# LOUDNESS ENCODING AT THE AUDITORY NERVE

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The 'sone' scale developed by Stevens (1956) describes the rate at which loudness grows with sound level. Using a method of magnitude estimation, human participants were required to quantify the loudness of a stimulus tone relative to a reference tone of some fixed level and frequency (or frequencies). For example, a 1 kHz reference tone at 40 dB SPL was assigned an arbitrarily scaled value of, say, 100. A 1 kHz stimulus tone deemed twice as loud would then be assigned a value of 200. After all stimulus tones were presented, the assigned values were then normalized such that the reference tone was given a value of 1 'sone'.

A full logarithmic plot of loudness (in sones) against sound level (in dB) yields a curve that is linear over much of its extent. The slope of the linear portion of this curve gives the loudness exponent, $n$, which describes the rate at which loudness grows with sound level. That is, the relationship between loudness, $L$, and sound level, $I$, is approximately

$$L \propto I^n \qquad (1)$$

where sound level is represented here as a linear measure.

The loudness exponent, $n$, is characteristic of the stimulus frequency (or frequencies) used for experimentation and varies from about 0.3 for 1 kHz tones to greater than 0.4 for pure tones of higher and lower frequencies. Whereas the 'Loudness function' in Equation (1) holds true for the human perceiver, we are interested in the extent to which this relationship is reflected at the auditory nerve.

In response to a tone stimulus of constant sound level, the stereocilia of a given inner hair cell within the cochlea become deflected resulting in a depolarization of the cell's receptor potential followed by the release of neurotransmitter. Approximately 20 auditory nerve fibers synapse onto this hair cell, each of which produce action potentials at a rate proportional to the amount of neurotransmitter release (Slepecky, 2000). The initial rate of neural firing, however, does not persist. For the duration of the stimulus, the neural response peaks immediately after onset of the tone and is followed by a component that adapts rapidly to a steady state.

As the sound level of the stimulus tone is increased, both the onset and steady state firing rates will become larger, but tend to saturate at higher intensities depending on the spontaneous rate of the nerve fiber. This feature is demonstrated in Figure 1, adapted from Smith (1979). Firing rate was measured from a single fiber of the auditory nerve in the Mongolian gerbil in response to a 50 Hz narrow-band stimulus of constant sound level centered around the characteristic frequency of the fiber at 1.86 kHz.

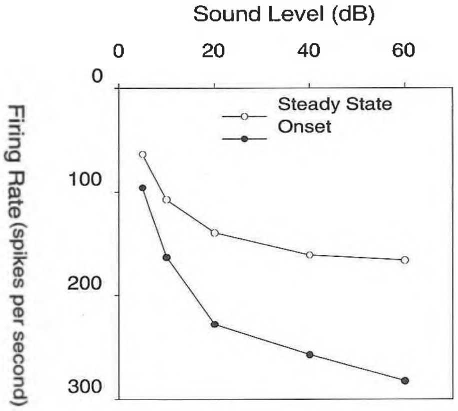

Figure 1

Neither the onset nor the steady state firing rate displays the necessary growth with sound level that would be characteristic of the loudness function. Similarly, Relkin and Doucet (1997) found that a gross measure of neural firing in the form of a perstimulus compound action potential taken from the chinchilla auditory nerve also does not demonstrate the required growth. That is, loudness is not simply proportional to the auditory nerve spike count.

Individual units of the mammalian auditory nerve fall into three categories, depending on their spontaneous firing rate. Units of high, medium and low spontaneous rates respond to low, medium and high sound levels respectively (Liberman, 1978). Hence, one might suggest that sound level is coded by the recruitment of subgroups of fibers in response to increasing sound levels. Nevertheless, if loudness were to be preserved amongst these fibers, each fiber would be required to encode the psychophysical growth of loudness, regardless of the limited dynamic range per fiber.

We propose that in each fiber of the auditory nerve, the loudness of a tone can be represented as an information such that the greater the loudness, the greater the information. Within information theory, information is defined as the difference between the stimulus uncertainty and the stimulus equivocation.

Consider a pure tone stimulus of 'constant' sound level acting on the inner hair cell. On a moment-by-moment basis, the square of the peak amplitude will fluctuate by an amount $\Delta I$ about the mean sound level $I$. That is, the hair cell is presented with a normal distribution of sound level values with a mean of $I$ dB and standard deviation of $\Delta I$ dB.

Similarly, the inner hair cell is by no means exact in its ability to detect the instantaneous sound level and will make errors, say by an amount $\sigma$ dB.

Taken together, $\Delta I$ and $\sigma$ determine the stimulus uncertainty and the stimulus equivocation respectively. Hence, one can calculate the information on a moment-by-moment basis simulating the process through which the inner hair cell samples the stimulus level. Figure 2 is a representative example of the information (in natural units [n.u.]) calculated as a function of the number of trials (or samples) for this process. Characteristically, the information rises to a peak and subsequently falls to an asymptotic value. For a given value of $\Delta I$, the peak and asymptotic values are completely determined by $\sigma$.

We propose that the calculated information is proportional to the firing rate one would observe in a single auditory nerve fiber in response to a constant sound level. Hence, the ratio of onset to steady state firing should equal the ratio of peak to asymptotic information.

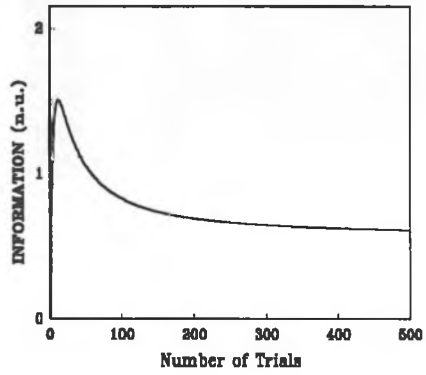

**Figure 2**

By way of example, let us use the data from Figure 1. At each stimulus level, one can calculate the ratio of onset to steady state firing rate. Using these ratios, one can generate the corresponding information curves.

First, however, we must define the value of $\Delta I$. We suggested above that the hair cell is presented with a stimulus uncertainty measurable in decibels. We simply assume here that $\Delta I = I/2$ dB corresponding to a square root law in linear space.

Using this relationship, one can now determine the values of $\sigma$ required to generate information curves such that the ratio of peak to asymptotic information corresponds to the ratio of onset to steady state firing rate at stimulus level.

Figure 3 represents a full logarithmic plot of variance, i.e. $\sigma^2$, against $\Delta I$ (already a logarithmic measure). Notably, the slope of the straight line is measured at 0.34 corresponding to the loudness exponent of Equation 1.

Hence, in every auditory nerve fiber, the loudness becomes encoded in the error intrinsic to the fiber as it samples the sound level of the stimulus tone.

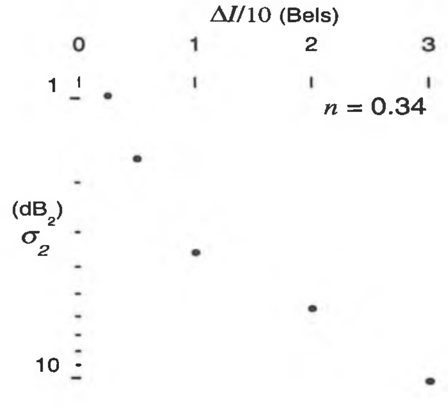

**Figure 3**

Liberman, M. C., (1978). Auditory-nerve response from cats raised in a low-noise chamber. *Journal of the Acoustical Society of America*, **63**, 442-455.

Relkin, E. M. & Doucet, J. R. (1997). Is loudness simply proportional to the auditory nerve spike count? *Journal of the Acoustical Society of America*, **101**, 2735-2740.

Slepecky, N. B., Galsky, M. D., Swartzentruber-Martin, H., Savage, J. (2000). Study of afferent nerve terminals and fibers in the gerbil cochlea: distribution by size. *Hearing Research*, **144**, 124-134.

Smith, R. L. (1979). Adaptation, saturation, and physiological masking in single auditory-nerve fibers. *Journal of the Acoustical Society of America*, **65**, 166-178.

Stevens, S. S. (1956). The direct estimation of sensory magnitudes-loudness. *American Journal of Psychology*, **69**, 1-25.