

The mammalian cochlear map is optimally warped^{a)}

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The form of the mammalian cochlear frequency-position map has been well described by Greenwood and empirical values found for its coefficients for a number of species. The apical portion of the mammalian map is spatially compressed relative to the base, and this nonuniformity in the representation of frequency is evidently consistent across species. However, an evolutionary reason for this consistency, encompassing critical band behavior with respect to position, is conspicuously missing. Likewise, the length of the cochlea in any mammal, including echolocating species, is related to body size, but attempts to explain the length in terms of frequency limits, range, or resolution have no general explanation. New insight stems from a hypothesis in which the map curvature may be appreciated as an adaptation for *optimal* frequency resolution over the auditory range. It is demonstrated numerically that the mammalian curve may be considered a member of a family of curves which vary in their degree of warp. The “warp factor” found to be common across mammals is an optimal trade-off between four conflicting constraints: (1) enhancing high-frequency resolution; (2) setting a lower bound on loss of existing low-frequency resolution; (3) minimizing map nonuniformity; and (4) keeping the whole map smooth, thereby avoiding reflections. © 2003 Acoustical Society of America. [DOI: 10.1121/1.1587150]

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I. INTRODUCTION

The form of the cochlear tonotopic map is very basic to the whole of auditory science, being considered at any stage in experimental and modeling investigations through to clinical work, cochlear evolution (Fay and Popper, 2000), and development (Echteler *et al.*, 1989), its extension to echolocating capabilities (Ketten, 2000), even to the fitting of cochlear implants (Skinner *et al.*, 2002).

The application which has triggered this investigation has to do with making sense of otoacoustic emissions, sounds which are emitted from the ear due to activity of the rows of outer hair cells (OHC) stretched along the length of the cochlear partition. In particular, the clinical usefulness of otoacoustic emissions could be greatly enhanced if the emission signal could be deconvolved in such a way as to reveal the extent of regions of dead or poorly functioning OHC. Since the development of the otoacoustic emission technique one should define at least two maps; a reception map and an emission map, which may be the same map for theoretical reasons (Shera and Guinan, 1999), but this needs to be more clearly defined for clinical use. It is not yet known how precisely the map for sounds emitted via reverse propagation overlays the map of forward-propagated sounds input to the ear and also how much emissions are a product of activity at any place or how much they depend upon secondary or multiple reflections. Fundamental to efforts towards a reconciliation is the need for a clear understanding of the form of the cochlear map relating characteristic frequency versus posi-

tion along the cochlear partition. En route to such a reconciliation, this paper revisits the receptive map for additional clues as to why the map has its particular form, effectively, low frequencies detected at the apex are spatially compressed relative to high frequencies detected at the base.

The generalized form of the mammalian reception cochlear map which is described by the Greenwood relation

$$f = \mathbf{A} \cdot (10^{ax} - \mathbf{k}), \quad (1)$$

where f is frequency (Hz), x is the distance from the apex of the cochlea (helicotrema end), \mathbf{A} , \mathbf{a} , and \mathbf{k} are coefficients (Greenwood, 1961, 1990, 1996). \mathbf{a} is the gradient of high-frequency end of the map, i.e., the coefficient of the derivative evaluated at the highest frequency, \mathbf{A} is a constant which shifts the curve as a whole along the log-frequency axis, and \mathbf{k} is constant, which introduces curvature into the frequency-position function so as to fit low-frequency data. The gradient \mathbf{a} may be expressed equivalently in two ways depending upon whether x is expressed in physical distance (mm) or is normalized to the range $[0, 1]$ ($[0, 100]\%$) to deal with variations in length of the cochlear partition which occur between individuals, between species (Bohne and Carr, 1979). The maps of specialized cochleae, such as those from echolocating species, deviate from this relationship and are treated separately below.

Table I shows values for these coefficients extracted from the publications listed and other discussions (Greenwood, personal communication). If x is measured in millimeters, then we denote that \mathbf{a}' is the gradient (oct/mm) of the log frequency-position map at the high-frequency end and is a constant which for humans is equal to 0.06 mm^{-1} . The parameter \mathbf{a} is the normalized value obtained multiplying \mathbf{a}' by the cochlear length L (mm). The table is listed in roughly

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TABLE I. Values of Greenwood model parameters A , a , and k extracted primarily from the references listed. The parameter a' are the non-normalized values obtained from dividing a by the cochlear length L (mm). The last for house mouse are recent estimates by Greenwood (personal communication) based upon the data of Ou *et al.* (2000). The last three columns indicate estimations of end frequencies F_{apex} and F_{base} , and the number of octaves reception subtended between the F_{apex} and F_{base} . Note the values of F_{apex} are zero for the cases where $k=1$, or the values indicated in parentheses if the warp theory is valid and $k \sim 0.85$.

Name	A	a	k	L (mm)	Reference	a' (mm^{-1})	F_{apex} (Hz)	F_{base} (Hz)	#Oct
Elephant	81	1.8	1	60	Greenwood (1961)	0.030	0 (12)	5 111	-8.7
Cow	52.6	2.1	1	38.3	Greenwood (1961)	0.055	0 (8)	6 622	-9.7
Human	165.4	2.1	1	35	Greenwood (1990)	0.060	0 (20)	20 772	-10
Macaque	360	2.1	0.85	25.6	Greenwood (1990)	0.082	54	45 321	9.7
Domestic cat	456	2.1	0.8	25	Lieberman (1982)	0.084	91	57 407	9.3
Guinea pig	350	2.1	0.85	18.5	Greenwood (1990)	0.114	53	44 062	9.7
Chinchilla	163.5	2.1	0.85	18.4	Greenwood (1990)	0.114	25	20 583	9.7
Rat	7613.3	0.928	1	8.03	Müller (1991)	0.116	0 (1142)	64 502	-5.8
Opossum	5821	1	0.564	6.4	Müller <i>et al.</i> (1993)	0.156	2538	58 210	4.5
Gerbil	398	2.2	0.631	12.1	Müller (1996)	0.182	147	63 079	8.7
Mouse	7130	0.99	1	6.8	Greenwood (pers.)	0.300	0 (1070)	105 262	-6.6

descending order of size of the mammal beginning with available data for elephant and ending with recent estimates of parameters for the house mouse by Greenwood based upon recent data (Ou *et al.*, 2000). The last three columns indicate estimations of end frequencies F_{apex} and F_{base} , and the number of octaves subtended between F_{apex} and F_{base} . Note the values of F_{apex} are either zero for the cases where k is designated equal to 1, or the values indicated in parentheses.

In the table there seems to be a pattern across all mammals for values of both a and k to cluster. However, there appears to be two forms of exception. First, for most primates plus chinchillas $a \sim 2.1$, while rats and opossum notably stand apart at $a \sim 1.0$. Second, the values of k seem to cluster between 0.5 and 1. Further examination allows three subclusters to be considered, *viz.*, values of $k \sim 1$, $k \sim 0.85$, and $k \sim 0.5-0.6$ (Müller, 1996). Values close to unity tend to be for larger mammals where the data is obtained behaviorally (Heffner and Heffner, 1982), while the values around 0.85 and below tend to be applied to the more precise morphological determinations such as those obtained with dye-injection techniques (Lieberman, 1982; Müller, 1991; Müller *et al.*, 1993; Müller, 1996). Echolocating mammals are a special case by virtue that they have multiple map regions, and are treated separately below. For species which have relatively small frequency spans, how the scale is represented (linear or log) is probably not so important. While Greenwood's analyses of the form of the map are extensive, a new reason is provided to show that for species whose range spans >8 octaves, the plotting of the spatial dimension versus the logarithm of frequency has particular advantages for understanding form.

Figure 1(A) shows, overlaid, the resulting maps for the species plotted versus the logarithm of frequency for the empirically determined values of A , a , and k in Table I. In each case the map referred to is the empirically found distance along the cochlear partition (ordinate values) versus the estimated best incoming frequency for any location (abscissa). As might be expected from the clustering of values mentioned above, the curves are mostly very similar in shape. The human and chinchilla curves almost overlay, as do

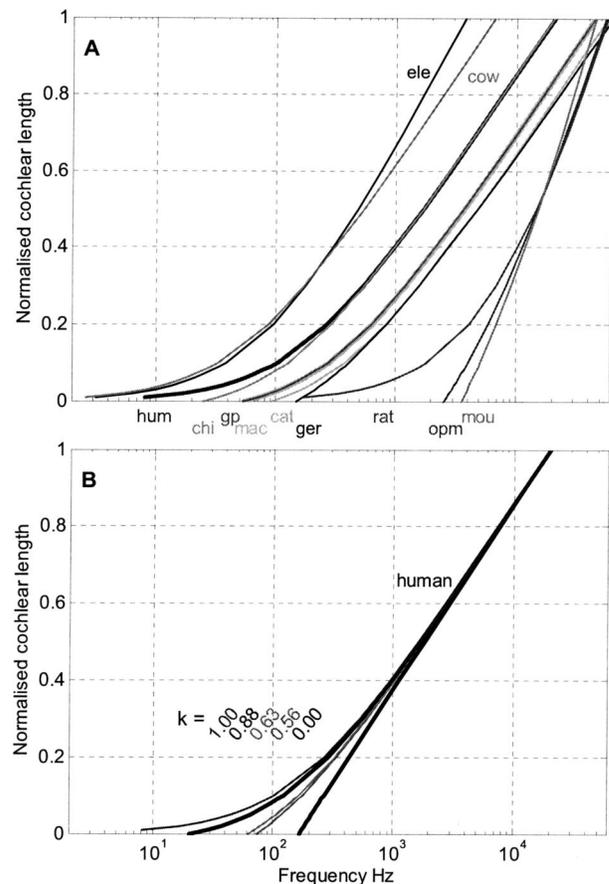


FIG. 1. Panels (A) and (B) show log frequency-position maps according to published values of the three coefficients of Eq. (1), for normalized distance from the apex towards the base. The top panel (A) shows the similarity of 8 maps from elephant (ele), cow, human (hum), chinchilla (chi), guinea pig (gp), macaque (mac), cat, Mongolian gerbil (ger), while the highest frequency maps, for rat, opossum (opm), and mouse (mou), which have shorter cochleae, have different basic gradients. The bottom panel (B) shows for the human case, the hypothetical effect of varying the third of the three parameters k over the values indicated in sequence. The higher the value of k , the bigger the correction. However, the value of unity quoted several times in Table I incurs the problem that the most apical region of the map is undefined. Any uncertainty in this value therefore generates considerable uncertainty as to the frequency associated with the most apical place.

guinea pig and macaque, and domestic cat and Mongolian gerbil. The notable exceptions in shape occur with the smaller mammals, opossum, rat, and mouse; plotting them on the same axes as the larger animals may lead to misinterpretation when the primary difference seems to be that the cochlea is shorter in these species. The parameter \mathbf{a} has its biggest effect on the slope of the curves; the higher the value the more extensive the frequency range of the cochlea.

Figure 1(B) illustrates the hypothetical effect of varying \mathbf{k} for the human case, a feature which is the focus of this paper. The straight dashed lines represent the case of $\mathbf{k}=0$. The value of \mathbf{a} (2.1 for human) plots as the number of decades spanned between the ends of the map for the $\mathbf{k}=0$ line. For each species five different curves are shown for the values of \mathbf{k} (0, 0.56, 0.63, 0.89, and 1.0) as indicated by the legend, chosen purely to coincide with the values quoted in Table I. As \mathbf{k} increases, the curvature increases so that the spatial representation of frequencies at the apex is compressed relative to the basal end (Greenwood, 1996). A common alternate view is to regard the high-frequency representation as greatly expanded relative to the apex. The question of which view to take becomes interesting in the context of cochlear evolution, but to make progress it is necessary to consider how precisely the available data define the low-frequency end of the curve.

Plotted versus log frequency, the high-frequency end of the map is almost straight. For the purposes of curve fitting to data, changing the value of \mathbf{k} has little effect at the high-frequency end, which is why it is generally taken to be straight (Robles and Ruggero, 2001). Values of $\mathbf{k}>0$ provide a better fit of the model specifically for low-frequency data points. The case of $\mathbf{k}=1.0$ is special. The latter leaves the map undefined at zero distance from the apex because it only reaches the abscissa at zero frequency. At first this seems a minor concern. Table I shows several species as having a value of $\mathbf{k}=1$, and presumably this is due to the sparsity or difficulty of obtaining low-frequency points with precision (Greenwood, 1996). While the high-frequency end of the map will be highly defined by high-frequency points, the same is not true of the low-frequency end, where sensitivity decreases more gradually as frequency is lowered depending upon the size of the helicotrema (Dallos, 1970). In this sense, the form of Eq. (1) is “open ended.”

The problem is that such values of \mathbf{k} are basically unsatisfactory because, although this end of the frequency range is important in behavioral terms, slightly differing values close to unity introduce huge variation of which frequency relates to which position. Indeed, while Table I quotes a value of unity, Fig. 1(B) shows that the most satisfactory value of \mathbf{k} for human is probably closer to 0.9 because this almost coincides with the empirically determined value of 20 Hz at which sensitivity drops. While the data may not support values of $\mathbf{k}<1$, similar theoretical concerns exist, therefore, for every instance of values of unity in Table I.

We are concerned here with how the form of the map came about in terms of evolution, and what general trends may exist, but may be obscured by the variations in the wealth of data for which the equation has been fitted. One of

the significant studies on the evolution of hearing is from Masterton *et al.* (1969). They note that the acquisition of high-frequency hearing in mammals is associated with the development of the system of three ossicles in the middle ear, a feature which was apparently present in early small mammals. One of the points of their article is not just the acquisition of high-frequency hearing in mammals, but indeed the apparent “loss” of high-frequency reception as the size of the species increased [see again Fig. 1(A)]. They postulate that since larger mammals were not so strongly dependent upon interaural level differences to achieve localization, localization could be achieved by interaural time differences as the head size grew larger. They suppose that loss of high-frequency sensitivity is a later development as the size of mammals increased.

We are concerned here about an earlier stage of evolution, around the Jurassic period, in which the acquisition of high frequencies apparently first took place. Fossils from that period have revealed the *Morganucodon* had an only partly coiled cochlea (like reptiles and birds) but which had early mammalian features—the characteristic beginnings of middle-ear ossicle formation (Kermack, 1989).

We are also concerned about what kinds of pressures led the basilar membrane to elongate, why the length is strongly species dependent, why the increase in length exceeds that expected on the basis of increase in high frequency (Manley, 2000), and ultimately what factors determine cochlear length, a question which remains unanswered (Popper and Fay, 1997; Ketten, 2000). In turn, we are trying to reconcile the “open-ended” form of Eq. (1) with the evolutionary pressures which led mammals to acquire high-frequency sensitivity (Popper and Fay, 1997). The considerations shed some light on the Masterton hypothesis, *viz.*, how larger mammals came to lose the highest frequencies.

Our quest for reconciliation leads directly to a paradox. It is a challenging paradox because we generally agree that the equation is a faithful model of most frequency-position data in generalist cochleae, certainly for high-frequency data tested against it. On the one hand, we conceive of high-frequency capability as having been “added on” to augment low-frequency reception in the archetypal cochleae of lower vertebrates, e.g., reptiles and turtles which hear up to about 1 kHz (Crawford and Fettiplace, 1980). On the other hand, the equation, in effect, treats the low-frequency region as having been added on to the primary first term, which defines the curve for high frequencies. So, if the high-frequency end of the cochlea is “newer” in evolutionary terms, how is it that the first term is decidedly the backbone of the relation? That is, how can we have a faithful model of the data in which the “older” end of the map (the archetypal low-frequency detection region) is handled by the second term, which is depicted in Fig. 1(B) essentially as an end correction?

One might suspect instead that during the process of selective adaptation to provide for high-frequency reception, the low-frequency end would have remained essentially invariant, while adaptations occurred to increase basilar-membrane stiffness at the high-frequency end, of the kinds which became extreme in the case of the odontocetes (dolphins and porpoises) and bats (Ketten, 2000). This ques-

tion divides into two alternate possibilities. We know that Eq. (1) does not cover such specialist cases, except maybe in piecewise fashion, but overall the equation, despite its minimal set of parameters needed for comparing species, sheds no light on how those parameters became set for any species. Is it possible that there exists a better overall characterization of mammalian frequency-position data?

One possible resolution of the paradox is that high-frequency reception has not simply been added on, in response to selective pressure, but has instead required a fundamental change to pre-mammalian cochlear mechanics. This idea is already embodied in the generally accepted traveling-wave theory (von Bekesy, 1960), but other views exist (Fay and Popper, 2000). An alternate resolution of the paradox may already be contained in the above-mentioned clustering of values of the coefficients seen in Table I. However, it is first necessary to disallow values of \mathbf{k} equal to unity on the grounds (1) that it is unacceptable for a model to leave the position of the very lowest frequencies undefined, and (2) the more precise (dye-injection) map data (Liberman, 1982; Müller, 1996) set the values of $\mathbf{k} < 1$. If, for example $\mathbf{k} \sim 0.85$, then two of the three coefficients (\mathbf{a} and \mathbf{k}) would be appear virtually constant, at least across eutherian mammals. Therefore, Eq. (1), simple as it is, may not necessarily be the simplest model because it suggests redundancy.

While treating Eq. (1) as a precise characterization of mammalian data, it would seem that the accuracy of the points is not weighted in any way by their thresholds which, by definition, rise at the frequency limits of reception.

A. Hypothesis

The existing data permit the recasting of Eq. (1) with different boundary conditions. Taking into account the rises in hearing threshold at the frequency limits which define the frequency span, we may replace the open-ended Greenwood model with a “closed-end” model. We achieve this by accepting the end frequencies to be those which are empirically determined. While there is still some uncertainty as to what the low-frequencies limits are because of the slow rise in thresholds, the principle can still be illustrated for the human case by taking the low-frequency limit to be 20 Hz and the high-frequency limit to be 20 kHz.

This hypothesis gives rise to a series of corollaries which can be tested in the same operation: (1) The map is nonuniform in the sense that it compresses the tonotopic representation towards the low-frequency end. (2) The resulting “warp” or smooth sag in the map is advantageous for mammals, i.e., the departure from a uniform map, which comes about by specific tapering of the mechanical properties (most probably stiffness) of the cochlear partition. (3) Evolutionary pressures (maybe over millions of years) have determined the degree of warp. (4) The “warp factor \mathbf{k}' ”, i.e., the degree of sag or “warp” in the map, is essentially common across mammals. (5) This warp factor has important consequences for all processes in the ascending auditory pathway which depend upon the resulting tonotopicity, such as resolution of separate frequency components. (6) The warp factor found is an optimal value in the sense that it is the best trade-off across mammals between conflicting conditions and seeks to

TABLE II. Values of \mathbf{A} and \mathbf{a} are uniquely determined by \mathbf{k} once the end frequencies are set (for human taken as 20 Hz and 20 kHz), establishing the family (Fig. 4).

\mathbf{k}	\mathbf{A}	\mathbf{a}
0.000	20.00	3.000
0.500	40.00	2.699
0.700	66.67	2.478
0.800	100.00	2.303
0.879	165.43	2.086
0.92	250	1.908
0.95	400	1.707
0.980	1000.00	1.322
0.990	2000.00	1.041
0.995	4000.00	0.778

fulfill the need for a simpler, more global basis (Fay, 1992) to “establish a minimal and/or optimal set of parameters for comparing species.”

What follows is a development and testing of the hypothesis and its corollaries, and it will be seen that there is a more generalized way of regarding the map which has widespread implications. The first is that this approach achieves an escape from the severely limiting concept that the basic curve is almost straight. We recognize instead that, plotted versus log frequency the map has the property that it is curved throughout its length, and for good reason. A second is that uncertainties which may arise in the determination of map estimates, e.g., Ou *et al.* (2000), may be partly due to the fact that the Greenwood model is open ended, particularly at the low-frequency end, so that there is no stronger basis for testing the quality of any particular set of data, e.g., whether \mathbf{A} has the value 3000 or 7900, than being totally at the mercy of sources of experimental error. A third application is to the area of genetic correlates of cochlear development, in particular to answering the question as to how the map becomes established during development (Echtemer *et al.*, 1989; Cantos *et al.*, 2000; Brigande *et al.*, 2000).

II. METHOD

The numerical exploration here examines the notion that a better way to think of the curvature of the mammalian frequency-place map is that it is warped. The advantages of the warp concept might be achieved more elegantly in other mathematical terms (Shera *et al.*, 2002), maybe based upon cochlear mechanical model parameters. However, it is not necessary to hypothesize a basis different from Eq. (1) to achieve a general appreciation of the concept and its applications. To the contrary, retaining the form of the Greenwood model with new boundary conditions has one big advantage. This exercise requires considering the map for the human case so that the variables in Eq. (1) are fixed while considering what happens as we allow the three coefficients \mathbf{A} , \mathbf{a} , and \mathbf{k} to vary. Once the end limits are fixed, changing the value of \mathbf{k} has the very different effect of generating a family of curves with different degrees of warp. Table II shows how various degrees of warp can be achieved within the terms of the basic relation [Eq. (1)]. This is because each value of \mathbf{k} uniquely sets the values of \mathbf{A} and \mathbf{a} as seen in Table II, except for the condition $\mathbf{k}=1$, which generates a singularity.

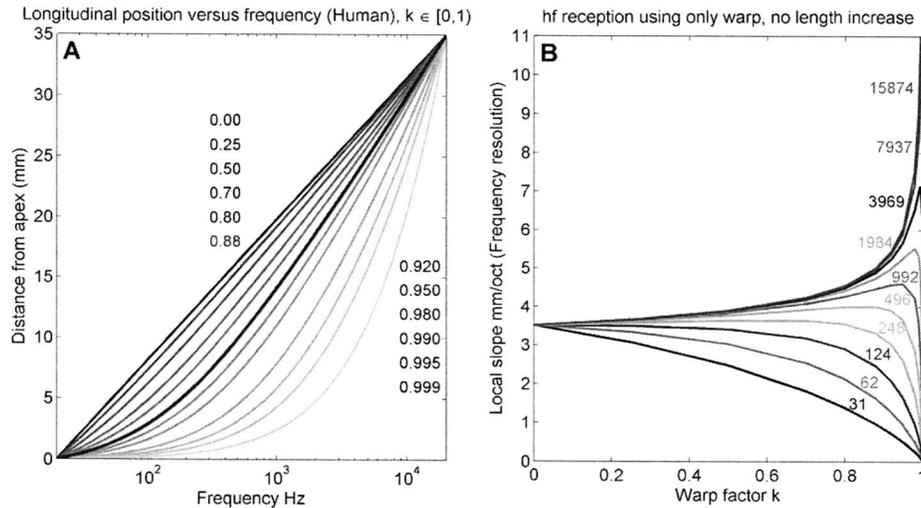


FIG. 2. Panels (A) and (B) show the effects of fixing both end coordinates of the frequency-position map, rather than allowing them to float in the data-fitting process. The justification for doing so is that it is important that the ends of the map be more or less defined by the decreases in hearing sensitivity. The new boundary conditions force the other two coefficients of Eq. (1) (A and a) to have values defined by the given values of k shown in the inset which generates a family of curves [panel (A)], each with a different degree of warp. The thick black line ($k=0$, $a=3.0$) in the top panel (A) is unwarped (undistorted). The most common allowed value of $k=0.88$ in the highlighted curve is thus seen to be a member of the family, each of which has different local values of frequency resolution (the gradient). As k rises towards unity, the frequency representation as a whole moves towards high frequencies. Panel (B) reprocesses the curves of panel (A) to show for representative frequencies, an octave apart, how the frequency resolution (mm/oct) changes with the warp factor (k). Very high values of frequency resolution may be achieved for high values of k without the need to elongate the cochlea. Conversely, the effect of changing k on low-frequency resolution is a steady decline.

The new constraints tie the value of a to that of k , so changing k changes the value of the high-frequency slope as well, unlike the original family of curves [Fig. 1(B)].

By setting the end limits to coincide with the limits of hearing sensitivity, we eliminate the possibility of having a very poorly defined lower-frequency limit. The “add-on correction factor” k is thus transformed into the generalized warp factor k' ($k=k'$). For the purposes of this exercise it suffices to assume, simultaneously, that the corresponding spatial limits are indeed the physical ends of the cochlear partition, i.e., for the human case, distances from the apex of 0 and 35 mm (normalized distances 0 and 1). An important by-product of not reformulating Eq. (1) is that any tentative conclusions about the near-constancy of k found across mammals carries across to the degree of warp (k').

III. RESULTS

Figure 2(A) shows for the human case the effect of varying warp by using the values of k in Table II. The order of the curves is reversed from Fig. 1(B), *viz.*, the $k=0$ case still gives rise to a uniform map throughout the length of the cochlea (3.5 mm/oct), but it is now located at the top and spans the 3 decades ($a=3$). The advantages of this approach become clear within the context that frequency resolution is directly proportional to the gradient of the frequency-place map (Greenwood, 1990). As the map becomes increasingly warped, the steeper is the local gradient at any cochlear position and the greater will be the number of independent resonators/channels serving any frequency range, giving rise to greater parallel processing capabilities (Manley, 2000). The salient feature of the left panel, therefore, is that different degrees of warp (12 values from 0 to 0.999 are shown) represent different degrees of trade-off between high- and

low-frequency resolution. Figure 2(B) displays the derivatives of the family of curves for octave steps throughout the human frequency range, increasing upward from midrange of the lowest octave (20 to 40 Hz). As the warp increases ($k' \rightarrow 1$), there is an accompanying steady gradual decline in the low-frequency resolution, whereas high values of resolution may be achieved at high frequencies, but only as $k' > 0.95$. In summary, fixing the lower-frequency limit eliminates the zero-frequency possibility as $k' \rightarrow 0$. Now, the map becomes increasingly warped instead, leading to very high values of high-frequency resolution.

It is helpful at this stage, but not essential, to suppose that the hypothesized warping seen in the mammalian cochlear map was not present in archetypal cochleae. This is reasonable considering the morphology of lower vertebrates (Wever, 1978; Fay, 1992). It is likely the case that they are too short for the form of the map to be questioned beyond whether it is simply logarithmic or linear.

A. Conclusion 1

For lower species to have evolved high-frequency hearing, this did not, in the first instance, require elongation of the cochlea. It only required arranging specialized tapering of the cochlear mass, stiffness, and damping to bend the map appropriately to whatever is the behavioral requirement.

Figure 2(B) clearly shows that spatial separation of frequencies within an octave, by substantial fractions of a millimeter, is achievable through warping, without cochlear elongation being essential. The question of what factors led to elongation of the cochlea may be logically separated from the factors leading to map warp and is addressed below. Increasing the warp from zero initially produces a slow change in the map gradients. This slow change with k' continues for

low frequencies, but as it rises above 0.9 there is a rapid rise in the local gradient for the high-frequency (basal) end. Figure 2(B) shows, however, this apparent advantage comes at a price. Actually, there are two obvious costs: (1) sacrifice of low-frequency resolution, which may already have been the indispensable product of substantial selective advantage, and (2) departure from a tonotopically uniform map (e.g., the constant mm/oct of the straight line at the top of the family of curves). Greenwood actually comments on the center region of the cochlear map with uniform gradient (Greenwood, 1997). The clue which flows from Fig. 2(A) is that one can see how the spatial extent of this central region varies with warp. For the case $k'=0$ we have 10 octaves of uniform map, but for $k'=0.999$ we only have about 1 octave of map with the original gradient. We can define this region retaining the uniform original gradient as having a certain “bandwidth.” It turns out that it is a very insightful exercise to compute this bandwidth as a function of warp.

We normally think of bandwidth as a concept of a band-pass filter in which the low-frequency and high-frequency slopes are very different in the passband than in the stop bands on either side. To make progress we generalize this notion of bandwidth so that the breakpoints are established where the local gradient differs from the uniform gradient by a set difference.

The three panels of Fig. 3 show how the “breakpoint” frequencies are calculated after establishing limits of gradient similarity. Panel (A) shows the derivatives of the curves in Fig. 2(A). Each member of the family has a region where the gradient (mm/oct) crosses the gradient of the unwarped map (horizontal line). Panel (B) is introduced because it is clear that the resulting departure of local gradient is asymmetric about the gradient of the top unwarped member of the family. If we want to compare the effects of warp upon bandwidth, our defined low-frequency and high-frequency limits of similarity should ideally be symmetric about the gradient of the central region. Hence, the logarithm of the gradient is obtained. A criterion for similar positive and negative thresholds can then be determined (here, the gradient threshold is chosen to be ± 0.14 , seen as the two horizontal dashed lines above 0 difference). The resulting dependence of the bandwidth upon map warp is shown in Fig. 3(C), where each of the log gradient curves crosses the gradient threshold limits. The higher the degree of warp, the greater the curvature of the family member and the smaller is the bandwidth of the “unwarped” (subthreshold) region of the map, as suggested in Fig. 2(A). Note that both the center frequency and the bandwidth vary systematically with the degree of warp.

B. Conclusion 2

For the value of warp apparent in most generalist mammalian cochleae, for which the map is precisely determined, the bandwidth seems to loosely coincide with the bandwidth of frequencies (*viz.*, ~ 100 Hz to 3 kHz), particularly implicated in neural phase-locking phenomena (Brugge *et al.*, 1969) and periodicity pitch determination important for speech (Sachs, 1984) and music (Tramo *et al.*, 2001).

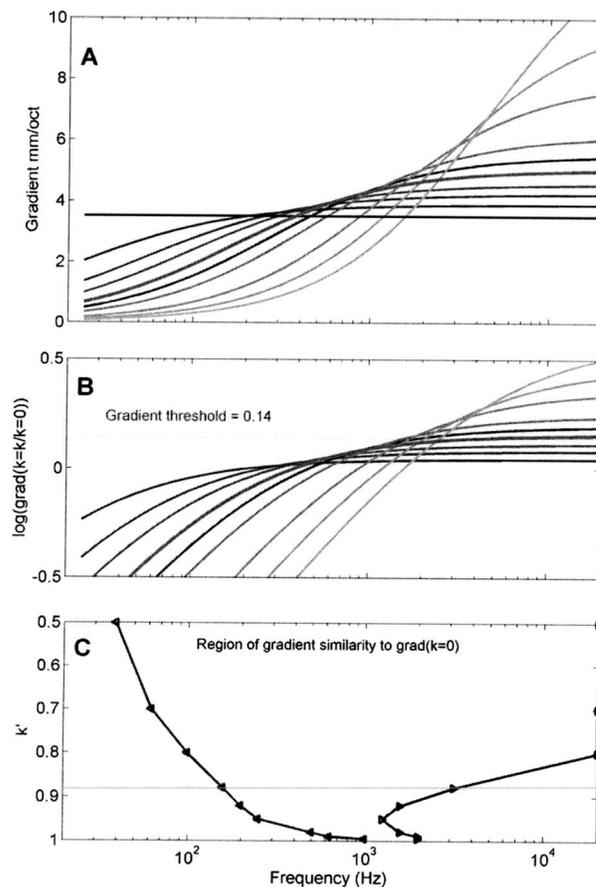


FIG. 3. This figure shows that the central region of each member of the family in Fig. 2(A) has a slope close to that of the unwarped map ($k=0$) and that its bandwidth varies systematically with the warp factor k . Each member of the family in (A) represents the gradient of the basic family which crosses the gradient of the uniform map (horizontal straight line). Panel (B) allows a method of determining the bandwidth of this region by establishing a threshold for gradient change. Panel (C) shows the frequency range between the left and right triangles which applies for each value of k less than the threshold value [± 0.14 in panel (B)]. This article was triggered by the realization that, although this bandwidth is seen here to vary markedly with k' , the common value of $k' \sim 0.88$ results in a bandwidth loosely coinciding with frequencies associated with neural phase locking (important for speech and music), supporting the notion that the common value of k is preset according to a best compromise situation.

IV. TESTING THE NOTION OF “OPTIMAL WARP”

If there is any merit to the general notion that the mammalian tonotopy is warped, it should be possible to show, on the basis of actual map data, that there exists some form of compromise between conflicting low- and high-frequency signal-processing requirements, or more general needs. Into this category falls the need for long-term stability of the tonotopic organization and, maybe in turn, protection of the cochlea against acoustic overload. This argument follows from the notion that damage will likely occur first at points of discontinuity of basilar-membrane impedance, or its derivative.

The last of the corollaries above is that the near invariance of k and a across species is the result of an optimal trade-off for mammals. The nature of the trade-off is therefore of interest. It is clear from Fig. 2 that raising high-frequency resolution by means of warping of the map, with-

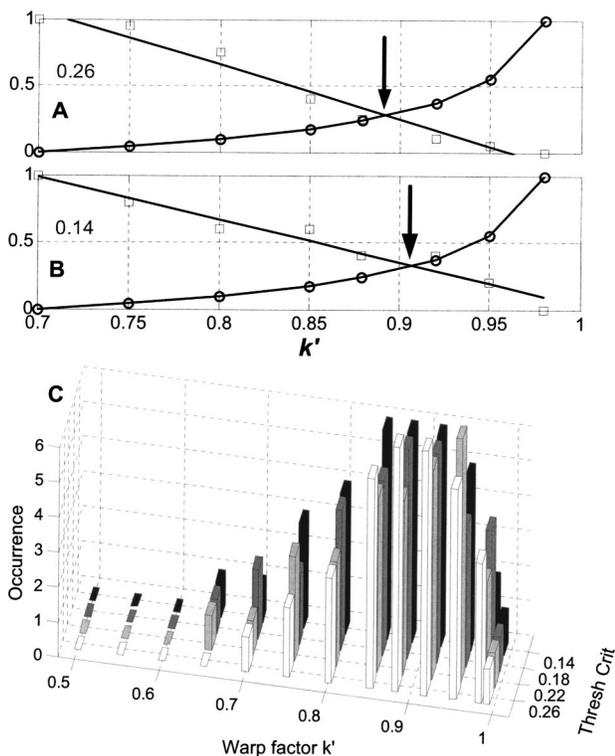


FIG. 4. If there is any merit to the generalized notion of the mammalian cochlear map being warped, it should be possible to show that there exists some form of compromise between conflicting low- and high-frequency signal-processing requirements. We hypothesize that the near invariance of k and a across species is the result of an optimal trade-off for mammals. Panel (A) shows two curves. The open squares fitted with the straight line shows the bandwidth of the apical unwarped region [from Fig. 3(C)] normalized to the interval [0,1], plotted versus value of k , for the criterion value 0.26. The curve defined by the circles shows the normalized frequency resolution [from Fig. 2(B)]. High values of both curves mean good map uniformity in the central region and improved high-frequency resolution, respectively. Since these two conditions vary inversely with rise in k , the place where they cross (arrow) represents the best trade-off. This value sits around a value of k of 0.9. Varying the threshold criterion of setting bandwidth of the central region does not change the condition of optimal warp [panel (B)]. Panel (C) extends the test for optimal trade-off further to include all threshold criteria and all appropriate ranges of the unwarped map gradient. The resulting histogram shows that the optimal value of k in the interval (0.85, 0.95) is robust. The result suggests that the mammalian cochlear map for all unspecialized ears is optimally warped for best high- and midfrequency resolution characteristics independent of length.

out simultaneously changing the length of the cochlea leads to loss of low-frequency resolution and a higher degree of curvature of the map in the central region (Fig. 3).

Figure 4 shows that the common value of $k \sim 0.85$ may be no accident. It is straightforward to plot both the bandwidth in octaves of this central region defined in Fig. 3 along with the high-frequency slope [Fig. 2(B)] versus the warp factor k' . In panels (A) and (B), the curve with the open circles represents high-frequency resolution as a function of k' . The straight line fitted to the open squares shows how the limit of map uniformity varies with k' . Both of these curves are normalized to vary in the interval [0, 1] in order to directly compare them. The two upper panels represent two different thresholds (0.14 and 0.26) for “gradient-departure” levels setting the “bandpass” breakpoints. In each panel the k' value where the lines intersect represents the warp factor condition for the *best trade-off between two conflicting con-*

ditions: maximizing the high-frequency resolution and maximizing the “bandwidth” of the uniformly mapped region. No matter which tolerance is considered, the optimal values of $k' \sim 0.9$. Since the reference gradient for this comparison is somewhat arbitrary [3.5 mm/oct; see Fig. 3(A)], it has further been shown that changing the value of the reference gradient for the comparison shifts the band limits but does not change the estimate of the optimal value of k , which remains close to 0.9. When all the likely combinations of reference gradient and gradient departure are tested grouped together, the result is the series of histograms shown in Fig. 4(C). Not only is there a strong clustering of values of optimal trade-off in the range k' in the interval (0.85 to 0.95), there is a steep decline for higher values of k' and no incidences of values of $k' < 0.65$.

A. Conclusion 3

There appears to be an optimal trade-off between two conflicting conditions: increasing high-frequency resolution and limiting the decline of the bandwidth of the central most-uniform-map region. Indeed, this conclusion appears to independently parallel the condition of “cochlear compromise” (Zweig *et al.*, 1976) between two conflicting requirements—maximizing both high-frequency resolution and avoidance of reflections of waves along the basilar membrane.

B. Conclusion 4

Subject to caveats, the optimal value of k' coincides with that value of k found to be most common for mammals. The correspondence is not perfect but is indeed remarkable. This has been achieved using the Greenwood relation, which guarantees that the map is smooth.

C. Conclusion 5

Mammals have arrived at a representation of frequency versus position along the cochlear partition which is an optimal trade-off between conflicting requirements. These requirements are: (1) high-frequency reception and resolution is enhanced; (2) the map remains smooth; and (3) the center region is maximally uniform (in terms of the longest possible length of near-equal spacing for adjacent octaves).

Returning to Fig. 1, it is possible now to view the shape of the map in a new context. In particular, the near-common value of the high-frequency slope finally has an explanation in terms of evolutionary forces. No reason has ever been supplied as to why the high-frequency slope should have any value in particular for any species, or why the frequency limits are not tied to body size, as is the frequency range (Ketten, 2000).

V. EVOLUTIONARY PRESSURE TO ELONGATE THE COCHLEA

If high-frequency resolution could be achieved by warping the map, why did mammals develop long cochleae, and what sets the length in any species?

Figure 5 illustrates that this manifestation of cochlear compromise provides an explanation. The warp ensures that the high-frequency slope (versus log frequency) may rise,

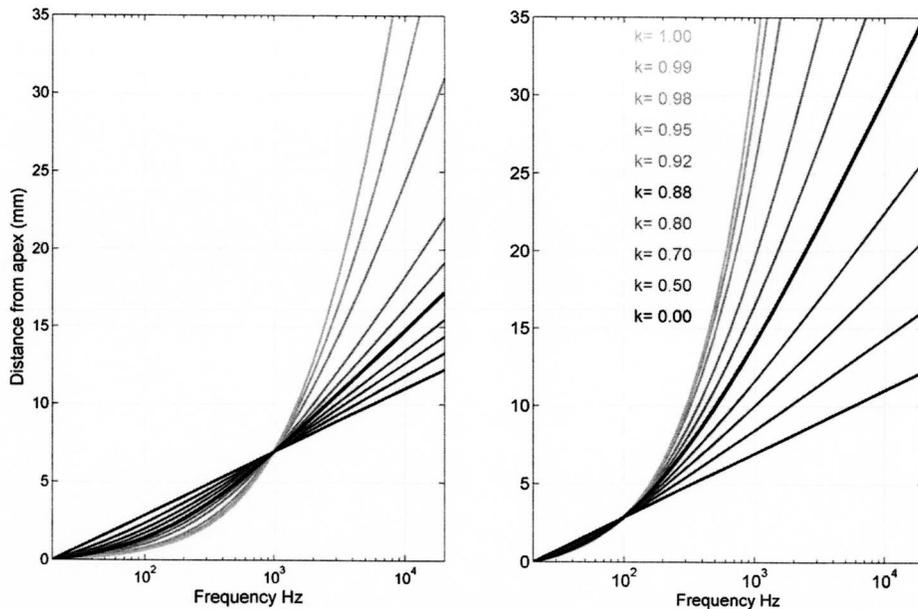


FIG. 5. Panels (A) and (B) demonstrate evolutionary pressure to elongate the cochlea. If warping the cochlear map can increase high-frequency resolution, why do cochleae vary in length? Panel (A) shows that if an archetypal short cochlea gains high-frequency resolution by evolving warp, it simultaneously loses low-frequency resolution [see again Fig. 2(B)]. If the existing low-frequency resolution has species advantage, selective pressure will act so as to offset that disadvantage. Panel (B) shows that simply elongating the cochlea can limit the loss of low-frequency resolution. The existence of the warp means that the whole cochlea does not need to elongate to the extent which would provide whatever required resolution; space saving can be achieved by warping the map as well, reducing the final extension.

but that at low frequencies the slope must drop correspondingly [Fig. 2(B)]. Taking a hypothetical example, the left panel (A) shows how, for a short cochlea (e.g., bird, reptile, even echidna (Ladhams and Pickles, 1996) handling a frequency range up to 10 kHz (say 4 to 7 mm in length) might tend to become warped to transduce higher frequencies. The warping process leads to reduced slope of the low-frequency range (the family of curves below the straight line, $k'=0$). This is a poor trade-off which does not constitute evolutionary advancement if existing low-frequency resolution is lost. The right panel (B) shows that if the warp is accompanied by elongation of the cochlea to exactly counteract the decrease in low-frequency resolution, loss of low-frequency performance can be avoided. However, the smooth map constraint requires that the whole cochlea is elongated in proportion. Figure 5(B) shows the result. The loss of low-frequency resolution is essentially avoided and the map elongates to (in the case of human) 35 mm long (the curve for $k\sim 0.88$).

A. Conclusion 6

The *lower* the (required) receptive frequency range, the *longer* must be the resulting cochlea. It is therefore simplistic to regard the archetypal cochlea as having elongated to provide high-frequency reception or even a given number of octaves frequency range. Economy dictates that limited increase in frequency resolution can be achieved in the first place purely by warping the map. Elongation occurred because even the optimally warped cochlea could not meet evolutionary demands (e.g., if the bandwidth of the uniform central region is too narrow, or much higher frequency channel separation is required for noisy environments).

B. Conclusion 7

Warping is an indispensable requirement for minimizing space—providing maximally compact cochleae by minimizing the length increase necessary. In other words, evolutionary pressure would first seek to extract the best compromise

over the desired frequency range and “top up” the frequency resolution by elongating the cochlea, but only so long as to maintain optimal trade-off.

C. Conclusion 8

There exists a frequency span limitation for mammals with generalist cochleae (i.e., echolocating animals excluded), which is about 10 octaves, and this appears to be a hard limit. The reason stems directly from Greenwood’s discovery that $a\sim 2.1$ is not exceeded by any species in which the map is smooth and free of kinks (discontinuous derivatives). The reason the limit is hard stems directly from the animal data. The octave range limit cannot be exceeded by further extending (and coiling) the cochlea, because 2.1 (maximum 2.2) is the value pertaining to the *normalized unity-length* cochlea. As observed by Ketten, odontocetes’ hearing may cover 12 octaves but this comes at the price of introducing a discontinuity into the map, or into the map gradient, resulting in specialized anisomorphic cochleae.

VI. DISCUSSION

The form of the frequency-position map has its origin in the shape of the critical band curve (Fletcher, 1940). The history of attempts to match frequency or pitch versus place has given rise to many estimations maps including early work (Koenig, 1949; Fant, 1973). The map has been extensively characterized and modeled (Zwicker and Terhardt, 1980; Traunmüller, 1990). With the exception of the first two early attempts, the modern estimates tend to be very similar up to about 3 kHz with the long-considered characterization (Greenwood, 1990) used as the starting point here. The warp hypothesis suggests by contrast that critical bands are established as a result of the optimal trade-off between conflicting requirements.

None of this exploration calls into question the validity of Greenwood’s formulation for adequately characterizing the frequency-position map across mammals for the bulk of

the available data. Moreover, none of the formulation loses any of its validity in approach by fixing the boundary conditions on the equation. To the contrary, this formulation adds credibility to the equation by virtue that the end-frequency limits are tied to where the sensitivity rises or by the corresponding physical limits of the cochlear partition. However, while the warp hypothesis should be tested against original morphological data, this task is beyond the scope here.

What is remarkable in light of Masterton's article is that the degree of warp for all the larger species listed (Table I) is about the same since the value of coefficient \mathbf{a} is about the same; indeed, there is a ceiling of maximum value of $\mathbf{a}=2.15$. It follows from the constraints that the increased sensitivity at lower frequencies in larger mammals is necessarily accompanied by a loss of high frequencies, unless high-frequency specializations such as basilar-membrane stiffening structures are introduced. It is tempting to speculate that the evolutionary process was necessarily constrained to weight the importance of low- and high-frequency information and, in humans, it chose to weight the low-frequency information as more important.

Two things follow from the evident 10-octave limitation. The first is that the notion of a grand basilar membrane (Ketten, 2000) from which a 10-octave segment is selected for any species has new merit. However, the notion of adjusting the taper is something which doesn't necessarily require long-term evolutionary forces. The optimal trade-off between frequency resolution in the various frequency zones is something which might even be dynamic—the result of OHC activity. Second, Masterton's hypothesis of the chronological loss of high frequencies might probably be relaxed. His speculation is that humans lost very high-frequency reception because as the head size grew the interaural time differences sufficed so that high frequencies were no longer needed. The alternate hypothesis here follows from the notion that the 10-octave limit is imposed by the need for a smooth map. Making more use of low frequencies necessitates loss of very high frequencies if the propagation of the traveling wave must be free of irregularities. It is not that large mammals with very low-frequency (infrasound) reception (e.g., great whales (Ketten, 1994) and elephants (Heffner and Heffner, 1982; O'Connell *et al.*, 1997) could not find a good use for higher frequencies and therefore "lost" high frequencies over time. Indeed, the odontocetes did get around the problem by introducing stiffening structures, such as the secondary outer-body lamina (Ketten, 2000). This exercise has illustrated that the form of the map likely has a specific origin which relates to forces which presumably came into play as the advantages of high-frequency reception evolved and which although sought has not had any extensive explanation before now.

A. Very highly warped maps and echolocating mammals

Considering the case of echolocating mammals (bats and cetaceans), it would appear that the constraints to provide a very wide bandwidth and very high-frequency resolution cannot be met while retaining a smooth map. Certainly some bats have regions receptive to usual audio frequencies, but

they possess a "fovea" in which the gradient is up to 60 mm/oct (Kössl and Vater, 1985). Ketten (2000) comments that while there are many sophisticated mathematical models of cochlear function, few are aimed at understanding species-specific variations. It may be consistent with our notion of warp that the price of higher resolution than the ceiling imposed by an $\mathbf{a}=2.1$ is a distinctly kinked and frequently discontinuous map (Henson and Henson, 1979; Vater and Lenoir, 1992) and not just the lack of need of intermediate frequencies as is generally presumed. We have demonstrated that situations may arise such that the advantages of maintaining optimal warp are outweighed by the advantages of rapid echolocation. Very high degrees of map curvature are conceivable in the limit, such as a map where $\mathbf{k}'=1$, resulting in a map which has a square corner, zero midregion bandwidth, zero low-frequency resolution, and infinite high-frequency resolution. Practically such a map can only be approached, and only to the extent that very rapid changes in cochlear mechanical parameters, e.g., mass, stiffness or damping can be achieved. Indeed, mammals with specialized cochleae do exist to provide very much higher high-frequency resolution but only at the cost when the map becomes discontinuous, or its gradient becomes discontinuous—a sufficient condition to establish reflections along the basilar membrane.

B. Cochleae of large mammals

The more pressing the need to accommodate low frequencies, the longer the length of the cochlea. The rapid rise in the required length with increase in value of \mathbf{k} provides a further reason (other than space limitations) as to why the mammalian cochlea cannot attain such lengths as to achieve arbitrary increases in high-frequency performance. Accordingly, in early animals which have made good use of its existing low-frequency resolution, but needed high-frequency capability, the cochlea as a whole has increased length in proportion to the degradation of low-frequency resolution. The cases of human, cow, and elephant (Table I) are receptive to very low frequencies and so the optimal warp hypothesis will ensure that the cochleae are proportionally longer (up to 60 mm). Whales which are sensitive to infrasound will predictably have longer cochleae again. Indeed, Ketten quotes 71 mm in the case of the blue whale. This may not necessarily be because the animal's cochlea scales to body mass, but because of the reception of very low ocean-transmitted frequencies and the need for uniform mapping in the middle of the hearing range.

C. Gender dependence

While convincing counterarguments may be advanced, it is at least qualitatively consistent with the above argument for elongation that cochleae of human males are 15% longer than the cochleae of females (Sato *et al.*, 1991)—the fundamental speech frequency is lower. Until now no explanation has been offered.

D. Cochleae of very small mammals including rodents

The value of k given for Mongolian gerbil is 0.63 and 0.56 for opossum. This lower value could possibly be due to a bad estimate, e.g., due to few data points in the low-frequency region, or it may be a fair estimate. The question arises, is there any room for the value to be consistent with the optimum-warp hypothesis? The value of 0.63 therefore is at the low end of the values of k seen in Fig. 4(C), but not inconsistent with the hypothesis.

In the cases of mice, rats, and opossum, the values of a are apparently more serious departures to be reconciled with the generalized model. Some of the departure may be explained by the different methods (normal or edge frequency) used to determine distance (Ou *et al.*, 2000). In these species notably the cochlea is much shorter and the number of octaves of audibility lower. As we saw in Table I, mice, rats, and opossum appear to have an a value of about 1.0 rather than the value of 2.1. Their estimated cochlear lengths are shorter and their frequency spans are only ~ 7 octaves. These cases are qualitatively consistent with the warp theory. Masterton hypothesized that they did not possess low-frequency reception and the resulting frequency span required was therefore less than the maximum possible. So, for the sake of economy, their cochleae only extended to the extent that the low-frequency characteristics they possessed were counteracted to meet their high-frequency requirement. It is consistent that the warp is less and the cochleae are shorter.

This exercise has also demonstrated that local increase in frequency selectivity can be achieved without length increase, simply by adjusting the tapering of mechanical parameters to warp the map. The significantly increased frequency selectivity in humans (Shera *et al.*, 2002) is directly predictable from the notion that it is basically tied to spatial constraints (Ehret, 1978; LePage, 1987).

VII. SUMMARY

The form of the Greenwood relation for mammalian tonotopicity initially appears paradoxical by virtue that the equation seems to cater to low-frequency curvature by applying a “correction” at what seems to be the “wrong” end of the map in evolutionary terms. Without loss of precision for its fit to many data, the paradox is resolved by changing the boundary conditions to fix the end-frequency limits in accordance with behavioral threshold data. This leads directly to the hypothesis that a better way to think about the form of the map is that it is warped. That is, its local gradient varies systematically with position from apex to base. In so doing it shows that the Greenwood relation actually represents a near-symmetric trend so that the correction thus applied to the low-frequency end actually applies neatly to the high-frequency end as well.

The hypothesis provides added meaning in terms that this warp actually evolved in the process of mammalian adaptation to high-frequency reception. Second, once the form of the map is questioned from an evolutionary context, the notion of warp becomes attractive, particularly when it is shown that the common value of k coincides with the value

which represents a state of warp for optimal trade-off. Third, “optimal warp” carries the added implication that the curve is smooth and that the length of the central region is maximally close to being uniform, for as long a distance along the cochlear partition as possible. Fourth, the concept of warp is seen as an important space-saving mechanism in the process of acquiring cochleae which transduce a wide range of frequencies. The notion of optimal warp leaves many aspects to explore, particularly the aspect that some measure of the warp may be due to cochlear activity, accounting for discrepancies in the passive stiffness range necessary for the full range of audio frequencies. The ultimate significance of this warp theory is at least fourfold. First, it provides a natural, encapsulated idea to reconcile with map data derived from various species. Second, it encompasses the “chicken-and-egg” problem as to whether critical band placement occurred as a result, i.e., subsequent to, the evolutionary optimization of the map or vice versa. Third, mathematical models may benefit from the process to arrive independently at the form of the map—rather than presuming it at the outset in order to set segmental parameters. Last, it may ultimately yield an added basis for regarding data produced by genetic studies of cochlear development, *viz.*, which end of the cochlea has extended (1) during the evolution process and (2) during maturation.

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