# A look at neural integration in the human auditory system through the stapedius muscle reflex

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**Ipsilateral and contralateral stapedius muscle contractions were studied as functions of the sound pressure level (SPL) and duration of 2-kHz tone bursts. The study complemented a preceding study in which temporal summation of stapedius muscle contractions produced by pairs of short tone bursts was determined and analyzed. The muscle contractions were determined indirectly by measuring changes in the acoustic impedance they produced at the tympanic membrane. The data for the stapedius muscle contraction as a function of tone-burst duration were derived from another study and analyzed in part with the help of the SPL functions obtained in the present study. According to the experimental results, the stapedius muscle contraction produced by contralateral stimulation follows a compressive power function paralleling both the cochlear output and loudness functions. The ipsilateral contraction follows an expansive power function. Mathematical analysis showed that the muscle tension due to contralateral stimulation increases with tone duration approximately according to the characteristic of a linear integrator having an exponentially decaying memory with a time constant that increases with SPL from ≈200 to 370 msec. The simple relationship appears to be possible because of mutual cancellation of neural-processing characteristics preceding and following the temporal integration.**

acoustic bridge | muscle tension | compressive power function | expansive power function | exponentially decaying memory

Responses of single afferent neurons of sensory systems can be measured with microelectrodes, but this is not true for meaningfully integrated responses of neural populations. Recording of summated neural potentials with larger electrodes may not provide functionally relevant information. Binaural reflex contractions of the stapedius muscles in the middle ear give us a rare opportunity to study natural neural integration. The reflex arcs of the muscles originate in the inner hair cells of the cochlea, the same cells that process most, if not all, neural information leading to conscious auditory experience (1–4). The compressive nonlinearity evident in the outputs of these cells (e.g., refs. 5–7), which reduces the enormous range of sound intensity processed by the auditory system to a biologically manageable one, is reflected in the responses of the muscles (8). The magnitudes of the contralateral muscle contractions produced by short, monaural bursts of a 3-kHz tone were found to parallel the compound action potential of the auditory nerve as a function of sound intensity (8). The similarity suggests that the populationwise neural processing involved, which includes three synaptic stages (1, 3), is linear between the auditory periphery and the muscle. The repeated finding that loudness also approximates the same function of sound intensity invites the speculation that global linear processing is widely spread in the auditory nervous system (8, 9), although intensity characteristics (input–output functions) of single neurons are nonlinear. Experimental results described in the present article indicate that the linear processing is not general, however. For example, it does not hold for the ipsilateral stapedius muscle responses whose reflex arc appears to contain an expansive nonlinearity.

Evidence for the linear global processing in the contralateral reflex arc of the stapedius muscle and the global neural processing underlying loudness sensation is strengthened by the finding of linear temporal integration in both the reflex and conscious responses (8, 10, 11). However, the overall response characteristics differ, suggesting differences in neural pre- and postprocessing.

In a preceding article (8), the temporal integration in the stapedius muscle reflex was studied by means of pairs of 20-msec bursts of a 3-kHz tone, which were presented with a variable time interval between them either contralaterally or dichotically. Mathematical analysis of the results indicated that the time constant of temporal integration was the same in both instances despite the evidence that the ipsilateral and contralateral tracks innervating the muscle appear to be separated beyond the cochlear hair cells (3). Because the time constant was much longer than the twitch time constant of the muscle fibers (12), the conclusion was reached that the dominant temporal integration took place at a neural stage preceding the motoneurons of the seventh cranial nerve driving the muscle (see, e.g., refs. 1–3).

The experiments and mathematical analysis described in the present article strengthen the evidence for the linear temporal integration by determining the relationship between the magnitude of the muscle contraction and the duration of a tone burst. Two complementary methods were applied. In one, the sound pressure level (SPL) was kept constant, and the contraction magnitude was measured as a function of sound-burst duration; in the other, the SPL was varied to keep the muscle contraction constant. In addition to confirming the process of linear temporal integration, the results, when combined with prior neurophysiological knowledge and mathematical analysis, revealed two phenomena that may be of more general interest than the stapedius muscle activity itself. According to one, the effects of neural processing at two different stages that act in series can cancel each other to become almost unnoticeable in the output of the total system. According to the other, the apparent rate of growth of an output magnitude can be increased by otherwise linear temporal integration when its time constant increases with stimulus intensity.

## Experimental Methods

The present article focuses on a mathematical analysis of experimental results obtained previously and published in part (13). The unpublished part is included in this article; some of the published results are reproduced for clarity and completeness. The fundamental methods of measurement were the same in both parts and have been described (8, 13, 14). They are summarized here for the convenience of the reader.

The muscle tension was determined indirectly by measuring the associated change in the acoustic impedance at the tympanic membrane. According to preceding studies, the impedance change is directly proportional to the muscle tension (2). It was measured with an acoustic bridge that compensated for the air volume of the ear canal interposed between the input end of the bridge tube and the tympanic membrane (8, 13, 14). When the

Abbreviation: SPL, sound pressure level.

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bridge was slightly unbalanced, its sensing microphone generated a small voltage directly proportional to the bridge mistuning, which was registered on the screen of an oscilloscope as the width of a horizontal time trace. At the low frequency of 500 Hz at which the bridge was energized, the resistance component of the acoustic tympanic-membrane impedance was relatively small and was easily balanced out by the variable bridge resistance. The compliance component was set to be slightly larger than that found at the tympanic membrane in the absence of muscle contraction. Contraction of the muscle increased the compliance imbalance, leading to a proportionately increased trace width on the oscilloscope screen. The increment served as a measure of the muscle tension. It was computed by taking the difference between the trace widths occurring in the presence and absence of the muscle contraction, respectively. By making direct measurements on the oscilloscope screen, delay times that could perturb the obtained time patterns of the muscle contractions were minimized.

Reflex contractions of the stapedius muscle were produced by single bursts of a 2-kHz tone. At this and higher frequencies, sound transmission through the middle ear is practically independent of the muscle tension, so that the muscle responses were studied under open-circuit conditions. The tone bursts were varied in duration from 10 to 3,000 msec and in SPL from 80 to 130 dB, depending on the particular experiment. They were turned on and off with transients of 5-msec effective duration. In the first experimental series, the SPL was set to produce saturation of the muscle tension beyond ≈400 msec of burst duration and was kept constant. In the second series, the SPL was varied as a function of the burst duration to keep the muscle tension constant. In the third series, the duration of the tone bursts was maintained at 20 msec, and the muscle tension was determined as a function of SPL. In all these series, the muscle tension was measured in one ear, and the tone bursts were delivered to the opposite ear. In the fourth series, which was similar to the third one, except that two burst durations of 20 and 500 msec were used, the tone bursts were delivered to the same ear in which the muscle tension was measured. They were produced by the same transducer that supplied the bridge signal of 500 Hz. The ipsilateral tone delivery required equipment modifications designed to protect the sensitive bridge microphone from the strong reflex-eliciting signals and to avoid recording artifacts. The first modification consisted of an acoustic low-pass filter made up of a partition placed symmetrically on each side of the bridge microphone and equipped with a round aperture of appropriate diameter. The diameter, together with the air volume enclosed between each partition and the microphone, determined the cutoff frequency. The second modification consisted of additional low-pass filtering in the recording circuit.

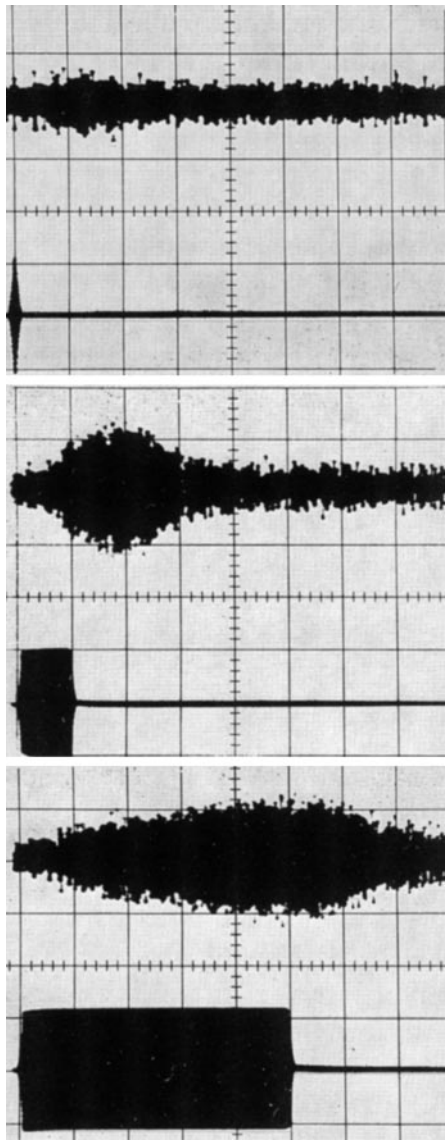

**Fig. 1.** Oscilloscope traces showing the temporal patterns of contralateral stapedius muscle contractions (upper traces) in response to tone bursts of constant SPL and variable duration (lower traces). (*Bottom*) The SPL was reduced, but the reduction was compensated for in the tone-burst channel by additional amplification. The spacing among vertical lines indicates 100-msec intervals; the vertical scale is arbitrary. The stimulus duration is 10 msec in *Top*, 100 msec in *Middle*, and 500 msec in *Bottom*. The difference between the trace widths recorded during muscle contraction and in its absence served as an indirect measure of muscle tension.

## Experimental Results

The data of the first experiment are reproduced from Djupesland and Zwislocki's article (13). An example of typical individual results is shown in terms of the widths of oscilloscope traces in Fig. 1. In all three parts of the figure, vertical scale lines indicate 100-msec time intervals. The lower trace belongs to the electrical signals that produced the reflex-eliciting tone bursts; the upper trace, to the stapedius muscle responses indicated by the acoustic bridge output. In Fig. 1 *Top* and *Middle*, the SPL was the same, but the tone-burst duration was increased from 10 msec in *Top* to 100 msec in *Middle*. According to a rough estimate, the 10-fold increase in duration produced a 10-fold increase in the magnitude of the muscle response, suggesting a process of linear temporal integration. Admittedly, a precise estimate was prevented by the noisy fluctuations in the oscilloscope traces, which resulted from the probabilistic nature of both the neuronal inputs to the muscle and the responses of the muscle fibers themselves. Attention may also be called to the diffuse patterns of the muscle responses as compared with the well defined patterns of the response-eliciting stimuli. The diffusion was most likely caused by the dispersion of synaptic delays whose overall effects can be seen in the overall response delays. The traces in Fig. 1 *Bottom* show the time pattern of the muscle response to a 500-msec tone burst. The SPL was reduced relative to that in Fig. 1 *Top* and *Middle* to minimize the effect of response saturation. The reduction is not evident in the signal channel, because it was compensated for by increasing the amplification. As is apparent in Fig. 1 *Bottom*, the muscle response increased gradually over a time span of ≈400 msec, then saturated. According to the analysis in the next section, the saturation occurred in the motor activity of the muscle rather than before or within the process of temporal integration.

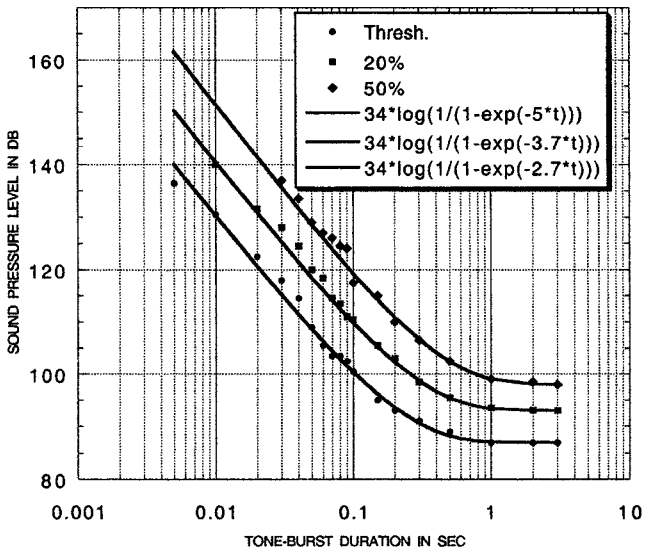


**Fig. 2.** SPL required for a constant muscle contraction as a function of tone-burst duration, determined at three levels of muscle tension: ≈50% (top) and 20% (middle) of the maximum, and at the visual detection threshold (bottom). The data points were obtained on a typical subject (13); the curves are theoretical.

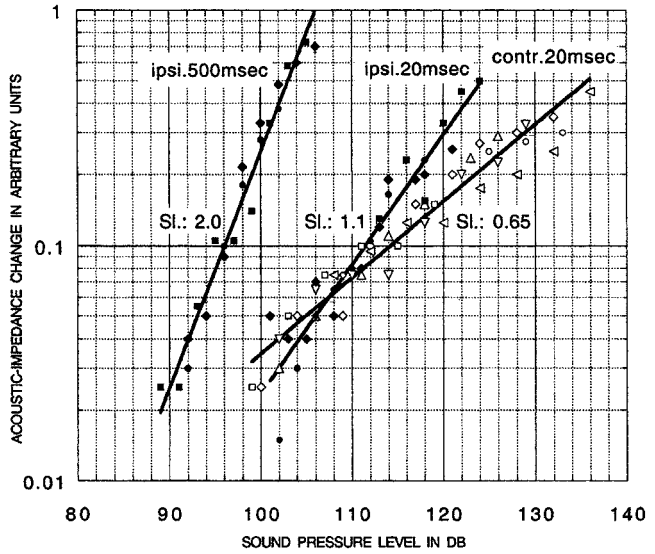


**Fig. 3.** Intensity functions (input–output functions) of ipsilateral (filled symbols) and contralateral (open symbols) stapedius muscle contractions. The symbols indicate the empirical data normalized to the grand mean of every set, and the curves indicate the straight-line least-squares fits to the data on double-log coordinates. The ipsilateral functions have been determined at two tone-burst durations, 20 and 500 msec, and the contralateral function has been determined only at 20 msec. The numbers by the curves indicate their slopes (Sl.). The fact that all of the data approximate straight lines on double-log coordinates means that the stapedius muscle contractions follow power functions of sound pressure.

The data points of Fig. 2 show the results of the second experiment, as obtained by Djupesland and Zwislocki (13) on a typical subject. Similar results were obtained on five other subjects, as is evident in their figure 2 (13). The solid lines are theoretical fits to the data points; their patterns are analyzed in the next section. The bottom set of points (circles) indicates the threshold response of the muscle, defined as the smallest increment in the oscilloscopic trace width that could be detected by eye. The middle set (squares) and the top set (diamonds) were produced by holding the muscle response at 20% and 50%, respectively, of the maximum response. At all three response levels, the SPL had to be steeply decreased as the burst duration was increased for the muscle response to remain constant. On logarithmic coordinates (the decibel scale is logarithmic), the data suggest a curve slope of slightly >30 dB per 10-fold increment in burst duration at small durations, nearly independent of the magnitude of the muscle contraction. At durations >1 sec, the SPL became practically independent of the duration, and the spacing among the curves associated with the different response levels decreased. Whereas a SPL increment of ≈10 dB was required to increase the muscle response from the threshold to 20% of response maximum, and a similar additional increment was required to reach the 50% level at short burst durations, the corresponding increments were reduced by almost half at long burst durations. The analysis in the next section suggests that this nonlinearity was due to a variation in the effective time constant of temporal integration, which appears to have increased with SPL.

The results of the third and fourth experiments in combination are represented graphically in Fig. 3. They have been obtained on different subjects than were the results of Djupesland and Zwislocki (13). The open symbols refer to experiments with the contralateral reflex, in which a group of five subjects with normal hearing participated; the filled symbols refer to experiments with the ipsilateral reflex performed on a subgroup of three subjects. The tone bursts used were, in the former experiments, only those of 20-msec duration and, in the latter, both those of 20- and 500-msec duration. The resulting data have been plotted on double-log coordinates. These coordinates made it possible to fit all three data sets with straight lines according to the method of least squares. Because, within each experiment, the individual data exhibited roughly the same dependence on SPL but varied considerably with respect to absolute reflex sensitivity, which was of secondary interest, they have been normalized accordingly. For every data set, a population grand mean has been obtained with respect to the vertical coordinate. Subsequently, the individual data have been multiplied by the ratio between their individual grand means and the population grand mean. The least-squares approximations have been applied to the data so normalized. They produced high correlation coefficients ranging from $R = 0.95$ for contralateral reflex stimulation to $R = 0.96$ for the ipsilateral one.

The finding that both the contralateral and ipsilateral stapedius muscle contractions depended on sound pressure according to straight-line functions on double-log coordinates means that they followed power functions. The exponents of the latter are given by the corresponding curve slopes. For the contralateral reflex, the curve of Fig. 3 has a slope of 0.65, reasonably close to the slope of 0.585 found in a preceding study (8) on a different group of subjects and also the slope implied by the results of Djupesland and Zwislocki (13). Somewhat surprisingly, the data of Fig. 3 indicate a slope of 1.1 for the ipsilateral reflex elicited by 20-msec tone bursts and of 2.0 when it was elicited by 500-msec bursts. The near doubling of the slope associated with the increased burst duration can be explained by the dependence of the effective time constant on SPL, as mentioned in connection with the results of Fig. 2. The 1.1 slope associated with the 20-msec tone bursts is more difficult to understand in view of cochlear compression that must affect all cochlear outputs, including both the contralateral and ipsilateral reflex arcs, and that is clearly evident in the contralateral reflex. The high slope implies a decompression following the compression. Neural decompression was suggested by Zeng (15) above the level of cochlear nuclei on the basis of electrical stimulation within the nuclei of deaf patients, but the phenomenon must be further investigated. It may be of more general interest.

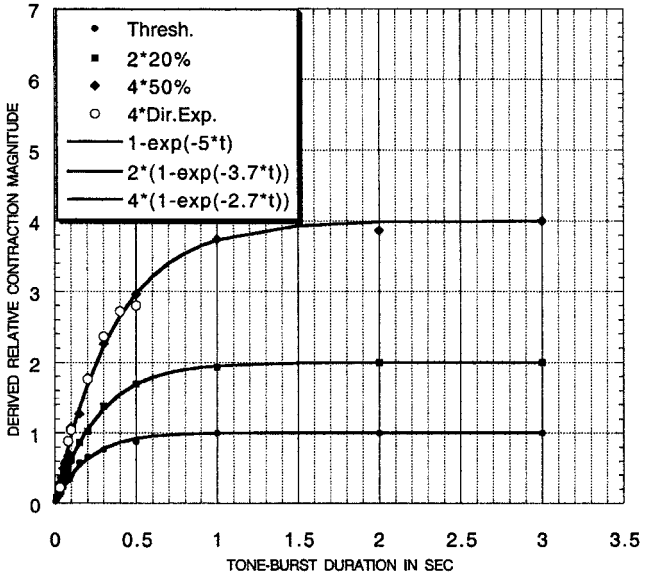


**Fig. 4.** Stapedius muscle contractions as functions of tone duration at three SPLs, plotted on linear coordinates. The data points indicated by the filled symbols have been derived from the data points of Fig. 2 by coordinate inversion and normalization with respect to SPL values at long tone-burst durations. The effect of the power exponent has been eliminated with the help of the contralateral curve slope of Fig. 3. To avoid ambiguity, the data corresponding to the 20% contraction in Fig. 2 have been multiplied by 2, and those corresponding to the 50% contraction have been multiplied by 4. The curves are theoretical and have been derived from those of Fig. 2 in the same way as the data points. The data points indicated by the open circles have been derived directly from the oscilloscope trace in Fig. 1 *Bottom* and normalized to coincide with the top curve.

## Mathematical Analysis

The mathematical analysis of this article is limited to the contralateral stapedius muscle reflex. First, the gradual growth of muscle tension shown in Fig. 1 *Bottom* by means of the width of the oscilloscope trace is approximated by an equation that describes the temporal output characteristic of a simple linear integrator having an exponential memory decay and a time constant $\tau_1$. This equation can be written in the form

$$\eta = C\tau_1\varepsilon[1 - \exp(-t/\tau_1)], \qquad [1]$$

where $\varepsilon$ is the constant magnitude of the input to the integrator; $t$ is the time elapsed from the input onset; $\eta$ is the integrator output at time $t$; and $C$ is a dimensional proportionality constant. The empirical result obtained by sampling the growth function of Fig. 1 *Bottom* is shown in Fig. 4 by means of the open circles. The corresponding theoretical curve is indicated by the top solid line. Both have been normalized to unity for $t > 3{,}000$ msec and multiplied by 4 to separate them from the other curves in the figure. A time constant $\tau_1 = 370$ msec fitting the data of Fig. 2 for a 50% muscle contraction has been assumed for the theoretical curve. Note the excellent agreement between the empirical data shown by means of the open circles and the theoretical curve, except for the highest point that undershoots the curve. As already mentioned, the deviation can be ascribed to saturation in the motor response of the muscle.

To analyze the data of Fig. 2 for which the muscle response, $\eta$, was kept constant and the input to the time integrator varied, Eq. **1** has to be inverted.

$$\varepsilon = \frac{\eta}{C\tau_1[1 - \exp(-t/\tau_1)]}. \qquad [2]$$

Furthermore, the input has to be expressed in terms of SPL. On the basis of Fig. 3 and associated discussion, it can be assumed to follow a power function. In mathematical nomenclature

$$\varepsilon = kP^\theta, \qquad [3]$$

where $\theta$ is the power exponent and $k$ is a dimensional proportionality constant. Accordingly,

$$P^\theta = \frac{\eta}{kC\tau_1[1 - \exp(-t/\tau_1)]}. \qquad [4]$$

In the logarithmic form used in Fig. 2, the equation can be rewritten as

$$20\log(P/P_0) = \frac{20}{\theta}\log(\eta_\infty/\eta_{0\infty}) - \frac{20}{\theta}\log[(1-\exp(-t/\tau_1)], \qquad [5]$$

where $P_0$ is the standard sound pressure reference and $\eta_\infty$ is the muscle response at $t \to \infty$, so that

$$20\log(P_\infty/P_0) = \frac{20}{\theta}\log(\eta_\infty/\eta_{0\infty}) \qquad [6]$$

for $t \to \infty$. By introducing Eq. **6** into Eq. **5**, we obtain

$$20\log(P/P_0) = 20\log(P_\infty/P_0) - \frac{20}{\theta}\log[1 - \exp(-t/\tau_1)], \qquad [7]$$

an expression corresponding to the coordinates of Fig. 2. The expression with $\theta = 0.585$ generated the solid curves of that figure. Note that the multipliers of the log terms in the legend result from $34 = 20/0.588$, and the numerical coefficients of 5, 3.7, and 2.7 in the exponents are the inverted values of $\tau_1$, having numerical values of 0.2, 0.27, and 0.37 $\text{sec}^{-1}$, respectively. By visual inspection, the theoretical curves fit the data points reasonably well. However, the latter suggest a systematic perturbation in the duration range between 0.02 and 0.1 sec. It probably resulted from neural processing preceding and following the temporal integration, as discussed further below. Beyond 0.1 sec, the curve fit is almost exact, suggesting that the assumed dependence of the time constant on stimulus magnitude is real.

The theoretical formulation should apply not only to the time domain but also to the domain of the response magnitude. If it is approximately correct, it should predict the difference in SPL required to increase the muscle response from 20% to 50% of the maximum. By rewriting Eq. **5** in terms of ratios of $P_1/P_2$ and $\eta_1/\eta_2$ and the corresponding time constants $\tau_{11}$ and $\tau_{12}$, we obtain

$$20\log(P_1/P_2) = \frac{20}{\theta}\log(\eta_1/\eta_2) - \frac{20}{\theta}\log(\tau_{11}/\tau_{12}) - \frac{20}{\theta}\log[1 - \exp(-t/\tau_{11})] + \frac{20}{\theta}\log[1 - \exp(-t/\tau_{12})]. \qquad [8]$$

At short durations, all of the terms containing the time constants cancel each other, so that Eq. **8** takes the simple form of

$$20\log(P_1/P_2) = \frac{20}{\theta}\log(\eta_1/\eta_2). \qquad [9]$$

For the ratio between the 50% and 20% contractions of 2.5, the difference in SPL becomes 13.53 dB, ≈2–3 dB larger than indicated by the empirical data in Fig. 2. The error can be considered as acceptable in view of the gross approximation of the data by the simple time-integration function and the rough estimation of the muscle contractions in percent of maximal contraction that was not sharply defined.

The percent muscle contraction at the response threshold can be calculated by inverting Eq. **9**. The SPLs required for the threshold curve were ≈10 dB below those required for the 20% response at short durations, giving a response ratio of 0.508, equivalent to 10.16% of maximum response.

At long stimulus durations, the exponential terms of Eq. **8** disappear, and the equation takes the form of

$$20 \log(P_1/P_2) = \frac{20}{\theta} \log(\eta_1/\eta_2) - \frac{20}{\theta} \log(\tau_{11}/\tau_{12}). \quad [10]$$

According to the latter, the SPL difference corresponding to the ratio between the 50% and 20% contractions and an associated time-constant ratio of 1.37 (0.37/0.27) should amount to 8.88 dB, between 2 and 3 dB greater than the corresponding empirical value. For the ratio of 1/0.508 between the 20% and the threshold responses and the corresponding ratio of time constants of 1.35, a SPL difference of 8.65 dB is obtained, again 2–3 dB greater than the empirical value. The almost constant error in all these calculations suggests that the actual ratios between the muscle contractions in percent may have been somewhat smaller than estimated.

The decreased SPL differences among the curves of Fig. 2 at long time durations may explain the slope difference between the two ipsilateral input–output functions of Fig. 3 determined with short and long tone bursts, respectively. The slope is inversely proportional to the SPL difference, as can be deduced from Eq. **6**.

The empirical data of Fig. 2 can be used to derive the integration functions of the temporal integrator hypothesized to precede the motor part of the contralateral stapedius muscle (8). For this purpose, Eq. **4**, when normalized to asymptotic values at large stimulus durations, $t$, can be rewritten in the form

$$\eta_t/\eta_\infty = (P_t/P_\infty)^\theta, \quad [11]$$

where $P_\infty$ is the asymptotic reference sound pressure at large stimulus durations, $P_t$ is the measured sound pressure at time $t$ from the onset of the stimulus, $\eta_\infty$ and $\eta_t$ are the corresponding output magnitudes of the integrator, and $\theta$ is the power exponent relating the sound pressure to the magnitude of the integrator input according to Eq. **3**. The data so transformed are plotted by means of filled symbols in Fig. 4. For clarity, the numerical values obtained for the 20% contraction have been multiplied by 2, and those for the 50% contraction, by 4. The solid curves are theoretical and have been generated by means of Eq. **1** normalized to the asymptotic value, $\eta_\infty$. The same integration time constants have been used as for Fig. 2. The open symbols have been derived directly from the oscilloscope recordings of Fig. 1, as already mentioned. Note the excellent agreement between the theoretical curves and the data points derived from the measurements. The agreement indicates that the stapedius muscle tension, as a function of sound duration, obeys approximately the time characteristic of a linear temporal integrator with an exponentially decaying memory.

The discovery that the stapedius muscle contraction as a function of stimulus duration follows the time characteristic of such an integrator is surprising because of the known temporal response decay in the auditory nerve (16) and the temporal integration at the muscle fibers (12) both having shorter time constants than the muscle contraction. Apparently, these effects cancel each other to a sufficient degree, even though they are separated by the assumed temporal integrator with a longer time constant and their time constants may not be identical. The mutual cancellation is made plausible by the evidence that, beyond the periphery, the system functions linearly and by the recognition that the neural response decay is equivalent to temporal differentiation counteracting approximately the temporal integration in the muscle. The cancellation can be derived mathematically.

When the rapid adaptation components that should be effective only for very rapid tone onsets (16–18) are neglected, the peripheral decay of the neural response can be described roughly by the function

$$\varepsilon = \varepsilon_\infty + \varepsilon_t \exp(-t/\tau_2), \quad [12]$$

where $\varepsilon_\infty$ means the asymptotic response, $\varepsilon_t \approx 2\varepsilon_\infty$ is the magnitude of the response decay, and $\tau_2 \approx 50$ msec is the decay time constant (19). On the assumption that the input to the integrator with the relatively long time constant is directly proportional to the neural response described by Eq. **12**, the output of the integrator should follow the convolution of this equation with the memory function of the integrator. Accordingly,

$$R(t) = E \int_0^t [(\varepsilon_\infty + \varepsilon_t \exp(-\tau/\tau_2)) \exp(-(t-\tau)/\tau_1)]\, d\tau, \quad [13]$$

where $R(t)$ is the output function and $E$ is a dimensional proportionality constant. In turn, if the input to the muscle obeys the function $R(t)$, the temporal integration in the muscle should lead to

$$\eta(t) = M \int_0^t [(R(t) - T) \exp(-(t-\tau)/\tau_3)]\, d\tau, \quad [14]$$

where $\eta(t)$ is assumed to be the muscle response, $T$ is the muscle response threshold, $\tau_3$ is a time constant similar in magnitude to the time constant $\tau_2$, and $M$ is a dimensional proportionality constant.

The mathematical result of the two convolution integrals is a sum of 10 terms. However, all of the terms containing as factors products or higher powers of the time constants $\tau_2$ and $\tau_3$ can be ignored, because these constants are small relative to the constant $\tau_1$, and their products or higher powers are small of the second order. When this is done, the solution of Eq. **14** can be simplified as follows:

$$\eta(t) \approx ME\tau_1\tau_3\varepsilon_\infty \left[ (1 - \exp(-t/\tau_1)) - \frac{T}{E\tau_1\varepsilon_\infty} (1 - \exp(-t/\tau_3)) \right]. \quad [15]$$

Except for the term containing the fraction $T/E\tau_1\varepsilon_\infty$, which is approximately constant beyond very short stimulus durations and is small for suprathreshold stimulation, the equation describes the temporal response pattern of a simple linear integrator with an exponentially decaying memory having a time constant $\tau_1$. Nevertheless, the empirical data points of Fig. 2 indicate small but systematic deviations from the theoretical curves generated on the basis of simple temporal integration. These deviations may reflect the effects of the threshold $T$ and of the small terms ignored in arriving at Eq. **15**.

## Summary and Conclusions

Reflex contractions of the stapedius muscle in the middle ear produced by loud sound afford us a rare opportunity to study natural neural integration in a sensory system. The contractions produce easily measurable changes in acoustic impedance at the tympanic membrane, which are directly proportional to changes in muscle tension. The impedance changes were measured with the help of an acoustic bridge that practically eliminated the effect of the ear-canal volume interposed between the end of the bridge tube and the tympanic membrane. As a consequence, the acoustic elements of the bridge were matched directly to the impedance components at the tympanic membrane, as had been described in greater detail (8). The inferred changes in muscle tension were studied as functions of SPL and the duration of a 2-kHz tone presented monaurally. Because, at this sound frequency, contraction of the stapedius muscle does not affect appreciably sound transmission through the middle ear, the functions reflect open-loop conditions.

Stapedius muscles contract binaurally in response to monaural stimulation, but the ipsilateral contraction follows a steeper function of SPL than the contralateral contraction. Measurements performed in connection with the present study indicate that both functions approximate power functions, but the ipsilateral function has an exponent almost twice as large as the contralateral function. Because the latter parallels the amplitude of the cochlear output at both the level of the inner hair cells and the integrated response of the auditory nerve, the neural processing involved appears to be globally linear. On the other hand, the steep ipsilateral function seems to require an expansive neural nonlinearity. This nonlinearity was found to be greater for stimuli of 0.5-sec duration than for short, 20-msec stimuli. The difference may be related to an unequal time constant of temporal integration. The time constant was demonstrated to depend on SPL in the contralateral muscle response.

The data on temporal integration evident in the stapedius muscle contractions were derived from a previous study (13). Mathematical analysis of these data revealed that they follow roughly the characteristics of a linear integrator with a constant input and an exponentially decaying memory. This outcome was surprising in view of the well known temporal decay of neural firing in the auditory nerve, which must precede the temporal integration. The possibility was investigated that the decay was compensated for by additional temporal integration known to take place in the stapedius muscle itself, both having similar time constants, much shorter than the overall time constant of the muscle reflex. According to mathematical analysis, almost complete compensation was possible even when the time constants were not exactly equal, provided they were sufficiently small. The demonstration supports a more general conclusion that simple relationships between biological output characteristics and the stimulus variables producing them may be deceiving and hide multiple processes with diverse characteristics, which cancel each other in the final outcome.

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