Psychophysical assessment of the level-dependent representation of high-frequency spectral notches in the peripheral auditory system

Ana Alves-Pinto[a] and Enrique A. Lopez-Poveda
Unidad de Audición Computacional y Psicoacústica, Instituto de Neurociencias de Castilla y León, Universidad de Salamanca, Avenida Alfonso X "El Sabio" s/n, 37007 Salamanca, Spain

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To discriminate between broadband noises with and without a high-frequency spectral notch is more difficult at 70–80 dB sound pressure level than at lower or higher levels [Alves-Pinto, A. and Lopez-Poveda, E. A. (2005). "Detection of high-frequency spectral notches as a function of level," J. Acoust. Soc. Am. **118**, 2458–2469]. One possible explanation is that the notch is less clearly represented internally at 70–80 dB SPL than at any other level. To test this hypothesis, forward-masking patterns were measured for flat-spectrum and notched noise maskers for masker levels of 50, 70, 80, and 90 dB SPL. Masking patterns were measured in two conditions: (1) fixing the masker-probe time interval at 2 ms and (2) varying the interval to achieve similar masked thresholds for different masker levels. The depth of the spectral notch remained approximately constant in the fixed-interval masking patterns and gradually decreased with increasing masker level in the variable-interval masking patterns. This difference probably reflects the effects of peripheral compression. These results are inconsistent with the nonmonotonic level-dependent performance in spectral discrimination. Assuming that a forward-masking pattern is a reasonable psychoacoustical correlate of the auditory-nerve rate-profile representation of the stimulus spectrum, these results undermine the common view that high-frequency spectral notches must be encoded in the rate-profile of auditory-nerve fibers. © *2008 Acoustical Society of America.*
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I. INTRODUCTION

The interference of sound waves within the pinna generates notches in the sound high-frequency spectrum (>6 kHz) (Shaw and Teranishi, 1968; Shaw, 1974; Lopez-Poveda and Meddis, 1996) that provide important information on the location of the sound source (reviewed by Carlile *et al.*, 2005). The usefulness of these notches as sound localization cues must depend on the quality of their representation in the peripheral auditory system, and in particular, at the auditory nerve (AN). The common notion (reviewed by Lopez-Poveda, 2005) is that spectral features beyond the cutoff frequency of phase locking (~4 kHz) (Palmer and Russell, 1986) must be represented in the AN by means of a rate-place code (Rice *et al.*, 1995; Lopez-Poveda, 1996). The quality of this representation is believed to gradually deteriorate with increasing sound level due to the broadening of the frequency response of AN fibers (Rose *et al.*, 1971) and to the saturation of their discharge rate (Liberman, 1978). The deterioration of this internal representation should impair the perception of these notches at high sound levels. However, discriminating between broadband noises with and without high-frequency spectral notches is, for most listeners, more difficult at around 70–80 dB sound pressure level (SPL) than at lower or higher levels (Alves-Pinto and Lopez-Poveda, 2005). This paradoxical result suggests either that the internal rate-place representations vary differently with level for human and lower mammals or that the quality of the rate-place representation of the spectral notch is not the only factor that determines performance on the spectral discrimination task. The present report describes a psychophysical study aimed at the following: (1) estimating the quality of the internal representation of a high-frequency spectral notch at increasing sound levels and (2) testing to what extent the quality of this representation is consistent with the noise-discrimination results described above.

The quality of the internal representation of the spectral notch was behaviorally estimated by comparing the masking patterns of forward noise maskers such as those used by Alves-Pinto and Lopez-Poveda (2005) in their spectral discrimination task. A masking pattern (or masked audiogram) is a graphical representation of the detection thresholds of masked probe tones of different frequencies as a function of probe frequency. Psychophysical forward masking is thought to reflect (to a large extent) the incomplete recovery of AN fibers from previous stimulation and/or the persistence of neural (post-AN) activity (Oxenham, 2001; Meddis and O'Mard, 2005). Whatever the case is, the detection of a low-level tonal probe is likely to depend on the discharge rate evoked by the probe in AN fibers with characteristic frequencies (CFs) approximately equal to the probe frequency. When preceded by a masker sound, this rate almost certainly

[a]Author to whom correspondence should be addressed. Present address: MRC Institute of Hearing Research, University Park, Nottingham NG7 2RD, United Kingdom. Electronic mail: ana@ihr.mrc.ac.uk.

depends on the discharge rate evoked on those same fibers by the masker (Harris and Dallos, 1979; Meddis and O'Mard, 2005). Furthermore, masker-probe interactions (e.g., suppression, distortion, or beating effects), which could potentially affect the detection of the probe, are minimized by presenting the probe after the masker. Therefore, the masking pattern of a forward masker possibly provides the best psychoacoustical correlate of the internal representation of the spectrum of the masker. Hence, it is reasonable to hypothesize that if discriminating between a flat-spectrum and a notched noise were more difficult at midlevels because the internal representations of the two spectra were more alike at those levels, then the masking patterns of the same stimuli should also be less distinguishable at those same levels.

Two sets of experiments were carried out on the same group of listeners to test the above hypothesis. The first set (experiment I) measured the threshold notch depth for discriminating between a flat-spectrum and a notched noise at increasing stimulus levels. The second set (experiments II and III) consisted of measuring the masking patterns of the two broadband noises used in the first set of experiments at different noise levels. The correlation between the results of the two sets of experiments provided the basis for testing the above hypothesis. It will be shown that the gradual deterioration in spectral discrimination with increasing level up to 70–80 dB SPL (Alves-Pinto and Lopez-Poveda, 2005) is consistent with a deterioration of the quality of the spectral-notch representation in the masking patterns. By contrast, the improvement in spectral discrimination above 80 dB SPL is *not* accompanied by an improvement in the quality of the representation of the spectral notch in the masking pattern.

The implications of these results in terms of the physiological mechanisms underlying the neural coding of high-frequency spectral notches will be discussed. It will be argued that the discrimination of high-frequency spectral features is unlikely to rely solely on comparisons of the representations of stimuli spectra in the rate profile of AN fibers, at least above 80 dB SPL. Other possible cues to discrimination at high levels will also be discussed.

II. EXPERIMENT I: DISCRIMINATION BETWEEN FLAT-SPECTRUM AND NOTCHED NOISES

The experiment was identical to the main experiment of Alves-Pinto and Lopez-Poveda (2005). It consisted of measuring the threshold notch depth for discriminating between a flat-spectrum broadband noise and a similar noise with a high-frequency rectangular spectral notch (Fig. 1) at increasing stimulus levels.

A. Methods

1. Stimuli

Stimuli consisted of bursts (total duration of 220 ms, including 10 ms cosine-squared rise/fall ramps) of random broadband (20–16 000 Hz) noise with either a flat spectrum or with a rectangular spectral notch (bandwidt of 2 kHz) centered at 8 kHz (Fig. 1). The noises were generated as described in the work of Alves-Pinto and Lopez-Poveda (2005). The reduced energy in the notch frequency band would have made the overall level of the notched noise slightly lower than that of the flat-spectrum noise. To prevent this level difference to be used as a cue for discrimination, the *overall* levels of the two noises were made equal by reducing the spectrum level of the flat-spectrum noise with respect to that of the notched noise. The reduction required for any given notch depth was always less than 0.58 dB and was determined as described by Alves-Pinto and Lopez-Poveda (2005). Level roving could have been alternatively used to prevent the use of overall level difference as a discrimination cue (Alves-Pinto and Lopez-Poveda, 2005). The level-equalization method was chosen instead because the resulting noises resembled more closely the noise maskers used to measure the masking patterns (experiments II and III).

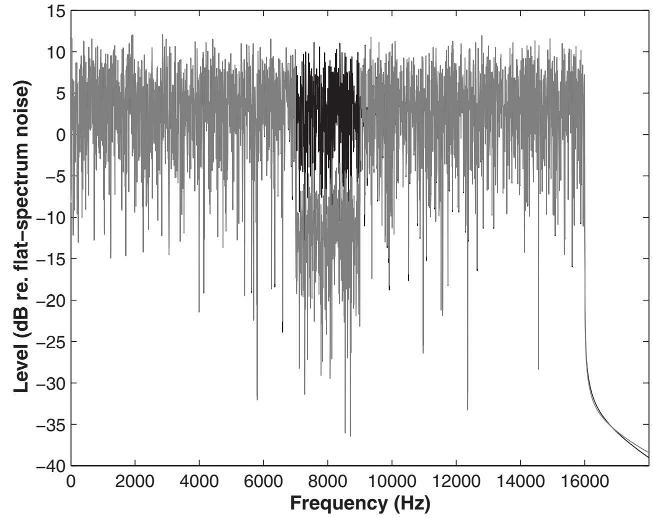

FIG. 1. Spectra of the flat-spectrum (dark trace) and notched (light trace) noises. The spectral notch was centered at 8000 Hz and its bandwidth was 2000 Hz. The notch illustrated had a depth of 15 dB relative to the spectrum level outside the notch band.

2. Procedure

The procedure was identical to that of Alves-Pinto and Lopez-Poveda (2005). Two flat-spectrum and one notched noise bursts were played in random order to the listener, who was instructed to identify the odd one out. The interstimulus period was 500 ms. A two-down, one-up adaptive procedure with feedback was employed to estimate the notch depth that produced 70.7% correct responses (Levitt, 1971). The initial notch depth was fixed at 20 dB below the reference spectrum level of the noise. The notch depth decreased or increased by 6 dB for the first six reversals and by 1 dB thereafter. Each block of trials consisted of 16 reversals and the threshold was estimated as the mean of the notch depths for the last ten reversals. When the corresponding standard deviation exceeded 6 dB, the measurement was discarded and a new threshold estimate was attempted. The thresholds reported correspond to the *geometric* mean of at least three valid measurements (see the work of Alves-Pinto and Lopez-Poveda, 2005 for details). Notch depths at threshold were measured for overall levels from 40 to 90 dB SPL, in 10-dB steps, and for an additional level of 95 dB SPL.

Listeners were tested individually in a double-wall sound attenuating chamber. Stimuli were generated digitally (24 bit, sampling rate of 48.8 kHz) with a TDT™ psychoacoustics workstation (system 3) and delivered via Etymotic™ ER2 earphones. The SPLs reported below correspond to calibrated values. The SPL reading of a sound level meter with its microphone coupled to a Zwislocki occluded ear simulator was 100 dB SPL for a 1 kHz pure tone with an amplitude of 2.3 V_{rms}.

3. Listeners

Seven volunteers (six women and one man, aged 22–35 years) participated in this experiment, all of whom had hearing thresholds within 20 dB re. ANSI 3.6-1996 (specifications for audiometers) at the audiometric frequencies (250–8000 Hz). All listeners were given at least one training session in the task before data collection. Listener S1 was one of the authors (A.A.P.).

B. Results and discussion

Figure 2 illustrates the threshold notch depth as a function of noise overall level. Each panel illustrates the results for a different listener. Error bars illustrate one standard error of the geometric mean. Triangles illustrate absolute thresholds for the flat-spectrum noise.

For most of the listeners, the threshold notch depth varied non-monotonically with level: it gradually increased with increasing level up to 70–80 dB SPL and then decreased with further increases in level. These results indicate that discrimination was more difficult at 70–80 dB SPL than at higher or lower levels. The nonmonotonic trend was less clear for S4 and S5. For S4, the threshold notch depth was still the highest at 70 dB SPL. In the case of S5, the threshold notch depth remained approximately constant above 60 dB SPL. Overall, these results were consistent with the nonmonotonic functions reported by Alves-Pinto and Lopez-Poveda (2005).

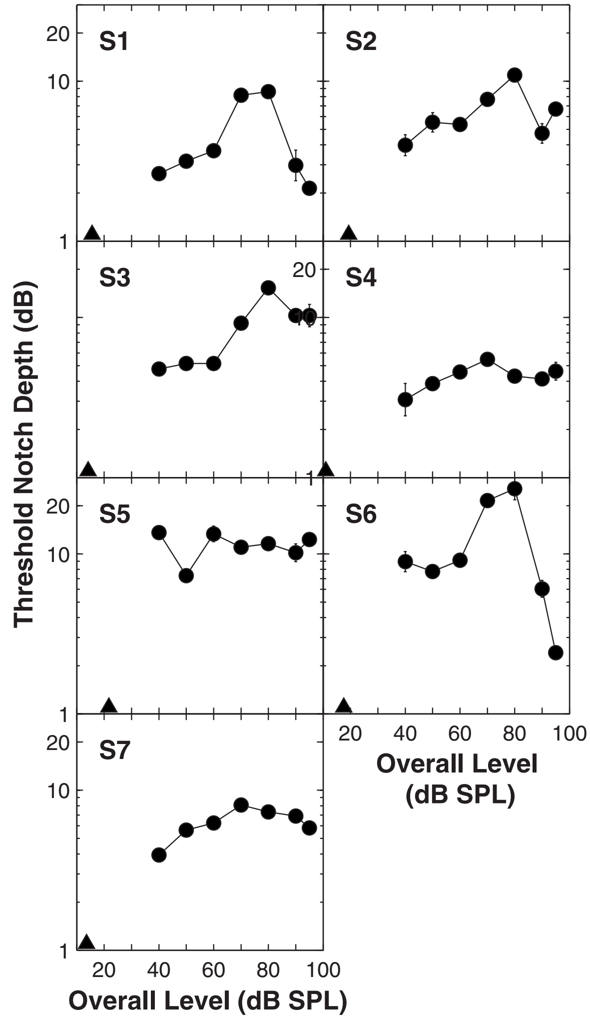

FIG. 2. Threshold notch depths for discriminating between a flat-spectrum noise and a notched noise plotted as a function of the stimulus overall level. Notches were centered at 8000 Hz and had a bandwidth of 2000 Hz. Each panel illustrates data for a single listener as indicated in the upper-left corner of each panel. Each data point corresponds to the geometric mean of at least three measurements. Error bars illustrate one standard error of the geometric mean. Shaded triangles indicate the listener's absolute hearing threshold for the flat-spectrum noise.

III. EXPERIMENT II: MASKING PATTERNS OF FLAT-SPECTRUM AND NOTCHED NOISES WITH A FIXED MASKER-PROBE TIME INTERVAL

A. Aim and rationale

The aim was to measure the forward-masking patterns of the flat-spectrum and notched noises used in experiment I for the same group of listeners. As argued in the Introduction, forward-masking patterns provide the best psychophysical estimate of the internal representation of the masker spectrum. Therefore, the overall difference between the internal representations of the flat-spectrum and the notched noise spectra can be inferred from the difference of their corresponding masking patterns. This method of estimating the internal representation of the spectral notch is based on the following two assumptions: (1) the decay of forward masking is independent of frequency and (2) the decay of forward masking is independent of probe level, at least over the range of probe levels considered in the present study. The first of these two assumptions is supported by other studies (e.g., Lopez-Poveda and Alves-Pinto, 2008). The second assumption relates to the effect of compression on forward masking and will be discussed in Sec. V. Masking patterns were measured for different masker levels to assess the effect of level on the quality of the internal representation of the masker spectrum.

B. Methods

1. Procedure

The thresholds for detecting probe tones of different frequencies in the presence of a forward noise masker were measured by using a two-interval two-alternative forced-choice adaptive paradigm. In one of the intervals, the masker was presented alone; in the other interval, the masker was followed by a brief probe tone. The two intervals were presented in random order (with an interstimulus period of 500 ms) to the listener, who was instructed to identify the interval containing the probe. Feedback was immediately given to the listener after his/her response. The initial probe level was set so that the probe was perfectly audible at the beginning of a trial, and a two-down, one-up adaptive procedure was used to estimate the probe level corresponding to 70.7% correct responses in the psychometric function (Levitt, 1971). The level of the probe was decreased or increased in 6 dB for the first two reversals and 2 dB thereafter. The measurement ended after twelve reversals, and the threshold was estimated as the arithmetic mean of the probe level for the last ten reversals. When the corresponding standard deviation exceeded 6 dB, the measurement was discarded and a new estimate was obtained. At least three thresholds were measured in this way and their mean was taken as the true threshold. When the standard deviation of those three estimates exceeded 3 dB, an additional estimate was measured and included in the mean.

Masking patterns were obtained by measuring the detection thresholds of 15 tonal probes of different frequencies (see the following text). Each experimental session consisted of measuring the thresholds for one group of 15 probe tones. Listeners were given a short (~5–10 min) resting period in the middle of each session to reduce fatigue. The absolute thresholds for the probes (i.e., without the masker) were also measured by using the same procedure. Listeners were tested in the same sound booth and with the same equipment as previously described for experiment I. The calibration procedure was also the same.

2. Stimuli

To measure a masking pattern consisted of measuring the masked detection threshold for tonal probes of the following frequencies: 5, 6, 6.5, 6.75, 7, 7.25, 7.5, 8, 8.5, 9, 9.25, 9.5, 9.75, 10, and 11 kHz. The probes had a total duration of 10 ms, including 5 ms onset/offset cosine-squared ramps, and no steady-state portion. Masking patterns were measured for two broadband (20–16 000 Hz) random-noise maskers with different spectra: one was flat and one was similar to the former except that it contained a rectangular notch centered at 8 kHz, with a bandwidth of 2 kHz and a fixed depth of 15 dB (Fig. 1). These noise signals were similar to those used in experiment I and were generated as described by Alves-Pinto and Lopez-Poveda (2005). The overall level of the notched noise masker was 0.56 dB lower than that of the flat-spectrum noise because it had less energy in the notch frequency band. Unlike in experiment I, this level difference was not compensated for and so the two maskers had identical spectral levels outside the notch band. Maskers had a total duration of 110 ms, including 5 ms onset/offset cosine-squared ramps. Masking patterns were measured for masker overall levels of 50, 70, 80, and 90 dB SPL. The masker-probe time interval (defined from masker offset to probe onset) was fixed at 2 ms for all masker levels.

3. Listeners

Five of the seven listeners who participated in experiment I took part in this experiment. They were given at least one training session on the task before data collection.

C. Results

Figure 3 illustrates the masking patterns for the flat-spectrum (open circles) and notched noises (filled circles) for different listeners at different masker levels. Each row corresponds to a different listener. Each column corresponds to a different masker level, as indicated at the top. Squares in the first column illustrate probe absolute thresholds. Error bars represent one standard error of the mean. Vertical dotted lines depict the notch frequency band.

For all listeners, masked thresholds increased as the masker level increased. Masked thresholds were also always higher than the probe absolute thresholds which confirm that there was a masking effect.

The masking patterns were not flat even when the spectrum of the masker was flat and their shape significantly varied across listeners. Nonetheless, for all listeners, the two masking patterns differed more clearly for probe frequencies around the notch frequency band, with masked thresholds for the notched noise masking pattern being clearly lower than those for the flat-spectrum masking pattern. Masked thresholds for probes outside the notch band were very similar for the two maskers. Although the notch was, in general, more evident in the masking patterns at 50 dB SPL, it was also clearly present for higher masker levels.

The effect of level on the relative shape of the masking patterns can be better seen by analyzing the difference masking pattern, that is, by analyzing the difference between the masked probe thresholds for the two maskers (notch-flat) as a function of probe frequency (Fig. 4). This form of analysis eliminates the dependence of the masked thresholds (hence, of the masking patterns) on the individual frequency sensitivity of the listeners. Furthermore, it minimizes the influence that different rates of decay across frequencies could have on the shape of the masking patterns.

Each row of Fig. 4 illustrates the difference masking patterns for a different listener and the bottom row illustrates the mean across the five listeners. Each column corresponds to a different masker level. Error bars in the bottom row represent one standard error of the mean across listeners. Error bars in the other rows represent one standard error of the mean difference. Dotted lines indicate the difference between the spectra of the two maskers. For most listeners, the spectral notch was visible in the mean difference masking patterns at all masker levels (bottom row of Fig. 4). It is also noteworthy that standard errors increased with increasing masker level. Furthermore, the notch became wider and its tip slightly shifted toward higher frequencies. The latter is consistent with the upward spread of masking (reviewed by Moore, 2005).

D. Discussion

Assuming that a forward-masking pattern is the best psychophysical correlate of the AN rate profile of the spectrum of the masker, then the physiological studies would suggest that the spectral notch would be less clearly represented at higher than at lower levels (see the Introduction). The clear presence of the spectral notch in the difference masking patterns of most listeners at high levels did not sup-

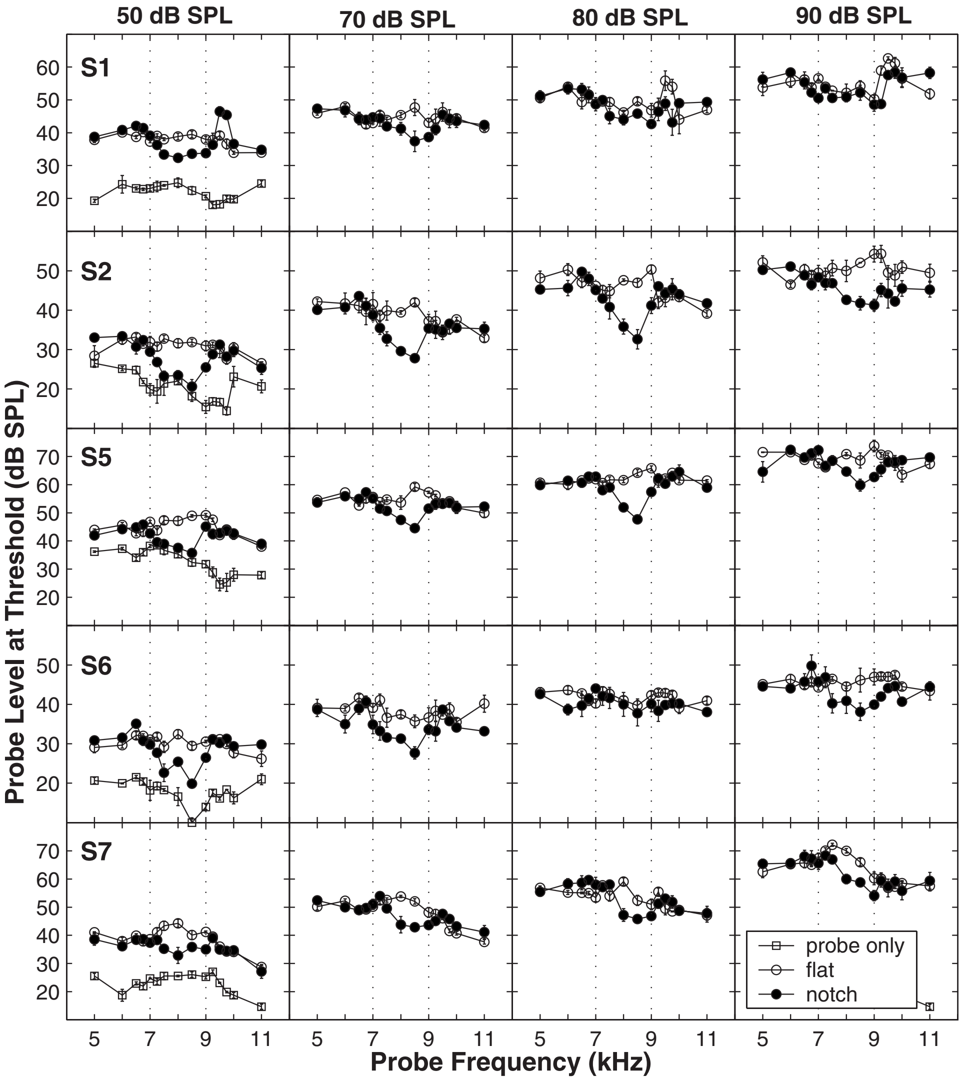

FIG. 3. Masking patterns for the flat-spectrum (open circles) and notched (filled circles) noise forward maskers for a fixed masker-probe interval of 2 ms across masker levels. Each panel illustrates the results for a different listener (rows) and level (columns). Masker levels are indicated at the top of each column. The squares in the first column represent the absolute detection thresholds for probes, i.e., the thresholds in the absence of the masker. Error bars represent one standard error of the mean. Dotted lines illustrate the boundaries of the spectral notch in the notched noise stimulus.

port this expectation (Fig. 4). Further, these masking patterns provide no explanation for the pattern of thresholds with increasing level in the discrimination task of experiment I. Given these inconsistencies, the possibility that the forward-masking patterns measured in this experiment do not capture level dependences that actually exist in the neural representation must be considered. It should be noted that probe thresholds increased with increasing masker level because the probe delay was fixed across masker levels (Fig. 3). As a result, high-level probes would have been subjected to the same processes that might have affected the quality of the neural representation of the masker spectrum. Hence, variations in probe threshold at high levels could be exaggerated (Figs. 3 and 4); they could result from changes not only in the internal representation of the masker but also of the probe.

The effects of peripheral auditory compression serve to illustrate this important point. In forward masking, it is commonly assumed that neural activity recovers exponentially after the masker offset (Harris and Dallos, 1979; Meddis and O'Mard, 2005) and that probe detection in the presence of a forward masker occurs when the response to the probe is as large as when the probe is presented alone (Harris and Dallos, 1979; but see the works of Relkin and Turner, 1988 and Meddis and O'Mard 2005). An alternative interpretation would be that the masker excitation decays exponentially with time and that probe detection occurs when the internal probe excitation just exceeds the residual masker excitation (Oxenham and Moore, 1994; Oxenham, 2001; Plack and Oxenham, 1998). Whatever the interpretation is, evidence exists that the time constants of recovery (or decay) are level independent over a wide range of levels (Plack and Oxenham, 1998; Harris and Dallos, 1979; Meddis and O'Mard, 2005). Hence, when the same masker-probe time intervals are used for all masker levels, probe detection thresholds will increase with increasing masker level. In addition, at levels of compression, the effects on the internal excitations of stimuli should be similar for the masker and the probe. As a result, the potential detrimental effects of peripheral compression on the internal representation of the masker spectrum would not be revealed in its corresponding masking pattern. Figure 5 illustrates this point. The right panel of Fig. 5(a) illustrates a hypothetical peripheral input/output (I/O) function (in log-log scale) with a linear segment (slope of 1 dB/dB) at low levels and a compressed segment at high levels (slope <1 dB/dB). The thick dark lines on the abscissa illustrate the notch depth (in decibels) for a low- and a high-level masker, respectively. Both of them have the same width to

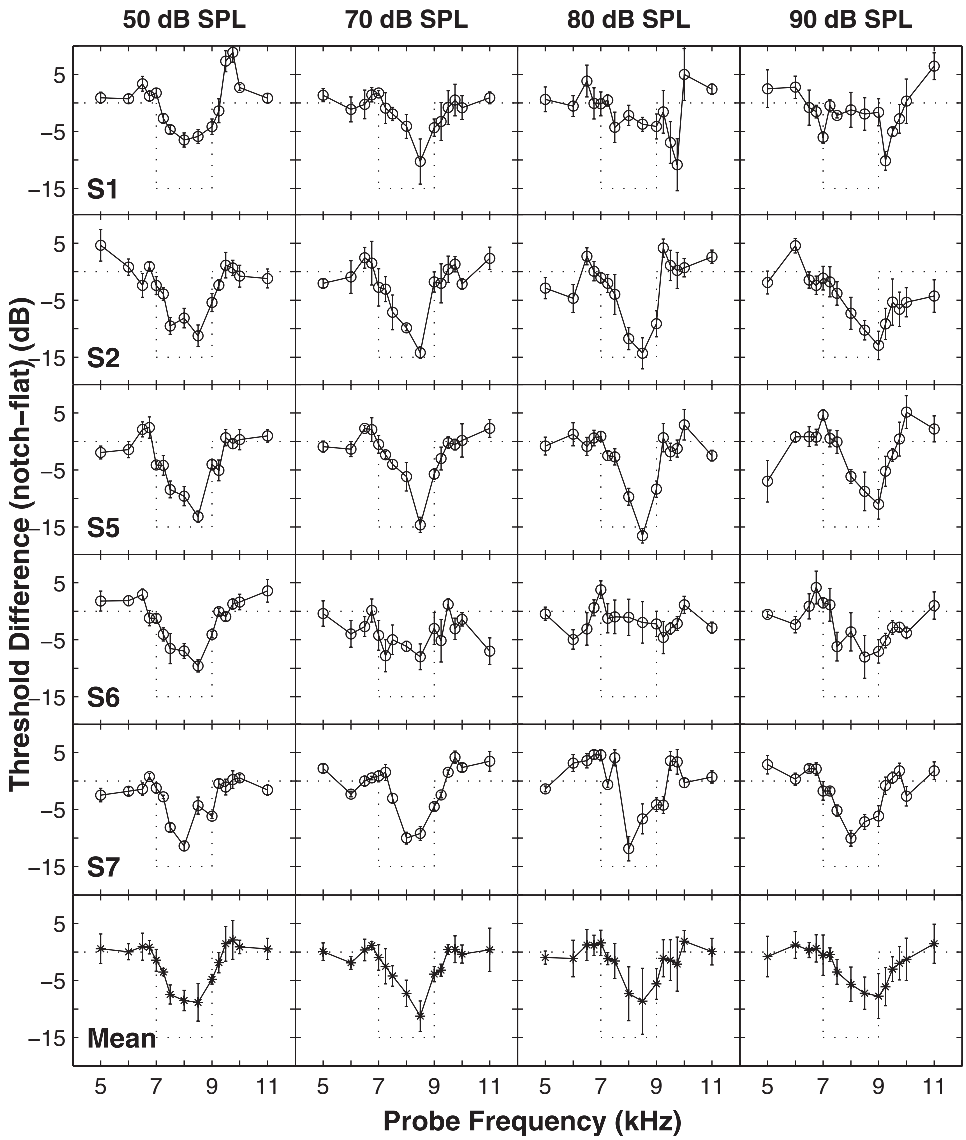

FIG. 4. The difference between the masking patterns for the flat-spectrum and notched noise maskers (notch-flat) for a fixed masker-probe time interval of 2 ms across masker levels. Each column illustrates the results for a different masker level (as indicated at the top). Each row contains the results for a different listener. Error bars represent one standard error of the mean difference. The bottom row illustrates the mean difference across listeners and the error bars illustrate one standard error of the mean. The dotted lines illustrate the difference between the spectra of the two noise maskers.

illustrate that the same notch depth is used for the two masker levels. The thick dark lines on the ordinate illustrate the corresponding internal representations of the notch (depth) for the two masker levels; i.e., the excitation at the output of the nonlinearity. Because of compression, the notch is shallower for the high-level masker than for the low-level masker in this representation.

The left panel of Fig. 5(a) is a hypothetical illustration of how the internal representation of the masker (notch) decays in time after its offset. This is based on the view that forward masking reflects persistence of neural activity, but its inverse could be interpreted as the time course of recovery from the internal masker effect. Evidence exists that this decay is exponential with two time constants (Oxenham and Moore, 1994; Plack and Oxenham, 1998). For simplicity, however, we illustrate here the case when the excitation exponentially decays in time with a single time constant, hence, the linear decay in a lin-log scale (note that time increases linearly to the left). Clearly, in this simplified model, the internal representation of the notch (depth) hardly changes in time. Assume now that masked (probe) threshold occurs when the probe excitation equals the residual masker excitation and that the masker-probe time interval is fixed at 2 ms for both masker levels, as shown in Fig. 5(a). From the excitation at time of 2 ms (vertical gray lines in the left panel), one can work backwards through the I/O function to estimate the range of (input) probe levels corresponding to the internal notch representations for the low- and the high-level maskers. The results are illustrated by the horizontal thick gray lines next to the abscissa in the right panel. Note that probe thresholds are much higher for the high-level masker than for the low-level masker. However, the range of probe levels (the width of the gray lines) is the same despite the internal representation of the notch being considerably worse (shallower) for the high-level masker. This would explain why the spectral notch was equally well represented in the masking patterns for different masker levels when the masker-probe time interval was fixed (Figs. 3 and 4). It also suggests that fixing the time interval may not be the most appropriate method to reveal the true representation of the masker spectrum at different masker levels.

Changes in the internal representation of the masker spectrum should, however, become apparent by considering different masker-probe time intervals for different masker

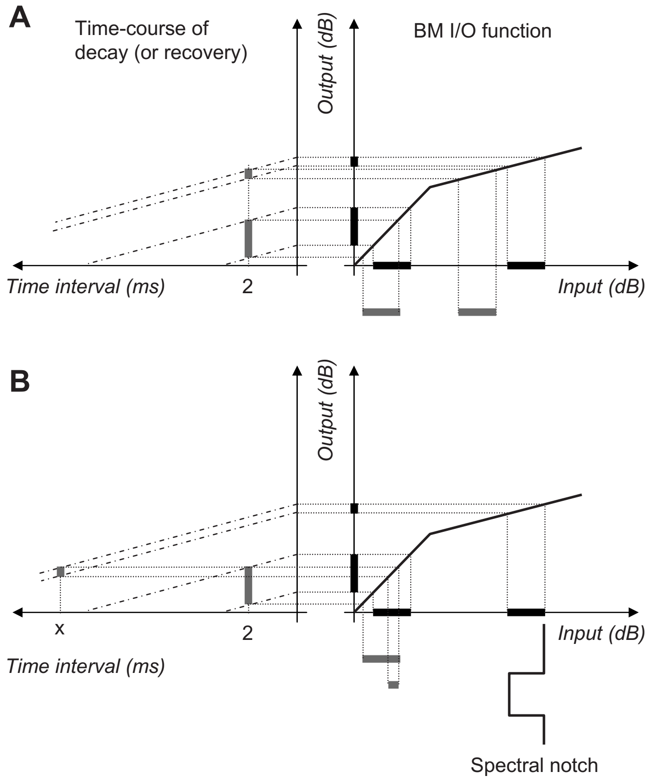

FIG. 5. Schematic explanation of the rationale of the method used to assess the internal representation of the spectral notch at different levels. (A) Representation for fixed a masker-probe time interval. The right plot illustrates a hypothetical peripheral input/output function with a linear segment at low levels (slope of 1 dB/dB) and a compressive segment at high levels (slope of <1 dB/dB). The thick dark lines on the abscissa represent the spectral notch and the width of the lines is proportional to the notch depth. The left panel illustrates a hypothetical internal representation of the spectral notch, the height of the thick gray lines being proportional to notch depth. Also illustrated is the exponential decay of the internal excitation along time, which is illustrated in a lin-log scale (see text for details). The internal representation of the notch is shallower at high levels as a result of compression. The thick gray lines on the abscissa of the right panel illustrate the range of probe levels corresponding to the internal representations of the notch for two level maskers. These were calculated by working backwards through the I/O function from the notch internal representation at time of 2 ms (vertical thick gray lines). (B) The same as in (A) but considering different masker-probe time intervals for different masker levels. Here, a longer masker-probe time interval is used for the higher-level masker, so that the resulting probe thresholds are comparable for the two masker levels. In this case, the range of probe levels (width of the horizontal gray lines) reflect the actual notch depth as internally represented (see text for details).

levels. Figure 5(b) illustrates how the internal representation of the notch (vertical dark thick lines) becomes clearly represented in the range of probe levels (i.e., in the width of the horizontal gray lines) by considering a longer masker-probe time interval for the higher-level masker. The intervals would need to be chosen such that the masked (input) probe thresholds remain approximately constant across masker levels. In this case masked probe thresholds are approximately the same for the two masker levels. Thus, any changes in the masking patterns may be mainly attributed to changes in the internal representation of the spectrum of the masker alone. The following section reports on an experiment aimed at measuring the masking patterns based on this principle.

IV. EXPERIMENT III: MASKING PATTERNS OF FLAT-SPECTRUM AND NOTCHED NOISES WITH VARIABLE MASKER-PROBE TIME INTERVAL

A. Aim and rationale

This experiment was similar to experiment II except that different masker-probe time intervals were used for different masker levels. The intervals were individually chosen for each listener such that masked probe thresholds remained approximately constant for the masker levels tested. Based on the rationale explained in the preceding section, the assumption was that the resulting masking patterns constitute the best possible psychophysical estimate of the internal representation of the masker spectrum at different levels.

B. Methods

1. Procedure and stimuli

The procedure and stimuli were similar to the ones used in experiment II except that, in this case, a 2 ms masker-probe time interval was used for the 50 dB SPL masker only, and longer masker-probe intervals were used for higher masker levels as necessary. The intervals were adjusted such that the masked threshold of an 8 kHz probe was approximately constant across masker levels. An 8 kHz tone was used because it was at the center of the notch frequency band. The actual intervals were determined as follows. The masked threshold for the 8 kHz probe tone was measured for the flat-spectrum noise masker for several masker-probe intervals, typically 2, 10, 20, and 30 ms. The flat-spectrum noise masker was used because it was the standard stimulus in experiment I. The resulting masking decay functions (shown in Fig. 6) were then fitted with either a first- or second-order polynomial (continuous lines in Fig. 6) depending on the number of points measured and the fit error. The fitted polynomial was then used to predict the masker-probe intervals that, for each masker level, gave a masked threshold for the 8 kHz probe approximately equal to the one observed for the 50 dB SPL masker. The predicted value was then experimentally confirmed (by measuring the masked probe threshold for the predicted time interval) and, if necessary, adjusted. This occurred, for example, for listener S3 at 80 and 90 dB SPL, for whom masked-probe thresholds varied ~6 dB across measures. In other words, the actual masker-probe intervals used (shown in Table I) differed slightly from fit predictions.

2. Listeners

Four listeners participated in this experiment (S1, S2, S3, and S4). Two of them (S1 and S2) participated also in experiment II. S3 and S4 were given at least one training session on the task before data collection.

C. Results

Figures 7 and 8 illustrate the masking patterns and the difference masking patterns, respectively, as in Figs. 3 and 4. Note first that for any given listener, masked thresholds were similar across masker levels as was intended (Fig. 7). Fur-

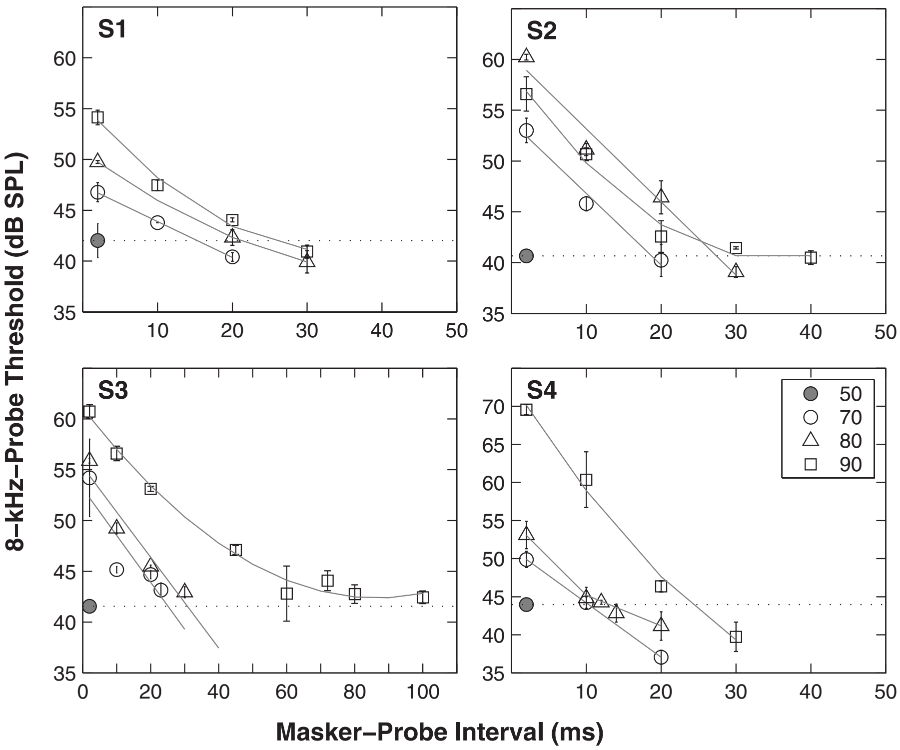

FIG. 6. Detection thresholds of an 8 kHz probe tone masked by a forward flat-spectrum-noise masker as a function of the masker-probe time interval. Each panel illustrates results for a different listener. Different symbols illustrate results for different masker levels, according to the inset in the lower-right panel. Error bars represent one standard error of the mean. The horizontal dotted line indicates the masked probe threshold for a masker level of 50 dB SPL and a masker-probe time interval of 2 ms. Continuous lines illustrate first- or second-order polynomial fits to the experimental functions.

ther, they were always higher than the probe absolute thresholds, which confirms that there was a masking effect.

As in the fixed masker-probe time interval condition (Fig. 3), the masking patterns were not flat. The notch was particularly evident in the masking pattern of the 50 dB SPL masker (Fig. 7). It was less obvious but still visible at 70 dB SPL, especially for listeners S2 and S4, and at 80 dB SPL for listener S4. At 90 dB SPL, the notch was barely visible in the masking pattern for all listeners. The difference masking patterns (Fig. 8) confirmed all these observations.

Peaks as high as 5 dB occurred at the notch edges in the difference masking patterns at 50 dB SPL for listeners S2, S3, and S4 (Fig. 8). These peaks are likely to occur as a result of cochlear suppression effects (Poon and Brugge, 1993).

D. Discussion

The forward-masking patterns of flat-spectrum and notched noises were measured for different masker levels, with different masker-probe time intervals set at different masker levels. The objective was to obtain a more realistic estimate of the internal representation of the notch at different masker levels.

Clearly, the effect of increasing masker level on the notch internal representation was very different for the fixed- and the variable-interval conditions (compare the bottom rows of Figs. 4 and 8). The notch was less clearly represented at high levels in the variable-interval condition (i.e., when the masked probe thresholds remained constant across masker levels) (Fig. 8) than in the fixed-interval condition (i.e., when masked probe thresholds increased with increasing masker levels) (Fig. 4).

Kidd and Feth (1981) reported that forward-masking patterns broadened as the masker-probe interval increased from 5 to 40 ms. This broadening would be consistent with a deterioration of the masker spectral features as represented in the masking pattern. It would also be consistent with the present results. In their study, however, the level of the (tonal) masker was fixed across masker-probe time intervals. As a result, probe thresholds decreased with increasing masker-probe time interval and, therefore, the changes in their masking patterns must have reflected changes in the internal excitation of the *probe*. In the present study, however, the masker-probe interval was precisely varied to maintain probe levels similar across masker levels (and time intervals).

The masking patterns of the flat-spectrum noise were not flat (as also reported in experiment II) and for some listeners, masked thresholds decreased with increasing frequency (e.g., S3 in Figs. 3 and 7). This may seem to be inconsistent with early studies that measured masked audiograms by using white noise as maskers and that reported a gradual increase in thresholds with increasing probe frequency (e.g., Reed and Bilger, 1973). Those early observations can be reasonably

TABLE I. Individual masker-probe time intervals (ms) used to measure the masking pattern for each of the four masker levels tested. The individual thresholds for the 8 kHz probe in the absence of masker are also shown.

Listener	8 kHz probe threshold (dB SPL)	Masker-probe time intervals (ms) for different masker levels (dB SPL)			
		50	70	80	90
S1	22.52	2	16	19	23
S2	27.61	2	19	27	34
S3	28.57	2	23	37	100
S4	19.50	2	11	12	24

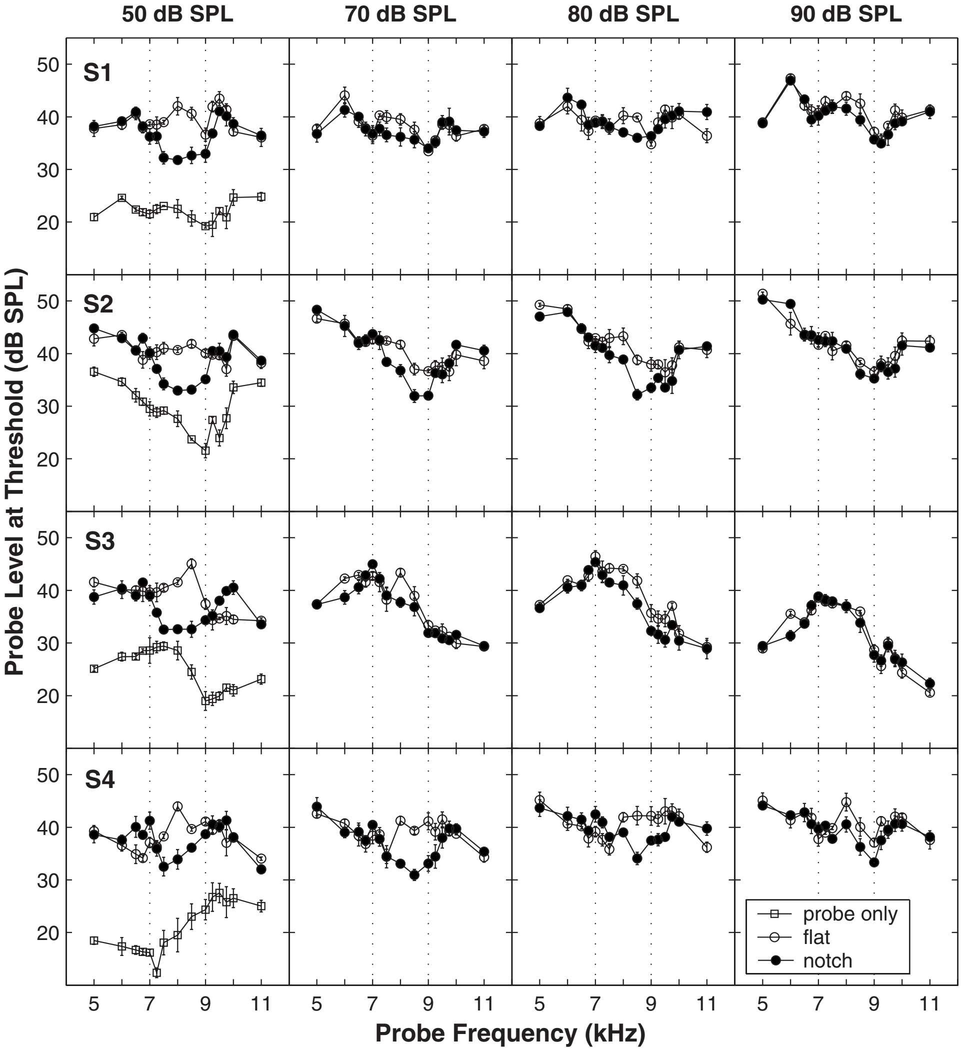

FIG. 7. The same as Fig. 3 but for a variable masker-probe time interval. The interval was varied to maintain the probe thresholds approximately constant across masker levels (see Fig. 6).

well accounted for in terms of the increasing bandwidth of auditory filters with increasing their center frequencies (Fletcher, 1940). In other words, the masking power of white noise is proportional to the width of the auditory filter centered at the probe frequency. It should be noted, however, that in the present study, the masker was not a white noise. Instead, its spectrum extended only up to 16 kHz. The lack of masking energy above that frequency could have reduced its masking power for probe frequencies close to 16 kHz. This may have facilitated the detection of higher-frequency probe tones (closer to 16 kHz) relative to that of lower-frequency tones. Furthermore, the individual listener's sensitivity to different frequencies might have also contributed to the shape of the masking pattern.

Whatever the reason is, the individual factors that determined the shapes of the masking patterns for the flat-spectrum masker will also have determined the masking pattern for the notched noise maskers. Such factors will have cancelled out in the *difference* masking patterns. Therefore, the idiosyncrasies in the shapes of the masking patterns do not compromise the conclusions on the internal representation of the spectral notch at different levels based on the difference masking pattern (bottom rows of Figs. 4 and 8).

The masked thresholds of listener S3 in the variable time interval condition (Fig. 7) were slightly lower for the 90 dB SPL masker than for the lower masker levels. Even so, the notch was already less clearly represented at 80 dB SPL and, therefore, also in this case, it can be concluded that the internal representation of the spectral notch deteriorates with increasing level. The results of this listener at 90 dB SPL should, nevertheless, be considered with reservation.

The shapes of the masking patterns may have also been influenced by off-frequency listening (Moore, 2005). Off-frequency listening, however, does not compromise the conclusion that the internal representation of high-frequency spectral notches gradually deteriorates as the stimulus level increases. One reason is that the amount (and effects) of off-frequency listening would have been approximately similar for the two noise maskers and, hence, would have cancelled out in the difference masking patterns. Second, masked thresholds were similar across masker levels and, hence, any off-frequency listening effects would have been comparable across masker levels.

A similar earlier study (Moore and Glasberg, 1983) investigated the effect of level on the quality of the internal representation of vowel formants by measuring the masking patterns of synthetic vowels in forward masking for overall levels of 50, 70, and 90 dB SPL. The masker was one of two synthetic vowels (/æ/ and /i/), both with a fundamental frequency of 100 Hz. Probe tones were immediately presented

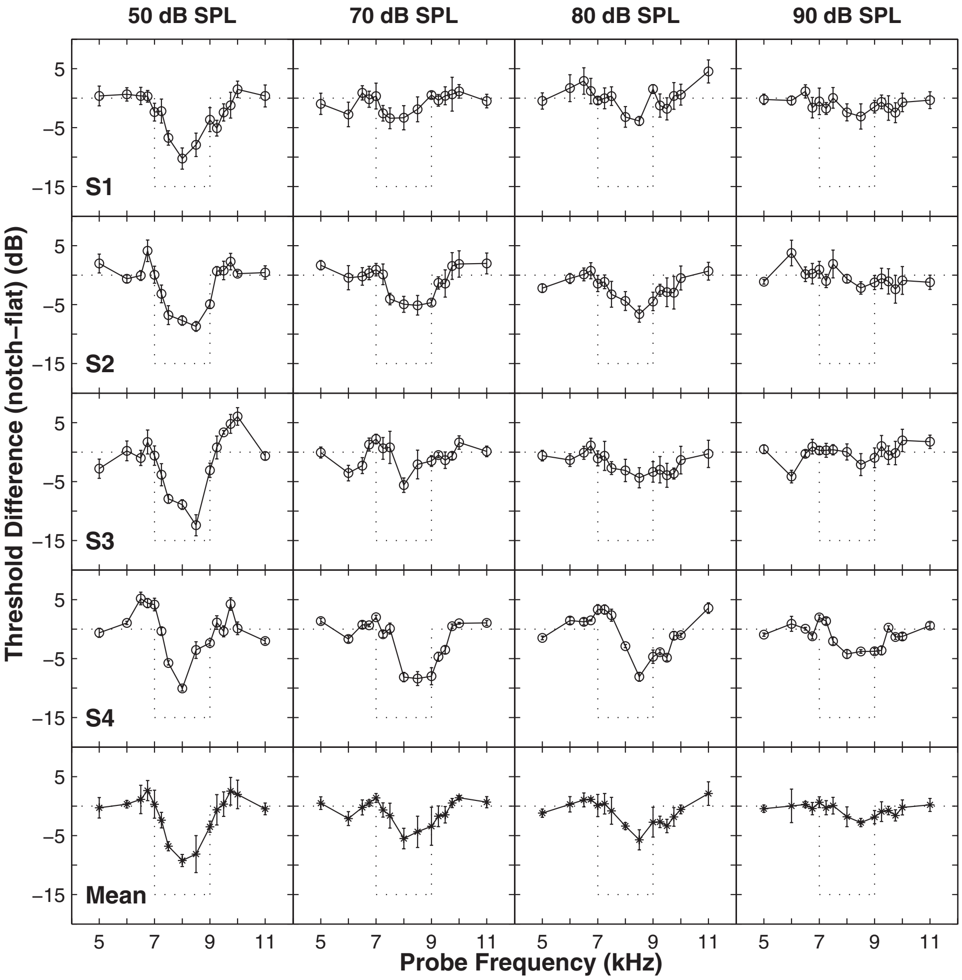

FIG. 8. The same as Fig. 4 but for a variable masker-probe time interval across masker levels.

after the maskers and their detection thresholds were measured as a function of probe frequency. Probe thresholds were expressed as the level of a broadband noise masker that would give a similar probe detection threshold. The authors concluded that the "representation of the formant structure was impaired only slightly at high masker levels" (p. 909). This conclusion is in agreement with the results reported here for the fixed masker-probe time interval condition (bottom row of Fig. 4) but not with those for the variable-interval condition (bottom row of Fig. 8). Moore and Glasberg (1983) used a fixed masker-probe time interval and, for the reasons described before, it is possible that any negative effect of level due to peripheral auditory compression was not revealed in their results. The transformation used to express probe thresholds was intended to compensate for the fact that the increase in probe thresholds was not equal to the increase in masker level. However, the compensation for the effects of compression may not have been sufficient. If probe detection had been affected by compression, the broadband noise level that corresponded to probe threshold may have also been affected by compression, even though the spectrum level of the broadband noise was much lower than the level of the probe tone.

Another possible reason for the apparent contradiction between the conclusion of Moore and Glasberg (1983) and the present results is that the spectral features considered in the two studies extended to very different frequency ranges: vowel formants were below 3.5 kHz, while the present notch extended from 7 to 9 kHz. The near-threshold bandwidth of AN fibers depends on the CF of the fiber; the higher the CF is, the wider the bandwidth is (Evans, 1975). Therefore, for broadband stimuli, the effective level driving an AN fiber is proportional to its bandwidth. As a result, a broadband stimulus that drives low-CF AN fibers below saturation might drive high-CF AN fibers at saturation. At high levels, this effect would be much stronger for high-CF units than for low-CF units, as their bandwidth increases substantially more with increasing level than that of low-CF units (Rose *et al.*, 1971). This might explain why the negative effect of increasing masker level was less obvious in the vowel masking patterns of Moore and Glasberg (1983) than in the present ones.

The results of experiments II and III, combined, are qualitatively consistent with the idea that peripheral compression contributes to a deterioration of the internal representation of the spectral notch at high levels. As previously explained, the masking patterns for the variable-interval condition probably provide a more realistic account of the quality of the internal representation of the spectral notch at different levels. For this reason, in the following section, the analysis and discussion of the results of the spectral discrimination task are based on the masking patterns for variable masker-probe time interval.

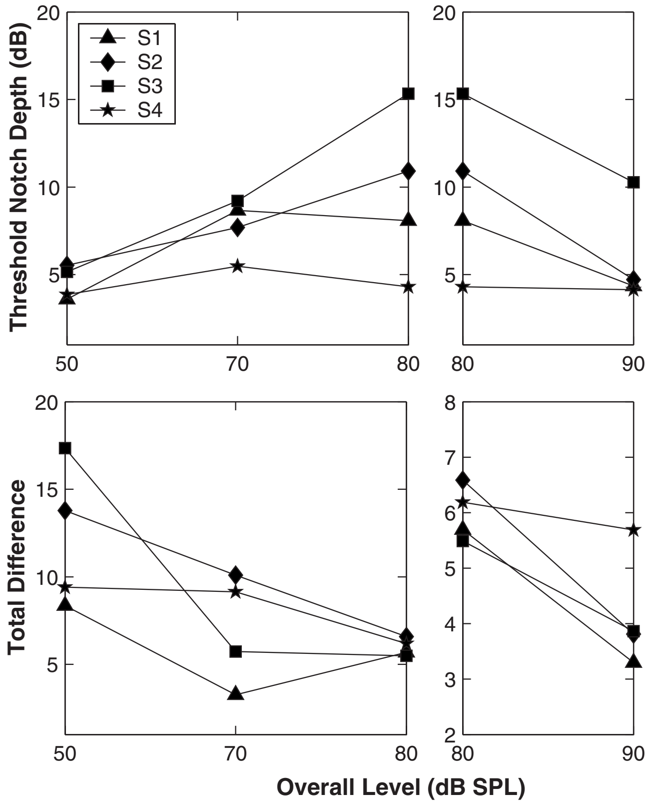

FIG. 9. The effect of increasing level on the threshold notch depths for discriminating between flat-spectrum and notched noise stimuli (upper panels, adapted from Fig. 2 for listeners S1–S4) and on the total difference between the masking patterns of flat-spectrum and notched noise maskers for variable masker-probe time intervals (lower panels, adapted from Fig. 8). Different symbols illustrate the results for different listeners. The left and right panels illustrate the results over two different level ranges: 50–80 (left) and 80–90 dB SPL (right).

V. CORRELATION BETWEEN THE RESULTS OF EXPERIMENTS I AND III

The masking patterns measured in experiment III are assumed to provide the best estimate of the internal representation of the flat-spectrum and notched noises used in the discrimination task of experiment I. These are assumed to be closely related to the excitation pattern representation of the spectra of the two noises in the peripheral auditory system, possibly in the AN (see Introduction). Therefore, the hypothesis that the discrimination is based on the comparison of the AN excitation pattern representations of the two noises was tested by correlating the shapes of the threshold notch depths versus level functions of experiment I with the total difference between the two masking patterns of experiment III. The latter was calculated as the square root of the sum (across frequencies) of the squared difference masking patterns (Fig. 8). This measure is akin to the Euclidean distance between the masked probe thresholds for the two maskers.

The lower panels of Fig. 9 illustrate the total difference between the masking patterns as a function of masker level. Different symbols illustrate the results for different listeners (results are shown only for the four listeners, S1–S4, for whom masking patterns were measured with variable masker-probe time intervals). For comparison, the upper panels of Fig. 9 show the discrimination threshold notch depths at the same four levels (adapted from Fig. 2). The results of both experiments are plotted separately for two level ranges: 50–80 (left panels) and 80–90 dB SPL (right panels). This facilitates the visual comparison of the results below and above 80 dB SPL, the level at which the trend in discrimination performance changed (from increasing to decreasing) with increasing level.

Discrimination threshold notch depths increased with increasing level from 50 to 80 dB SPL, while the total masking-pattern difference decreased over the same level range. In other words, discriminating between flat-spectrum and notched noise stimuli became more difficult as the level increased from 50 to 80 dB SPL and this is consistent with the masking patterns of the two stimuli becoming gradually more similar with increasing masker level over the same range. Strikingly, the total difference between the masking patterns continued to decrease as the level increased from 80 to 90 dB SPL and yet discrimination *improved* (or remained approximately constant for S4). Thus, above 80 dB SPL, the increasing similarity between the masking patterns does not correlate with the improvement on the discrimination task.

VI. GENERAL DISCUSSION

The aim of this study was to behaviorally investigate to what extent discriminating between broadband noise stimuli with and without *high*-frequency spectral notches relies on the comparison of the internal (supposedly AN) representation of the spectra of the two noises. The approach consisted of comparing the results of the spectral discrimination task with the shapes of the forward-masking patterns of the corresponding two noises. The forward-masking patterns were assumed to provide the best psychophysical correlate of the internal excitation patterns of the masker at the auditory periphery. The hypothesis was that if high-frequency spectral discrimination relied on comparisons of the internal representation of the spectra of the two noises, then the more similar the masking patterns are, the worse listeners should perform in the discrimination task. The results suggested that this hypothesis holds true below but not above 80 dB SPL (Fig. 9).

Assuming that a forward-masking pattern is a reasonable approximation of the AN rate-profile representation of the stimulus spectrum (see Introduction), then the deterioration of the internal representation of the spectral notch with increasing level would be consistent with the notion that the rate-profile representation of spectral features deteriorates with increasing stimulus level. This deterioration would be due to the broadening of the frequency response and to the saturation of the response of AN fibers (Rice *et al.*, 1995; Lopez-Poveda, 1996). However, rate profiles and masking patterns are different measures. Despite precautions have been taken to maximize the correspondence between the two (e.g., by using forward masking and by ensuring that the probe level was approximately constant for all masker levels), the correspondence may not be straightforward.

Indeed, the quality of the notch representation in the present masking patterns varies with level in a way consistent with most, but not all, studies on the AN rate-profile representation of high-frequency spectral notches. Physiological (Rice *et al.*, 1995) and simulation (Lopez-Poveda, 1996) studies have shown that the AN rate-profile representation of high-frequency spectral notches gradually deteriorates with increasing level, which is consistent with the trend in the present making patterns for the variable-interval condition. This trend is also consistent with the quality of the level-dependent representation of the spectral notch in the simulated excitation pattern of inner hair cells (Lopez-Poveda *et al.*, 2008). By contrast, a related physiological study (Alves-Pinto, 2007; Lopez-Poveda *et al.*, 2007) suggests that the spectral notch is *better* represented in guinea-pig AN rate profiles at around 70–80 dB SPL than at lower and higher levels, which appears to be inconsistent with the trend suggested by the present masking patterns as well as with the results of the spectral discrimination task (Fig. 2). The reason for this inconsistency is unclear. Maybe a mismatch exists in the SPL calibration between the physiological and psychophysical studies. It is also possible that the masking patterns were measured for a range of levels insufficient to reveal any improvement in the representation of the spectral notch. Alternatively, the discrepancy might relate to differences in signal processing between the guinea-pig and human peripheral auditory systems. In any case, it is important to bear in mind that forward masking is not only the result of a poststimulatory reduction in AN activity and/or the persistence of neural activity but also of efferent inhibitory processes (see the work of Meddis and O'Mard, 2005 for a brief review on the topic).

Assuming that masking patterns reflect the AN rate-place representation of the spectra of the two noises, the present results suggest that discriminating between the two noises is unlikely to rely on comparing the rate-profile representations of their spectra, at least above 80 dB SPL. This undermines the conjecture of Alves-Pinto and Lopez-Poveda (2005) that the improvement in performance above 80 dB SPL could reflect an improvement in the quality of the representation of the spectral notch in the rate profile. This would occur as a result of the notch being essentially encoded by low-spontaneous–rate fibers, which have higher thresholds and wider dynamic ranges (Evans and Palmer, 1980; Sachs and Abbas, 1974). If this had been the case, the notch would have been more clearly observed in the difference masking patterns at high levels.

If the quality of the representation of high-frequency spectral notches in the excitation pattern gradually deteriorates with increasing level, what explains the improvement in spectral discrimination above 80 dB SPL (Fig. 2)? One possibility is that it is based on temporal information. It is possible that above 80 dB SPL, when the rate-place representation of the different spectra becomes statistically indistinct, the information carried in the discharge *times* of AN fibers evoked by the different spectra may become more relevant to discrimination. This is supported by a related computational modeling study on the representation of spectral notches at the level of the inner hair cells (IHCs) (Lopez-Poveda *et al.*, 2008). The simulations show that the quality of the IHC excitation pattern representation of the spectral notch decreases as sound level increases (consistent with the present masking patterns for the variable-interval condition). By contrast, when the frequency information of the receptor potential waveforms is considered, the quality of the IHC representation of the spectral notch improves above 80 dB SPL (consistent with what occurs in the spectral discrimination task). According to the model, the improvement could be possibly related to IHC nonlinearities. The plausibility of this mechanism would require almost certainly that AN responses be phase locked to the IHC receptor potential waveforms for frequencies much higher than the conventionally accepted limit for phase locking (around 4 kHz according to Palmer and Russell, 1986). On the other hand, recent studies have shown that although the number of AN spikes phase locked to the stimulus waveform rapidly rolls off with increasing frequency, statistically significant phase locking may still occur for stimulus frequencies as high as 14 kHz (Recio-Spinoso *et al.*, 2005). Therefore, the proposed mechanism is at least plausible.

The conjecture that some form of temporal code may mediate the discrimination of high frequencies *when rate cues are not available* is original as far as it refers to *aperiodic*, high-frequency stimuli. A similar conjecture was put forward long ago by Sachs and Young (1979) and Young and Sachs (1979) based on the representation of vowel spectra in the discharge pattern of the AN. It has also been suggested based on a computational model of the limits of human auditory perception for single tones (Heinz *et al.*, 2001). It is also consistent with the results of a recent modeling study (Holmberg *et al.*, 2007) according to which rate-place codes do not explain the good performance of human listeners in speech recognition at high speech levels, particularly in the presence of background noise. Speech recognition accuracy in their model improved, however, when the rate-place code information was combined with temporal information.

Another alternative explanation for the improvement in spectral discrimination at high levels could be that it reflects the activation of acoustic reflexes. The medial olivocochlear reflex activates at high level and its effect is to shift the dynamic range of AN fibers toward higher levels (Guinan, 2006). Therefore, one might think that the improvement in spectral discrimination above 80 dB SPL [Fig. 2, Alves-Pinto and Lopez-Poveda (2005)] relates to the activation of this reflex (Winslow and Sachs, 1987; Pickles, 1988). This, however, is unlikely. If it had been the case, it would have almost certainly led to a clearer representation of the spectral notch in the masking patterns above 80 dB SPL and this was not the case (Figs. 3 and 7).

One final remark: the conclusions of this study would have been markedly different if the masking patterns had been measured only with a fixed masker-probe time delay for all masker levels, as is commonly the case. The differences between the masking patterns obtained with fixed and variable masker-probe intervals demonstrate (1) the importance of choosing the correct psychophysical method to infer the internal representation of the spectrum of a sound and (2) the extent to which this representation can be affected by peripheral compression.

VII. CONCLUSIONS

The shape of the masking patterns of broadband noise forward maskers with and without a high-frequency spectral notch becomes gradually more similar as the overall level of the masker increases (at least when measures are taken for masked probe thresholds to remain constant across masker levels). This suggests that the AN rate-place representation of high-frequency spectral notches gradually deteriorates with increasing level. The result is consistent with the increased difficulty in discriminating between flat-spectrum and notched noise stimuli for stimulus levels increasing between 50 and 80 dB SPL but not with the improvement observed for further level increases above 80 dB SPL. This suggests that a form of representation other than rate place (possibly temporal) is likely to mediate high-frequency spectral discrimination, at least above 80 dB SPL.

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