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NEURAL CODING OF HIGH-FREQUENCY TONES

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NEURAL CODING OF HIGH-FREQUENCY TONES

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SUMMARY

Available evidence indicates that neural discharges in the auditory nerve display characteristic periodicities in response to any tonal stimulus including high frequency stimuli, and that this periodicity corresponds to the subjective pitch.

INTRODUCTION

If a low-frequency tone stimulus (<5 kHz) is imposed on a monkey (or presumably on a human being), the impulsive electrical discharges observed in individual auditory-nerve fibers tend, over many periods of the stimulus waveform, to be correlated with the stimulus waveform (ref. 1). More specifically, the number of discharges as a function of the phase of the stimulus wave tends to reproduce graphically that part of the waveform exceeding some reference amplitude, whereas essentially no discharges occur throughout the rest of the period of the wave. As the stimulus frequency is increased this correlation tends to fade out. At stimulus frequencies greater than 5 kilohertz, all evidence of correlation disappears, and the number density of discharges becomes uniform over the period of the wave. One interpretation of these results is that low-frequency acoustic stimuli are coded in the peripheral nervous system by the periodicity of the neural discharges. But the method of coding high frequencies is not evident. How, then, do the peripheral neurons transmit the attribute of frequency for high-frequency stimulation?

Over the years several methods for coding high frequencies have been proposed. For example, it is commonly believed that for high-frequency stimulation the attribute of frequency must be coded according to the place of stimulation of the fiber along the cochlear partition (refs. 2 to 4). Since each fiber has a broad frequency response, the place of stimulation for a given frequency extends over a relatively large interval along the cochlear partition (refs. 4 and 5). Therefore, it becomes difficult to associate any

specific frequency with a particular place of stimulation. Moreover, the subjective aspect of frequency displays no characteristics that would suggest a different objective form of coding at high frequencies (ref. 3).

Another possibility is that the high-frequency coding involves two, or more, interacting fibers (ref. 2, chap. 8). But if the fibers interact to produce a periodicity at high frequencies, then they must also independently produce periodic discharges at some lower frequency harmonically related to the stimulus frequency. These periodicities should be observable over many realizations of the stimulus. Apparently these periodicities are not observed, at least in the manner that periodicities due to low-frequency stimuli are observed.

Finally, if it were possible that high frequencies are represented by periodicities in individual fibers, some specific point along the discharge signature would have to specify the beginning of each period since the duration of each impulse is then comparable to the period of the tone. More importantly, since they require a refractory period between discharges, neurons are unable to transmit successive discharges in the short time interval corresponding to the period of a high frequency.

PROPOSED CODING OF HIGH FREQUENCIES

Since each of the proposed methods of neural coding of high frequencies suffers from serious drawbacks, it seems worthwhile to reconsider another possibility, apparently originated by Wundt in 1880 (see ref. 6), which does not appear to have been tested at high frequencies. Specifically, because the subjective nature of a tone, other than its pitch, seems no different at high frequencies than at low frequencies, it is reasonable to suspect that the coding at high frequencies may be the same as at low frequencies. If so, why haven't the periodicities been observed at high frequencies? The fact is that periodicities do exist at high frequencies, but appear to have been overlooked.

To show how high frequencies might be coded and to show how the coding may be observed in the peripheral nervous system, consider first that two frequencies are associated with any tone stimulus, namely, the objective frequency of the stimulus and the subjective frequency of the sensation, better known as pitch. The objective frequency (henceforth called the stimulus frequency) may be viewed as the input to, and the pitch may be interpreted as the conscious output of, the nervous system. The frequency is measured physically, whereas the pitch is crudely estimated by subjective judgment of the ratio of the apparent frequency to that of a standard tone. According to one common pitch scale, a 1-kilohertz tone is defined to have a pitch of 1000 mels (ref. 7). For low-frequency stimuli, say for tone frequencies less than 1 or 2 kilo-

hertz, the pitch in mels has usually been judged to be near the imposed frequency. (See refs. 7 to 10 and see fig. 1). For higher frequency stimuli the pitch falls well below the imposed frequency. For example, for a frequency of 15 kilohertz the pitch may only be about 2500 mels.

Since the peripheral nervous system is unable to code high frequencies in terms of the periodicity of discharges, an alternative possibility is that it is the pitch, not the frequency, which is coded. According to this argument the pitch is not simply an unexplained psychological phenomenon, but rather, is the conscious correspondent of physical processes occurring in the nervous system. The pitch is, thus, the conscious representation of the periodicity of discharges observed in the peripheral nervous system. One important consequence of this assumption is that little reinterpretation of low-frequency information is required because the pitch nearly equals the frequency. More importantly, for high-frequency stimuli this assumption may overcome the problem of the minimum achievable period of discharges since the period of the pitch in this case tends to be much greater than that of the associated frequency.

TESTS OF CODING PROPOSAL

The periodicities of neural discharges are commonly displayed in the form of period histograms or of interspike-interval histograms. A period histogram shows the temporal density of discharges in a neuron within a typical period of the stimulus. This density is obtained from measurements over many periods. An interspike-interval histogram displays the temporal density of discharges in a neuron as a function of time between discharges, again from measurements over many periods.

For low-frequency stimuli both types of histograms display periodicities corresponding to the frequency of the stimulus. For high-frequency stimuli the period histograms tend to display a uniform number density (ref. 1), that is, no periodicity. This should be expected if the discharges are associated with pitch rather than frequency because, as the pitch increasingly differs from the frequency, a uniformly distributed, more rapidly time-dependent phase shift must generally exist between the pitch and frequency. More importantly, however, in contrast with the period histograms, the interval histograms continue to display a periodicity for high-frequency stimulation simply because the number density of discharges is peaked and not uniform (ref. 11), as shown in figure 2. It is this periodicity which has been disregarded, which is the dominant period between discharges, and which may correspond to the pitch.

Data that might verify the preceding proposal are minimal. Kiang (ref. 11) displayed interval histograms from a cat's auditory nerve fiber stimulated at its best

frequency, 9800 hertz. From his histograms it is evident that the dominant period is less than 4 milliseconds, corresponding to a frequency (pitch?) of at least 250 hertz. Other sources (ref. 2, p. 159; ref. 12, p. 81) report a minimum period of approximately 0.4 millisecond between successive discharges in peripheral, type A fibers. In the references cited the stimulus frequency and characteristic frequency of the neuron were not given. Rose found from his data that this minimum interval limit is not violated in auditory neurons with high characteristic frequencies in squirrel monkeys. In addition, the peaks of interval histograms like that shown in figure 2 were found to be broad compared with the average interval between discharges.

If it is assumed that the minimum interval between discharges is approximately 0.4 millisecond and that the periodicity of discharges determines pitch, then the maximum distinguishable pitch must be about 2500 mels.

The most widely accepted psychoacoustic studies of the functional dependence of pitch on frequency are those by Stevens, et al. (refs. 7 and 8). In the 1937 experiment (ref. 7) judgments were made to find the frequency of a tone with one-half the pitch of a reference tone. In the 1940 experiment (ref. 8) two reference tones were subjectively bisected by a third tone. The lowest reference tone was only a 40-hertz tone so that the bisecting tone had one-half the pitch of the upper reference tone when its frequency was high. Neither experiment was a "blind" experiment because the listener was able to adjust the bisecting tone. The great disagreement between the two experimental results, shown in figure 1, is indicative of experimental bias since in each test the scatter of judgments was less than the difference between the two experimental curves. Subsequent blind experiments involving single judgments of pitch presumably have less bias and yield yet different estimates of the relation between pitch and frequency (refs. 9 and 10, and fig. 1).

The preceding psychoacoustically generated pitch functions are to be compared with an estimate of the pitch function based on physiological arguments. Assume that the dominant period of the discharges equals the reciprocal of the pitch; at low frequencies the pitch equals the stimulus frequency; the maximum pitch is determined by the minimum observed interval between discharges; and the pitch function is monotonically increasing. The resulting estimated pitch function (where the minimum discharge interval is assumed to occur at 15 kHz) is in excellent agreement (fig. 1) with that psychoacoustically generated function (ref. 10; ref. frequency, 528 Hz) which may be expected to possess the least bias. The psychoacoustically generated pitch function with least bias is assumed to be that obtained by single magnitude estimates of pitch relative to a higher reference pitch, in analogy with minimally biased loudness judgments (ref. 13). Finally, it is important to note that the physiological estimate was generated without knowledge of the results in reference 10.

CONCLUSIONS

In conclusion, it is evident that neural discharges stimulated by a tone display a characteristic periodicity for high, as well as low, frequencies and that this periodicity may be associated with subjective judgments of pitch.

Lewis Research Center,
National Aeronautics and Space Administration,
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505-03.

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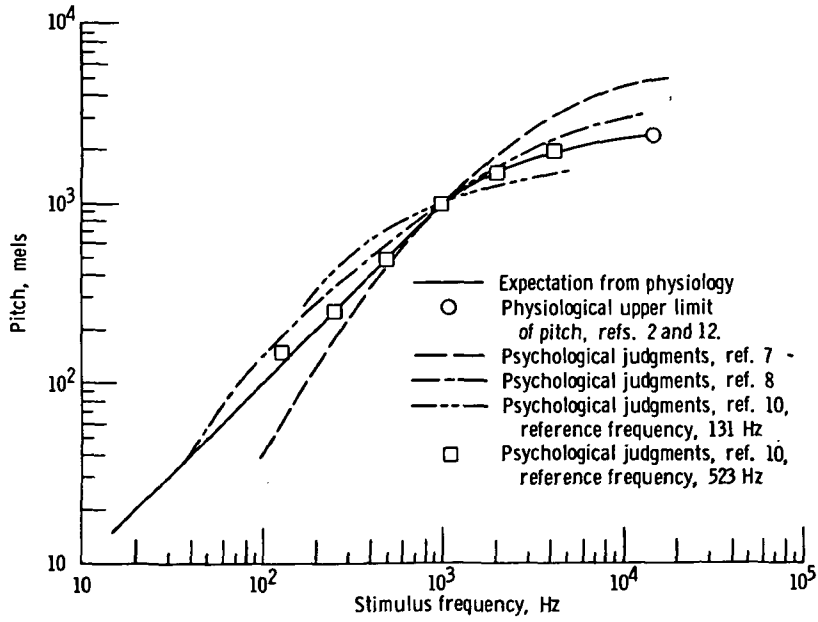


Figure 1. - Pitch as function of stimulus frequency.

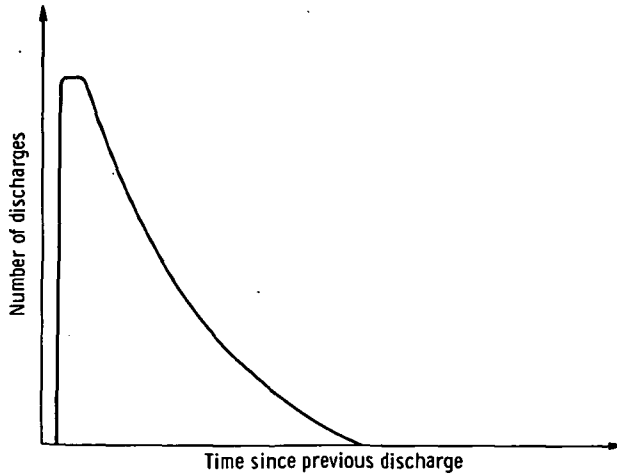


Figure 2. - Typical interval histogram for high-frequency stimulus.



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