The pulse-train auditory aftereffect and the perception of rapid amplitude modulations

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Prolonged listening to a pulse train with repetition rates around 100 Hz induces a striking aftereffect, whereby subsequently presented sounds are heard with an unusually "metallic" timbre [Rosenblith *et al.*, Science **106**, 333–335 (1947)]. The mechanisms responsible for this auditory aftereffect are currently unknown. Whether the aftereffect is related to an alteration of the perception of temporal envelope fluctuations was evaluated. Detection thresholds for sinusoidal amplitude modulation (AM) imposed onto noise-burst carriers were measured for different AM frequencies (50–500 Hz), following the continuous presentation of a periodic pulse train, a temporally jittered pulse train, or an unmodulated noise. AM detection thresholds for AM frequencies of 100 Hz and above were significantly elevated compared to thresholds in quiet, following the presentation of the pulse-train inducers, and both induced a subjective auditory aftereffect. Unmodulated noise, which produced no audible aftereffect, left AM detection thresholds unchanged. Additional experiments revealed that, like the Rosenblith *et al.* aftereffect, the effect on AM thresholds does not transfer across ears, is not eliminated by protracted training, and can last several tens of seconds. The results suggest that the Rosenblith *et al.* aftereffect is related to a temporary alteration in the perception of fast temporal envelope fluctuations in sounds.
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I. INTRODUCTION

Prolonged exposure to a constant or repeating stimulus can induce a transient alteration in the perception of subsequent stimuli, which is commonly referred to as an "aftereffect" in the psychophysical literature. In some cases from the visual domain, the aftereffect manifests itself as an "afterimage." Perhaps the simplest and most familiar visual aftereffect is experienced when closing one's eyes after staring at a bright light. Another famous example is the "waterfall" illusion in which, after watching a waterfall for several seconds, one sees fixed objects (such as nearby rocks) "as if in upward motion" (Addams, 1834). The waterfall illusion is just one example of a large set of motion aftereffects, wherein exposure to movement in a certain direction causes a following stationary stimulus to be perceived as moving in the opposite direction [see Wade (1994) for a historical review of motion aftereffects]. Other types of aftereffects are produced using stationary stimuli. These include tilt aftereffects, wherein an oriented stimulus appears to be rotated away from the orientation of a prior stimulus (Gibson and Radner, 1937; Mitchell and Muir, 1976; Magnussen and Johnsen, 1986; He and McLeod, 2001). In fact, aftereffects have been identified, not just for motion and orientation, but for almost all features of visual perception, including spatial frequency, contrast, color, stereoscopic depth, size, and others (e.g., MacKay, 1964; Blakemore and Sutton, 1969; Blakemore and Campbell, 1969; Blakemore and Julesz, 1971).

Common explanations for aftereffects are couched either in terms of sensory persistence, or in terms of neural adaptation. According to the latter type of explanation, prolonged exposure to a stimulus causes a reduction in the responsiveness of neurons that are specifically activated by certain features of that stimulus—a view supported by physiological findings (Barlow and Hill, 1963; Movshon and Lennie, 1979; Maffei *et al.*, 1973; Barlow, 1990). This selective "adaptation" biases subsequent responses of the corresponding array of feature detectors (which are systematically tuned to different values of the stimulus parameter) toward activation patterns shifted away from that previously evoked by the adapting stimulus (Clifford *et al.*, 2000). Alternative and more elaborate explanations involve release from inhibition (Sekuler and Pantle, 1967; Mather *et al.*, 1998), shifts in tuning (Jin *et al.*, 2005), or other neural mechanisms. Perceptual aftereffects provide a unique psychophysical tool as evidence for the existence of specific feature detectors in a sensory system.

While the visual psychophysics literature abounds with examples of aftereffects, examples of analogous phenomena in the auditory modality are much less common. Compared to their visual counterparts, auditory aftereffects remain rather elusive and often require very specific and somewhat unnatural test conditions in order to reveal themselves (e.g., Shu *et al.*, 1993). One example is the so-called "Zwicker

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tone," in which an illusory tonal sensation is heard for a few seconds following the presentation of a broadband noise containing a spectral notch about one-third octave in width, with relatively sharp edges (Zwicker, 1964; Lummis and Guttman, 1972; Wiegrebe *et al.*, 1996; Norena *et al.*, 2000, 2002). The Zwicker tone has been described as a "negative auditory afterimage," because the pitch of the transient illusory tone corresponds roughly to the center frequency of the spectral notch in the preceding noise. While the mechanisms responsible for the generation of the Zwicker tone are still not entirely clear, neurophysiologically inspired models (e.g., Norena *et al.*, 2000; Franosch *et al.*, 2003) have been offered, and potential neural correlates for the phenomenon have been identified at the level of the auditory cortex (Hoke *et al.*, 1996; Norena and Eggermont, 2003). It appears that the aftereffect is related to a temporary enhancement of responsiveness, possibly related to a release from inhibition, in central auditory neurons with best frequencies within the spectral notch, which were least stimulated during the presentation of the inducer.

Another example of an auditory aftereffect is when a stimulus with a uniform (or "flat") spectrum acquires a timbre that is related to the complement (or "negative") spectrum of a preceding stimulus. A compelling demonstration of this type of aftereffect was provided by Summerfield *et al.* (1984). By removing from a series of equal-amplitude harmonics three harmonics, the frequencies of which were close to those of the first three formants in a vowel, Summerfield *et al.* generated precursors that resembled spectral complements of the vowel. When listeners were presented with such precursors followed by the whole series of equal-amplitude harmonics, they heard the latter as an identifiable vowel, despite its physically flat spectrum. A simpler demonstration of a potentially related effect involves removing just one component in a complex tone; when that component is later reintroduced, it stands out perceptually (Wilson, 1970; Viemeister, 1980; Viemeister and Bacon, 1982). The mechanisms underlying such "auditory enhancement" effects remain unclear. The most common explanation involves adaptation, such that the neural responses to subsequently presented stimulus components that were not part of the precursor are enhanced relative to the (adapted) responses to components that were in the precursor.

Another interesting auditory aftereffect appears to have been forgotten soon after its initial description by Rosenblith *et al.* (1947). These authors discovered that, after listening for 1 to 2 min to a train of rectangular pulses repeating at a relatively fast rate (e.g., 100 Hz), listeners experienced various environmental sounds, such as their own voice, a typewriter, a handclap, or the sound of rubbing sandpaper as having an unusually "metallic" timbre—also described as an added "jangly," "twangy," or "like a rasping file" quality. Rosenblith *et al.* explored the influence of various stimulus parameters, including the pulse rate, duration, and level of the inducer. They found that the strength of the aftereffect increased with inducer level and that inducer pulse rates between 30 and 200 Hz were most effective. Using inducer durations ranging from 5 to 240 s, they showed that the duration of the aftereffect increased as a function of exposure time. Based on these results, they suggested exposure times of 20–30 s as a "convenient compromise between the listener's impatience and the experimenter's desire to produce a measurable effect."

Initially unaware of the Rosenblith *et al.* aftereffect, we were recently led to rediscover it during a series of magnetoencephalography experiments (Gutschalk *et al.*, 2007), which involved the continuous presentation of pulses repeating at 80 Hz over tens of minutes. At the end of such experiments, many listeners spontaneously reported experiencing a noticeable change in the perceived quality of sounds, which invariably subsided within a few minutes. Listening to these sounds, we also noted a second feature, which was not reported by Rosenblith *et al.* (1947): When the pulse train is played for longer than 1 min, it appears to serve as its own test stimulus, and prominently changes its sound character. At its beginning, the pulse train sounds like one coherent source, with a buzzing pitch and a certain roughness. After about 20–30 s, however, the roughness appears to slowly die away, while a buzzing, which was previously only a minor element of the coherent percept, becomes increasingly prominent and segregated from the first. In informal listening, the latter percept has been likened to the sound of cicada or midges. Similar to the afterimage, this phenomenon is more prominent when the pulse train is high-pass filtered above 2000–4000 Hz, while low-pass filtering attenuates it, such that the effect is completely abolished for low-pass cutoff frequencies below about 2000 Hz.

Unlike the Zwicker tone, the Rosenblith *et al.* (1947) auditory aftereffect has been the object of very little research up to now, and the perceptual and neural mechanisms underlying it remain essentially unknown. Based on the observations of Rosenblith *et al.* (confirmed by informal listening experiments on ourselves) that the aftereffect was largest for inducer pulse rates between 30 and 200 Hz, and could be eliminated or greatly reduced by low-pass filtering, we hypothesized that the effect was (a) dependent upon the presence of relatively fast and marked temporal envelope fluctuations in the outputs of peripheral auditory filters stimulated by the inducer, and (b) related to an alteration of the perception of such fast temporal envelope fluctuations in subsequently presented sounds. In order to test this hypothesis, we measured how amplitude modulation (AM) detection thresholds for probe noise bursts were influenced by the prior presentation of three types of inducers: (1) A high-pass-filtered 100-Hz harmonic complex with components in sine phase, the temporal waveform and spectrum of which are similar to those of a pulse train with a corresponding rate, (2) a 100-Hz "jittered" pulse train, wherein the timing of each pulse was randomly shifted forward or backward relative to its nominal position, resulting in a stimulus that was aperiodic, but still had marked temporal envelope fluctuations, and (3) an unmodulated noise inducer, which was expected to produce no aftereffect, and so served as a control.

In addition to a main experiment, in which we compared the influence of these three types of inducers on thresholds for the detection of AM imposed onto short noise-burst carriers for different AM frequencies, we performed three further experiments. Experiment 2 measured the time course of the threshold recovery. Experiment 3 was sparked by the informal observation of Rosenblith *et al.* (1947) that the aftereffect reported in their study was not elicited when the test stimulus was not presented to the same ear as the inducer; this prompted us to test whether the aftereffect on AM detection thresholds in the present study would also not be present under such listening conditions. Experiment 4 was motivated by a recent report that AM threshold adaptation effects can disappear with protracted task practice (Bruckert *et al.*, 2006); in order to test whether the effects observed in the present study were also susceptible to training, some of the listeners who had already taken part in the previous three experiments were tested further.

II. GENERAL METHODS

A. Listeners

Four listeners (one female, three male; age 24–32) participated in all experiments, except that listener 1 did not participate in experiment 4. They had normal hearing, defined here as pure-tone thresholds below 20 dB HL at octave frequencies between 250 and 8000 Hz, and reported no history of peripheral or central hearing disorders. The listeners were tested individually in a double-walled sound-attenuating chamber. They were paid an hourly wage for their participation. The study protocol was approved by the institutional review board of the Massachusetts Institute of Technology.

B. Apparatus

The stimuli were generated digitally under MATLAB (The MathWorks, MA), stored onto the computer hard disk, and played out at a 48-kHz sampling rate using the 24-bit digital-to-analog converter of a LynxStudio LynxOne soundcard. They were delivered diotically (except in experiment 3) to the listener via HD580 circumaural headphones (Sennheiser, Old Lyme, CT). The overall sound intensity for inducers as well as probes was set to 46 dB SPL. This moderate level was chosen based on preliminary listening tests, indicating that this level was sufficient to induce a strong aftereffect while still falling well below levels that could cause some listeners discomfort during protracted listening.

III. EXPERIMENT 1: INFLUENCE OF INDUCER TYPE AND AM FREQUENCY TUNING

A. Stimuli and procedure

In this experiment, modulation detection thresholds for probe noise bursts were measured in the absence and in the presence of an "inducer" or "adaptor." Three different inducers were tested in separate conditions: (1) A 100-Hz F0 harmonic complex with all harmonics starting in sine (i.e., 0°) phase, which approximates a regular pulse train with a repetition rate of 100 Hz; (2) a train of temporally jittered pulses with a 100-Hz average rate, which was obtained by shifting randomly and independently the timing of each pulse in an original 100-Hz pulse train over a 10-ms range (i.e., from −5 to +5 ms around the pulse's nominal temporal position with uniform distribution); and (3) a Gaussian noise. The probe stimuli were three 150-ms noise bursts, including 20-ms on and off raised-cosine ramps. One of the three bursts, chosen at random with equal probability on each trial, was sinusoidally modulated in amplitude. Both the inducer and probe stimuli were bandpass filtered using a sixth-order, zero phase-shift Butterworth filter with 6-dB cutoff frequencies of 4 and 16 kHz.

An adaptive tracking procedure was used to estimate the detection threshold for the sinusoidal amplitude modulation. At the beginning of each run, the adaptor was played for 60 s. Two seconds before the end of the adaptor, listeners were visually alerted that the first test trial was about to begin. Following a 200-ms silent interval after the offset of the adaptor, the three probe bursts were presented, separated from each other by 200 ms. The amplitude of one of the three bursts was modulated with a modulation index (m) of −2 dB (i.e., the modulator was 2 dB below the level required for 100% sinusoidal amplitude modulation). The third probe burst was followed by a 200-ms silent interval, after which the inducer was resumed for 4 s and the next trial (i.e., series of probe bursts) began. This alternation of 4-s inducer and probe tones continued until the termination of the threshold-tracking procedure, which occurred after the tenth reversal in the direction of the changes in AM depth. The step size, by which the modulation index was changed, was initially set to 4 dB; it was reduced to 2 dB after the second reversal, and to 1 dB after the fourth reversal. The threshold was computed as the mean of the modulation index (in decibels) across the last six reversals. Listeners had a time window of 2 s after the end of the third probe burst to indicate which of the three probe bursts they thought was amplitude modulated, and they were instructed to respond before the end of that time period, as far as possible. In rare cases where they failed to respond within this time window, the AM depth was left unchanged for the next trial. Otherwise, the AM depth was reduced after any two consecutive correct responses, and increased after any incorrect response.

The following five AM frequencies for the probe bursts were tested in separate conditions: 50, 100, 150, 250, and 500 Hz. These five AM rate conditions, combined with the three inducer conditions and the baseline (no-inducer) condition, yielded a total of 20 different test conditions. The no-inducer condition was tested first. When data collection in this condition was completed, the inducer was introduced. Listeners were given the opportunity to practice the task with the inducer present before data collection for the different inducer conditions started. The different AM rate conditions with the inducer present were tested in randomized order, but the inducer was always the same within one session. Each listener performed a minimum of four runs in each condition; the thresholds measured on the last four runs were averaged.

B. Results

Figure 1 shows how the AM depth (AMD) at threshold, defined in terms of the modulation index (m), varied as a function of the probe-burst modulation rate in the different test conditions of experiment 1. The four panels of Fig. 1(a) show individual data; Fig. 1(b) shows the average across the

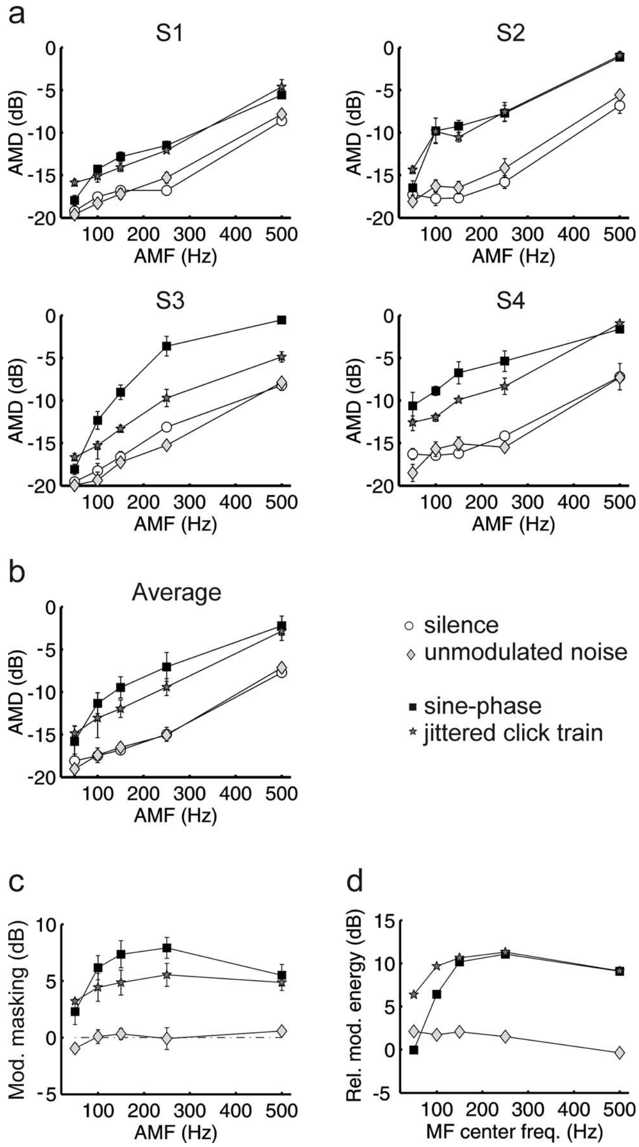

FIG. 1. (a) Individual thresholds for detecting sinusoidal AM imposed on a bandpass noise carrier in silence (open circles), in the presence of the two pulse-train inducers (sine-phase pulse train, closed squares; jittered pulse train, closed stars), and in the presence of unmodulated bandpass noise (closed diamonds) are plotted in terms of $20\log_{10}(m)$, where m is the modulation index, as a function of modulation frequency (AMF). Error bars represent ± 1 standard error of the mean. (b) Mean of the individual results; error bars represent ± 1 standard error across listeners. (c) Elevation of AM detection thresholds in the presence of the three inducers compared to silence (averaged across listeners $\pm$ standard error). The data represent the difference between the conditions shown in (b) and thresholds in silence. (d) Output of a modulation filterbank in response to the inducers of experiment 1, based on the filterbank parameters of Ewert and Dau (2000). Filtered modulation power is considerably higher for the periodic and jittered pulse trains than for bandpass noise at most frequencies, and shows a broad peak at modulation-filter center frequencies around 200 Hz, in general agreement with the psychophysical data.

four listeners. The threshold AMD is expressed in decibels, as $20\log_{10}(m)$, such that lower values correspond to better detection. In all conditions, AM detection thresholds increased with the AM frequency (AMF). The thresholds measured in the absence of any inducer (silence condition, open circles) and those measured following the unmodulated noise inducer (gray diamonds) were usually the lowest and were not significantly different from each other ($F_{1,3}=0.00$, $p=0.975$). Thresholds measured following the sine-phase complex tone inducer (closed squares) were usually the highest, and were significantly higher than those measured in quiet ($F_{1,3}=45.05$, $p=0.0068$). Thresholds measured following the jittered pulse train inducers were slightly, but not significantly different from the regular pulse train ($F_{1,3}=2.24$, $p=0.232$), but were significantly higher than those found in the quiet condition ($F_{1,3}=35.25$, $p=0.0095$).

Figure 1(c) illustrates the "tuning" of the inducer effect with respect to the AMF. The data shown in Fig. 1(c) were obtained by subtracting the thresholds measured in the silent condition from those measured in the different inducer conditions. Accordingly, higher values indicate larger increases in threshold caused by the inducer. The mean increase in AM depth at threshold across listeners for the sine-phase-complex inducer was 2.3 dB (range: 0.8–5.7 dB) at 50 Hz, 6.2 dB (3.3–8.0 dB) at 100 Hz, 7.4 dB (4.0–9.5 dB) at 150 Hz, 7.9 dB (5.2–9.5 dB) at 250 Hz, and 5.5 dB (3.0–7.7 dB) at 500 Hz. For the jittered-pulse-train inducer, the mean increase was 3.2 dB (range 2.9–3.7 dB) at 50 Hz, 4.4 dB (2.4–7.9 dB) at 100 Hz, 4.9 dB (2.7–7.1 dB) at 150 Hz, 5.5 dB (3.4–8.2 dB) at 250 Hz, and 4.9 dB (3.3–6.3 dB) at 500 Hz. As can be seen, for those inducers that had a significant effect (i.e., the complex tones and jittered pulse trains), the effect was broadly tuned, with a peak usually corresponding to around 250 Hz AMF—higher than the 100-Hz AMF of the probe stimulus. As indicated by significant interactions between the "AMF" and "condition" factors in two-way analyses of variance (ANOVA) on the data from the silent and inducer conditions, the influence of the periodic, but not the irregular pulse train, depended on the AMF of the probe [sine phase inducer: $F_{4,12}=10.70$, $p=0.0125$ (including a Greenhouse–Geisser, GG, correction for lack of sphericity where appropriate); irregular pulse train: $F_{4,12}=2.30$, $p=0.2012$]. Student's t-tests for the 50-Hz AMF were only significant for the jittered pulse train compared to silence ($t=16.35$, $p=0.0005$). For all other AMF conditions, the difference between inducers and the silent condition was significant in paired t-tests for both the periodic and jittered pulse trains. No significant interaction with AMF in the contrast of periodic pulse train and silence was observed when the 50-Hz-AMF condition was not included in the ANOVA, indicating that the observed tuning of the periodic pulse train inducer shows mainly a high-pass characteristic above the F0. However, the frequency interaction between periodic and aperiodic pulse trains missed significance in the two-way ANOVA when a GG sphericity correction was applied [$F_{4,12}=4.08$, $p=0.0259$ (uncorrected); $p=0.1146$].

The high-pass nature of the adaptation pattern is similar to what might be expected, given what is currently known about modulation masking and modulation frequency selectivity (e.g., Bacon and Grantham, 1989; Houtgast, 1989; Ewert and Dau, 2000). The modulation spectrum of the 100-Hz pulse train has components at multiples of 100 Hz. Given the broad tuning of the hypothesized modulation filters, with postulated Q values of 1 or less (e.g., Ewert and Dau, 2000), one would not expect to see distinct masking peaks at 100, 200, and 300 Hz, but rather a broadly tuned response. This is illustrated in Fig. 1(d), which shows the time-averaged output of a modulation filterbank, generated using the parameters proposed by Ewert and Dau (2000), operating on the different inducer stimulus waveforms, after processing designed to simulate the effects of the peripheral auditory system. This included passing the stimuli through a gammachirp auditory filter (Irino and Patterson, 1997) with a characteristic frequency of 5 kHz (i.e., within the stimulus passband) and phase response modified according to Oxenham and Dau (2001a, b), and extracting the envelope through halfwave rectification. Additionally, a low-pass filter (first order) with a cutoff frequency of 150 Hz was applied, to account for the relative reduction of sensitivity at higher modulation frequencies (Kohlrausch *et al.*, 2000; Ewert and Dau, 2000). The center frequencies of the modulation filters (Ewert and Dau, 2000; Q value=1) were chosen to coincide with the AM frequencies of the probe tones. Finally, the energy at the output of these filters was computed. The resulting modulation-filter responses are broadly consistent with the psychophysical findings shown in Fig. 1(c) in that both the periodic and jittered pulse trains exhibit a broadly tuned bandpass shape peaking around 200–300 Hz, although some discrepancies between the model predictions and the data are apparent for the lowest probe modulation frequencies.

IV. EXPERIMENT 2: TIME COURSE OF THE EFFECT

A. Rationale, stimuli, and procedure

This experiment sought to measure the time course of the change in AM detection thresholds following the offset of a 60-s, 100-Hz sine-phase harmonic complex inducer, similar to that used in experiment 1. The bandwidths of the inducer and probe were the same as in experiment 1. Each run started with the presentation of this inducer, followed after a 200-ms silent interval by a first triplet of probe bursts. As in experiment 1, one of the three probe bursts (the target burst) was modulated in amplitude, and the listener's task was to indicate which one. Based on the results of experiment 1, which showed the largest effect at an AM frequency of 250 Hz, the target probe was modulated at a rate of 250 Hz here. Also based on the results of experiment 1, the following four modulation indices were selected: −6, −10, −14, and −18 dB. On each run, one of these four depths was randomly selected, and applied to all target bursts. Following a 3-s silent interval after the end of the first triplet, another triplet was presented, again with the position of the target probe randomized. This was done repeatedly over a period of 60 s, during which a total of 20 probe triplets was presented. Each run was followed by a 30-s silent interval. Following this fixed period of silence, listeners could initiate the next run with a button press. To establish a baseline, the same four modulation indices were also tested in silence at the beginning of the experiment, in the same random order.

Listeners had a time window of 2.5 s after the offset of the last stimulus in each triplet to respond. Rare trials on which listeners failed to respond within the time window were discarded. Each listener performed 50 runs at each of the five AM depths. For each of the 20 triplet positions, the estimated correct-response probabilities were plotted as a function of the AM depth and fitted with a logistic function using a maximum likelihood procedure. This permitted the estimation of the 70%-correct AM detection thresholds as a function of the delay between the offset of the 30-s inducer and the onset time of each probe triplet.

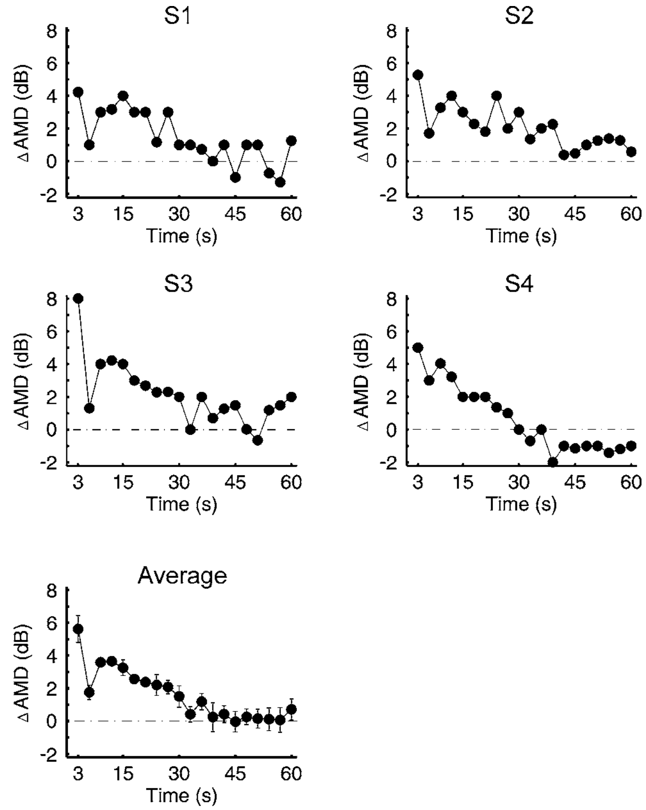

FIG. 2. Recovery of AM detection thresholds over time. Each data point represents the difference of the AM threshold determined after the inducer and the AM threshold in silence (ΔAMD), as determined at the beginning of experiment 2. The inducer was 60 s long, and adapted thresholds were determined in 3-s steps after the end of the inducer (a sine-phase pulse train). The AM depth of the probe was −6, −10, −14, or −18 dB. Thresholds corresponding to 70% correct on the psychometric function were calculated using a maximum likelihood procedure. The bottom panel shows the mean across listeners, and the error bars in that panel correspond to 1 standard error of the mean across listeners.

B. Results

The results of experiment 2 are shown in Fig. 2, where the upper four panels show individual data, and the lower panel shows the mean across listeners. The data points in these plots were obtained by subtracting the AM detection threshold in the absence of the inducer, as determined by the same procedure at the beginning of the experiment, from that measured in the presence of the inducer at each probe-triplet position, across all triplet positions. Thus, these data points reflect the influence of the sine-phase inducer on AM detection thresholds at different times after the offset of the inducer: Positive values along the Y axis indicate an increase in threshold compared to the reference (quiet) condition; the zero point is marked by a horizontal dashed-dotted line.[1]

As can be seen, the effect of the inducer usually decreased over the first 30 s following the offset of the inducer, after which it remained roughly constant on average, and not significantly different from zero [main effect over the whole 1- to 60-s period: $F_{19,57}=12.03$, $p=0.0020$ (GG); main effect over the 1- to 30-s period: $F_{9,27}=7.05$, $p=0.0102$ (GG); linear contrast over the same period: $F_{1,3}=12.10$, $p=0.0401$; (third- and fifth-order contrasts, not reported here, were also significant); main effect over the 31- to 60-s period: $F_{9,27}=0.85$, $p=0.4769$ (GG); linear contrast over the same period: $F_{1,3}=1.34$, $p=0.3302$ (second-order contrast significant); main effect of interval, i.e., contrast between 1- to 30-s and 31- to 60-s periods: $F_{1,3}=58.61$, $p=0.0046$].

One unexpected feature of the results, which is apparent in both the individual and the average data in Fig. 2, relates to the presence of a "kink," indicating a decrease of the inducer effect, at the second probe-triplet position. As revealed by the results of *t*-tests contrasting the effect at the second triplet-position with those at the surrounding, first and third positions, this effect was significant (First versus second triplet: $t=3.88$, $p=0.0304$; second versus third triplets: $t=5.23$, $p=0.0136$). However, we have no explanation for the effect at this time.

V. EXPERIMENT 3: IS THE EFFECT EAR SPECIFIC?

A. Rationale

Rosenblith *et al.* (1947) mentioned in passing near the end of their article that the aftereffect measured in their study did not transfer across ears. This anecdotal observation, which can easily be verified by listening, is particularly interesting, not only for its potential implications regarding the neural substrate of the aftereffect, but also because it can be used as a tool to further investigate the relationship between the aftereffect described by Rosenblith *et al.* (1947) and the elevation in AM detection thresholds measured in the present study. If the two are related, the induced increase in AM detection thresholds should not be observed when the inducer and probe stimuli are presented to opposite ears.

B. Methods

This experiment used a procedure similar to that of experiment 1, with probe-burst triplets presented at regular time intervals between 4-s bursts of a 100-Hz F0 sine-phase harmonic complex tone or unmodulated noise inducer. Each run started with the uninterrupted presentation of the inducer for 60 s. The unmodulated noise inducer was used as a control. The sine-phase complex inducer and a probe AMF of 250 Hz were selected because this combination yielded the largest effects in experiment 1. The main difference between this and previous experiments was that instead of presenting the inducer and probe diotically, the probe was presented monaurally to the right ear and the inducer was presented either to the same ear (ipsilateral-inducer condition) or to the opposite ear (contralateral-inducer condition).

C. Results

As can be seen in Fig. 3, the results of experiment 3 were consistent across listeners. There is a clear interaction between the inducer type and stimulation mode ($F_{1,3}=620.13$, $p=0.0001$): For the sine-phase complex inducer

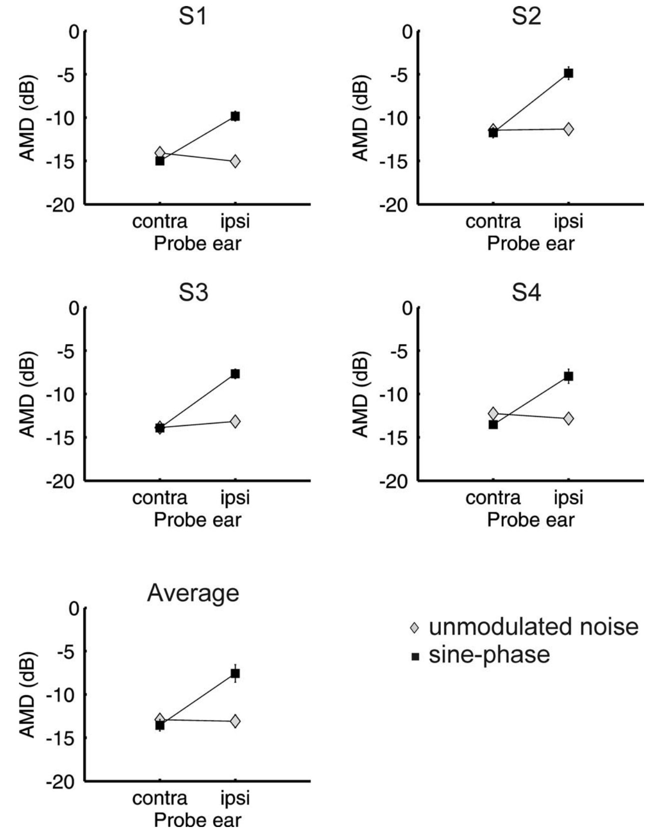

FIG. 3. Amplitude modulation detection thresholds for the right ear, with the sine-phase complex tone (squares) or unmodulated noise (diamonds) inducer presented either to the ipsilateral (right) or the contralateral (left) ear. The probe was sinusoidally amplitude modulated at 250 Hz. Each data point in the four upper panels is an average across four runs of the adaptive procedure, and the error bars in those panels indicate the corresponding standard errors. The bottom panel shows the mean across listeners, and the error bars in that panel correspond to 1 standard error of the mean across listeners.

(closed squares), AM detection thresholds were significantly larger in the ipsilateral-inducer condition than in the contralateral-inducer condition ($F_{1,3}=252.63$, $p=0.0005$). In the contralateral condition, they were not significantly different from those measured with the unmodulated noise inducer ($F_{1,3}=4.94$, $p=0.1127$), which were not different between the ipsilateral- and contralateral-inducer conditions ($F_{1,3}=0.23$, $p=0.6657$). In contrast, in the ipsilateral-inducer condition, the thresholds measured in the presence of the sine-phase inducer were significantly larger than those measured with the unmodulated noise inducer ($F_{1,3}=261.45$, $p=0.0005$). Thus, like the aftereffect discovered by Rosenblith *et al.*, the modulation-adaptation effect measured in the present study does not transfer across ears.

VI. EXPERIMENT 4: DOES THE EFFECT DISAPPEAR WITH PRACTICE?

A. Rationale and procedure

Although numerous investigators have reported significant adaptation effects in the detection of amplitude or frequency modulation (Kay and Matthews, 1972; Green and Kay, 1973, 1974; Regan and Tansley, 1979; Gardner and Wilson, 1979; Davidson *et al.*, 1981; Cole *et al.*, 1981; Tansley and Suffield, 1983; Wojtczak and Viemeister, 2003, 2005), some results suggest that these effects can substantially diminish (Moody *et al.*, 1984; Wakefield and Viemeister, 1984) and even completely vanish (Bruckert *et al.*, 2006) within the course of a few to several hours of practice. For instance, Bruckert *et al.* (2006) found that a 5-kHz pure-tone carrier inducer modulated at a 16-Hz rate, which initially caused a substantial increase in AM detection thresholds measured with probe tones of the same carrier frequency and modulation rates between 4 and 64 Hz, completely lost its effect during the course of 10–12 h of practice. Although they were observed under testing conditions substantially different from those used in the present study, these findings prompted us to add one additional experiment at the end of this study, in order to check whether the inducer still had a significant effect following the many hours of testing accumulated by the listeners during the course of the previous three experiments.

B. Stimuli and procedure

This experiment involved a single 2-h session, during which AM detection thresholds for 250-Hz AMF probe bursts were measured after exposure to a 100-Hz F0 sine-phase complex tone, using the same procedure as in experiment 1. At the beginning of the session, thresholds were measured four times in the absence of the inducer, in order to obtain a baseline. The stimuli in this experiment were presented diotically. Three of the four listeners who had taken part in experiment 3 could be tested in this final experiment. Thus, prior to beginning this final experiment, all listeners had accumulated at least 14 h of experience with the task (18 h when including the control conditions).

C. Results

The results of experiment 4 are shown in Fig. 4. The first three panels show individual data. Listener 2 performed only 9 runs; listener 3 performed 15, and listener 4 performed 20. The average data, including only the first 9 runs in which data from all subjects are available, are shown in the lower right-hand corner. The data points that are shown on the right part, corresponding to the "avr" mark on the X axis, represent the mean thresholds (across runs) measured in the presence of the sine-phase inducer (closed square) or in quiet (open circle) in this experiment. The rightmost data points, which correspond to the "E1" mark, are replotted from the 250-Hz condition of experiment 1.

When averaged across listeners, thresholds remained fairly constant across repetitions, and no statistically significant variation across repetitions was observed ($F_{8,16}=0.73$, $p=0.5225$). However, some interindividual differences were apparent in the data. While listener 3's thresholds tended to decrease across repetitions, listener 4's thresholds showed a trend in the opposite direction.

When comparing these data to those of the same three listeners in experiment 1 ("E1"), a reduction in effect size is evident. Whereas the average threshold increase in experiment 1 was 8.8 dB (8.1, 9.5, and 8.8 dB for listeners 2–4), in the current experiment, the average attenuation was only

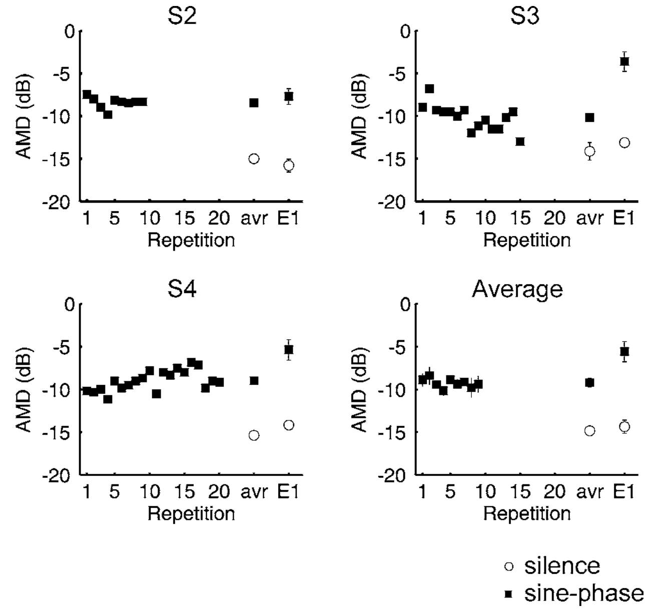

FIG. 4. Amplitude modulation detection thresholds measured in three listeners (2–4) in the presence of a sine-phase pulse train. The data points situated second from the right in each panel correspond to the mean thresholds (across runs) measured in the presence of the sine-phase inducer (closed squares) and in quiet (open circles) in this experiment ("avr"). The rightmost data points replot the two corresponding conditions from experiment 1 ("E1"), for comparison. The lower right panel shows the average across listeners; error bars denote the standard error of the mean across the three listeners.

5.6 dB (6.6, 3.9, and 6.3 dB for listeners 2–4); this corresponds to an average reduction of the effect of approximately 3 dB between the two experiments. This difference was statistically significant ($t=6.65$, $p=0.0219$). Thus, although some effects of learning are evident, the effect remains robust even after 16 h or more of practice.

VII. GENERAL DISCUSSION

A. Summary of results

The main results of this study can be summarized as follows: (1) Following the presentation of a 60-s long pulse train with an average rate of 100 Hz, sinusoidal AM detection thresholds for noise bursts with AM frequencies between 100 and 500 Hz were significantly elevated. (2) Unmodulated noise had no significant effect as an inducer. (3) The elevation in AM detection thresholds induced by a 60-s 100-Hz pulse train decreased over approximately 30 s following the offset of the inducer, after which it was no longer significant. (5) When the inducer and probe were presented to opposite ears, no significant threshold elevation was observed. (6) A significant effect of the inducer was still present in listeners who had received about 16 h practice in the task.

B. Temporal amplitude fluctuations as an essential determinant of the aftereffect

Our use of a relatively low stimulus repetition rate (100 Hz) and a high-pass filter with a relatively high lower cutoff frequency (4 kHz) imposes strong constraints on the factors and mechanisms responsible for the perceptual effects observed in this study. Because the bandwidths of auditory filters with center frequencies above 4 kHz exceed the spacing between consecutive spectral components in a 100-Hz pulse train, these spectral components are not individually resolved in the auditory periphery. This has two important consequences. First, it makes it very unlikely that the results obtained in this study were mediated by spectral cues. Second, the interaction between multiple spectral components within the auditory-filter bandwidths resulted in the auditory-filter outputs fluctuating in amplitude at a rate corresponding to the stimulus F0 or pulse rate. In the following two sections, we discuss how these amplitude modulations may have interfered with the external amplitude modulations imposed on the target probe burst, which the listeners had to detect, and how this may relate to the aftereffect first described by Rosenblith *et al.* (1947).

The finding that the temporally jittered pulse train yielded a significant increase in AM detection thresholds reveals that precise temporal periodicity is not a prerequisite to elicit the aftereffect. The jittered pulse train did not show the same marked high-pass characteristic observed with the periodic inducers, which is compatible with the predictions of an auditory modulation filterbank [see Figs. 1(c) and 1(d)]. On the other hand, in contrast to the predictions of the modulation filterbank, the effect of the jittered pulse train appeared to be somewhat less than that of the periodic sine-phase inducer, although this difference was not statistically significant in our small sample of four subjects. Based on these considerations, we suggest that the effects observed in the present study were mediated by mechanisms, the operation of which was based on relatively fast (100–500 Hz), but not necessarily periodic, amplitude fluctuations in the peripheral auditory responses to the inducer and probe stimuli. Of course, we cannot rule out the possibility that the inducer affects other aspects of perception, which may not involve the coding of rapid temporal fluctuations. Clearly, an exhaustive exploration of the many possible perceptual effects of inducers such as those used here and in the study of Rosenblith *et al.* will require many additional experiments. Exploratory experiments, which we performed in a single listener prior to those described here, showed no evidence for an effect of the pulse-train inducer on either pitch discrimination measured using pulse trains with an F0 close to the inducer, or on detection of identically bandpass filtered noise bursts.

C. Can the effect be explained by AM adaptation?

A possible explanation for the finding of elevated AM detection thresholds following the prolonged presentation of temporally modulated stimuli is in terms of modulation adaptation. Several investigators have found that prolonged exposure to an amplitude- or frequency-modulated tone could cause a temporary impairment in the ability to detect subsequent amplitude or frequency modulation (Kay and Matthews, 1972; Green and Kay, 1973, 1974; Regan and Tansley, 1979; Gardner and Wilson, 1979; Davidson *et al.*, 1981; Cole *et al.*, 1981; Tansley and Suffield, 1983; Moody *et al.*, 1984; Wakefield and Viemeister, 1984; Wojtczak and Viemeister, 2003, 2005). Although this adaptation to modulation has traditionally been studied using pure-tone stimuli, the same phenomenon may have mediated the elevation in AM detection thresholds that was observed here using a noise carrier as a target, and pulse-train inducers, which have significant inherent amplitude modulations. However, there are several differences between the present study and earlier studies on AM adaptation. First, the inherent modulation frequencies in our inducer were all at rates of 100 Hz and above. These rates are substantially higher than those used in earlier studies on AM adaptation, which were usually below 30 Hz, and adaptation effects have been reported to be most prominent around 16 Hz (Tansley and Suffield, 1983). From a phenomenological point of view, amplitude modulations with rates below 30 Hz usually evoke a sensation of flutter; they are effectively perceived as fluctuations in the level of the sound. In contrast, modulations with rates between about 100 and 500 Hz, the range over which the inducer was found to produce a significant elevation in thresholds here, usually evoke a sensation of pitch and/or roughness (Burns and Viemeister, 1976). These phenomenological differences may also reflect, or result in, differences in the underlying adaptation mechanisms.

A second important difference between this study and earlier studies on AM adaptation is that the adaptation observed in our experiments does not appear to transfer across ears. Using frequency-modulated tones, Kay and Matthews (1972) and Green and Kay (1973) found that the adaptation effect transferred largely between the two ears: When the inducer was presented to one ear and the probe to the contralateral ear, the size of the effect was still around 80% of that observed in a condition where inducer and probe were presented to the same ear. This may be a difference between AM and FM adaptation, or may be a result of the different range of modulation frequencies tested. In any case, it suggests the possibility that the effects are mediated by different neural mechanisms, which take place at different levels of the auditory system.

Third, our study showed that adaptation persisted despite considerable exposure and training. This appears to be consistent with early investigations on modulation adaptation, which used subjective measures and reported large and durable effects (e.g., Kay and Matthews, 1972; Green and Kay, 1974; Tansley and Suffield, 1983). However, more recent studies using forced-choice procedures (Moody *et al.*, 1984; Wakefield and Viemeister, 1984; Bruckert *et al.*, 2006) found that the adaptation effect decreased in an orderly fashion across practice sessions; in some cases, after approximately 10–12 h of testing, the effect had completely disappeared (Moody *et al.*, 1984; Bruckert *et al.*, 2006). In contrast, in the present study, despite the different experiments involving approximately 16 h of testing and one of the listeners having even more extensive experience listening to the stimuli, the effect was still present at the end of the study. Although the effect observed in the final experiment was reduced compared to that measured using comparable stimulus conditions in the same three listeners in the first experiment, the finding that the effect is still present after 16 h of training indicates that the effect observed here is less susceptible to practice than that observed in earlier studies on AM adaptation using pure tones at much lower modulation frequencies.

In summary, differences in stimulus characteristics limit direct comparisons between the adaptation effect observed in the present study and those observed in earlier studies on AM adaptation. However, dissimilarities in the characteristics of the adaptation effect observed in this study compared to earlier studies suggest that the form of AM adaptation suggested by the present results is functionally dissimilar from the AM adaptation observed at lower frequencies in earlier studies (Kay and Matthews, 1972; Green and Kay, 1974; Tansley and Suffield, 1983; Wakefield and Viemeister, 1984; Bruckert *et al.*, 2006). The existence of different mechanisms for AM perception at low and high rates has been suggested in different contexts (e.g., Wright and Dai, 1998; Sheft and Yost, 2005). Possibly related neural phenomena could be the decrease of phase locking along the ascending auditory system (Creutzfeld *et al.*, 1980), or the more recent evidence for two separate temporal codes in monkey auditory cortex (Lu *et al.*, 2001) for pulse rates above and below about 20 Hz. It may, for instance, be that modulation rates coded primarily by temporal mechanisms in cortex exhibit different adaptation characteristics from those that are coded by a cortical rate code.

D. Relationship to the Rosenblith *et al.* aftereffect

The stimuli that were found to elevate AM detection thresholds in the present study are similar to those that Rosenblith *et al.* (1947) found to induce a temporary change in the timbre of sounds, and informal listening tests confirmed that they exerted a similar subjective aftereffect. Like Rosenblith *et al.* (1947), we noticed that if the inducer was sufficiently long, the subjective aftereffect could persist for over 10 s; experiment 2 revealed that the aftereffect on AM detection thresholds also took over 10 s to subside. Finally, we confirmed the Rosenblith *et al.* (1947) finding that the subjective aftereffect was not elicited when the inducer was presented to a different ear than the subsequent probe sounds; experiment 3 revealed that the aftereffect on AM detection thresholds did not transfer across ears. Therefore, it seems reasonable to suggest that the subjective aftereffect discovered by Rosenblith *et al.* (1947) is related to the "objective" aftereffect on AM detection thresholds characterized in the present study.

The use of stimuli with specific spectral and temporal characteristics in the present study imposes some new constraints on possible explanations of the timbre modification, which Rosenblith *et al.* (1947) described as an added "metallic" quality. In particular, the present findings suggest that both effects have their origin in the altered perception of temporal envelope fluctuations between about 100 and at least 500 Hz. One possible explanation is that the change in timbre and the elevation in AM detection thresholds are both due to the inducer causing a decrease in AM sensitivity over that range of AM frequencies. It is possible that a subjective attenuation of fast amplitude fluctuations could change the timbre to a metallic quality, by changing the natural roughness of sound to an unnatural quality, which is then perceived as metallic. This might be similar to the slight timbre change sometimes caused by artificial reverberation, which tends to smear the temporal envelope of sounds, thereby effectively low-pass filtering the envelope spectrum. The perception of some listeners, which referred to the aftereffect as "spatial," or "like stepping into another room," might be attributed to a similar association. On the other hand, most sounds take on an unnatural, unpleasant quality, which can be described as "rough," "chopped," or "metallic," when they are amplitude modulated at relatively fast rates. In fact, we noticed in informal listening experiments that recorded speech or environmental sounds with added amplitude modulations in the 100- to 500-Hz range sounded more similar to what the original sounded like when presented immediately after a 100-Hz pulse train inducer. Based on these observations, the auditory aftereffect discovered by Rosenblith *et al.* (1947) may alternatively be due to a form of "persistence," rather than adaptation, in the perception of AM. According to this interpretation, the reason that AM detection thresholds were elevated after the presentation of the inducer is not that listeners were less able to hear the AM imposed onto the target probe burst (as assumed by the "AM adaptation" explanation), but rather that they heard at least one of the other two probe bursts as modulated too, because some of the modulations present in the inducer persisted beyond its termination. The interpretation in terms of persistence is consistent with reports from some listeners, who reported having sometimes had the impression that more than one probe sound in the trial was modulated. Further study is required in order to determine whether adaptation or persistence is actually responsible for the aftereffect.

E. Neural locus?

The neural substrates of visual aftereffects have received substantially more attention than those of auditory aftereffects. The results of several studies in the visual modality indicate selective adaptation at the cortical level as a key mechanism behind various aftereffects (Movshon and Lennie, 1979). For example, the motion aftereffect has been attributed to the adaptation of motion-selective neurons in area V5 (Kohn and Movshon, 2004). However, it should be noted that some visual aftereffects may be explained by adaptation at the retinal level (Barlow and Sparrock, 1964). As mentioned earlier, neural correlates of the Zwicker tone have been proposed at the cortical level in both humans (Hoke *et al.*, 1996, 1998) and cats (Norena and Eggermont, 2003). Psychophysical results alone cannot precisely pin down the neural locus of the Rosenblith *et al.* aftereffect, or that of AM adaptation. The observation that the effect of the inducer in both the present study and that of Rosenblith *et al.* was strongly ear-specific might suggest a fairly peripheral neural locus, prior to binaural integration. Neurons that exhibit bandpass tuning to AM have been described as early as in the ventral cochlear nucleus (Møller, 1972; Frisina *et al.*, 1990). Such neurons might also mediate selective adaptation to AM. On the other hand, we cannot rule out the possibility that selective adaptation effects in the AM domain originate at a higher level of processing in the auditory system, where neural responses may be selective to spatial location, rather than simply ear of entry. For example, selective adaptation to AM has been demonstrated in the auditory cortex (Barlett and Wang, 2005). At this point, further insights may be gained from physiological studies into the underlying mechanisms of those effects.

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[1]On the first triplet, listener 3 was unable to detect the AM above chance level in any of the AM depth conditions tested. The corresponding data point was artificially set to an AMD of 6 dB, the highest modulation depth tested. The threshold AMD measured in the absence of the inducer in this listener was 14 dB, yielding an estimated attenuation of 8 dB, as plotted in the graph.

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