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ON THE PLACE CODE FOR PITCH: A PSYCHOPHYSIOLOGICAL PARADOX IN THE CLASSICAL CONCEPT

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The place of maximum excitation in the cochlea has been believed to be the code for the pitch of tones since mid 19-th century. More recent physiological experiments have revealed that, in a healthy cochlea, the maximum is displaced gradually toward the cochlear base (input) as the sound pressure is increased, whereas the pitch remains practically constant. This paradox suggests that the maximum excitation may not be the adequate code for the pitch after all. In the presence of hearing loss of cochlear origin, the pitch appears higher than normal. As the sound pressure level is increased, it changes gradually back to normal. By contrast, the maximum of cochlear excitation in the presence of cochlear damage, although displaced toward the cochlear base, remains independent of sound pressure level. In both situations, normal and pathological, the apical cut off of cochlear excitation depends on the sound pressure level in the same way as does the pitch. Could the cut off be the adequate place code for the pitch?

Keywords: pitch, place code, cochlea, maximum excitation, sound pressure level.

1. Introduction

According to an almost general belief, pitch of pure tones is determined by the location of maximum vibration of the basilar membrane that courses along the cochlea, a spirally wound canal of the inner ear, filled with fluid. To the basilar membrane is attached the organ of Corti over its entire length. It holds two kinds of hair cells, the inner and outer hair cells, which are the sensory cells of hearing. The outer hair cells serve as amplifiers for the basilar-membane vibration and the organ of Corti responses. The inner hair cells, on which end almost all the fibers of the auditory nerve, when stimulated by the vibration of the basilar membrane, excite the nerve fibers. The latter, then, send nerve impulses to the brain.

When sound waves enter the ear, they proceed through the outer ear and the middle ear to the inner ear, where they produce transversal waves on the basilar membrane.

The waves run from the oval window, where they enter the cochlea, and the basal part of the cochlea to the apex of the cochlea. The basilar membrane is narrow in its basal part and becomes gradually wider toward the apex. It contains, among other structures, fibers that span its width. HELMHOLTZ [5] proposed in the mid nineteenth century that the fibers were tuned like piano strings and responded maximally to high sound frequencies where they were short and to low sound frequencies where they were long. In the first half of the twentieth century, BÉKÉSY (Nobel Prize, 1961) ([1] for review) confirmed Helmholtz's hypothesis to the extent that, in post-mortem preparations of human inner ears, he was able to see a vibration maximum of the basilar membrane at a location depending on sound frequency — in the basal part, for high frequencies, and in the apical part for the low ones. However, the maximum was very flat and in no way consistent with human sensitivity to changes in sound frequency. At a frequency of 1000 Hz, musicians can detect a change of only 3 Hz – 0.3%. Békésy suggested therefore that the maximum was sharpened in the nervous system. Indeed, GALAMBOS and DAVIS [4] and, more systematically, KIANG [7] and his associates seemed to find such a sharp tuning in the fibers of the auditory nerve. An example obtained by LIBERMAN and KIANG [8] of what has become known as tuning curves is shown in Fig. 1.

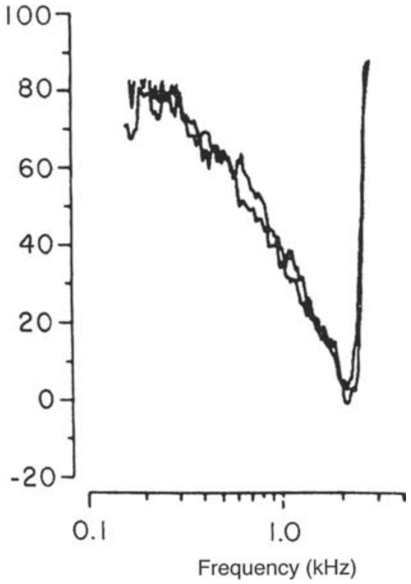

Fig. 1. Tuning curve of an auditory-nerve fiber of a domestic cat recorded twice. According to LIBERMAN and KIANG [8]. From ZWISLOCKI [14].

Other investigators demonstrated that basilar-membrane tuning in live animals was much sharper than in post-mortem preparations of Békésy's, e.g. [6, 9]. All these results, and many other similar ones, solidified the notion that the subjective pitch of pure tones was coded in terms of the location of maximum basilar-membrane vibration to a dogma that has withstood all the subsequent evidence against it.

2. The paradox

The paradox in the assumed pitch coding by the maximum basilar membrane vibration, as possibly sharpened by the nervous system, is hidden in the tuning curves based on firing rates of the auditory-nerve fibers. A tuning curve is expressed in terms of sound pressure measured as a function of sound frequency for a constant nerve-fiber response. Because the sound pressure constitutes the input to the system, and the fiber response the output, the tuning curve is equivalent to an inverse transfer function. However, the ear responds to sound stimuli according to forward transfer functions that are defined in terms of the fiber responses as functions of sound frequency for given sound pressures.

In a linear system, an inverse transfer function is simply an inversion of a forward transfer function but, according to numerous experiments, the cochleae of mammals and, as a result, the nerve fibers that innervate them do not function as linear systems. The cochlear response is compressed. When the sound pressure at the input is increased by a factor x, the amplitude of the basilar membrane is increased by about $x^{0.6}$. When, for example, the sound pressure is increased by 10, the amplitude is increased by only approximately 6. As a result, the forward tuning curves (transfer function) are flattened, and the inverse tuning curves sharpened. RUSSEL and SELLICK [10] discovered that the tuning of the inner hair cells was about the same as of the nerve fibers, so that no sharpening took place in between. The discovery was confirmed repeatedly.

Experiments performed on diverse mammals, following those of RUSSELL and SELLICK [10], showed that the outer hair cells and the adjacent supporting cells have about the same sharpness of tuning (for review see [14]). As a consequence, cochlear frequency characteristics can be studied conveniently by recording alternating potentials produced by sound in any of these cells. We have found that Hensen's cells that are adjacent to the outer hair cells are particularly suitable for the purpose. The following two figures compare the corresponding frequency characteristics of an inner hair cell and a Hensen's cell. Both were obtained on Mongolian gerbils that tolerate the necessary anesthesia particularly well.

The characteristics shown in Fig. 2 were recorded on an inner hair cell with the help of an intracellular microelectrode, so that no spread of the internal electric field was possible [3]. They were determined at a set of sound pressure levels in 10 to 20 dB steps. Several features of the characteristics are noteworthy. First of all, they are broader than the tuning curve of Fig. 1, and their peaks are more rounded. Second, and most importantly, the peaks do not occur at the same sound frequency but are gradually shifted toward lower frequencies as the sound pressure level is increased. In Fig. 2, the peak shift exceeds somewhat one octave for a change in sound pressure level of 50 dB. The subjective pitch of tones in the same frequency range, measured psychophysically on human listeners, is known to be practically independent of sound pressure (for review see [14]). How, then, can it be coded by the peak cochlear response the frequency of which depends strongly on sound pressure? Because the cochlear peak shift has been encountered in all experimental mammals, the probability that it does not occur in humans is small.

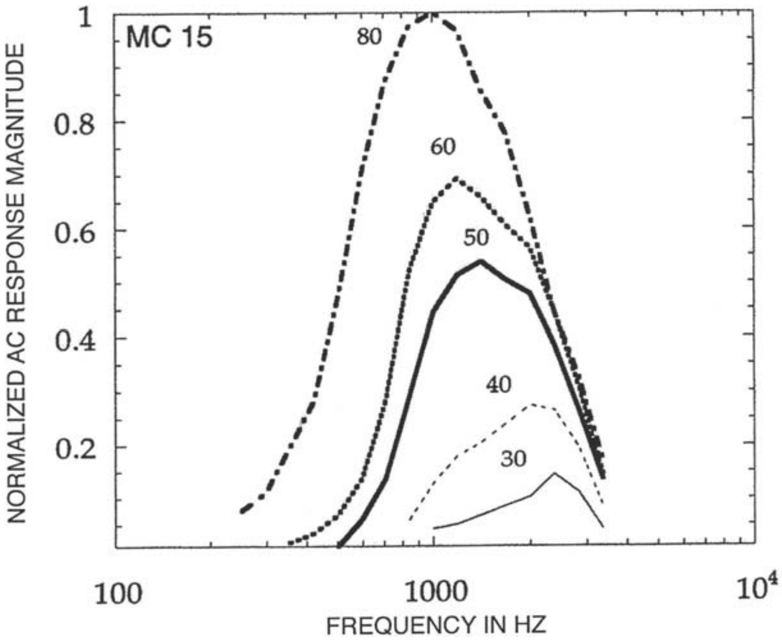

Fig. 2. Intensity series of intracellular frequency characteristics of a Mongolian-gerbil inner hair cell. Corresponding sound pressure levels are indicated at the curves. According to CHATTERJEE and ZWISLOCKI [3]. From ZWISLOCKI [14].

The possibility that the peak of the hair-cell response determines the pitch is further reduced by its substantial width. It contrasts with the great sensitivity of human listeners to changes in sound frequency, as already mentioned.

To document the generality of the phenomenon of the peak shift and emphasize another phenomenon, Fig. 3 reproduces an intensity series of frequency characteristics of a Hensen's cell also recorded intracellularly [15]. The peak shift is of about the same magnitude as in Fig. 2 for the inner hair cell. But note in addition the approximate invariance of the high-frequency cut off. It is present in Fig. 2 also but, because of the way the curves are plotted there, it is less apparent.

Because of the cochlear tonotopic organization, the high-frequency cut off in frequency characteristics is a mirror image of the apical cut off of vibration in the cochlea. The reciprocity is demonstrated in Fig. 4 that shows cochlear frequency characteristics determined intracellularly on Hensen's cells at two locations separated by 226 μm along the cochlear spiral. The characteristics marked by the darker lines belong to a more basal location, those marked by the lighter lines, to a more apical one. The frequency difference between the response cut offs corresponding to the cochlear separation are clearly apparent. On the other hand, the locations of the corresponding response peaks strongly overlap. Could the the apical cut off of cochlear excitation constitute the code for auditory pitch?

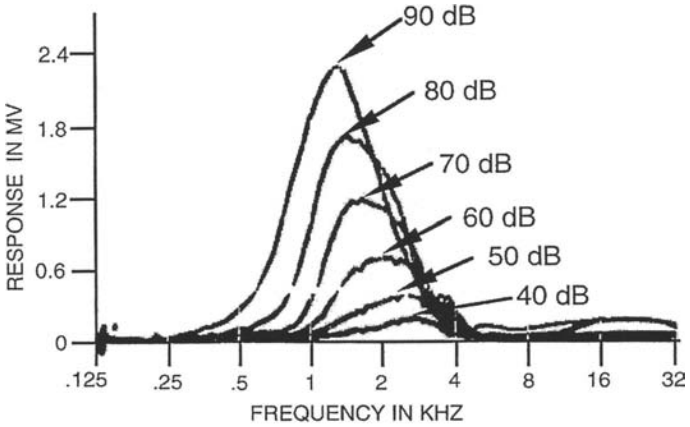

Fig. 3. Intensity series of intracellular frequency characteristics of a Mongolian-gerbil Hensen's cell. Corresponding sound pressure levels are indicated at the curves. According to ZWISLOCKI and NGUYEN [15]. From ZWISLOCKI [14].

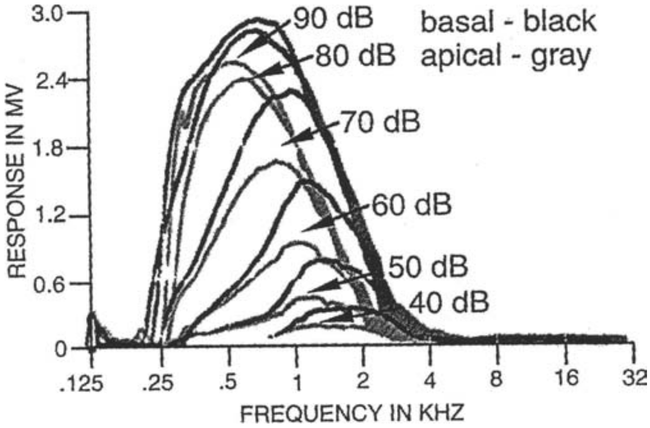

Fig. 4. Intensity series of intracellular frequency characteristics of two Mongolian-gerbil Hensen's cells separated by 226 μm along the cochlea. Corresponding sound pressure levels are indicated at the curves. According to ZWISLOCKI and NGUYEN, [14]. From ZWISLOCKI [15].

3. Evidence from cochlear pathology

Hearing loss of cochlear origin provides an additional opportunity for testing the nature of the place code for pitch. In its presence, even when it is evenly distributed across the audible sound frequencies, the pitch of test tones appears higher than normal (e.g. [2]). This is particularly true at near-threshold sound pressure levels. As the sound pressure is gradually increased, the pitch becomes lower, converging on normal. Thus, it depends on the sound pressure, in contradistinction to its independence of sound pressure in normal hearing.

To determine the changes in cochlear response characteristics underlying the psychophysical changes described above, we exposed Mongolian gerbils to wide-band noise at a sound pressure level of 100 dB. The noise exposure lasted for 140 minutes [11], also [12, 13]. The response characteristics were determined by recording intracellularly alternating potentials of Hensen's cells, which reflect faithfully those of the outer hair cells. The resulting frequency characteristics obtained before noise exposure from a Hensen's cell at 5 sound pressure levels ranging from 20 to 60 dB in 10 dB steps are plotted in the left panel of Fig. 5; those obtained after the noise exposure from a neighboring cell at the sound pressure levels of 40 to 70 dB in 10 dB steps, in the right panel. Whereas the characteristics obtained before the noise exposure resemble the normal characteristics of Figs. 2 to 4, those obtained after the exposure are severely altered. They have been amplified by a factor of 4 relative to those determined before the noise exposure. As a whole, the noise exposure produced a shift of the characteristics to lower frequencies, the peak became independent of sound pressure, and the high-frequency skirts became widely scattered.

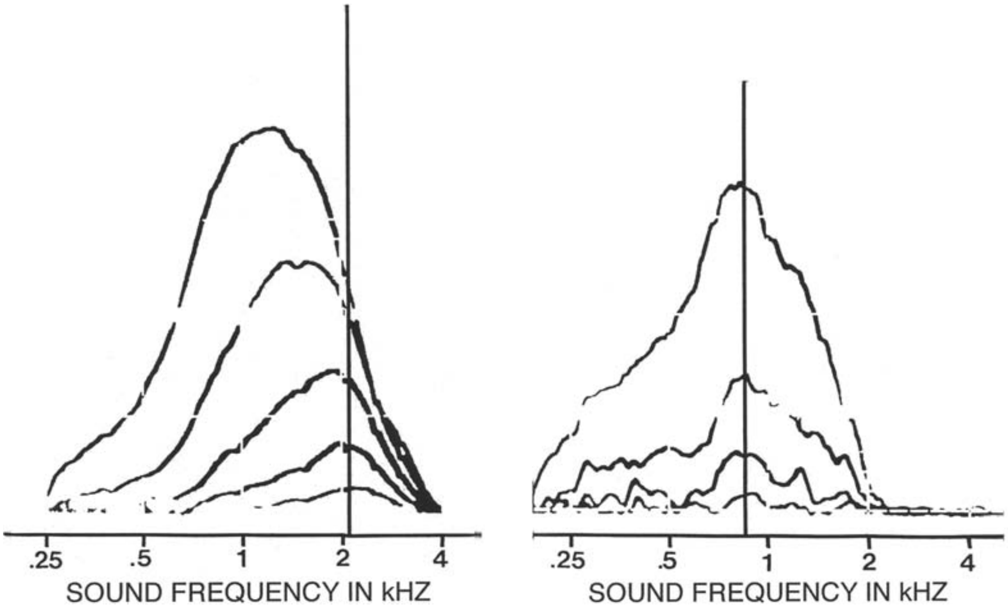

Fig. 5. Intensity series of intracellular frequency charactristics of two neighboring Mongolian-gerbil Hensen's cells recorded before noise exposure (left panel) and after noise exposure (right panel), respectively. The sound pressure level ranged from 20 to 60 dB in 10-dB steps before noise exposure and from 40 to 70 dB in 10-dB steps after noise exposure. According to ZHANG [11]. From ZWISLOCKI [14].

The shift of the frequency characteristics to lower frequencies is consistent with the higher pitch found in the presence of hearing loss attributed to cochlear malfunction. Remember that the characteristics are the mirror image of the cochlear tonotopicity. However, the independence of the peak location of sound pressure is not. Such dependence is found in the high frequency skirts of the frequency characteristics. Note in particular that the skirts are not bunched together, as in the left panel associated with the healthy cochlea not exposed to noise, but are displaced toward higher frequencies with the increasing sound pressure. Because of the mirror-image relationship, the displacement signifies a displacement of the apical excitation cut off in the cochlea toward the apex. This is consistent with the gradual lowering of the pitch with increasing sound pressure, as was found by BURNS and TURNER [2].

4. Conclusions

The pitch of pure tones is known to be practically independent of sound pressure level. On the other hand, the peak of the frequency characteristics of cochlear responses, in particular those of the inner hair cells innervated by the fibers of the auditory nerve, moves toward lower sound frequencies as sound pressure is increased. The difference suggests that the location of the peak of cochlear excitation is not the adequate code for the pitch. In contrast, the high-frequency cut off of the characteristics does not depend on sound pressure. This is consistent with the pitch invariance. In addition, in the presence of hearing loss of cochlear origin, the pitch is shifted upward at sound pressure levels close to the threshold of audibility but becomes more normal, as sound pressure is increased. Frequency characteristics of cochleae damaged by noise and recorded in cochlear Hensen's cells, which are known to parallel those of the outer and also inner hair cell, are moved according to the mirror image toward lower frequencies. However, their peak becomes independent of sound pressure. By contrast, their high-frequency skirt moves toward higher frequencies as sound pressure is increased. Because of the mirror-image relationship, this is consistent with lowering of the pitch. Thus, according to the psychophysiological relationships described in this article, the low-frequency (apical) cut off of cochlear excitation appears to be a better correlate of tonal pitch than the maximum excitation.

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