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Psychophysical laws revealed by electric hearing

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PSYCHOPHYSICAL laws relate the intensity of a physical stimulus to its perceived magnitude. G.T. Fechner hypothesized 150 years ago that the psychophysical law can be derived by measuring intensity discrimination, but modern scientists favor a direct magnitude estimation approach and are still divided on whether and how intensity discrimination is related to sensation magnitude. This controversy is partially due to the uncertainty of the role of the sensory organ in the psychophysical law. Here we bypass the auditory sensory organ with electric stimulation of the human auditory nerve and find a close coupling between intensity discrimination and loudness functions in electric hearing. Our results support Fechner's hypothesis in principle but not the exact relationship from which he derived his logarithmic law. *NeuroReport* 10:1931–1935 © 1999 Lippincott Williams & Wilkins.

Key words: Auditory nerve; Cochlear implant; Electric stimulation; Intensity discrimination; Loudness function; Psychophysical laws

Introduction

Whether and how the just-noticeable-difference (jnd) in intensity is related to its subjective magnitude is a long-standing problem in psychophysics [1–4]. Weber first noticed that a stimulus jnd ($\Delta\phi$) is approximately proportional to its magnitude (ϕ), so that the so-called Weber fraction, $\Delta\phi/\phi$, is a constant. Fechner gave this constant a perceptual meaning by assuming that the Weber fraction is equal to a constant change in the sensation magnitude ($\Delta\psi=\theta\Delta\phi/\phi$, where θ is a scaling factor). Integrating Fechner's equation results in a logarithmic function between sensation and stimulus magnitude ($\psi=\theta\log\phi$). On the other hand, Brentano [1] assumed that Weber's law holds in both sensation and stimulus domains ($\Delta\psi/\psi=\theta\Delta\phi/\phi$). Integrating Brentano's equation results in a power function ($\psi=\phi^{\theta}$), which later was promoted by Stevens as a universal law of sensation magnitude across all sensory modalities [5].

Because the direct magnitude estimation method used to validate Stevens' power law does not relate sensation magnitude to stimulus jnd, the relationhsip between stimulus jnd and sensation magnitude remains controversial to this date. Some researchers have argued against the existence of the loudness and jnd relationship, but they appear to base their argument on totally opposite grounds. Stevens downplayed intensity discrimination because he viewed this measure as merely gauging the system noise. On the contrary, Viemeister and Bacon [6] viewed direct loudness estimation as a measure involving "non-sensory factors, we did not attempt to relate these data to those for intensity discrimination." Other researchers have argued for the existence of a loudness and jnd relationship, but they differ significantly on the exact form of such a relationship [7–11]. One major reason for these disagreements is the uncertain role that the sensory organ may have played in this relationship. For example, cochlear hearing loss changes the slope of the loudness function but not the jnd size.

In this study, we used the cochlear implant to bypass the auditory sensory organ by stimulating the auditory nerve directly with electric currents. In addition, we took advantage of the frequency dependence of loudness in electric hearing; loudness is an exponential function of electric amplitude for high-frequency stimuli and a power function for low-frequency stimuli [12,13]. Here we report the jnd function for both low- and high-frequency stimuli in the same cochlear implant listeners from whom the loudness balance functions have been obtained [12]. If loudness and jnd functions were tightly coupled as Fechner hypothesized, then the same frequency dependency should be observed for the jnd function in these listeners.

Materials and Methods

Subjects: Six post-lingually deafened adults (two females and four males) participated in this study. All subjects were users of the Ineraid cochlear implant device and had extensive experience in various psychophysical tests. Informed consent was approved by the local Institutional Review Board and obtained from each individual subject after the nature and possible consequences of the study were explained.

Stimuli: Sinusoids and biphasic pulses were used in the experiments. The sinusoid stimulus had a frequency of either 100 Hz or 1000 Hz. The pulse stimulus had a frequency of 100 Hz only and consisted of 100 μs/phase biphasic pulse trains. All stimuli were 200 ms in duration and delivered through a constant current source to the most apical electrode inside the cochlea and a remote reference electrode outside the cochlea.

Procedures: We used a tracking procedure to measure the threshold and the maximum comfortable loudness level. The threshold was estimated from an ascending sequence and a descending sequence, whereas the maximum loudness level was estimated from an ascending sequence only. We used a two-alternative, forced-choice, adaptive procedure to measure the jnd in intensity. On each trial, the subject heard two electric stimuli that differed only in amplitude and had to judge which of the two stimuli was louder. Initially, the amplitude difference was large and then decreased after three consecutive correct responses or increased after one incorrect response. Such a procedure converged to an amplitude difference that produced a 79.4% correct response [14].

Data analysis: Because the absolute amplitude of threshold and maximum loudness in electric hearing is determined by physical parameters such as the distance between the electrode and the nerve, there are vast differences in dynamic range among cochlear implant listeners. To compensate for individual differences in dynamic range, the individual loudness and jnd data were normalized as a percentage of each individual subject's dynamic range in μA. The following mathematical derivations verify the use of the dynamic range normalization in comparing the loudness and jnd relationships. We showed previously [12] that there is a logarithmic relation in producing equal loudness between the dynamic range normalized amplitude at 1000 Hz and that at 100 Hz

$$\frac{A_{1000} - T_{1000}}{M_{1000} - T_{1000}} = \theta \log \frac{A_{100} - T_{100}}{M_{100} - T_{100}} \quad (1)$$

where A denotes electric amplitude in μA, T denotes the threshold in μA, and M denotes the maximum comfortable loudness in μA. Differentiating both sides of the above equation with respect to the electric amplitude, we obtain:

$$\frac{\Delta A_{1000}}{M_{1000} - T_{1000}} = \frac{\theta}{\ln 10} \frac{\Delta A_{100}}{M_{100} - T_{100}} \Big/ \frac{A_{100} - T_{100}}{M_{100} - T_{100}} \quad (2)$$

Rewriting the above equation based on dynamic range normalization:

$$\Delta E_{1000} = \frac{\theta}{\ln 10} \frac{\Delta E_{100}}{E_{100}} \quad (3)$$

where ΔE is the jnd and E is the pedestal normalized by the dynamic range (M−T).

Results

We first present the measured electric dynamic range as a function of stimulus frequency and waveform (Fig. 1) in six cochlear implant listeners. The lower boundary of the dynamic range was the electric current amplitude that evoked just audible hearing, or threshold, and the upper boundary was the maximum comfortable loudness level. The 100 Hz sinusoid produced the lowest threshold and the greatest mean dynamic range of 30 dB, while the 100 Hz pulse produced the highest threshold and a significantly narrower 14 dB dynamic range (t(df =

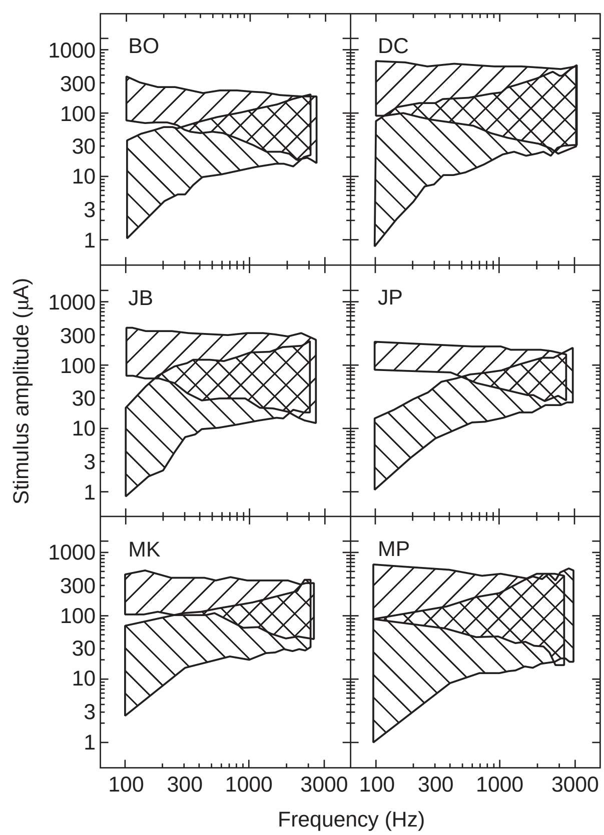

FIG. 1. Individual thresholds (bottom boundary) and maximum comfortable loudness levels (top boundary) as a function of frequency for sinusoid (left-slanted, hatched area) and pulse (right-slanted, hatched area).

10) = 5.60, $p < 0.01$). The 1000 Hz dynamic range was not significantly different between the sinusoid and pulse (19 dB *vs* 18 dB; t(df = 10) = 0.37, $p > 0.6$).

We then present the measured jnd functions for sinusoids at 100 Hz and 1000 Hz (Fig. 2) and for pulses at 100 Hz (Fig. 3). For the 100 Hz sinusoid, the jnd increased from 1–5% dynamic range near threshold to 6–17% near maximum loudness. In contrast, the jnd was relatively constant between 2% and 8% over the entire dynamic range for the 1000 Hz sinusoid. Despite their large differences in waveform, threshold and dynamic range, the 100 Hz pulse and the 100 Hz sinusoid showed a similar sloping jnd function. The individual data were averaged (Fig. 4) to derive three linear regression functions, in which the slope, intercept and correlation coefficient were 0.11, 2.00 and 0.99 for the 100 Hz sinusoid, 0.15, 0.09 and 0.95 for the 100 Hz pulse, and −0.02, 5.83 and 0.60 for the 1000 Hz sinusoid. These averaged results indicate that the jnd function was significantly different from a horizon-

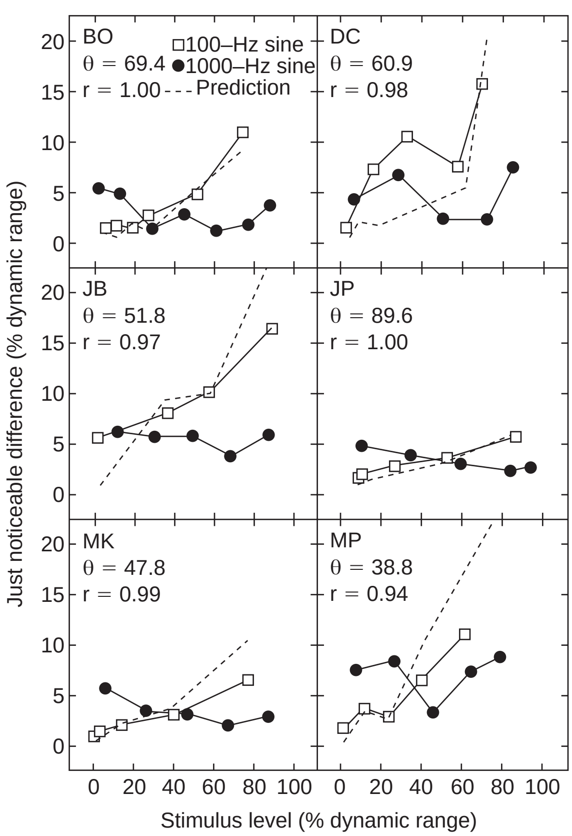

FIG. 2. Normalized individual jnd data for the 100 Hz sinusoid (open squares) and the 1000 Hz sinusoid (filled circles). The normalization was performed according to the stimulus dynamic range (in μA) in each individual listener. Dashed lines represent the prediction of the individual 100 Hz jnd data from the 1000 Hz jnd data and the slope of the loudness balance function between the 100 Hz and 1000 Hz sinusoids (see Equation 5). θ is the slope of each individual's loudness balance function (Equation 4) and r is the correlation coefficient of the fitted function.

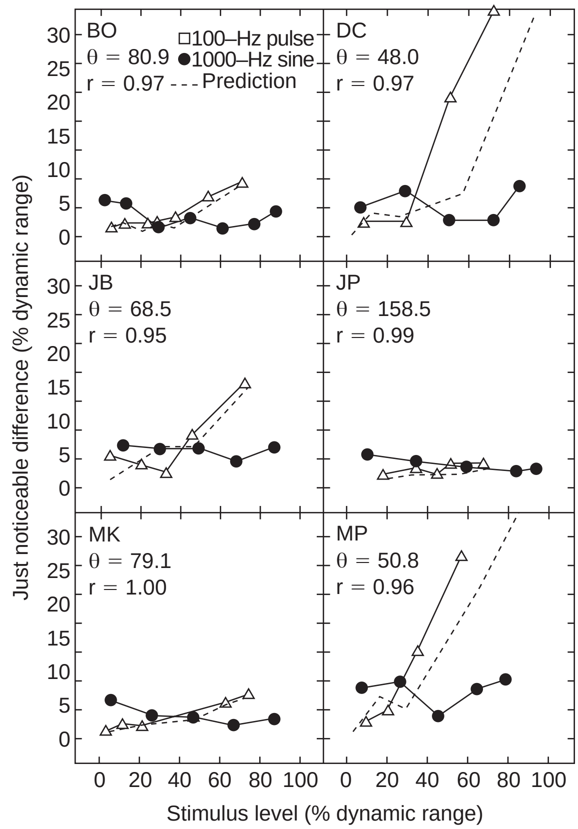

FIG. 3. Normalized individual jnd data for the 100 Hz pulse (open triangles) and the 1000 Hz sinusoid (filled circles, the same as in Fig. 2) stimuli. Dashed lines represent the prediction of the individual 100 Hz jnd data from the 1000 Hz jnd data and the slope of the loudness balance function between the 100 Hz pulse and 1000 Hz sinusoid (see Equation 5). θ is the slope of each individual's loudness balance function (Equation 4) and r is the correlation coefficient of the fitted function.

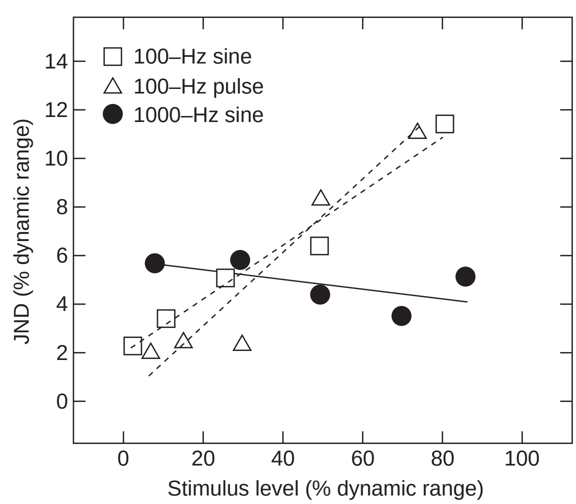

FIG. 4. Averaged jnd data for the 100 Hz sinusoid (open squares), 100 Hz pulse (open triangles), and 1000 Hz sinusoid (filled circles). Linear regression functions are also shown as dashed lines for the 100 Hz stimuli and the solid line for the 1000 Hz sinusoid. Fitting parameters are discussed in Results.

tal line for both the 100 Hz sinusoid ($t(df=3)=12.16$, $p<0.01$) and the 100 Hz pulse ($t(df=3)=5.27$, $p<0.01$), and abided by Weber's law. On the contrary, the 1000 Hz sinusoid jnd function was not significantly different from a horizontal line ($t(df=3)=1.30$, $p>0.10$), indicating a constant jnd with intensity and a violation of Weber's law.

Discussion

Here we demonstrate that these frequency-dependent jnd functions have a simple relation to the loudness functions. We showed previously for both the sinusoid and pulse that cochlear implant listeners produced a logarithmic loudness balance function between the 1000-Hz stimulus amplitude (E_{1000}) and the 100 Hz stimulus amplitude (E_{100}) [12]:

$$E_{1000} = \theta \log E_{100} \tag{4}$$

where θ is the slope of the above loudness balance function which was measured previously. If we assume that the size of the jnd is inversely proportional to the slope of the loudness function, then we can simply differentiate Equation 4 and obtain the approximate relationship between the 100 Hz and the 1000 Hz jnd functions:

$$\Delta E_{100} = \frac{\ln 10}{\theta} \Delta E_{1000} E_{100} \tag{5}$$

Equation 5 allows us to predict the 100 Hz jnd function from the slope of the loudness balance function (θ) and the 1000 Hz jnd (ΔE_{1000}) at equal loudness to the 100 Hz stimulus level (E_{100}). The predicted 100 Hz jnd functions are shown individually for the sinusoid (Fig. 2) and the pulse (Fig. 3). Although deviations from the data occur, the prediction has quite accurately captured the general pattern of each individual's data. We note that most deviations occur at high stimulus levels and for small θ values (e.g. JB, MK, MP for the 100 Hz sinusoid, and DC, MP for the 100 Hz pulse). Equation 5 shows that such error patterns are due to the fact that the predicted 100 Hz jnd is directly proportional to the 100 Hz amplitude (E_{100}) and inversely proportional to the θ value. The accuracy of prediction is striking, considering that the prediction is based on three independent perceptual measures (the loudness balance function, the 100 Hz jnd function, and the 1000 Hz jnd function) and that the prediction is free of free parameters (Equation 5).

Fig. 5 presents a phenomenological model that summarizes the relationship between loudness and intensity jnd in both acoustic and electric hearing. In the loudness model (left side), a logarithmic compression in the periphery and an exponential expansion in the brain combine to produce a power function between sensation magnitude (L) and stimulus intensity (I). In the jnd model (right side), the logarithmic compression converts a relative difference in the stimulus level (ΔI/I) into an absolute difference in the neural count (ΔN), which is then exponentiated by the brain to restore a relative difference in the sensation magnitude (ΔL/L).

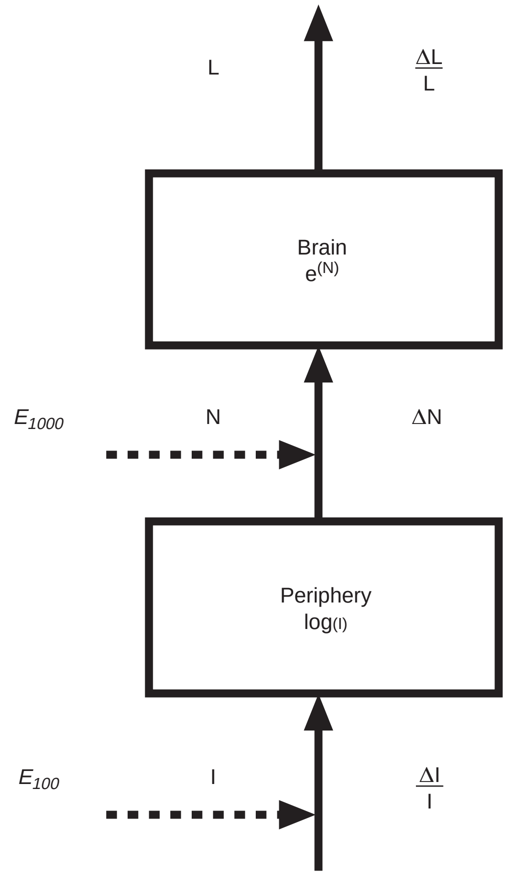

FIG. 5. The loudness and jnd relationship, in which I represents the normal acoustic stimulus, N represents the neural count, L represents the sensation magnitude, E_{100} represents the 100 Hz electric stimulus, and E_{1000} represents the 1000 Hz electric stimulus.

The present model is similar to previous models in vision [15] and is consistent with the present loudness and jnd data. For high-frequency stimuli, the logarithmic compression is mechanical and located in the cochlea. In this case of electric stimulation, this compression is bypassed so that loudness is an exponential function of electric amplitude (E_{1000}):

$$L = ae^{E_{1000}} \tag{6}$$

Differentiating Equation 6 with respect to E_{1000} we obtain:

$$\frac{\Delta L}{\Delta E_{1000}} = ae^{E_{1000}} \tag{7}$$

Rewriting Equation 7 we have:

$$\frac{\Delta L}{L} = \Delta E_{1000} \tag{8}$$

The present 1000 Hz jnd data show that Equation 8 is a constant, which is consistent with the model prediction for the high-frequency electric stimuli: Weber's law holds only in the sensation domain but not in the stimulus domain.

For low-frequency stimuli, the peripheral logarithmic compression is presumed to occur in cochlear nuclei and may be related to extraction of neural synchrony information for fibers of different diameters [16]. For example, both anatomical and physiological data show that cochlear nuclei receive differential inputs from fibers of different diameters [17,18] and processes synchrony information up to 300 Hz [19,20]. Therefore, loudness (L) of low-frequency stimuli, similar to acoustic stimulation, is a power function of electric amplitude (E_{100}):

$$L = \mathrm{a}E_{100}^{\theta} \tag{9}$$

Differentiating Equation 9 with respect to E_{100} we obtain:

$$\frac{\Delta L}{\Delta E_{100}} = \theta\, aE_{100}^{\theta-1} = \theta\frac{aE_{100}^{\theta}}{E_{100}} = \theta\frac{L}{E_{100}} \tag{10}$$

Rewriting Equation 7 we have:

$$\frac{\Delta L}{L} = \theta\frac{\Delta E_{100}}{E_{100}} \tag{11}$$

The present jnd data show that Equation 11 is a constant, validating the model prediction for the 100 Hz stimulus that Weber's law holds in both sensation and stimulus domains.

The simple relationship between loudness and jnd in electric stimulation is not always observed in acoustic stimulation, however. It has been shown that the loudness-jnd relationship can be either enhanced or weakened, or even totally abolished, depending on the nature of the internal noise in acoustic hearing that may limit intensity discrimination [7–11]. In electric stimulation of a deafened ear, the spontaneous activity is absent, the statistical independence among neurons is lost, and the temporal firing pattern is artificially synchronous [21–25]. This more deterministic neural activity and resulting reduced level of internal noise in the auditory nerve may be the reason that the loudness–jnd relationship is clear with electric stimulation but is not always apparent with acoustic stimulation.

Conclusion

Although the successful prediction of the jnd data from the loudness data supports Fechner's hypothesis that the sensation magnitude and the stimulus jnd are closely related, the exact relationship seems to be as suggested by Brentano rather than by Fechner. Specifically, Weber's law in the stimulus domain is due to a logarithmic compression in the periphery, and Weber's law in the sensation domain is due to an exponential expansion in the brain. The present data from electric hearing help distinguish peripheral and central contributions to the relationship between stimulus and sensation magnitude.

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