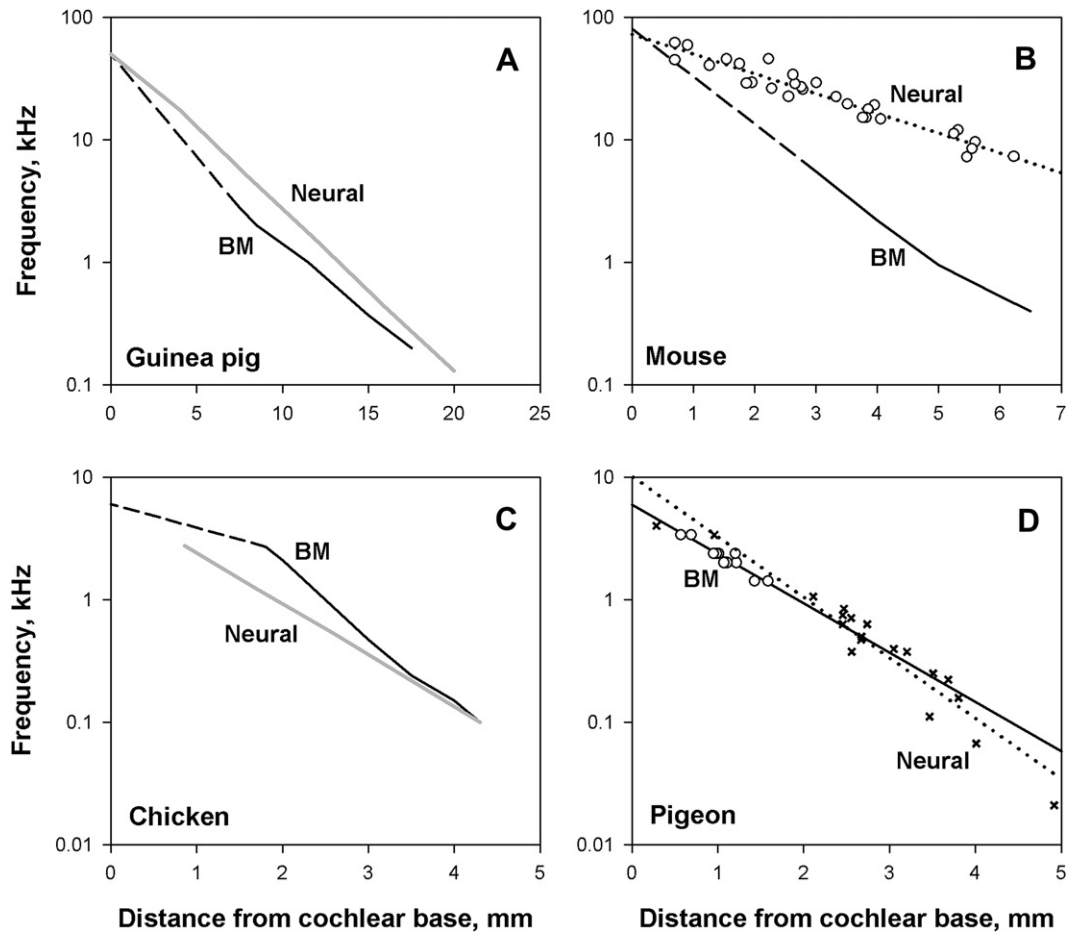
Fig. 2. A comparison between two frequency maps for four species. In A and B, the frequency maps generated by Békésy for A the guinea pig and B the mouse are each shown as solid black lines, with a dashed line as an added extension of the data to the putative upper frequency limit. In comparison, frequency maps made by tracing characterized and stained single auditory-nerve fibers are shown as a gray line (A) or a dotted line through data points (B). The data are taken for the guinea pig from Tsuji and Liberman (1997), for the mouse from Müller et al. (2005). In C and D, data for two bird species, the chicken (C) and the pigeon (D) are shown. Neural data in C (gray line) are from Manley and Gallo (1997), in D the BM data (open circles, continuous regression line fit) are from Gummer et al. (1987); the neural data (crosses, dashed regression line fit) are from Smolders et al. (1995).

techniques. It should, however, be noted that under the conditions available to Békésy, better measurements would not be possible, even today. The main difference between "then and now" is that we now know that cochlear amplifiers exist that have a huge influence on cochlear sensitivity and frequency selectivity and that the frequency response of the BM plus the "passive" organ of Corti is tuned to a lower frequency and with much less sensitivity and selectivity than the "active" component.

2.2. Békésy's concept of evolution

In one further respect, Békésy was the victim of the times in which he lived. His concept of evolutionary trees and "progress" was typical for the non-expert of the times (and sometimes even today!). For example, after commenting on the "great increase in the length of the basilar membrane" (von Békésy, 1960a, p. 485) during the evolution of the cochlea, he writes "If we go along the line from bird, alligator, and Duckbill to man…", thus revealing that his understanding of the evolution of vertebrates was severely deficient. Even at that time a quick reference to a book on the subject of vertebrate evolution would have made clear that such a "line" never existed and that birds and alligators (Archosauria) and mammals were always separate lineages, stemming independently from early amniote ancestors. Békésy was probably led astray by Retzius' (1884) statement that alligators have inner and

outer hair cells as do mammals. Békésy also worked with frogs, commenting on the function of their middle ears (e.g., von Békésy, 1960a, p. 181–183), but where he placed them in the evolutionary scheme of things is not known. Of course, had this mythical "line" between birds and human beings not been imagined, however incorrectly, it is not likely that Békésy would have made any of his comparative observations on other species.

What was perhaps more important to Békésy was the similarity of the solutions to the same evolutionary problems posed by the development of auditory sensitivity via middle ear and cochlear response patterns. It is exactly this aspect that has dominated comparative physiology since that time — the similarity and differences of structures and physiological response patterns in fishes, amphibians, lizards, crocodilians, birds and the different mammal groups help understand how their ears — and the ears of humans — actually work.

The next sections of this review seek briefly to describe what we have learned since Békésy's times through studies of non-human, especially non-mammalian, groups that have helped in establishing the theories that now dominate auditory neuroscience.

3. Fishes

Békésy did not consider fishes at all, probably because von Frisch (1938) had stated early on that the fishes do not possess

a basilar membrane or likely have a "place principle" – the saccule and two other otolith organs (utricle and lagena) seem responsible for all auditory responses in fishes. This was interpreted as an indication that whatever analysis took place among fishes was likely due to processing exclusively in the time domain (through a mechanism similar to Wever's (1949) "volley principle"). Nevertheless, it is now known that the goldfish (and presumably other "otophysan" fishes having Weberian ossicles mechanically linking the swim bladder and saccule, giving them sensitivity to sound pressure), and perhaps all fishes, have a sense of hearing not unlike mammals and birds. Physiological responses of the auditory nerve and brain of fishes are functionally very much like those found in other vertebrates, including mammals (e.g., Lu and Fay, 1995). These similarities include the perception of sound determined behaviorally (e.g., Fay, 2009), the responses of peripheral and central auditory neurons (Lu and Fay, 1996), and the structures of the brain's ascending auditory system which, while not established as homologous with those of other vertebrates, are certainly closely analogous at hindbrain and forebrain levels (e.g., McCormick and Hernandez, 1996).

Some of the most interesting things about the fishes (at least in Otophysi) are their behavioral hearing capacities. Goldfish are capable of something similar to pitch perception (Fay, 2005), analytic listening (Fay, 1992), and auditory source segregation (Fay, 1998), among many other auditory capacities that have been determined (Fay and Megela Simmons, 1999). The basis for these capacities is apparently the frequency selectivity of auditory afferents (saccular nerve fibers) with at least two channels tuned at near 170–200 Hz and 600–900 Hz (Fay, 1997), a feature apparently not arising from a "traveling wave" on the receptor organ surface. The origin of this selectivity is not known, but is likely caused by the micromechanics of saccular hair cells and their stereocilia, something Békésy did not consider. Békésy could not have known that this sort of behavioral and physiological functionality could occur without a basilar membrane and without a "place principle."

4. Amphibians

Another vertebrate taxon received little attention from Békésy – the amphibian. Nevertheless, it is perhaps not surprising that Békésy's wide range of interests did include speculating on the mechanics of the frog ear and how its function related to that of the mammalian cochlea (von Békésy, 1959). For example, building on van Bergeijk's (1957) modeling of the high-frequency hearing organ in the frog inner ear – the basilar papilla (or BP, one of two organs in the frog inner ear dedicated to the detection of airborne sound; the other is the amphibian papilla, or AP), Békésy suggested that a traveling wave could be supported by the semi-circumferential BP membrane and would travel from its outer margins radially inward to the central mass. This hypothesis has not been directly tested to date, despite recent modern mechanical measurements of the BP motion (Schoffelen et al., 2008, 2009). There is evidence however, that a traveling wave may be supported by the tectorial membrane in the low-frequency amphibian papilla (Hillery and Narins, 1984).

Yet in his magnum opus, *Experiments in Hearing*, von Békésy (1960a) makes only passing mention of the amphibian ear, about which his remarks are restricted to speculation on (1) the mechanisms by which the frog inner ear is protected from damage during high-intensity vocalizations, and (2) the function of the structural attachment of the ossicular chain to the eardrum. With regard to (1), Békésy surmised that when the frog vocalizes with his mouth open, the high-level calls would strike both sides of the tympanic membrane, thus reducing its displacement and limiting the input to the inner ear. He suggested that this mechanism would be valid over a wide range of low frequencies. Unfortunately, this explanation applies to only very few species since the large majority of frogs that have been studied in fact vocalize with their mouths closed. Nevertheless, Békésy was correct in that the eardrum motion is attenuated during vocalizations, since sound pressure striking the external surface of one eardrum is partially canceled by sound pressure on the internal surface of that same eardrum. It is now known that with the mouth closed, this "internal sound" enters through the contralateral ear, travels through the wide buccal cavity and Eustachian tubes and strikes the internal surface of the ipsilateral eardrum (Narins, 1992). The situation in the frog is further complicated since there are multiple inputs to the buccal cavity that can affect the eardrum responses, including a pathway via the lungs (Narins et al., 1988; Ehret et al., 1990).

Békésy described a second method used by roosters, and more recently shown to be used by elephants (O'Connell-Rodwell, 2007), to reduce inner ear input during calling. This involves closing off the external auditory meatus just prior to vocalizations.[1] Yet at least one species of frog, *Amolops tormotus* from Central China, has evolved a variant of this method involving the closing of the Eustachian tubes, which simultaneously protects the inner ear from overstimulation during vocalizations and improves the ear's high-frequency sensitivity (Gridi-Papp et al., 2008).

Laser Doppler measurements of the contact membranes of the AP and BP in the frog inner ear suggest yet another way that frogs avoid inner ear overstimulation from high-intensity sound. It has been shown that the responses of these membranes correspond to the frequency ranges associated with the associated papillae (Purgue and Narins, 2000a). Modeling the ear based on these measurements, Purgue and Narins (2000b) were able to identify three frequency-dependent pathways for energy flow in the frog ear: (1) through the periotic canal for DC and low-frequency sound; (2) into the AP recess via the endolymphatic space for mid-frequency sound; and (3) into the BP recess via the endolymphatic space for high-frequency sound. It was suggested by these workers that the first of these pathways represents an adaptation to protect the ear from high-intensity, low-frequency input (for example, during vocalization and breathing), by shunting the energy away from the sensory epithelia. The mechanics of the frog ear is the subject of ongoing studies, many of which have been recently summarized in comprehensive reviews (Mason, 2007; van Dijk et al., 2011).

The second topic mentioned by von Békésy (1960a) concerned the amphibian middle ear ossicles, their rotation and the connection of the stapes to the tympanic membrane. He noted that suppression of lateral movements would be advantageous to the frog in reducing detection of unwanted transients, and that optimally, this could be done by "having a small rod lying radially in the eardrum and then to attach the piston (stapes) to this rod". Békésy also noted that if one grasps one of the ossicles in the frog with forceps, it becomes clear that there is only one degree of freedom in its movements. These fundamental observations inspired a series of laser Doppler vibrometry studies of the vibration velocity along the ossicular apparatus of the bullfrog in response to free-field sound. These measurements demonstrated that the ascending process, first pictured as a tendon (von Békésy, 1960a), then as a ligament (Capranica, 1976) and later correctly identified as a strap-like cartilaginous process (Wever, 1985), supports a rocking motion of

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[1] In the case of the rooster, closure of the ear canal is achieved by compression of a cartilaginous ring surrounding the external auditory meatus when the rooster raises its head to crow (von Békésy, 1960a). In contrast, both the African and Asian elephant have a novel sphincter-like skeletal muscle surrounding the external auditory meatus of the ear that contracts on tactile stimulation, occluding the opening of the ear canal (O'Connell-Rodwell, 2007).

the extrastapes (extracolumella) and restricts ossicular motion to one plane, as predicted by Békésy. Thus, the ascending process is critical to the normal function of the ossicular apparatus (Mason and Narins, 2002a). The latter workers also found that the operculum and stapes footplate are coupled (Mason and Narins, 2002b). As a result of this unusual morphology, the opercularis muscle, which connects the operculum with the shoulder girdle, is likely to be involved in the protection of the inner ear from high-amplitude displacements of the stapes footplate during respiration and vocalization (Mason and Narins, 2002b).

Anurans (frogs and toads) have often proven to be appropriate subjects for studies of the neural mechanisms underlying auditory and seismic behavior. For example, saccular hair cells are exquisitely sensitive to substrate-borne vibrations, but also respond to high-level, low-frequency airborne sound. Nevertheless, anurans are unique among vertebrates in that they possess two distinct organs that detect airborne sounds: the basilar papilla (BP) and amphibian papilla (AP). The BP functions as a single auditory filter and its ca 60 hair cells make synaptic contact with auditory-nerve fibers tuned as high as 8 kHz (Loftus-Hills and Johnstone, 1970), although recent reports speculate on the existence of BP fibers tuned to frequencies more than two octaves higher in some Asian species (Feng et al., 2006; Arch et al., 2012).

The bullfrog AP contains roughly 1000 hair cells. There is no analog of the basilar membrane in this organ; instead, shearing forces necessary for displacement of the stereovillar bundles result from the differential movement of the tectorial membrane (TM) relative to the stationary hair cell receptors. The TM itself is a highly fenestrated, acellular structure that overlies the hair cells and is coextensive with the AP. Intracellular dye-injections of physiologically-identified AP fibers have revealed a rostrocaudal tonotopic organization, with low- and mid-frequency fibers innervating rostral and caudal hair cells, respectively (Lewis et al., 1982). The former fiber population exhibits two-tone rate suppression, whereas the latter group does not.

Despite middle and inner ear structural differences between the amphibian and mammalian auditory systems, the frog ear has served as a valuable model for understanding the physiology of sensory hair cell transduction (Hudspeth and Corey, 1977; Hudspeth, 1985; Smotherman and Narins, 2000). The recent suggestion that some frogs are capable of producing and detecting ultrasound (up to 38 kHz), however, highlights the fact that that we know less about the high-frequency behavior of the auditory periphery of frogs than previously believed (Narins et al., 2004; Feng et al., 2006; Arch et al., 2009). The frog inner ear thus has and will continue to provide a rich substrate for the examination of the mechanics, transduction and neural function subserving vertebrate hearing (Narins et al., 2007), which Békésy could not have known at the time.

5. Lizards

Békésy did not measure frequency maps from lizards (von Békésy, 1960a). This may or may not be fortunate, since had he done that, he might have been diverted from further work by trying to explain the differences to humans and we have no idea where that may have led. Nonetheless, lizard papillae are highly interesting objects for comparative auditory studies, since the structure of the papilla varies widely and is to a large extent family-specific. In addition, the TM varies equally widely in its form and in some papilla types is absent altogether (Wever, 1978).

In lizards, the BM, which is thick and often stiffened (Wever, 1978) is not locally tuned. Measurements of basilar-membrane tuning in two quite different species with very different BM lengths, a short (0.4 mm, alligator lizard, Peake and Ling, 1980) and

a long (2 mm, bobtail skink, Manley et al., 1988) BM indicates that each location along the BM length shows the same tuning. This tuning is equivalent to that of the middle ear (Manley et al., 1988). Thus the BM itself shows no difference in tuning selectivity at different locations on the BM and its selectivity is poor (Fig. 3). The very sensitive and much more frequency-selective responses of auditory afferents (Fig. 3) are due to relative movements at the level of the hair-cell stereovillar bundles and an active process found in the bundles (Manley et al., 2001). Fig. 3 shows only the response of a single nerve fiber, other nerve fibers would have similar curves that, however, show a sharply-tuned peak at a different best frequency.

Numerous studies of the frequency selectivity of lizard auditory papillae have established that — as in fishes and amphibians — frequency tuning does not require a flexible BM as a substrate for the organ. Early observations of hair-cell stereovillar bundles in alligator lizards, that have no TM over most of their papilla, used stroboscopic techniques to follow the motion of the tall stereovillar bundles of the basal hair cells in isolated preparations of the papilla as seen under the microscope (Frishkopf and DeRosier, 1983; Holton and Hudspeth, 1983). Rocking motions of the basilar membrane were observed, which pivoted about the neural limbus. The largest relative displacement between stereovillar bundles and hair-cell bodies (the stimulus for these cells) was seen in cells with short bundles at high frequencies. Correspondingly, displacement of the bundles of the hair cells with the longest stereovilli (that lie apically in this area) was seen at low frequencies. Bundle resonant frequencies varied inversely along the papilla with bundle height and were similar to the best frequencies of auditory-nerve fibers measured in vivo at corresponding locations in the nerve. Thus relative bundle motion forms the basis of a tonotopic organization in these papillae.

In general, the TM is lacking only in short papillae (<500 μm). Other lizard papilla do have a TM, sometimes a continuous one (varanid and teeid lizards), sometimes a chain-of-pearls-like "salletal" system (skinks, geckos; Manley, 1990). There are clear correlations between the structural variation and physiological responses (Manley, 1997). In general, there is not a great difference in the frequency response range of lizard papillae whether they have a TM or not. However, in those without a TM, the frequency
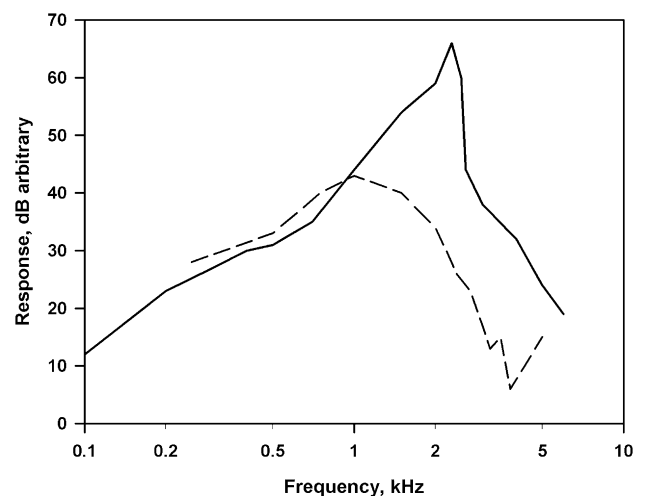

Fig. 3. A comparison of the tuning selectivity of the basilar membrane (dashed line) and a single auditory-nerve fiber (continuous line) in the bobtail skink *Tiliqua rugosa*. For purposes of this comparison, dB scales have been arbitrarily moved on the ordinate so that the low-frequency slopes correspond. The sensitivity scale of the nerve fiber has been reversed so as to indicate a response level. It can be seen that, in comparison to the BM response, the nerve fiber shows a region, in this case near 2.3 kHz, of high frequency selectivity. After Manley et al. (1988).

selectivity is approximately half of that seen in papillae that have a TM (Manley, 2000a). In lizards with a TM, its characteristics work together with the hair-bundle characteristics to determine the response frequencies of the hair cells at different papillar locations. Since these features vary between lizard families, the tonotopic organization also varies and can even be reversed — as in geckos — as compared to all other amniote papillae (Manley et al., 1999; Manley, 2002).

As in mammals, non-mammalian papillae also have an active process (Manley, 2001) that is based within the stereovillar bundle (Manley et al., 2001; Hudspeth, 2008). This process provides the energy necessary for the bundles to overcome fluid viscosity and resonate in the cochlear fluids (Manley, 2011a). In fact, the hair-cell bundles are in general continuously generating oscillations at their preferred frequency and these spontaneous oscillations can be measured as spontaneous otoacoustic emissions (SOAE) in the lizard ear canal (Manley and Köppl, 2008). These signals are so weak, however (mostly <10 dB SPL), that even had he tried, Békésy would not have been able to measure them in his day. With modern equipment, SOAE have provided a very powerful tool for "remote sensing" of cochlear responses. In lizards, these SOAE are usually present in all ears and there may be up to 14 obvious sound-energy peaks per ear (Manley and Gallo, 1997). SOAE frequency patterns correlate with papillar anatomy; they vary with temperature and respond to sounds presented to the ear in complex ways (Manley, 1997, 2000a, Manley and Van Dijk, 2008). Through the use of SOAE and other otoacoustic emission types, it has been possible to non-invasively study the ears of most lizard families and elucidate their sensitivity, frequency response range, frequency selectivity, etc. Through this, it has become obvious that lizards, also, evolved highly sensitive and selective hearing organs independently of the other groups of land vertebrates (Manley, 2011b).

6. Birds

A comparison of Békésy's chicken BM measurements to more recent chicken neural data shows that they differ in a way that would not be expected from a comparison of equivalent mammalian data, but of course Békésy could not have been aware of this. In the chicken, he was also able to measure a traveling wave, which did not surprise him since, as noted above, he assumed that there was some evolutionary line between birds and mammals. However, at the high-frequency end of the chicken cochlea, the frequency maps of von Békésy (1960a) and Manley and Gallo, 1997 diverge by more than an octave (Fig. 2C), but are essentially the same at low frequencies. The comparison between BM and neural maps in the chicken thus behaves differently (diverging to higher frequencies instead of lower) and this is likely explained by the different anatomy.

In birds, the hearing organ, the basilar papilla, is only partly placed over the free BM. The entire neural section of the papilla sits over the neural limbus, a thick, cartilage-like structure (review in Gleich et al., 2004). Most afferent neurons (that were used to generate modern frequency maps) do not innervate cells over the free BM, but mainly — or only — more neural "tall" cells. Thus these neural hair cells lie in a location that would not have been measurable by Békésy and, indeed, is not measurable today either. There is as yet no evidence to confirm the assumption that the frequency responses of neural- and abneurally-lying hair cells are, for a given location, the same. It is thus not possible to directly compare the frequency maps in birds (BM and neural) in the same way as in mammals. Although there are no more recent measurements of the chicken BM, Gummer et al. (1987) carried out measurements of the pigeon BM. In the best preparations, the pigeon BM showed a fairly crude traveling wave, with a frequency

map (measured on the free BM below the short hair cells at some basal locations) where each location represented 70–80% of the frequency revealed by sensitive afferent fibers from these locations (Fig. 2D; Gummer et al., 1987). This difference between BM and neural representations is in fact similar to most of those demonstrated for the mammalian species studied by Békésy and unlike the chicken comparison to his data outlined above. This suggests that Békésy's chicken data are seriously flawed, in spite of his observing a traveling wave. In the caiman basilar papilla, which strongly resembles (and is evolutionarily closely related to) that of birds (Manley, 1990), Wilson et al. (1985) were also able to measure a crude traveling wave. At present, it is not possible to decide whether the avian and crocodilian BM below the short hair cells is really relatively poorly tuned or whether there are technical problems in obtaining reliable measurements. In any case, most tall hair cells — which receive all or most of the afferent innervation — do not sit over the free basilar membrane and thus the BM data from birds cannot describe the stimulus to this group of hair cells.

The avian and mammalian hearing organs are the product of more than a hundred million years of independent evolution (Manley and Köppl, 1998; Manley, 2000b). In contrast to the mammalian organ, the avian papilla is wider, with many more hair cells in a given transverse section (Gleich et al., 2004). Even though the avian papilla is relatively short and its frequency responses generally limited to below ∼10 kHz, the number of hair cells and nerve fibers can be as high as in longer mammalian organs. Thus the innervation density and the possibilities of parallel processing of information to the brain are high (Gleich et al., 2004). As noted above, the afferent fibers almost all innervate neurally-lying ("tall") hair cells, yet their mechanical input presumably arises indirectly from the movement of the BM. It has been suggested that in birds, the TM plays an important role in transferring energy to these neural hair cells (Gleich et al., 2004). Indeed the stimulus to the hair cells from the TM may be larger over the neural hair cell area than over the abneural area due to putative active processes in the hair cell bundles of short hair cells of the abneural papilla (Steele, 1996). The presence of such an active process is indicated by otoacoustic emissions that have been measured in birds, although so far SOAE have only been seen in barn owls (Taschenberger and Manley, 1997). Békésy's work was the first physiological study of the avian auditory papilla, but its relative inaccessibility has made it very difficult to make substantial progress in further exploring its macro- and micro-mechanics. Progress in understanding the physiology of hair cells and especially the afferent nerve-fiber discharge activity has, however, been very substantial (Manley, 1990; Gleich et al., 2004).

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