Recovery from prior stimulation II: Effects upon intensity discrimination

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We obtained just-noticeable differences (jnds) for the intensity of pure tones following a forward masker. The masker was a 100 ms burst of narrow-band noise centered at 1000 Hz presented at 90 dB SPL; the pure-tone signal was at 1000 Hz and was 25 ms in duration. The masker-signal delay was 100 ms. Under these conditions, there is no threshold shift for the detection of the pure-tone signal following the forward masker. In contrast with the absence of a forward-masker effect upon detection thresholds, unusually large midlevel (40-60 dB SPL) jnds were observed. These large midlevel jnds were measured as a function of signal delay, revealing that they are not completely recovered to the normal (unmasked) values by 400 ms. We interpret these data as a consequence of the slower recovery of low-spontaneous rate, high-threshold neurons following prior stimulation (Relkin and Doucet, 1990). These experiments may therefore provide psychophysical evidence that the low-spontaneous rate, high-threshold neurons are a necessary physiological component in the coding of the large dynamic range for intensity. In addition, the present data provide evidence that the assumption that the effect of forward masking is limited to 100-200 ms is inappropriate, as this recovery time does not necessarily apply to suprathreshold tasks.

Intensity discrimination; Forward-masking; Auditory neurons; Spontaneous rate

Introduction

In a normal-hearing listener, both the growth of loudness sensation and the ability to discriminate small changes in intensity extend across a large dynamic range of stimulus energy (as great as 120 dB). This range is in contrast to that shown by the majority of individual auditory peripheral neurons, which have a relatively limited operating range (about 30-50 dB in most cases; e.g., Evans and Palmer, 1980; Kiang et al., 1965). Attempts to resolve this dynamic range mismatch between psychophysical and physiological results have focused primarily on two types of peripheral neural coding schemes that might serve to encode intensity: spread of excitation along the frequency continuum and a distribution of thresholds along the intensity continuum.

The hypothesis that psychophysical intensity is encoded by a group of neurons having the same characteristic frequency (CF), but different thresholds was popular in the 1950s (e.g., Davis, 1961, p.123), following Tasaki's (1954) finding that the thresholds of individual neurons at a given CF are distributed across a wide range. However, Kiang's report (1968) that the majority of neurons have a very limited threshold distribution range of about 20 dB led most theorists to consider the alternative coding hypothesis in which a spread of excitation along the frequency domain was responsible for coding increases in sound intensity. Most models in the following years incorporated the spread of excitation as the critical mechanism to explain the wide dynamic range exhibited in intensity discrimination (Siebert, 1965; Teich and Lachs, 1979), loudness growth (Goldstein, 1974; Howes, 1974; Lachs and Teich, 1981) and also to explain loudness recruitment (Evans, 1975).

Recently, the importance of this coding scheme has been challenged by the psychophysical findings that neither the magnitude of loudness nor the size of the jnd for a pure-tone changes greatly in cases which a tone's spread of excitation is altered or restricted by using either a high-pass and/or low-pass noise as a masker (Hellman, 1974, 1978; Moore et al., 1985; Moore and Raab, 1974; Schneider and Parker, 1987, Viemeister, 1974) or by the presence of a high-frequency hearing loss (Hellman and Meiselman, 1986; Zeng and Turner, 1990). Perhaps more importantly, Liberman's (1978) report that there exists a bimodal distribution in the physiologically-recorded spontaneous rate of individual auditory neurons, with the existence of a significant population of low-SR neurons that possess high thresholds, has revived the hypothesis that the large range of intensity is coded by a distribution of neuronal thresholds. Subsequently, a number of...
physiology-based models incorporating such a distribution of thresholds have been proposed to resolve the dynamic range problem (Delgutte, 1987; Vieimeister, 1988; Winslow and Sachs, 1988).

Although the importance of low-SR auditory neurons for intensity coding, especially at higher stimulus levels, is strongly suggested, there have not yet been psychophysical experiments that directly support this hypothesis. The reason for this would appear to be a lack of experimental conditions that can restrict the contribution of one group of SR neurons, in the way in which the previously mentioned class of experiments attempted to restrict the contribution of spread of excitation along the frequency continuum. Based upon Relkin and Doucet's (1990) recent finding that the time course of recovery from forward masking in the auditory neuron is related to spontaneous rate, with low-SR neurons recovering at a much slower rate than high-SR ones, it may be possible to limit the contributions of low-SR neurons if a sound is presented at an appropriate signal delay (e.g., 100 ms) following an intense masker. If low-SR (or high-threshold) neurons are indeed needed to encode the full dynamic range of a stimulus, then one should be able to observe a behavioral change in the ability to code intensity when the low-SR fibers are selectively adapted. Under such conditions where high-SR neurons are recovered while low-SR ones are not, the distribution of neuronal thresholds present in a normal auditory system should be disrupted. With low-SR neurons having higher-than-normal thresholds, an artificial threshold gap between high-SR and low-SR neurons would be created.

The effects of an adapting stimulus upon the detection threshold have been well-documented in the psychophysical forward-masking literature. The time course of recovery of the forward-masked detection threshold is usually well fit by a straight line in logarithmic time coordinates. In general, investigators have found that the threshold of detection following a masking signal of 90-100 dB SPL or less recovers completely in approximately 100-200 ms, with less than 10 dB of threshold shift existing at 100 ms (e.g., Zwischocki et al., 1959; Smiarowski and Carhart, 1975; Jesteadt et al., 1982). In contrast, the effects of an adapting stimulus upon suprathreshold thresholds have been rarely investigated. Coats and Dickey (1972) reported that a preceding adaptor stimulus could reduce the judged loudness of a click signal for certain combinations of signal level and delay period between the two signals. Zwischocki and Sokolich (1974) and Zwischocki et al., (1974) reported that a preceding stimulus may enhance or reduce the loudness of a following stimulus depending upon the stimulus conditions, but they also reported variability across subjects on the loudness task when the delay period was less than 80 ms. Widin et al., (1986) measured intensity discrimination of pure tones following a forward masker and reported that in some cases, the resulting increase in the jnd was greater than that expected on the basis of a shift in the sensation level of the tone alone. They however, used a signal delay between the masker and the test signal of only 5 ms; this delay, in view of the results of Relkin and Doucet (1990), was probably too brief to produce a condition where only the low-SR neurons were adapted.

The present study measured the intensity jnd of a brief pure tone presented 100 ms following an intense forward masker. Intensity jnds were obtained across a wide dynamic range of signal levels, in order to investigate possible effects of an altered distribution of neural thresholds that should result due to the adapting stimulus. In addition, jnds were obtained across a range of signal delays, to investigate the course of recovery of suprathreshold intensity discrimination following the adapting stimulus. These experiments were designed to correspond to the conditions reported in Relkin and Doucet (1990), in order to investigate the possible contribution of low-SR neurons to the dynamic range of hearing.

Methods

Subjects

Three young (20–27 years old), normal-hearing listeners served as subjects in the present study. Air-conduction thresholds for 204 ms pure tones were determined using an adaptive threshold-tracking procedure that tracked the 71% level of correct responses. The thresholds in all three subjects were better than 20 dB HL (ANSI, 1969) at the test frequencies from 125 Hz to 8000 Hz. Subject FG, the first author, had considerable previous experience in various psychophysical experiments, while subjects Ay and RB had a more limited experience with this type of study. Extensive training (10–20 h) was employed and formal data collection was not started until subjects reached a stable level of performance.

Stimuli

The temporal paradigm employed here was the same as that used in the companion physiological experiment (Relkin and Doucet, 1990). The masker was a narrow-band (900–1100 Hz) noise with a presentation level of 90 dB SPL and a duration of 100 ms (steady-state). We used a narrow-band masker instead of a pure tone (as used in the companion paper (Relkin and Doucet, 1991)), in order to provide a qualitative listening difference between the masker and signal in order to reduce possible confusion in the subjects as to which stimulus was to be judged in intensity. The masker was generated by passing a white noise (MDF Inc., Model 8156) through a Kemo (Type VBF 8) low- and high-pass filter
with cut-off frequencies at 900 Hz and 1100 Hz, respectively. Our choice of a constant level masker (90 dB SPL) is different from the levels of masker used in the companion physiology paper (Relkin and Doucet, 1991). In their physiological study, masker levels were chosen for each fiber individually; masker levels were set to insure saturation of the neuron's response (average level 55 dB SPL). Either method of determining masker level should produce the same amount of adaptation in the low- and high-SR fibers, as the degree of adaptation in auditory-nerve fibers is determined by the fiber's driven rate in response to the masker (Smith, 1977). In addition, Relkin and Turner (1989) have shown that maskers that produce a maximum firing rate also produce a maximum threshold shift. Therefore all maskers in both studies would be assumed to produce an essentially saturated response and therefore a maximum threshold shift. If the low-SR fibers (which sometimes show a sloping-saturation response) in Relkin and Doucet's physiology experiment were not completely saturated by the maskers used in their study, then it is most probable that the observed differences between the recoveries of the two fiber types was actually greater than that reported.

The 1000 Hz, 25 ms (steady-state duration) probe tone was synthesized and stored on a Macintosh IIx computer. Both masker and probe tone had 2 ms, cosine-squared onset and offset ramps. The probe tones were output by a 16-bit digital-to-analog converter (Sound Accelerator-Digidesign) at a sampling rate of 44.1 kHz. The synthesized tones were smoothed by a 20 kHz low-pass filter and presented to the subject via a Beyer dynamic DT 48 A.0 headphone. Intensity increments were created in one randomly-selected interval of the 2AFC paradigm by adding a same-frequency, in-phase increment signal to the standard, or pedestal tone. Attenuation of the incremental signal was achieved by a Wilsonics Model PATT unit under control of the laboratory computer. Sound levels were expressed as the values measured with the headphone in an NBS-9A coupler.

Procedure

A 2IFC paradigm was used to measure intensity jnds. Each interval within a trial contained a puretone following an intense NB noise masker, and had an overall duration consisting of the masker duration, the signal delay (Δt) and the puretone signal duration. The subject's task was to choose the interval with the more intense puretone signal. The silent period between two intervals within a trial was 500 ms, while that between consecutive trials was 2200 ms plus the subject's response time. This long interval between trials was used in order to minimize possible cumulative adaptation effects upon low-SR neurons, as Relkin and Doucet (1990) have shown that the recovery time for some low-SR neurons can be as long as 2 seconds. The 500 ms between intervals was a compromise between adaptation and memory effects. We believe that this was acceptable because the effect of the masker in the first interval upon the tone in the second interval is negligible compared with that of the masker in the second interval. A series of control conditions were also run, in which the recovery of the detection threshold for the 25 ms probe tone following the forward masker was measured. In these experiments, the same 2IFC procedure was employed with the exception that no pedestal tone was present in either interval; instead the listener was instructed to choose the interval containing the signal.

A standard 2-up, 1-down 2IFC adaptive procedure tracking the 71%-level of correct response was employed in the intensity discrimination experiment (Levitt, 1971). Trial-by-trial feedback was given to the subject regarding the correct response. The decrement or increment step for the increment signal was 6 dB until the fourth reversal and after that was changed to a 2 dB step. The procedure automatically terminated following the 14th reversal for each sequence. The intensity jnd value in each run was estimated from the arithmetic mean of the last 10 reversals. The jnd values reported here were the average of 6 such runs.

Results

Recovery of detection threshold

Mean thresholds for the recovery of detection threshold following the forward masker as a function of Δt are plotted in Fig. 1. The symbols represent the mean thresholds of a probe tone following a 90 dB SPL masker. The standard deviations across the three subjects are also plotted as the vertical bars. For comparison, the threshold of the 25 ms probe tone in quiet is displayed as the arrow line in Fig. 1. It is evident from these data that the mean detection threshold is essentially recovered by 100 ms. The mean threshold shift at 100 ms for the three subjects was 1.5 dB. It should be noted however, that for one individual subject (RB), the detection threshold remained slightly elevated at the 100 ms delay (5 dB).

Intensity discrimination at 100 ms signal delay

The results of the forward-masked intensity jnd experiments are shown in Fig. 2. The jnds, expressed as $10 \log (1 + \Delta I/I)$, are plotted as a function of the level of the standard tone. The delay between the masker and the signal was 100 ms. Using the open squares, panels (a), (b) and (c) show the results of the three individual subjects, while panel (d) displays the mean results across the subjects. Shown by the filled circles is the intensity jnd for a quiet (no masker) control condi-
Fig. 1. Mean thresholds for the 25-ms probe tone following a forward masker presented at 90 dB SPL (open squares). The masker-signal delay was 100 ms. The quiet threshold is shown as the arrow line. Standard deviations across the three subjects are also shown as the vertical bars.

The jnds measured in the absence of the forward masker (filled circles in Fig. 2) are similar to those reported in the previous literature (Jesteadt et al., 1977; Turner et al., 1989). In contrast, the unusual result shown in Fig. 2 is that for all three subjects, there is an unusually large forward-masked intensity jnd at the medium intensity levels between 40–60 dB SPL (about 30–50 dB SL), even though the threshold shift under this forward masking condition is minimal. This provides a striking example that having a normal detection threshold does not necessarily correspond to normal suprathreshold performance. Somewhat different from the first two subjects (Figs. 2a and b), for the third subject (RB, Fig. 2c), the jnd at the lowest sensation levels was elevated when compared to the unmasked condition. This subject's data are in agreement with the previous observation that RB's detection

Fig. 2. Panel (a), (b) and (c): Intensity jnds from three subjects as a function of the stimulus level under two conditions: quiet (filled circles) and forward masking (open squares). Standard deviations across runs for each individual subject are plotted as the vertical bars; panel (d): mean results of the three subjects, with standard deviations across subjects are plotted as the vertical bars in this panel. The forward masker for all subjects is a 90 dB SPL, narrow-band (900–1100 Hz) noise.
threshold was slightly elevated at the 100 ms masker-
signal delay.

Further examination of Fig. 2 indicates that while
the largest difference in jnds between the forward-
masked condition and the quiet condition occurs at the
mid-intensity levels, at the low or high intensity levels
the two conditions produce similar jnds. Under the
conditions of 100 ms signal delay and a standard tone
level of 40–60 dB SPL, physiological data indicate that
low-SR neurons have not yet recovered from the inten-
tense masker while high-SR neurons, while recovered,
are saturated (Relkin and Doucet, 1990). Our interpre-
tation is that the large jnd at these medium levels
reflects the limited contributions from low-SR neurons,
whose thresholds and corresponding dynamic ranges
have been shifted upward due to the preceding masker.

Intensity discrimination as a function of signal delay

If the large jnds at the medium intensities are due to
incomplete recovery of the low-SR neurons, as hypothe-
sized above, then we should observe that these larger
jnds have a slow time course of recovery to normal
values which corresponds to the physiologically mea-

ured recovery course of low-SR neurons (Relkin and
Doucet, 1990). To address this hypothesis, we mea-
sured the jnd recovery as a function of signal delay
using a fixed, mid-level standard tone. The level of the
standard tone was chosen individually for each subject
and was based upon the level at which each individual
subject had the largest jnd at 100 ms signal delay. The
probe tone levels for three subjects AY, FG and RB
were therefore chosen as 60, 50, and 40 dB SPL,
respectively (see Fig. 2). Fig. 3 shows the effect of
signal delay on jnds at the fixed probe tone level which
was chosen for each individual subject. The solid arrow
line at the bottom of the figure shows the group mean
jnds in quiet. It can be seen in Fig. 3 that the jnds
under the present forward masking condition have not
recovered to the normal value (in the quiet case) at up
to 400 ms signal delay.

Discussion

Following Relkin and Doucet’s (1990) finding that
low-SR neurons’ recovery from forward masking is
significantly slower than that of high-SR fibers, we
measured pure tone intensity discrimination over a wide
range of probe levels at a 100 ms signal delay, where
the high-SR neurons are presumably recovered while
the low-SR ones are not. The group mean results (Fig.
2d) indicate that there is an unusually large jnd differ-
ence between the forward-masked condition and the
quiet condition at the mid-intensity levels, while at the
low or high intensity levels the two conditions produce
similar jnds. We interpret the observed results as fol-

ows: 1) for low probe-tone presentation levels, the
recovered high-SR neurons can presumably code inten-
sity changes as they are not driven to saturation by the
pure tone test signal; 2) for high tone levels, we hy-
pothesize that the low-SR neurons, while not fully
recovered in terms of threshold, can however respond
to the highest-level tones and can therefore contribute
to the intensity discrimination task; 3) the unusually
large jnd at some medium intensity levels was accord-
ingly hypothesized to reflect the restricted contribution
from low-SR neurons under these conditions.

Fig. 4 summarizes our interpretations in a highly
schematic fashion. In the quiet condition (upper panel),
there is presumably a smooth transition between the
high-SR, low-threshold neurons and the low-SK, high-
threshold neurons with respect to their contribution to
intensity discrimination. At low stimulus levels (<40
dB SPL in Fig. 4), it is high-SR neurons that are
responsible for the intensity discrimination as the low-
SR neurons have not reached their thresholds; at high
levels (>40 dB SPL), the low-SR neurons take over
(indicated by the left shaded area) as the high-SR
neurons have been saturated. The smooth transition
that occurs in quiet between high- and low-SR neurons
is disrupted in the forward masking condition (signal
delay is 100 ms in this case), due to the different
recovery time courses following prior stimulation. This
is displayed in the lower panel of Fig. 4, in which the
high-SR neurons are recovered to normal while the
low-SR neurons are not (the arrow shows the shifted
threshold). It can be noted that forward masking cre-
ates a gap between intensity levels of 40 and 60 dB
SPL, in which the low-SR neurons are not recovered

Fig. 3. Intensity jnds for a fixed level (60 dB SPL for AY, 50 dB SPL
for FG and 40 dB SPL for RB) probe tone plotted as a function of
signal delay. Standard deviations across runs for each individual
subject are plotted as the vertical bars. Mean results of the three
subjects are plotted as the thick, dashed line. The group mean jnd
obtained in quiet from the three subjects at the given tone levels is
shown by the arrow line in the bottom of the graph. The same
forward masker was used as in figure 3.
Forward Masking

I I I I I
60 100
+ 20 40 80
d0 SPL

Fig. 4. Schematic comparison between high-SR and low-SR neurons with respect to their contribution to intensity discrimination. The shaded area indicates the operating range of each group of neurons under conditions in quiet (upper panel) and in the presence of forward masking (lower panel). The arrow shows the shifted threshold of low-SR neurons due to their slower recovery from forward masking. See text for the significance of such threshold shift.

While the high-SR neurons, though recovered, are saturated. Therefore, neither group of neurons can effectively contribute to intensity discrimination. In our schematic model, we have assumed that the rate-intensity functions for the adapted low-SR neurons have a shifted threshold but normal contribution at high stimulus levels. This would be in agreement with our experimental result that the forward-masked jnds are normal at the highest signal levels. Until rate-intensity functions for adapted low-SR fibers are available, this would seem to be a reasonable working assumption for our simple model.

The conclusion that low-SR neurons may be necessary for the encoding of intensity was further supported by the second experiment which measured jnds as a function of signal delay and showed that the jnd under the present forward masking condition has not recovered to normal values at up to 400-ms signal delay. We consider this an important finding in the sense that: 1) it may provide psychophysical evidence that low-SR neurons are a necessary and important component in accounting for the large dynamic range of intensity coding; 2) the assumption that the effect of forward masking is limited to 100–200 ms delay may be inappropriate, as the current study shows that, under some conditions, suprathreshold intensity discrimination has a much longer time course of recovery from forward masking than detection does.

Relations to previous studies

In contrast to the detection results, the effect of forward masking on intensity discrimination observed in the present study may be regarded as unusual. It is generally assumed that that suprathreshold performance has a recovery course similar to the threshold recovery. The only published study specifically on the effect of forward masking on intensity discrimination (Widin et al., 1986) chose 5 ms as the masker-signal delay. The general conclusion in the study by Widin and co-workers was that forward masking had a greater-than-simultaneous-masking effect on intensity discrimination due to some additional process, such as adaptation. A close examination of their results indicates that the greatest effect under their conditions occurred primarily in cases of high masker and signal levels. This is consistent with the present finding that low-SR neurons have a slower recovery, and their effect would only show up for conditions of an intense masker level and a relatively high signal level. However, as stated earlier, a 5 ms delay time probably did not serve to selectively adapt only low-SR neurons, but instead adapted both groups of neurons with the low-SR neurons showing a greater amount of adaptation (Relkin and Turner, 1988). Therefore the effects resulting from forward masking that Widin et al. (1986) observed were small.

Psychophysical and physiological recoveries from forward masking

It seems interesting, and also possible, to compare the recoveries following a forward masker obtained from psychophysical and physiological measurements. We have reasoned previously that the detection threshold for the probe tone as a function of signal delay may provide a psychophysical counterpart to the recovery of high-SR neurons. On the other hand, the jnd of that tone at medium intensities (where we showed large jnds – as shown in Fig. 3) expressed as a relative measure, may be able to provide a psychophysical measure of the recovery of low-SR neurons. Fig. 5 displays such a comparison. In order to compare the threshold shift and the jnd recovery on the same scale, we applied the following normalization measures to the data of Fig. 1 (detection) and Fig. 3 (jnd):

relative threshold shift (Δt)

\[
\text{relative threshold shift (Δt)} = \frac{\text{threshold (Δt)} - \text{threshold (quiet)}}{\text{threshold (Δt = 0)} - \text{threshold (quiet)}}
\]  

(1)

relative jnd (Δt)

\[
\text{relative jnd (Δt)} = \frac{\text{jnd (Δt)} - \text{jnd (quiet)}}{\text{jnd (Δt = 0)} - \text{jnd (quiet)}}
\]  

(2)
The experimental data, normalized as in the above equations, are shown in Fig. 5, where the filled symbols represent the relative threshold shift and the open symbols represent the relative jnd for a 25 ms probe tone at a fixed level from each subject. Compared with the recovery functions for high- and low-SR neurons (Relkin and Doucet, 1990, Fig. 3), the parallel between psychophysical and physiological data is striking in that the forward-masked threshold data resemble the recovery of high-SR neurons, while the intensity jnd values for a mid-level tone resemble the recovery of low-SR neurons.

Fig. 5 suggests that recovery of detection and recovery of medium-level intensity jnds can provide behavioral parallels to the recovery of high- and low-SR neurons, respectively. While this correspondence between the detection threshold recovery and high-SR units is striking, we must point out that this similarity only exists for the normalized data. Relkin and Turner (1988) showed that the amount of masking (in dB) for individual neurons was much less than that observed in the behavioral experiments, if one assumes optimal central processing of the information from auditory nerve responses. In contrast, Relkin and Smith (1990) observed that the amount of forward masking and its time course based upon the whole-nerve AP response corresponds very closely to the behavioral results. Thus our attempt to use the time course of recovery of the behavioral detection threshold as an indication of the time course of recovery for detection by individual neurons must be taken with some caution, until the discrepancy between single-unit and whole-nerve forward masking data and their relation to behavioral data is resolved.

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