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LOUDNESS FUNCTION DERIVED FROM DATA ON ELECTRICAL DISCHARGE RATES IN AUDITORY NERVE FIBERS

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16. Abstract

Judgments of the loudness of pure-tone sound stimuli yield a loudness function which relates perceived loudness to stimulus amplitude. In this report a loudness function is derived instead from physical evidence alone without regard to human judgments. The resultant loudness function is $\mathscr{L} = K(q - q_0)$, where $\mathscr{L}$ is loudness, q is effective sound pressure (specifically q_0 at the loudness threshold), and K is generally a weak function of the number of stimulated auditory nerve fibers. The predicted function is in agreement with loudness judgment data reported by Warren, which imply that, in the suprathreshold loudness regime, decreasing the sound-pressure level by 6 decibels results in halving the loudness.

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LOUDNESS FUNCTION DERIVED FROM DATA ON ELECTRICAL DISCHARGE RATES IN AUDITORY NERVE FIBERS

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SUMMARY

Judgments of the loudness of pure-tone sound stimuli yield a loudness function, or psychoacoustic "law," which relates perceived loudness to stimulus amplitude. In this report a loudness function is derived instead from physical evidence regarding the number of stimulated auditory nerve fibers and the electrical discharge rates in each fiber, without regard to human judgments. The physical evidence is combined with the assumption that loudness is proportional to the total "phase-locked" discharge rate above its threshold value. The resultant loudness function is $\mathscr{L} = K(q - q_0)$, where $\mathscr{L}$ is loudness, q is effective sound pressure (specifically q_0 at the loudness threshold), and K is generally a weak function of the number of stimulated fibers. The predicted function is in good agreement with loudness judgment data reported by Warren, which imply that, in the suprathreshold loudness regime, decreasing the sound-pressure level by 6 decibels results in halving the loudness.

As previously suspected, loudness is found to depend primarily on the total number of active fibers rather than on variations of the discharge rate per fiber averaged over the ensemble of active fibers as the stimulus amplitude is changed.

INTRODUCTION

It is well known that a sound stimulus (measured as pressure fluctuations) imposed on a listener induces impulsive electrical discharges (the "action" potentials) of constant amplitude in many of the 30 000, or so, individual fibers of the auditory nerve. These discharges advance along successive neurons toward the higher nervous system wherein an auditory sensation is induced. The magnitude of this auditory sensation is called loudness.

It has often been proposed that the electrical discharge rate induced in the auditory nerve by the sound stimulus is a measure of its loudness (refs. 1; 2, p. 302; 3, pp. 112, 263-272). Fletcher made a numerical estimate of the relation between electrical discharge rate and loudness level which yielded a function in fairly good agreement with contemporary psychoacoustic data relating loudness to loudness level (ref. 3, p. 271). A subsequent attempt by Zwislocki (ref. 4) was less successful. The fact that discharge rates in individual fibers, like the whole-nerve potential (the potential due to all fibers as measured by a macroelectrode), become saturated within sound-pressure ranges constituting only a small fraction of the total acoustic range has proved especially perplexing (refs. 2, p. 146, and especially p. 196f; 5; 6, p. 79; and 7). However, as shown in the following analysis, this phenomenon creates no difficulty in quantitatively relating psychoacoustic and electrophysiological observations.

Although the exact behavior of a given physiological system as it responds to physical stimuli might appear complex beyond the scope of any mathematical model, the essential features of the behavior can be approximated. A simple model is proposed which incorporates essential features of the relation between the physical (sound), electrophysiological (neural discharge), and psychoacoustic (loudness) observations for pure tones. The best argument for any model is, of course, its ability to correlate observational data while obeying known physical principles. It will be shown that, in this sense, the present model appears more successful than its predecessors.

LOUDNESS FUNCTIONS

Assume that a listener with "normal" hearing ability is exposed to a pure-tone sound stimulus in a manner intended to minimize psychological biases in judging loudness. The available data consist of the judged loudness $\mathscr{L}$ and neural discharge rates r for individual auditory nerve fibers as functions of the effective sound pressure $(\tilde{p^2})^{1/2}$ of the stimulus, where p is pressure and the time average, denoted by the tilde, is over the auditory integration time ($\approx$0.2 sec). Subjective judgments of loudness as a function of the stimulus sound pressure by listeners yield the well-known loudness function, or psychoacoustic "law,"

$$\mathscr{L} = k\left(\tilde{p^2}\right)^{\alpha} \tag{1}$$

for suprathreshold loudnesses, where k is a function of the tone frequency and $1/4 \leq \alpha \leq 1/2$ is a function of the experiment (e.g., refs. 7 to 12). (All symbols are defined in the appendix.) A more general, but less widely accepted, loudness function, which nevertheless satisfactorily represents available data for both suprathreshold and near-

threshold loudnesses and has some physical basis (ref. 7), is

$$\mathscr{L} = k\left[\left(\tilde{p}^2\right)^{\alpha} - \left(\tilde{p}_0^2\right)^{\alpha}\right] \tag{2}$$

where $\left(\tilde{p}_0^2\right)^{1/2}$ is the effective sound pressure at the loudness threshold (ref. 12).

In order to incorporate neural discharge rates in the model, mathematical relations between sound pressure and neural discharge rates are needed.

PHYSIOACOUSTIC FUNCTIONS

The relations between sound pressure and neural discharge rates, namely the physioacoustic functions, are determined from measurements on animals since data for human beings do not exist. The sound stimulus induces electrical impulses of constant amplitude (action potentials) to be transmitted along the individual fibers of the auditory nerve toward the brain. In general, the rate at which impulses are generated in each fiber is a function of the imposed sound pressure. The electrical response threshold and the dynamic response range (discharge rate strongly affected by stimulus magnitude) vary among the fibers. In its inactive state (no external stimulus imposed), each fiber may, or may not, conduct random spontaneous action potentials, which are often observed in the absence of a stimulus (ref. 6, ch. 8, p. 93ff). If the fiber exhibits spontaneous activity, the first indication of a threshold response to a stimulus is "phase-locking." That is, a correlation appears between the phase of the stimulus waveform and the occurrence of the originally spontaneous discharges without the discharge rate necessarily being affected (refs. 13 to 15). Even in the absence of the stimulus there may be, on the average, a very slight apparent phase-locking of the spontaneous discharges at possible stimulus frequencies simply because the spectrum of the spontaneous discharges may include the stimulus frequency. As the stimulus amplitude is increased the discharge pattern tends, upon summing discharges in each phase interval over repeated realizations of the waveform, to reproduce a partial-wave rectification of the original stimulus waveform (refs. 13 and 16). Phase-locking is detectable at all stimulus amplitudes for which there is a neural response and for all stimulus frequencies up to approximately 5 kilohertz (ref. 17), which includes the dominant frequencies in most sounds.

Electrical Discharge Rates in Individual Fibers

Much of the reported data on neural discharge rates exhibit insufficient regularity to be useful for theoretical purposes. Conceivably, for fibers with high spontaneous

discharge rates, this may result from failure to subtract the residual spontaneous discharge rate from the rate measured in the presence of a stimulus, especially at low stimulus amplitudes (ref. 13). Regularity is to be expected since the neural activity is an intermediary between the stimulus and the sensation, which exhibit a regular relation, as evidenced by equation (1). Exceptionally regular sets of rate data for typical individual nerve fibers in squirrel monkeys exposed to pure tones are presented in reference 13. In reference 13 these data are depicted as "spike" (impulse) rate as a function of sound-pressure level, where sound-pressure level S is defined by

$$S = 10 \log\left(\frac{\tilde{p}^2}{\tilde{p}^2_{ref}}\right) \tag{3}$$

with $\tilde{p}^2_{ref}$ a reference mean-square pressure corresponding to the loudness threshold for a 1-kilohertz tone; specifically, $\tilde{p}^2_{ref} = 4\times10^{-10}\ N^2/m^4$. The mathematical regularity of the data is not completely evident in the semilogarithmic plots in reference 13. The regularity usually becomes more evident by plotting the logarithm of the neural discharge rate r as a function of S, as shown in figure 1. Each curve shows the discharge rate for an individual fiber stimulated at its best, or characteristic, frequency (frequency of maximum sensibility). Clearly, each curve can be split into two segments. Each segment can be approximated mathematically by a numerical power law since each segment can be approximated by a straight line. Remarkably, the corresponding segments of each curve approximately satisfy the same, very special, power law. Specifically, for any given fiber denoted by the subscript j, the discharge rate r_j is given by

$$r_j = \begin{cases} \lambda_j\left(\tilde{p}^2\right)^{1/2} & \text{(lower stimulus amplitudes; dynamically active rate)} \quad (4a) \\ \left(\lambda_s\right)_j\left(\tilde{p}^2\right)^{0.03} & \text{(higher stimulus amplitudes; saturated rate)} \quad (4b) \end{cases}$$

where λ_j and $(\lambda_s)_j$ are proportionality constants. In the saturation range it will be assumed, because r_j is a weak function of $\tilde{p}^2$, that

$$r_j \equiv \left(r_s\right)_j = \text{Constant} \tag{5}$$

where $(r_s)_j$ is the discharge rate of the jth fiber when it is saturated. There is often a tendency for the discharge rate to decline slightly for the highest stimulation amplitudes. However, neglect of this effect is compatible with the assumption that $(r_s)_j$ is constant, which is, of course, not exactly true. It is important to note that, with regard to

equations (4) and (5), "lower" and "higher" are relative to the stimulus range, perhaps 40 decibels, over which the fiber displays a variable response. This is much less than the total acoustic amplitude range of hearing, which is approximately 120 decibels.

Equation (4a) is very special because it indicates that, for each fiber, the discharge rate at the lower stimulus amplitudes is proportional to the effective sound pressure $(\tilde{p^2})^{1/2}$. When similar plots of log r_j as a function of S are made using the data in figures 1, 2, 4, 5, 6, and 8 of reference 13, equations (4) generally represent the results satisfactorily, although the agreement is not always as good as that shown here in figure 1. However, in general, equations (4) provide a reasonable fit to the data, not only for stimulation at the characteristic frequency, but for stimulation at other frequencies as well. It is assumed that the activity in the vast majority of auditory nerve fibers in response to a tonal stimulus is typified by equations (4) and (5).

Number of Stimulated Fibers

Let N denote the total number of auditory nerve fibers which are capable of transmitting coherent (phase locked) electrical discharges to the higher nervous system in the presence of a given maximal tonal stimulus within the hearing range. For any lesser stimulus amplitude, the N fibers can be divided into three groups, namely, the group of inactive fibers, the group of dynamically active fibers, and the group of saturated fibers. In the absence of a stimulus, all fibers are defined to be inactive. The group of inactive fibers thus includes truly inactive fibers as well as spontaneously active fibers, which may, as already explained, exhibit some minimal apparent phase-locking at a stimulus frequency in the absence of the stimulus. The group of dynamically active fibers consists of those whose electrical activity obeys equation (4a). The group of saturated fibers includes those whose activity obeys equation (4b), which has been approximated by equation (5). Those fibers whose dynamic response thresholds are exceeded are designated simply as active fibers. Thus, the group of active fibers consists of both the dynamically active fibers and the saturated fibers.

The total number of active fibers and the relative numbers of dynamically active and saturated fibers are functions of the stimulus amplitude. The number density of active fibers at threshold as a function of sound-pressure level has been reported in reference 18. The results have been used to obtain the number distributions of active fibers presented logarithmically in figure 2. The curves in figure 2 show the number distributions of small samples of active fibers excited at their characteristic frequencies, rather than at a fixed stimulus frequency. (The characteristic frequency of the fiber, that is, the frequency which most readily activates the fiber, is determined by the location of the origin of its discharges along the basilar membrane within the cochlea.) However, the frequency bandwidth encompassed by each set of data is limited. The curves are similar

for widely differing frequency bands. There is no reason to believe they would be significantly different in shape if a single-frequency stimulus were employed and if all fibers were sampled, except that the dynamic segments of the curves would tend to extend over a greater dynamic range of the stimulus. The corresponding subdistributions of dynamically active and saturated fibers are unknown. As shown in figure 2, the number distributions of active fibers for different stimulus frequencies bear approximately the same remarkable relation to sound-pressure level as does the discharge rate for a single fiber. Specifically, if a denotes the total number of active fibers, then

$$a \approx \begin{cases} \mu\left(\overline{p^2}\right)^{1/2} & \text{(lower stimulus amplitudes)} \quad (6a) \\ \mu_s\left(\overline{p^2}\right)^{0.03} & \text{(higher stimulus amplitudes)} \quad (6b) \end{cases}$$

where μ and μ_s are proportionality constants associated with lower and higher acoustic amplitudes, respectively. Here "lower" and "higher" now refer to the total acoustic range of hearing (about 120 dB) rather than to the dynamic range of an individual fiber. Equations (6) yield essentially the same curve as that assumed by Fletcher (ref. 3, p. 264) on the basis of electrical discharge thresholds from nerve endings in the eye rather than in the ear. For the higher stimulus amplitudes it will be assumed that

$$a = N = \text{Constant} \tag{7}$$

The total number of fibers which can be activated is given by

$$N = i + a = i + d + s$$

where i is the number of inactive fibers, d is the number of dynamically active fibers, and s is the number of saturated fibers. The numbers i, d, and s depend upon the amplitude of the sound stimulus. Thus, equation (7) implies that, at the higher stimulus amplitudes, $i \rightarrow 0$, as it must since N includes only those fibers capable of being stimulated by the tone.

In conclusion, physical evidence implies that the simple equations (4a) and (5) may adequately represent the coherent discharge rate from a single fiber and that the equally simple equations (6a) and (7) may similarly represent the total number of fibers activated by the stimulus. In both cases the effective sound pressure of the stimulus is the independent parameter. With a few additional assumptions a simple model consistent with equations (4) to (7) can be constructed to represent the total coherent discharge rate R for an assemblage of N fibers as a function of the effective sound pressure $\left(\overline{p^2}\right)^{1/2}$.

Model for Total Coherent Discharge Rate R

The model for the electrical activity of auditory nerve fibers is shown in figure 3. Each individual fiber, denoted by the subscript j, is assumed to begin contributing coherent discharges at the same rate r_t in response to the sound stimulus when the effective sound pressure of the stimulus reaches the particular threshold value $(q_t)_j$ for the fiber. For brevity the symbol q is used to denote $\left(\overline{p^2}\right)^{1/2}$. The number j is assigned in the order of decreasing sensibility of the fibers; that is, j = 1 denotes the first fiber to become active, and j = N the last one, as the sound pressure is increased. The discharge rate in each fiber rises linearly as a function of q according to equation (4a) until the saturation rate is achieved, after which the discharge rate remains effectively constant, according to equation (5). Similarly, the number of active fibers also increases as a linear function of q, given by equation (6a), until all N fibers are active (cf. eq. (7)).

The simplifications involved in the model obviously preclude its being an exact representation of the system. However, its simplicity allows quantitative calculation of overall discharge rates throughout the acoustic range. The utility of the model will then depend on the degree to which predicted rates correspond to observed rates and on the extent to which implicit features of the model correspond to reality.

At the lower end of the sound-pressure range, where the total response results from a very small number of units, departures from the simplified model might produce answers noticeably different from those predicted. However, the departures are not likely to have serious consequences in predicting loudness because loudness judgments are also of low precision in this sound-pressure range. For greater sound pressures, where the active units number in the hundreds or thousands, it seems reasonable to expect that individual variations among units may average out, so that the model might be quite adequate if it is functionally sound. For example, in the model shown in figure 3 it is assumed that the order in which the fibers saturate is the same as the order in which they achieve the threshold of stimulation. Because the data in figure 1 show a tenfold variation of the saturation discharge rate r_s, the fibers may not, in fact, always saturate in the same order in which they achieve dynamic threshold. However, since the discharge rate for each fiber obeys equation (4a) and the threshold sound pressure over all fibers will be found to cover a range greater than 10^4, it is evident that, on the average, the fibers will saturate in the approximate order in which they achieve threshold stimulation.

For any given stimulus amplitude the total coherent discharge rate R in the presence of a sound stimulus equals the sum of the coherent discharge rates of all fibers. Hence,

$$R = \underbrace{\left[\sum_{\sigma} (r_i)_\sigma\right]_{inact}}_{\text{Inactive fibers}} + \underbrace{\left[\sum_{\sigma} (r_d)_\sigma\right]_{dyn}}_{\text{Dynamically active fibers}} + \underbrace{\left[\sum_{\sigma} (r_s)_\sigma\right]_{sat}}_{\text{Saturated fibers}} \tag{8}$$

where the subscripts i, d, and s refer to inactive, dynamically active, and saturated fibers, respectively. The coherent discharge rates of inactive fibers are likely to be small or zero and, hence, of possible significance only near the loudness threshold. The coherent discharge rate of each dynamically active fiber and of each saturated fiber is represented by equations (4a) and (5), respectively, as a function of the effective sound pressure of the stimulus. The incoherent discharge rate of each fiber presumably does not contribute to the loudness of the stimulating tone. Thus, it is emphasized that the total coherent discharge rate R represents the measured total discharge rate minus the total incoherent discharge rate (cf. ref. 17).

Let $\langle r \rangle$ denote the average discharge rate over an ensemble of fibers. Then, consistent with the proposed model, equation (8) becomes

$$R = i\langle r_i \rangle + d\langle r_d \rangle + s\langle r_s \rangle \tag{9}$$

in terms of products of numbers of fibers and their average discharge rates. These numbers and rates are to be expressed as functions of the effective sound pressure q.

The numbers of dynamically active and saturated fibers are evaluated first. Let the subscript t refer to conditions at the dynamic response threshold of a fiber. From equation (6a) it follows that the effective sound pressure at which the jth fiber becomes dynamically active is given by

$$(q_t)_j = \frac{j}{\mu} = j(q_t)_1$$

In particular,

$$\mu = \frac{1}{(q_t)_1}$$

The corresponding discharge rate at threshold is $(r_t)_j$, so that

$$\lambda_j = \frac{(r_t)_j}{(q_t)_j}$$

which follows from equation (4a). The effective sound pressure q_s at which the jth fiber becomes saturated is given by

$$(q_s)_j = \frac{(r_s)_j}{\lambda_j} = \frac{j}{\mu}\left(\frac{r_s}{r_t}\right)_j = j(q_t)_1\left(\frac{r_s}{r_t}\right)_j$$

which results from the preceding equations. Incidentally,

$$\left(\frac{q_s}{q_t}\right)_j = \left(\frac{r_s}{r_t}\right)_j$$

Assume on the average that with increasing sound pressure the fibers become saturated in the same order of occurrence as that in which they become dynamically active and that the values of r_t and r_s are the same for each fiber (see fig. 3). Then, if there exist any saturated fibers, it follows from the previous equation that the total number of saturated fibers s is approximated by

$$s = \left(\frac{r_t}{r_s}\right)\mu q = \left(\frac{r_t}{r_s}\right)\frac{q}{(q_t)_1} \qquad (1 \leq s < N) \tag{10}$$

Since $a = d + s$, it follows that the total number of dynamically active fibers is approximated by

$$d = a - \left(\frac{r_t}{r_s}\right)\mu q = \left(1 - \frac{r_t}{r_s}\right)\frac{q}{(q_t)_1} \qquad (1 \leq s < N) \tag{11}$$

when some fibers are saturated. Equations (10) and (11) constitute the required expressions for the numbers of fibers in the saturated and dynamically active groups, respectively, as functions of q.

Next, the discharge rates are evaluated. There is considerable variation of discharge rates among individual inactive and saturated fibers. Apparently, fibers with greater sensibility at their characteristic frequency possess greater spontaneous discharge rates (ref. 13). However, coherent spontaneous rates are generally very small relative to coherent active rates, so that r_i can be replaced by $\langle r_i \rangle$, in conformity with the proposed model. With regard to saturated discharge rates r_s, note that $\langle r_s \rangle \geq \langle r_d \rangle$ are of the same order of magnitude when fibers begin to saturate; and $r_t \ll r_s$. Also, $a < N$ until all fibers are active. Considering these conditions, it is apparent from equations (9) to (11) that the number s of saturated fibers does not significantly affect the total discharge rate R until s becomes of the same order as the number d of dynamically active fibers. This occurs only when the effective sound pressure q is very large in comparison with the threshold value $(q_t)_1$ at which the first

fiber becomes dynamically active. Therefore, r_s only affects R significantly when s, and hence q, is large. For this reason, in equations (10) and (11), r_s may be replaced by the ensemble average $\langle r_s \rangle$ over s fibers without appreciably changing the value of R. This is also in accordance with the proposed model.

It is apparent from the data of reference 13 that the saturation discharge rate for each fiber depends on the stimulus frequency. Moreover, it appears that the saturation discharge rate is not a function of the sensibility of the fiber at the stimulus frequency. This was found by plotting discharge rate as a function of sound pressure for a given stimulus frequency, using data for several fibers from reference 13. Each curve looked like those in figure 1 with no systematic change in saturation discharge rate for decreased fiber sensibility. Hence, it may be assumed that $\langle r_s \rangle$ is independent of q.

The average discharge rate $\langle r_d \rangle$ among the dynamically active fibers is a function of the number d of dynamically active fibers since both r_d and d are functions of q. By definition and by virtue of equation (4a),

$$\langle r_d \rangle = \left(\frac{1}{d}\right)\left[\sum_{\sigma} (r_d)_\sigma\right]_{dyn} = \left(\frac{q}{d}\right)\left[\sum_{\sigma} \lambda_\sigma\right]_{dyn}$$

Hence,

$$\langle r_d \rangle = \langle \lambda \rangle q$$

However, $\langle \lambda \rangle$ is also a function of q since each fiber generally has a different sensibility to a stimulus and since the number of dynamically active fibers is a function of q (cf. eq. (6)). The preceding equation can be rewritten as

$$\langle \lambda \rangle = \frac{\langle r_d \rangle}{q} = \left(\frac{1}{d}\right)\left[\sum_{\sigma} \frac{(r_d)_\sigma}{\hat{q}}\right]_{dyn}$$

Here $\langle \lambda \rangle$ is determined by summing rates r_d over the ensemble of dynamically active fibers for fixed $q \equiv \hat{q}$. Alternatively, $\langle \lambda \rangle$ can also be determined by summing effective sound pressures q over the same ensemble of fibers for a fixed discharge rate, $r_d \equiv \hat{r}_d$. The preceding expression for $\langle \lambda \rangle$ is equivalent to

$$\langle \lambda \rangle = \left(\frac{1}{d}\right)\left[\sum_{\sigma}\left(\frac{\hat{r}}{q_\sigma}\right)\right]_{dyn} = \frac{\hat{r}}{d}\left[\sum_{\sigma}\left(\frac{1}{q_\sigma}\right)\right]_{dyn} = \hat{r}\left\langle\frac{1}{q}\right\rangle_{dyn}$$

The average over r for fixed q has been replaced by the equivalent average over 1/q

for fixed r. This is permissible because, for each fiber, r(q) is linear. If one sets $\hat{r} = r_t$, then, since $1/(q_t)_j = \mu/j$ for the jth fiber, it follows that

$$\langle\lambda\rangle = r_t\left\langle\frac{1}{q_t}\right\rangle_{dyn} = \left(\frac{\mu r_t}{d}\right)\sum_{\sigma=1+s}^{d+s}\left(\frac{1}{\sigma}\right) = \left(\frac{\mu r_t}{d}\right)g(d,s)$$

where

$$g(d,s) \equiv \sum_{\sigma=1+s}^{d+s}\left(\frac{1}{\sigma}\right) = \sum_{\sigma=1}^{d+s}\left(\frac{1}{\sigma}\right) - \sum_{\sigma=1}^{s}\left(\frac{1}{\sigma}\right)$$

$$= g(d+s,0) - g(s,0) \tag{12}$$

If $s = 0$, $g(0,0) = 0$ and

$$g(d,0) \equiv \sum_{\sigma=1}^{d}\left(\frac{1}{\sigma}\right) \approx \ln d + C + \left(\frac{1}{2d}\right) - O(d^{-2}) \tag{12a}$$

is a weakly increasing function of d, hence of q, and $C = 0.577$ is Euler's constant (ref. 19). (For example, if $d = 1$, then $g(d,0) = 1$; whereas, if $d = 10^4$, then $g(d,0) \approx 10$.) For $s \neq 0$ and $a < N$, equations (12), (12a), (10), and (11) yield

$$g(d,s) \approx \ln\left(\frac{d+s}{s}\right) \approx \ln\left(\frac{\langle r_s\rangle}{r_t}\right) \tag{12b}$$

whereas for $a = N$, they yield

$$g(d,s) \approx \ln\left(\frac{N\langle r_s\rangle}{\mu r_t}\right) - \ln q \tag{12c}$$

Finally, when expressed as a function q, the average discharge rate of the dynamically active fibers is then found to be given by

$$\langle r_d\rangle = \left(\frac{r_t}{d}\right)g(d,s)\mu q \tag{13}$$

Equations (9) to (13) can be combined to yield an expression for the total discharge rate R as a function of the effective sound pressure q in each of four nontrivial subranges shown in figure 4. In order of increasing stimulus amplitude these subranges and the resulting formulas for R are as follows:

(1) Dynamically active subrange I ($(q_t)_1 \leq q < q_a$): Some fibers are dynamically

active, but none are saturated. In this range $d = a = \mu q$ (cf. eq. (6a)). Also, $i = N - a$ and $s = 0$, so that equation (9) reduces to

$$R = a\left(\langle r_d \rangle - \langle r_i \rangle\right) + N\langle r_i \rangle \tag{14a}$$

or, in terms of q,

$$R = \left[r_t g(d, 0) - \langle r_i \rangle\right] \mu q + N\langle r_i \rangle \tag{14b}$$

Because $g(d, 0)$ is a weak function of q, it is concluded that R is an almost-linear function of q. At the lower limit of this subrange, that is, at $q = (q_t)_1$,

$$R = N\langle r_i \rangle$$

whereas at the upper limit, $q = q_a = \langle r_s \rangle / \mu r_t$ (cf. eq. (10)), so that

$$R = \left[r_t g(d_a, 0) - \langle r_i \rangle\right] \mu q_a + N\langle r_i \rangle \tag{15}$$

where $d = d_a$ at $q = q_a$.

(2) Active subrange II ($q_a \leq q \leq q_b$): Some fibers are dynamically active, and some are saturated. By introducing equations (6a), (10), (11), and (13) and the relation $i = N - a$ into equation (9), the expression for R as a function of q is found to be

$$R = \left\{r_t[g(d, s) + 1] - \langle r_i \rangle\right\} \mu q + N\langle r_i \rangle \tag{16}$$

where, in this range, $g(d, s)$ is independent of q (cf. eq. (12b)). Hence, R is a linear function of q. For $q = q_a$ this reduces to equation (15) because $g(d, s) = g(a - 1, 1) = g(a, 0) - 1$, and $a = d_a$. At the upper limit of this subrange, that is, at $q = q_b = N/\mu$,

$$R = r_t[g(d_b, s_b) + 1] \mu q_b \tag{17}$$

where

$$d_b = N - \left(\frac{r_t}{\langle r_s \rangle}\right) \mu q_b = N\left(1 - \frac{r_t}{\langle r_s \rangle}\right) \quad \text{(cf. eq. (11))}$$

and

$$s_b = \left(\frac{r_t}{\langle r_s \rangle}\right) \mu q_b = \frac{N r_t}{\langle r_s \rangle} \quad \text{(cf. eq. (10))}$$

Thus far, it has been assumed that, as the stimulus amplitude is increased, the number of active fibers increases. Eventually, an amplitude is reached for which no more fibers can be activated.

(3) Fiber saturation subrange III ($q_b \leq q < q_c$): All fibers are active. This implies that $a = N$ and $i = 0$. Otherwise, proceeding as in the case of subrange II, equation (9) reduces to

$$R = r_t[g(d, s) + 1]\mu q \tag{18}$$

in which R is again an almost-linear function of q (cf. eq. (12c)). For $q = q_b = N/\mu$, equation (18) specializes to equation (17). At the upper limit of this subrange, $q = q_c = (N/\mu)(\langle r_s \rangle / r_t)$ and

$$R = N\langle r_s \rangle \tag{19}$$

because

$$g(d, s) \rightarrow g(1, N - 1) = \sum_{\sigma=N}^{N} \left(\frac{1}{\sigma}\right) = \frac{1}{N} << 1$$

$$r_t \mu q = s\langle r_s \rangle \qquad \text{(cf. eq. (10))}$$

and

$$s \approx N$$

(4) Fiber- and rate-saturation subrange IV ($q_c \leq q$): In the limit when all available fibers are saturated, $s = N$ and $d = \langle r_d \rangle = 0$, so that equation (9) reduces to

$$R = N\langle r_s \rangle = \text{Constant} \tag{20}$$

in agreement with equation (19) at $q = q_c$. Now, R is independent of q.

These and subsequent results are summarized in table I for all subranges.

The preceding physioacoustic functions relate the total discharge rate R to the effective sound pressure $q \equiv \left(\tilde{p}^2\right)^{1/2}$. The analysis indicates that R is an almost-linear, increasing function of q, except at the highest stimulus amplitudes, where R is constant. The transitions between the four ranges are smooth.

ACOUSTIC PSYCHOPHYSIOLOGIC FUNCTION

The psychoacoustic and physioacoustic functions may now be combined to yield an acoustic psychophysiologic function which relates the total neural discharge rate R to the loudness $\mathscr{L}$. Alternatively, a simple acoustic psychophysiologic function can be assumed on the basis of physical principles. It can, then, be shown that this function, when combined with the preceding physioacoustic functions, leads to the psychoacoustic equations (1) and (2) plus an additional psychoacoustic function for the highest stimulus amplitudes within the acoustic range. This alternative approach is used herein.

Equation (1) is empirical (refs. 8 and 9). The only derivation of equation (2) uses equation (1) plus empirical relations among loudness, whole-nerve action potentials, and the mean-square sound pressure (ref. 7). (The whole-nerve action potential consists of a weighted sum of the impulsive action-potential discharges over all fibers at any instant, as determined by using a gross (or macro) electrode in contact with the nerve.) It is shown in reference 7 in a very crude analysis that the loudness of a pure-tone stimulus is given by equation (2) herein if the empirical formula $\Phi \propto P^{2\alpha}$ relating the whole-nerve action-potential amplitude Φ to the sound-pressure amplitude P is combined with the assumption that loudness is proportional to the excess amplitude of this potential relative to its value at the loudness threshold. (Incorporating time integration should only change the proportionality constant in the case of a pure-tone stimulus.) Unfortunately, because this potential formula results from an instantaneous weighted sum of action potentials over all auditory nerve fibers (because a gross electrode cannot contact all fibers), its observed range (50 or 60 dB) is far less than the sound-pressure level range (120 dB) associated with loudness variability.

This weighting effect associated with gross potential measurements can be overcome by more detailed measurements, using microelectrodes, of action potentials from individual fibers. The total discharge rate R measured over all auditory nerve fibers is proportional to a time-averaged, unweighted, action potential, since each potential impulse possesses the same amplitude. Hence, the assumed psychophysiologic function based on whole-nerve measurements (ref. 7) can be replaced by the more fundamental acoustic psychophysiologic function

$$\mathscr{L} = \kappa(R - R_0) \tag{21}$$

based on single-unit (fiber) measurements, where R_0 represents the total coherent discharge rate at the loudness threshold, and κ is a constant. The loudness threshold, of course, differs from the dynamic thresholds of individual fibers, denoted by the subscript t.

Equation (21) indicates that, for a pure-tone sound stimulus, loudness is proportional to the excess total coherent discharge rate over its coherent value at the loudness

threshold. Throughout the greater portion of the loudness range, $R \gg R_0$, so that, except in the vicinity of the loudness threshold, $\mathscr{L} \approx \kappa R$. The idea that loudness is proportional to the total discharge rate has been commonly suspected for many years (e.g., ref. 2, p. 302; ref. 3, pp. 263-272).

LOUDNESS FUNCTION DERIVED FROM TOTAL NEURAL DISCHARGE RATE

When the preceding physioacoustic functions for each stimulus subrange are inserted in equation (21), new loudness functions result.

Dynamically Active Subrange I ($q_0 \leq q < q_a$)

The loudness threshold determines the lower bound of this subrange. At the loudness threshold, denoted by the subscript "0," $q_0 \geq (q_t)_1$, and equation (14b) becomes

$$R_0 = \left[r_t g(d_0, 0) - \langle r_i \rangle\right] \mu q_0 + N\langle r_i \rangle$$

By combining this with equations (14b) and (21), the result is

$$\mathscr{L} = \kappa\left\{\left[r_t g(d, 0) - \langle r_i \rangle\right] \mu q - \left[r_t g(d_0, 0) - \langle r_i \rangle\right] \mu q_0\right\}$$

Now $r_t g(d, 0) > r_t g(d_0, 0) \gg \langle r_i \rangle$. Hence, the resultant loudness function is found to be

$$\mathscr{L} = \kappa r_t \mu g(d, 0)\left[q - q_0 + \frac{g(d, 0) - g(d_0, 0)}{g(d, 0)} q_0\right] \tag{22}$$

At the loudness threshold, $d_0 \geq 1$ fiber. If the total range of R is to correspond to the known range of $\mathscr{L}$ (cf. eq. (21)), d_0 must be small. Suppose $d_0 \leq 10$ fibers. Then, since $d \propto q$ in subrange I (cf. eq. (6a)) and this subrange is found experimentally to be of the order of 40 decibels or less (see, e.g., refs. 7, 11, and 12), the corresponding total subrange of $g(d, 0)$ is about 2 or 3 in comparison with a total subrange of q of the order of 100. Hence, $g(d, 0)$ is a weak function of q. The third term in equation (22) is negligible because

$$\frac{g(d, 0) - g(d_0, 0)}{g(d, 0)} \to 0$$

as $d \to d_0$, that is, near the loudness threshold; whereas $q \gg q_0$ as

$$\frac{g(d,0) - g(d_0,0)}{g(d,0)} \rightarrow 1$$

that is, near the upper limit of the subrange. Hence, there results an approximate formula

$$\mathscr{L} = k(d)(q - q_0) \tag{23}$$

for the loudness function, where

$$k(d) = \kappa r_t \mu g(d,0) \tag{24}$$

is a weakly increasing function of d, and hence of q.

As the upper limit of this subrange is approached, $q >> q_0$, so that

$$\mathscr{L} \rightarrow k(d)q \tag{25}$$

Equation (23) has the same form as the loudness function chosen by Lochner and Burger (ref. 12) to fit loudness judgment data, except that their mean-square pressure exponent is 0.27, rather than 1/2. Equation (23) was also derived in reference 7 by using electrophysiological data for the whole nerve.

Active Subrange II ($q_a \leq q \leq q_b$)

When equations (16) and (21) are combined with the preceding expression for R_0, the result is

$$\mathscr{L} = \kappa\left(\left\{r_t[g(d,s) + 1] - \langle r_i \rangle\right\}\mu q + N\langle r_i \rangle - \left[r_t g(d_0,0) - \langle r_i \rangle\right]\mu q_0 - N\langle r_i \rangle\right)$$

Now $r_t[g(d,s) + 1] > r_t g(d,0) > r_t g(d_0,0) >> \langle r_i \rangle$, so that

$$\mathscr{L} = \kappa\left\{r_t[g(d,s) + 1]\mu q - r_t g(d_0,0)\mu q_0\right\}$$

However, in this range $q >> q_0$. Therefore,

$$\mathscr{L} = K(d,s)q \tag{26}$$

where

$$K(d,s) = \kappa r_t \mu[g(d,s) + 1] \tag{27}$$

Equation (26) has the same form as a commonly accepted loudness function (ref. 9), except that the exponent of the mean-square pressure is now 1/2, rather than 0.3. The

loudness is an almost linear function of the effective sound pressure q. As $q \to q_a$, $K(d, s) \to k(d)$, and equation (26) approaches equation (25) (since $q_a >> q_0$).

The preceding derivation implies that $R >> R_0$, so that equation (21) can be approximated by

$$\mathscr{L} = \kappa R$$

in this and all subsequent subranges.

Fiber Saturation Subrange III ($q_b \leq q < q_c$)

Equations (18) and (21) combine to yield

$$\mathscr{L} = K(d, s)q \tag{26}$$

which is the same result as in subrange II, and where $K(d, s)$ is given by equation (27). For $q \to q_c$, equation (26) reduces to

$$\mathscr{L} \to K(1, N - 1)q_c$$

where $K(1, N - 1) \approx \kappa r_t \mu$ because $g(d, s) = g(1, N - 1) << 1$ in equation (27).

Fiber- and Rate-Saturation Subrange IV ($q_c \leq q$)

Equations (20) and (21) combine to yield

$$\mathscr{L} = K(0, N)q_c = \text{Constant} \tag{28}$$

because, in equation (20), $s = N = (r_t/\langle r_s \rangle)\mu q_c$, and $K(0, N) = \kappa r_t \mu$.

In summary, the assumed acoustic psychophysiologic function (eq. (21)) and the empirical physioacoustic functions combine to yield the psychoacoustic function (cf. eq. (2)),

$$\mathscr{L} = K(d, s)\left[\left(\tilde{p}^2\right)^{1/2} - \left(\tilde{p}_0^2\right)^{1/2}\right] \tag{29}$$

where

$$K(d, s) = \kappa r_t \mu[g(d, s) + 1] \tag{27}$$

and

$$g(d,s) \equiv \sum_{\sigma=1+s}^{d+s} \frac{1}{\sigma} \tag{12}$$

These results should be valid throughout the loudness range, except possibly very near the loudness threshold. The loudness $\mathscr{L}$ is an almost-linear function of the effective sound pressure $\left(\overline{p^2}\right)^{1/2} \equiv q$ throughout nearly the entire dynamic range of loudness. At higher sound pressures, when both the number of active fibers and the discharge rate in each fiber reach saturation, loudness is found to be independent of sound pressure. These results are based on an assumed psychophysiologic relation and physical measurements rather than on relatively inaccurate human loudness judgments, the usual basis for the loudness function.

QUANTITATIVE REPRESENTATION OF LOUDNESS FUNCTION

The results of the preceding analysis permit a quantitative determination of the loudness function, as follows:

The unit of loudness is the sone, which is defined as the loudness of a 1-kilohertz tone imposed frontally on a listener as progressive plane waves at a sound-pressure level of 40 decibels. Any other equally loud sound also has a loudness of 1 sone. From equation (3) it follows that a 1-kilohertz tone has a loudness of 1 sone if $q = 2\times10^{-3}$ N/m^2, where $q_{ref} = 2\times10^{-5}$ N/m^2. Note that $q >> q_{ref}$ when the loudness is 1 sone. From this and equation (29) the loudness of the tone relative to 1 sone is given by

$$\mathscr{L} = 5\times10^2 \frac{K(d,s)}{K_1(d,s)} (q - 2\times10^{-5}) \tag{30}$$

where $K = K_1$ when $\mathscr{L} = 1$ sone. Equation (30), which is dimensionless but yields numerical values equal to the loudness in sones, eliminates the necessity for evaluating the psychoacoustic conversion factor κ in equation (27). Hence, equation (30) expresses the loudness solely in terms of physical quantities.

The appropriate expression for K in terms of numbers of fibers, or of the sound pressure, is a function of the subrange. The subranges can be related to the sound-pressure level. Thus, at the lower limit of the active subrange II, there must exist one saturated fiber. Hence, at this limit, $\mu q_a \approx \langle r_s \rangle / r_t \approx 50$ (cf. eq. (10)) if it is assumed that $\langle r_s \rangle \approx 1.5\times10^2$ coherent discharges per second (ref. 13) and that $r_t \approx 3$ coherent discharges per second. (The selected value of r_t is based on the fact that near the loudness threshold the integration time of the auditory system is of the order of 0.5 second (ref. 20, p. 358). Moreover, the sensation of pitch is detectable after only one or

two cycles of stimulation (ref. 20, p. 554). Near threshold, only one coherent discharge might occur within one cycle of stimulation. Thus, a minimum of only one or two coherent discharges occurring repetitively within successive auditory integration periods should be sufficient to produce a continuous sensation of pitch.) The data of reference 18 in figure 2 indicate that $\mu = a/q \approx 5\times10^4\ m^2/N$ for a 1-kilohertz tone at the lower sound pressures (dynamic range). Hence, $q_a \approx 50/\mu \approx 10^{-3}\ N/m^2$, so that $q_a/q_{ref} \approx 50$, which corresponds to a sound-pressure level $S_a \approx 34$ decibels at the lower limit of subrange II. This, of course, is also the upper limit of the dynamically active subrange I. Since $S_a < 40$ decibels (for which the loudness = 1 sone), K_1 must be given by equation (27) with $s \neq 0$.

Assume that K_1 is in subrange II. Then,

$$K_1 = \kappa r_t \mu \left[\ln\left(\frac{\langle r_s\rangle}{r_t}\right) + 1\right] \approx 5\kappa r_t \mu$$

because $g(d,s) \approx \ln(\langle r_s\rangle/r_t) \approx 3.9$, since $s \neq 0$. Therefore, equation (30) may be rewritten in the approximate form

$$\mathscr{L} = 10^2[g(d,s) + 1](q - 2\times10^5) \tag{31}$$

Equations (30) and (31) can be used to obtain simple approximate formulas for loudness in each subrange.

(1) <u>Dynamically active subrange I ($0 \leq S \leq 34$ dB)</u>: Equation (31) becomes

$$\mathscr{L} = 10^2(\ln q + 12.4)(q - 2\times10^{-5}) \tag{32a}$$

because $g(d,s) + 1 \approx \ln d + 1.6 = \ln q + \ln \mu + 1.6$ when $s = 0$.

At the upper limit of subrange II, $q_b = N/\mu = 0.6\ N/m^2$ if $N = 3\times10^4$ fibers (see Discussion). Therefore, at the upper limit of subrange II, $S_b = 90$ decibels, which is obtained by using equation (3).

(2) <u>Active subrange II (34 dB $\leq S \leq$ 90 dB)</u>: Equation (30) reduces to

$$\mathscr{L} = 5\times10^2\ q \tag{32b}$$

since in this subrange $K(d,s) = K_1(d,s) = \text{Constant}$ and $q >> q_0$. Note that equation (32b) applies over much of the normal range of hearing.

At the upper limit of subrange III, $q_c = N\langle r_s\rangle/\mu r_t = 30\ N/m^2$. Therefore, $q_c/q_0 \approx 10^6$, so that $S_c \approx 120$ decibels.

(3) Fiber saturation subrange III (90 dB $\leq$ S < 120 dB): Equation (31) becomes

$$\mathscr{L} = 10^2(4.4 - \ln q)q \tag{32c}$$

since $g(d,s) \approx \ln(N\langle r_s\rangle/r_t\mu) - \ln q = 3.4 - \ln q$.

(4) Fiber- and rate-saturation subrange IV (120 dB $\leq$ S): Equation (30) reduces to

$$\mathscr{L} = 10^2\, q_c = 3\times10^3 \tag{32d}$$

since, in this subrange, $K(d,s)/K_1(d,s) = K(0,N)/K_1(d,s) = 1/5$, and $q_c = 30\ N/m^2$. Thus according to equation (32d) the maximum achievable loudness is approximately 3000 sones.

The quantitative loudness function indicated by equations (32) is displayed in figure 5. This theoretical curve is in excellent agreement, except for sound-pressure levels greater than 80 decibels, with that obtained by Fletcher (ref. 3, p. 271), which was based on similar assumptions but utilized different data in a different analysis. Fletcher's curve (fig. 171 in ref. 3) is presented in figure 5 as well. (In comparing Fletcher's curve, note that, for a 1-kilohertz tone, loudness level equals sound-pressure level.) Over the greater portion of the suprathreshold loudness regime, decreasing the sound-pressure level by 6 decibels results in halving the loudness. This is in contrast with the commonly accepted value of 9 or 10 decibels for loudness halving (ref. 3, p. 192; 9). Loudness judgment data from 720 subjects reported by Warren (ref. 21) are also shown in figure 5. Experimental biases in previous studies have presumably been eliminated in obtaining these data. Warren's data consist of "standard," sound-pressure levels (which have been chosen to lie on the theoretical curve) of 1-kilohertz tones paired with sound-pressure levels of "comparison," 1-kilohertz tones judged to be one-half as loud as the standards. The 95 percent confidence limits of the comparison tones are also shown. The theoretical curve nearly always lies within these limits.

DISCUSSION

At the highest stimulus levels for a given discharge-rate curve (cf. fig. 1), the discharge rate of a given fiber sometimes tends to decline. This decline would tend to cause a diminution of loudness. A diminution of loudness has been observed at low frequencies (ref. 20, p. 264). However, the discharge-rate data are not sufficient to determine the rate of decrease of the discharge rate. Moreover, the actual measured decrease is within the saturation range given by equation (5) in which $(r_s)_j$ was assumed to be constant. Hence, the possible diminution of loudness at high stimulus amplitudes has

not been incorporated in the present model.

In subrange I, $d = a = \mu q$; and $g(d, 0)$ is essentially a logarithmic function, that is, a weak function, of d for $d > 1$. Hence, by virtue of equation (13), $\langle r_d \rangle$ is a weak function of d. Therefore, by virtue of equation (14a), R is an explicit function of d and a weak implicit function of d through $\langle r_d \rangle$. Similarly, in subranges II and III, $\langle r_d \rangle$ is a weak function of d and s and, hence, R is a weak implicit function of d and s through $\langle r_d \rangle$. In subrange IV, R is, of course, independent of d and s. Therefore, throughout the entire acoustic amplitude range, the total discharge rate R and the loudness $\mathscr{L}$ are affected principally by variations of the number of active fibers and only weakly by variations of the ensemble average $\langle r \rangle$ of discharge rates over all the active fibers.

The behavior predicted by the model might appear to be contradicted by the data in figure 2. The calculation of q_c implies that q_c corresponds to 90 decibels, whereas the data in figure 2 seem to imply a value of only about 40 decibels. It should be noted, however, that figure 2 illustrates the number distribution function for a small sample of fibers, each stimulated at its best frequency. In the model, on the other hand, a set of N fibers is assumed which includes all those capable of responding to a given stimulus frequency. Consequently, it includes fibers whose characteristic frequencies are far removed from that of the stimulus. Their dynamic response thresholds are raised correspondingly. These two factors, namely the sampling of all N fibers and the raised thresholds, account for the difference between the theoretical and experimental ranges. Clearly, data are needed on the number density over all fibers at dynamic threshold as a function of sound pressure for a fixed-frequency stimulus, preferably a 1-kilohertz stimulus.

The detailed loudness values arising from the model are obviously dependent to some extent on the assumption as to the fraction of the total number of fibers responsive to the given stimulus and the values taken for r_s and r_t. When they are represented by equations (6), the two segments of the active-number-distribution curve for the eye used in Fletcher's theory (ref. 3, p. 264) intercept in the neighborhood of $a/N = 1$, $S = 84$ decibels. If it is assumed that only one-half of the total number of fibers can be stimulated by a 1-kilohertz tone, then in the present model, $N \approx 1.5 \times 10^4$, so that $S_b = 84$ decibels, in agreement with the curve assumed by Fletcher. In addition, since r_t cannot be determined precisely, it is reasonable to assume that $r_t \approx 1.5$ coherent discharges per second, so that $S_c \approx 120$ decibels, as before. However, then $S_a = 40$ decibels, rather than 34 decibels. The effects of these adjustments on the theoretical loudness function shown in figure 5 are negligible.

The various published values of the exponent α in the loudness function (eq. (1)) often appear to be functions of artifacts in various psychoacoustic experiments (ref. 21). By virtue of the present theory, there are now three independent reasons for believing

that $\alpha = 1/2$. Firstly, loudness judgment tests by Warren (ref. 21), in which all known artifacts in previous tests were presumably eliminated, yielded $\alpha = 1/2$. The present theory, which incorporates the electrophysiological measurements of references 13 and 18, also shows, without consideration of psychoacoustic tests, that $\alpha = 1/2$ and, hence, that loudness is proportional to effective sound pressure over a large part of the dynamic response range of hearing. Finally, Fletcher's earlier theory (ref. 3, pp. 263-272) leads to the same result.

The subjective judgment of loudness ratios is very difficult. This is well illustrated, for example, by Warren's data (ref. 21), as well as by those of Stevens and Guirao (ref. 22). Judged loudness ratios have always been used to determine α. The assumption $\alpha = 1/2$ attaches physical significance to loudness which is missing with other proposed values of α. Thus, in the suprathreshold regime it would seem more reasonable to let selected physical stimulus ratios define psychological loudness ratios, rather than the reverse. In other words, the listener would be exposed to a tone at two amplitudes differing by 6 decibels and would be told that one sound is twice as loud as the other. All subsequent judgments would be based on this initially defined observation.

Warren and Sersen (ref. 23) and Warren (ref. 24) theorized that a listener's loudness judgments are based upon his experience in estimating how the sensation varies with his distance from the sound source. In concurrence with this theory they found that halving the loudness corresponds approximately to a 6-decibel decrease in sound-pressure level. In contrast Stevens (ref. 25) rejected this proposition on the basis that, in his opinion, loudness is determined by the operational characteristics of the auditory system and that other judgment tests indicate that a 10-decibel decrease in sound-pressure level corresponds to halving the loudness. Warren (ref. 24) agreed that if loudness, and not distance, is primary, then it should be possible to establish neurophysiological functions related quantitatively to the psychophysical functions. Such functions have been derived in this report. Hence, the present model supports Stevens' thesis. On the other hand, the loudness function predicted in this report quantitatively agrees with the function found from loudness judgments by Warren. The fact that the two functions agree results from the very special operational characteristics of the neural system (eqs. (4) and (6)).

CONCLUSIONS

On the basis of published electrophysiological data from the auditory nerve, a model was proposed which yields a loudness function not dependent on human loudness judgment tests but which does agree with loudness judgment tests reported by Warren. The following specific results were obtained:

1. Electrophysiological data of Rose, Hind, Anderson, and Brugge indicate that over the lower response ranges of individual auditory nerve fibers the action-potential

discharge rates are proportional to the effective (rms) sound pressure of a sinusoidal sound stimulus, whereas over the higher response ranges the discharge rates are essentially independent of sound pressure.

2. Electrophysiological data of Katsuki, Suga, and Kanno indicate that over the lower range of subjective response to a sinusoidal sound stimulus the total number of stimulus-activated, auditory-nerve fibers is proportional to the effective sound pressure, whereas over the higher range of response the total number of activated fibers is essentially independent of sound pressure.

3. It was shown by using a model consistent with the preceding data, that, throughout the dynamic range of hearing, the total neural discharge rate in the auditory nerve is an almost linear function of the effective sound pressure, except near the threshold of feeling, where the total discharge rate becomes independent of sound pressure. These functions were designated herein as physioacoustic functions.

4. By assuming that the loudness of a pure tone is proportional to the difference between the total coherent discharge rates with and without the stimulus, the loudness function was found to be approximated by

$$\mathscr{L} \approx 10^2(\ln q + 12.4)(q - 2\times10^{-5}) \qquad (0 \leq S \leq 34 \text{ dB})$$

$$\mathscr{L} \approx 5\times10^2\, q \qquad (34 \text{ dB} \leq S \leq 90 \text{ dB})$$

$$\mathscr{L} \approx 10^2(4.4 - \ln q)q \qquad (90 \text{ dB} \leq S < 120 \text{ dB})$$

$$\mathscr{L} \approx 3\times10^3 \qquad (120 \text{ dB} \leq S)$$

where $q \equiv \left(\overline{p^2}\right)^{1/2}$ is the effective sound pressure. The formulas are displayed graphically in this report. Over its range the second equation implies that decreasing the sound-pressure level by 6 decibels results in halving the loudness.

5. Loudness was found to be dependent primarily on variations in the total number of active fibers rather than on variations of the discharge rate per fiber averaged over the ensemble of active fibers.

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APPENDIX - SYMBOLS

a	number of active fibers
C	Euler's constant, 0.577
d	number of dynamically active fibers
$g(d, 0)$	$\approx \ln d + C + (1/2d) - O(d^{-2})$
$g(d, s)$	$\equiv \sum_{\sigma=1+s}^{d+s} (1/\sigma)$
i	number of inactive fibers
j	integer number of fiber
$K(d, s)$	proportionality function in loudness function for higher stimulus amplitudes
$K_1(d, s)$	value of $K(d, s)$ when loudness is 1 sone
$k(d)$	proportionality function in loudness function
$\mathscr{L}$	loudness
N	total number of fibers available for activation
O	order
P	pressure amplitude
p	instantaneous sound pressure
$\left(\tilde{p^2}\right)^{1/2} \equiv q$	effective sound pressure
$\left(\tilde{p^2_{ref}}\right)^{1/2} \equiv q_{ref}$	effective sound pressure corresponding to loudness threshold of 1-kHz tone, 2×10^{-5} N/m^2
$q \equiv \left(\tilde{p^2}\right)^{1/2}$	effective sound pressure
R	total coherent, action-potential discharge rate over all fibers
r	coherent, action-potential discharge rate in individual fiber
r_d	coherent discharge rate in dynamically active fiber
r_i	coherent discharge rate in inactive fiber
r_s	coherent discharge rate in saturated fiber

S	sound-pressure level
s	number of saturated fibers
α	exponent in loudness function
κ	proportionality constant in acoustic psychophysiologic function
λ	proportionality constant in discharge-rate equation for dynamic range
λ_s	proportionality constant in discharge-rate equation for saturation range
μ	proportionality constant in active-fiber-number equation for dynamic range
μ_s	proportionality constant in active-fiber-number equation for saturation range
σ	integer
Φ	whole-nerve, action-potential amplitude indicated using a gross electrode
$\langle\ \rangle$	average over ensemble of fibers

Subscripts:

a	upper bound of dynamically active subrange I and lower bound of active subrange II
b	upper bound of active subrange II and lower bound of fiber saturation subrange III
c	upper bound of fiber saturation subrange III and lower bound of fiber and rate saturation subrange IV
dyn	dynamically active
inact	inactive
j	integer number of fiber
sat	saturated
t	dynamic response threshold of fiber
0	loudness threshold

Superscripts:

$\sim$	time average over auditory integration time (≈ 0.2 sec)
$\hat{}$	fixed value

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TABLE I. - SUMMARY OF PHYSIOACOUSTIC AND PSYCHOACOUSTIC FUNCTIONS FOR ALL SUBRANGES

Subrange	Number and nature of active fibers	Discharge rate formula, R =	Loudness function[a], $\mathscr{L} \approx$	Equations
I - Dynamically active ($0 \le S \le 34$ dB)	$d < N$ $s = 0$	$[r_t g(d,0) - \langle r_i \rangle]\mu q + N\langle r_i \rangle$	$10^2 (\ln q + 12.4)(q - 2\times10^{-5})$	14b, 32a
II - Active (34 dB $< S \le 90$ dB)	$d + s < N$	$\{r_t[g(d,s) + 1] - \langle r_i \rangle\} \mu q + N\langle r_i \rangle$	$5\times10^2 q$	16, 32b
III - Fiber saturation (90 dB $\le S <$ 120 dB)	$d + s = N$	$r_t[g(d,s) + 1]\mu q$	$10^2 (4.4 - \ln q)q$	18, 32c
IV - Fiber and rate saturation (120 dB $\le S$)	$s = N$ $d = 0$	$N\langle r_s \rangle$ = Constant	3×10^3	20, 32d

[a]Loudness functions follow from assumption: $\mathscr{L} = \kappa(R - R_0)$.

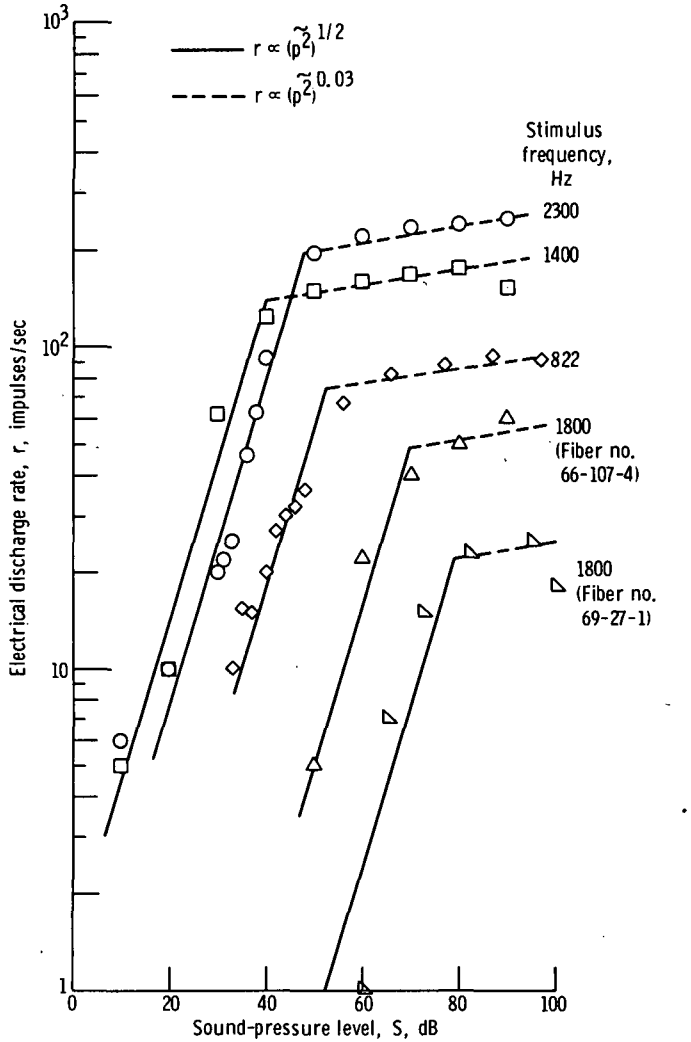

Figure 1. - Electrical discharge rates of typical neurons in the auditory nerve of squirrel monkeys as function of sound-pressure level. (Data from ref. 13, fig. 9.)

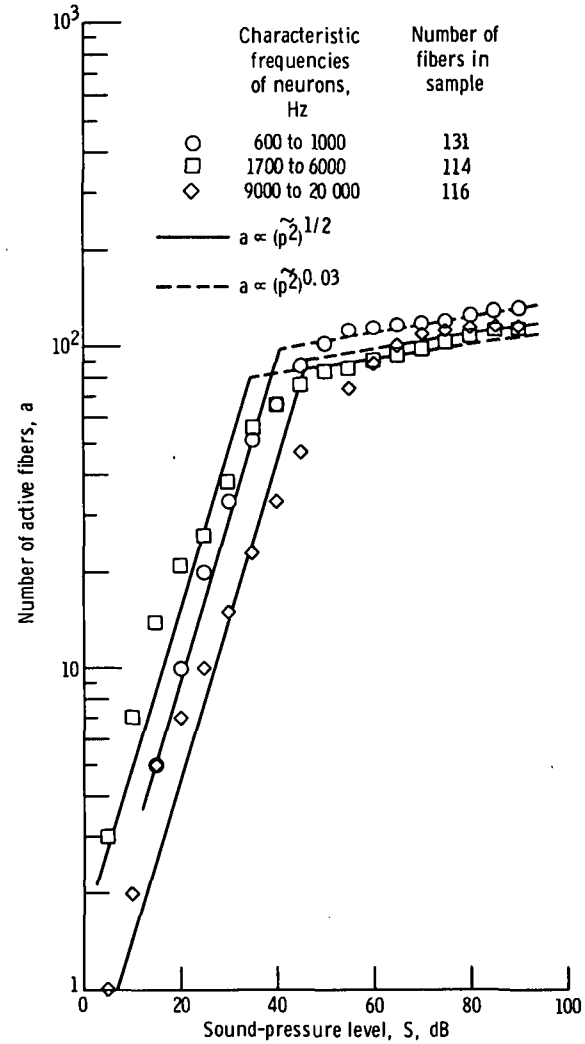

Figure 2. - Small-sample number distributions of active neurons in the auditory nerve of monkeys as function of sound-pressure level. (Data from ref. 18, fig. 4.)

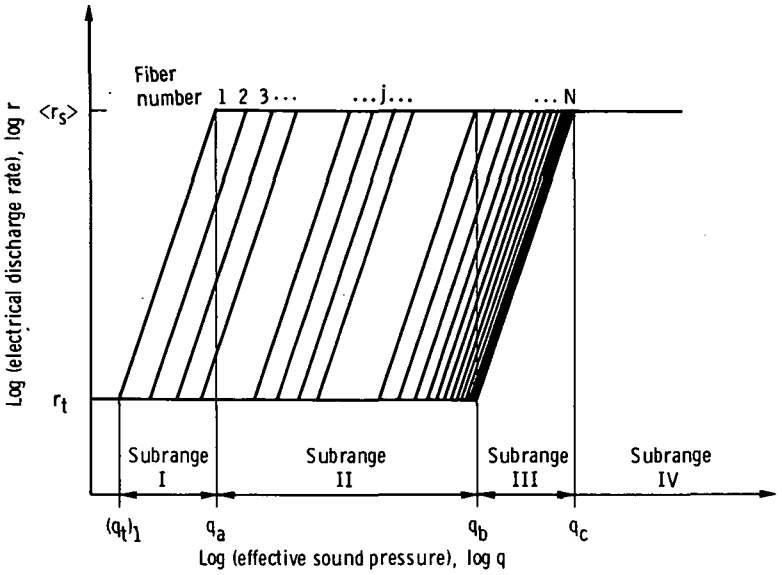

Figure 3. - Model of coherent electrical discharge rates in individual auditory nerve fibers as function of effective sound pressure.

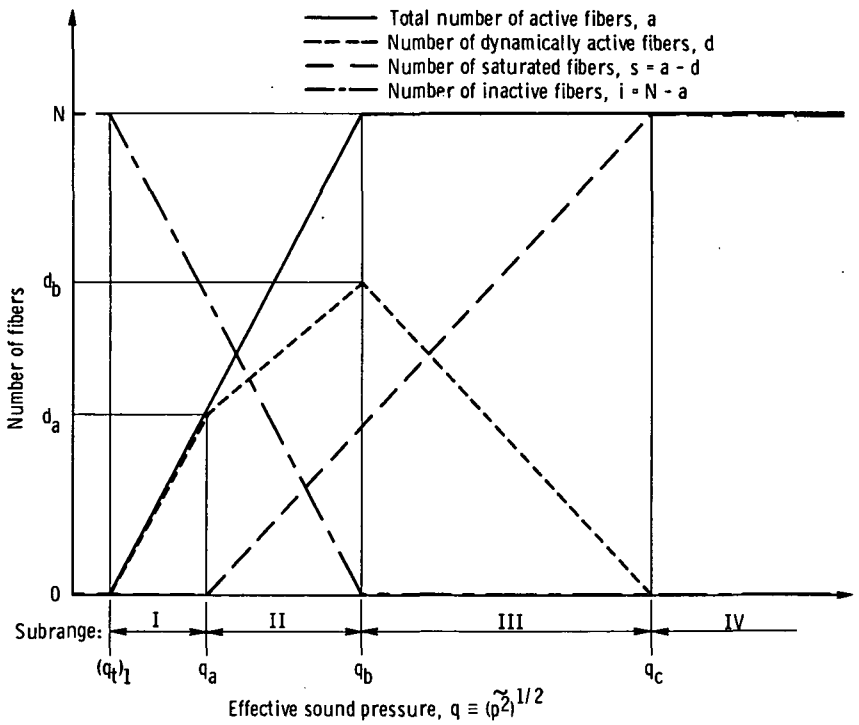

Figure 4. - Number distribution of fibers as function of effective sound pressure. (Not to scale.)

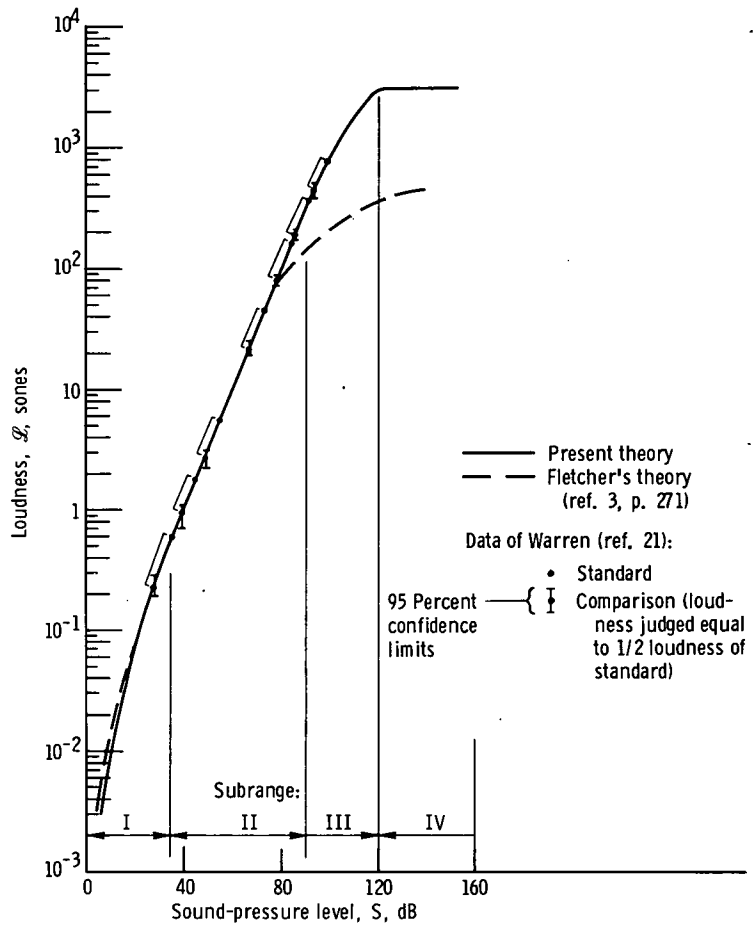

Figure 5. - Predicted loudness function.

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