7. SYMPOSIUM ON SIMULATING WITH SPREADSHEETS

Chaired by Russell Church, *Brown University*

Lotus 1-2-3 simulation of frequency encoding on the basilar membrane

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A spreadsheet simulation was designed to describe frequency encoding on the basilar membrane according to the place theory (Greenwood, 1961). For any given frequency, the simulation displayed the location of maximum amplitude on the basilar membrane and the relevant critical bandwidth. The authors found a very high correlation between data given by the simulation and data from empirical research. The high correlation indicates the validity of the place theory of frequency encoding and the usefulness of this simulation for future research purposes.

In this study, a neurophysiologically valid spreadsheet model of the cochlear mechanics involved in the process of pitch discrimination was designed. This study simulated only a portion of the physiological process related to pitch discrimination. In particular, the simulation reflected the transduction process from the cochlea's reception of a sound wave to the innervation of specific hair cells in the auditory transducer. In constructing this simulation, the validity of the place theory of frequency encoding was assumed. The decision to design this spreadsheet model of the auditory transducer according to the propositions of the place theory, rather than another theory of frequency encoding, was based on the fact that in the past 4 decades research has supported the place theory (Gulick, Gescheider, & Frisina, 1989).

This simulation utilized several specific concepts posited by the place theory. For example, the simulation accounted for Békésy's (1960) "traveling wave." Békésy envisioned that the vibrations transmitted to the cochlea through the movement of the stapes set up a traveling wave along the basilar membrane. The traveling wave would progress down the basilar membrane over time, growing in size until it peaked at a specific location, and then abruptly disappear. Due to the tonotopic organization of the hair cells (Netter, 1986), the location of the peak of the traveling wave represented a certain band of frequencies; thus, the location also represented what pitch we would perceive.

Békésy's concepts of the traveling wave and the maximum displacement were supported by the way in which the places for frequency transduction are distributed on the membrane. This distribution depends primarily upon the stiffness gradient along the basilar membrane (Ehert, 1978; Tonndorf, 1970). The stiffness gradient is exponential and, therefore, the places along the membrane are a function of log frequency. A constant logarithmic relationship holds true for all frequencies except those less than 1000 Hz. Whereas the exponential relationship of frequencies greater than 1000 Hz to places along the basilar membrane is represented by a straight line on a log-linear plot, the line on the log-linear plot for frequencies less than 1000 Hz is not linear (Greenwood, 1961). Greenwood argues that this is not devastating to the place theory, though, because below 1000 Hz the abscissa approximates the linear distance on the basilar membrane less than it does above 1000 Hz. The evidence that frequencies below 1000 Hz do not have a constant logarithmic relationship to positions on the basilar membrane seems to corroborate other evidence of synchronous firing in acoustic neurons for low-frequency stimuli. However, according to Gulick et al. (1989), this evidence is outweighed by research on acoustic nerve projections to the brain, which strongly supports the concept of place in frequency encoding. Overall, the evidence against the place theory for low-frequency stimuli did not seem convincing enough to abandon it; therefore, the authors relied on the place theory for encoding all frequencies.

The evidence that the stiffness gradient on the basilar membrane is exponential not only gave credence to the traveling wave theory (Yost & Nielsen, 1985) but enabled

Requests for a copy of the spreadsheet program should be accompanied by a DOS-formatted floppy disk and sent to F. J. Bremner, Psychology Department, Trinity University, San Antonio, TX 78212.

researchers to devise logarithmic equations to relate the frequency of a tone to position of maximum displacement on the basilar membrane. Greenwood (1961) synthesized a knowledge of critical bandwidths and log-frequency relations in order to create an equation to plot frequency on the basilar membrane. First, frequencies greater than 1000 Hz are distributed so that they approximate a logarithmic function on the basilar membrane. Second, locations of critical bandwidth also have a logarithmic relationship to the basilar membrane, as a function of center frequency. Third, each critical bandwidth physically corresponds to about 1 mm on the basilar membrane. These three facts indicated to Greenwood that a frequency scale could be constructed by stacking critical bandwidths end to end on the basilar membrane. Thus, he wrote empirical functions to relate critical bandwidth to frequency and to position on the basilar membrane. One function specifically related frequency to position of maximum amplitude along the basilar membrane,

$$f = 165.4(10^{0.06x} - 1),$$

where f was frequency in hertz and x was the position of the maximum displacement expressed in millimeters from the helicotrema. In order that the function better fit this study's purpose, the authors solved for x :

$$x = \text{Log}(f/165.4 + 1)/0.06.$$

When given a frequency, f , the simulation determined the location of maximum amplitude on the basilar membrane.

Thus far, we have considered only how and where a sound wave of a certain frequency affects the basilar membrane. However, it is equally important to discuss the hair cells that line the membrane, because these cells hold the key to the actual transduction process. In all, there are between 15,500 and 23,500 hair cells that are arranged in the organ of Corti in two distinct groups. The first group, and the one most relevant to this simulation, is the inner hair cells (IHCs). There are approximately 3,500 IHCs, all of which are located in a single row that runs the length of the basilar membrane (Netter, 1986). There is some controversy over the number and arrangement of the second group of nerve cells, the outer hair cells (OHCs). Netter stated that there are 12,000 OHCs arranged in rows of three. Gonong (1987) stated that there are 20,000 OHCs arranged in rows of three to five.

These two segregated groups of cells differ not only in number, but more importantly, in their pattern of connection with the auditory nerve (Spoendlin, 1988). The far more numerous OHCs are sparsely represented in the auditory nerve. Only 5% of the afferent auditory nerve neurons are associated with the OHCs. Moreover, each afferent neuron innervates many OHCs. The remaining 95% of the afferent neurons entering the organ of Corti lead directly, unbranched, to the nearest IHCs. Dallos (1985) and Shepherd (1988) attempted to explain the role of the OHCs since they have such poor afferent innervation when compared with the IHCs. Dallos (1984) reported that only the cilia from the OHCs make contact

with the tectorial membrane. Also, when electrical currents are in the OHCs, they produce a motor response in which the actin filaments contract and expand the cilia along their longitudinal axis. Therefore, when a sound causes the basilar membrane to vibrate, the OHCs move back and forth and their cilia are stretched and relaxed. This motion sets up an alternating current within the hair cells. This alternating current further stimulates the OHC cilia to contract and expand, and thus the tectorial membrane is pulled and pushed even more. The rapid movement of the tectorial membrane serves to amplify the movement of the fluid within the cochlea. The amplified movement of the fluid displaces the IHCs by a greater amount than they would have been without the contractions of the OHC cilia membrane. Dallos (1985) and Shepherd (1988) concluded that there is not extensive afferent innervation to the OHCs because, although the OHCs have electrical and mechanical roles crucial to the transduction process, they probably do not participate in direct neural transmission to the central nervous system. Since the OHCs are apparently not involved in the actual frequency transduction process, the present authors decided to represent only the IHCs in the simulation.

The purpose of our simulation was to represent on a spreadsheet the relationship among the frequency of a tone, its critical bandwidth, and position on the basilar membrane at which the membrane vibrates maximally. We used the rows-and-columns layout of a spreadsheet to map the anatomical arrangement of the IHCs along the basilar membrane. With this representation of the basilar membrane, we displayed, for any given frequency within the human audibility range, both the location of maximum amplitude and the subjective range of the relevant critical bandwidth.

Method

The simulation used the spreadsheet Lotus 1-2-3 and represented the basic structure and shape of the basilar membrane. The basilar membrane was constructed with 160 spreadsheet cells in a shape similar to the cochlea, a spiral with two and one half turns. There was an approximately 22:1 reduction between the IHCs and the spreadsheet cells (i.e., each spreadsheet cell represented 22 IHCs in order to account for the 3,500 IHCs). The relationship between length of the human basilar membrane was 1 mm to 4.57 spreadsheet cells. This measurement also implied that each critical bandwidth included approximately 4.57 spreadsheet cells. For practical purposes, each critical bandwidth was represented by the activation of 5, rather than 4.57, spreadsheet cells.

From the user's perspective, the basilar membrane is displayed on the screen by rows and columns of 0s in a spiral configuration. After the user enters a frequency in response to the prompt, the entire basilar membrane changes from 0s to 1s, signifying the wave traveling from the stapes to the helicotrema. Next, the membrane returns to 0s except for the location of the maximum bulge, which remains "activated," indicated by a cell status of 1. Fi-

nally, the simulation provides the user with the exact distance of the maximum bulge from the helicotrema and the subjective range in hertz of the critical bandwidth.

The spreadsheet accomplishes this simulation of frequency encoding through a series of macro commands. First, the user is presented with an “inactive” basilar membrane and asked to input a frequency between 20 Hz and 20000 Hz. When the user enters a frequency, it invokes a macro that sends a traveling wave down the basilar membrane. The frequency f is sent to a macro containing the equation for determining location of maximum amplitude on the human basilar membrane, $x = \text{Log}(f/165.4 + 1)/0.06$. The value is multiplied by 4.57 in order to transform the location of maximum amplitude on the human basilar membrane to a matching location on the simulated basilar membrane. The numerical value of the location of the maximum displacement on the simulated basilar membrane is sent to another macro to classify its magnitude. This macro places the value in a specific numerical interval and then branches to one of 160 similar, but individualized, macros. This set of macros determines and activates the cells in the membrane to be included in the maximum displacement. These macros also provide the display of information informing the user of the exact lo-

Table 1
Correlation of the Simulation Data With Békésy (Zwislocki, 1965)

Frequency (in Hertz)	Sim Data	Békésy	Sim * Bék
25	1.02	1	1.02
50	1.92	2.5	4.8
100	3.42	4	13.68
110	3.69	4.1	15.129
200	5.74	6	34.44
300	7.49	9	67.41
400	8.9	9	80.1
440	9.39	8.8	82.632
800	12.77	12.5	159.625
1000	14.13	14.1	199.233
1700	17.54	17.8	312.212
2000	18.62	18.2	338.884
4000	23.35	25.8	602.43
8000	28.22	29	818.38
total	156.2	161.8	2,729.975

Note—SDs = 8.029 and 8.261. $M_s = 11.157$ and 11.557. $r[\text{Sim Bék}] = 0.995971$. $r[\text{Sim*Bék}]^2 = 0.991958$.

cation of the maximum displacement and the number of hertz included in the bandwidth.

Results

Positions of maximum amplitude on the basilar membrane for frequencies, given by Greenwood’s (1961) function, were compared with data randomly selected from a pool of Békésy’s empirical measurements and data relating maximum hearing loss to locus of maximum damage on the basilar membrane (see Zwislocki, 1965). Pearson’s product-moment correlations performed on the two data sets resulted in $r > .99$ and $r^2 = .99$, $ps < .01$.

Discussion

The high correlation between our simulation and the pool of Békésy’s data and the hearing loss data was not surprising, because Greenwood derived his function in accordance with place-frequency data. However, this does tell us that our simulation accurately reflects both Greenwood’s function and the pool of data. Moreover, the high correlation validates the exclusive use of the place theory to describe frequency encoding. As stated earlier, there is some support for the frequency theory of encoding for tones of less than 1000 Hz. However, this simulation and the correlation demonstrate how a place theory accounts for the encoding of all audible frequencies on the basilar membrane, including those below 1000 Hz. This proposition is further supported by the fact that the majority of the data points compared were for tones of less than 1000 Hz.

The sine qua non of modern neurophysiology is that the nervous system is dynamical (Mpitsos, 1987). This means that the nervous system organizes itself functionally as the task dictates. In fact, dynamic organization may be very irregular or even chaotic (Mpitsos & Cohan, 1986); that is, the neat anatomical organization of the cortex is misleading (Mountcastle, 1978). In particular, the predisposition among neural scientists to champion chaotic organization in the nervous system is in sharp contrast

Figure 1. Innervation of inner hair cells on the simulation of the basilar membrane for frequencies of (A) 75 Hz and (B) 3037 Hz. The central cell of status “1” shows the location of maximum amplitude. Cells of status “1” on either side of maximum amplitude reflect the critical bandwidth.

to the near logarithmic organization of the auditory transducer. It is common in computer-driven neural network simulations to initially randomize all synaptic connections and then let the network learn the correct function by dynamically adjusting its synaptic weights. The authors wonder if a neural network could be designed that would learn to organize itself in the logarithmic fashion of the hair cells. Therefore, the authors are designing another simulation, in order to test the constraints of mapping the logarithmic functioning of the hair cells onto a dynamic neural network.

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