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Transfer of learning across durations and ears in auditory frequency discrimination

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Frequency-discrimination thresholds (FDTs) for 1-kHz tone pips with durations of 40, 100, and 200 msec were measured in the left and right ears of 10 normal-hearing listeners, before and after six 2-h frequency-discrimination training sessions involving, exclusively, the 200-msec duration and the right ear. In the trained ear, highly significant improvements in FDTs were observed at all durations. Further inspection of the data suggested complete generalization between 200 and 100 msec, but not at 40 msec. Post-training FDTs were not found to differ between the two ears for the two untrained durations, but proved significantly smaller in the right (trained) than in the left (untrained) ear at the trained (200-msec) duration only. A control experiment involving 10 additional subjects allowed us to establish the absence of intrinsic differences in pretraining FDTs between the right and left ears. Overall, these findings indicate that frequency-discrimination learning generalizes widely across stimulus durations and across ears, but that part of the improvement is specific to the range of durations and to the ear used in training.

Several previous studies have shown that performances in a variety of perceptual tasks can improve with practice. In the visual modality, marked improvements in performance have in particular been demonstrated for vernier acuity (Beard, Levi, & Reich, 1995; Fahle, Edelman, & Poggio, 1995; McKee & Westheimer, 1978; Poggio, Fahle, & Edelman, 1995; Saarinen & Levi, 1995), spatial frequency discrimination (Fiorentini & Berardi, 1980, 1981), orientation discrimination (Karni & Sagi, 1991; Vogels & Orban, 1985), texture discrimination (Karni & Sagi, 1993), and motion discrimination (Ball & Sekuler, 1982, 1987). In the somatosensory modality, improvements in tactile-discrimination performance over time have been reported (Sathian & Zangaladze, 1997; Spengler et al., 1997).

In spite of the important role played by the auditory modality in humans, relatively little is known at present about how performance in basic perceptual auditory tasks improves with practice. Although most of the numerous existing publications on auditory perception specify that subjects received training in the task before actual data collection, the authors have very rarely provided detailed information on how performance improved during the training period. Furthermore, even if they had provided it, this information would most of the time be hard to interpret since psychoacoustic investigations often involve listeners with previous experience in psychoacoustic tests—sometimes, being the authors of the study themselves—rather than naive subjects. On the other hand, the number of publications devoted specifically to the influence of practice on perceptual auditory performance has remained surprisingly small in comparison with the large number of questions that are still unanswered in this area. Basically, leaving aside studies devoted to auditory learning in speech perception (e.g., Bradlow, Pisoni, Akahane-Yamada, & Tohkura, 1997), only a few studies have been devoted specifically to perceptual auditory learning for detection (Gundy, 1961; Zwislocki, Maire, Feldman, & Rubin, 1958) and discrimination in frequency (Campbell & Small, 1963; Demany, 1985; Wyatt, 1945) or duration (Wright, Buonomano, Mahncke, & Merzenich, 1997) of pure tones presented either in isolation or as part of complex temporal sequences (Leek & Watson, 1984; Spiegel & Watson, 1981; Watson, Kelly, & Wroton 1976; for a re-

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view, see Watson, 1980). Scarce information is also available in the literature regarding practice effects on auditory localization (Hofman, Van Riswick, & Van Opstal, 1998; Recanzone, 1998) and timbre perception (Bech, 1993). Thus, only very scarce information is currently available in the literature regarding what aspects of perceptual auditory performance improve significantly with practice, what the extent is of these improvements, how much practice in a given task is necessary before performance stabilizes, what conditions are required for performance to change, whether these changes affect other aspects of auditory perception, as well as many other fundamental questions. Answering such questions is important for several reasons. Besides being helpful in the design of future auditory perception studies, answers to these questions could lead to the development of new training programs (or to the improvement of existing ones) designed to rehabilitate those individuals with perceptual auditory deficit (e.g., Merzenich et al., 1996; Tallal et al., 1996). Furthermore, the answers could significantly improve our understanding of the underlying mechanisms of auditory perception in humans. In particular, studies on the transfer of perceptual learning across tasks or stimuli could provide valuable information regarding whether different aspects of auditory perception share a common basis or not (e.g., Grimault, Micheyl, Carlyon, & Collet, 2002).

In this context, the present study was first of all performed with the general aim of further documenting some of the effects of practice on frequency discrimination. Frequency discrimination, which refers to the ability to detect fine differences in frequency between successive tones, has been the object of numerous studies during the past 50 years, and it probably is the aspect of auditory perception for which practice effects have been the most largely studied. Several investigators have noted that the performance of inexperienced listeners in frequency-discrimination tasks increases drastically with practice (Campbell & Small, 1963; Demany, 1985; Harris, 1952; Moore, 1973; Turner & Nelson, 1982; Wyatt, 1945). Yet, several important aspects of frequency-discrimination learning remain incompletely documented, if not completely undocumented. In particular, a series of questions relates to the generalization—or transfer—of frequency-discrimination learning across stimuli (i.e., does practice in frequency discrimination with a given stimulus lead to improved performance with stimuli having different characteristics?). So far, the only stimulus dimension across which the generalization of frequency-discrimination learning that has been documented is frequency (Demany, 1985). The results of the study by Demany have demonstrated that frequency discrimination thresholds (FDTs) at 200 Hz improve as much with training at 200 Hz as with training at 360 or 2500 Hz, thus suggesting that frequency-discrimination learning transfers widely across frequencies.

In the present study, transfer of learning in frequency discrimination across a second potentially important stimulus dimension—namely, duration—was investigated, together with another interesting question about frequency-discrimination learning—namely, the generalization of learning between the two ears. In a recent investigation, Demany and colleagues (Demany & Semal, in press; Demany, Semal, Maubaret, & Noblia, 2000) found that frequency-discrimination learning with tones presented to a single ear generalized widely to the opposite, untrained, ear. Therefore, a secondary aim in the present study was to further document across-ear transfer in frequency discrimination by comparing the discrimination performance of the untrained ear with that of the trained ear.

EXPERIMENT 1

Subjects

Ten subjects (4 male and 6 female, between the ages of 19 and 24 years) took part in Experiment 1. They were all right handed (means score = 91.98 and *SD* = 18.23 on the Edinburgh handedness questionnaire). None had prior experience in psychoacoustic testing. All were paid an hourly wage for their services.

Procedure

The subjects went through eight test sessions that took place on different days during a total of 4 weeks. The first session was devoted to familiarizing the subjects with the test material and procedures, measuring their hearing thresholds, and collecting initial measures of FDTs for tones with durations of 40, 100, and 200 msec, including 20-msec raised-cosine ramps, in the right and left ears. At each duration and for each ear, the subjects performed three runs of an adaptive psychophysical procedure (detailed below) that converged toward 70.7% correct responses in a variable number of trials, generally around 50. The measurements were performed in a pseudo-randomized order: Namely, although the different duration conditions were tested in a random order varying across subjects, FDT measurements in the left ear began only after completion of right-ear measurements. The six following test sessions were devoted to training in frequency discrimination at the 200-msec duration in the right ear. In each session, the subjects performed 15 runs of the FDT measurement procedure, so that 90 estimates were obtained overall during the training period, which spanned 3 consecutive weeks with two sessions on a different day of the week. The last, posttraining test session was similar to the pretraining session and involved three FDT measurements at each of the three different durations, presented in a random order, which varied across subjects, first in the right ear, then in the left.

The psychophysical procedure used for FDT measurements was a three-interval, two-alternative, forced-choice (3I-2AFC) procedure. On each trial, the subject heard three successive tones: a first tone having a fixed frequency of 1000 Hz followed by two tones, one that had the same frequency and one that had a frequency at 1000 + df Hz, where df represents a variable frequency increment. The interstimulus interval was 900 msec long.[1] The subject's task was to indicate whether the second or the third tone had a different frequency from the other two. The subjects gave their responses by pressing keys marked "2" and "3" on the computer keyboard. Visual feedback was provided following each response. Owing to a two-down one-up adaptive tracking rule, the variable frequency increment df was divided by 2 or $\sqrt{2}$ after two consecutive correct responses and multiplied by 2 or $\sqrt{2}$ after each incorrect response; the $\sqrt{2}$ factor was used after the fourth reversal in the direction of df size change. The procedure stopped after 16 reversals in the variation of df. The FDT was computed as the geometric mean of FDTs over the last 12 reversals.[2] The level of the tones was fixed at 50 dB above the subjects' absolute detection threshold for a 1-kHz tone of the corresponding duration in the corresponding ear. Absolute thresholds in these different conditions were collected prior to the initial FDT measurements on the pretraining session, using a 2I-2AFC procedure.

Apparatus

The stimuli were generated digitally in the time domain and output at a sampling rate of 44.1 kHz through a 16-bit digital-to-analog converter. They were delivered to the subject's right or left ear via dynamic stereo headphones (Sony MDR-CD470).

Results

Figure 1 shows the FDTs measured in the right ear on the initial test session. The FDTs represented in this graph were computed as the geometric means across subjects of the geometric mean FDTs across the three runs performed in each condition by each subject; they are thus based on a very large number of responses. These data were analyzed using a two-way repeated measures analysis of variance (ANOVA) with duration and repetition as factors and the log-transformed FDTs as the dependent variable. The results indicated a highly significant main effect of duration [$F(2,18) = 12.8$, $p = .0003$]. An HSD Tukey test revealed that the FDTs measured using tones of 100 and 200 msec were not significantly different ($p = .42$), but differed significantly from those measured at 40 msec ($p = .0055$ for 40 vs. 100 msec, and $p = .00044$ for 40 vs. 200 msec).

Figure 2 represents the FDTs obtained during the training sessions, as a function of the run number (i.e., the geometric mean FDTs measured during each of the six training sessions). These data were analyzed using a two-way ANOVA, with the log-transformed DLF as the dependent variable and the session and run numbers as within-subjects factors. The results revealed highly significant main effects of the session [$F(5,45) = 5.80$, $p < .001$] and run [$F(14,126) = 5.14$, $p < .001$] and a significant interaction between the two [$F(70,630) = 1.39$, $p < .05$].

In order to check whether the visible trend on the graph for DLFs to improve over the first four sessions but not over the last two was statistically significant, a contrast analysis was performed. The results indicated that the effect of the *run* factor was significantly different between the first four and the last two sessions [$F(1,9) = 13.90$, $p < .005$]. When the data of the first four sessions were analyzed separately, significant differences were found across runs [$F(14,126) = 5.87$, $p < .00001$] and almost across sessions [$F(3,27) = 2.83$, $p = .056$]. With the data of the last two sessions, neither of these two factors had any significant effect.

As revealed by the individual learning curves plotted in Figure 3, there were substantial differences across subjects, not only in overall performance levels, but also in the rate of improvement across sessions and in the over-

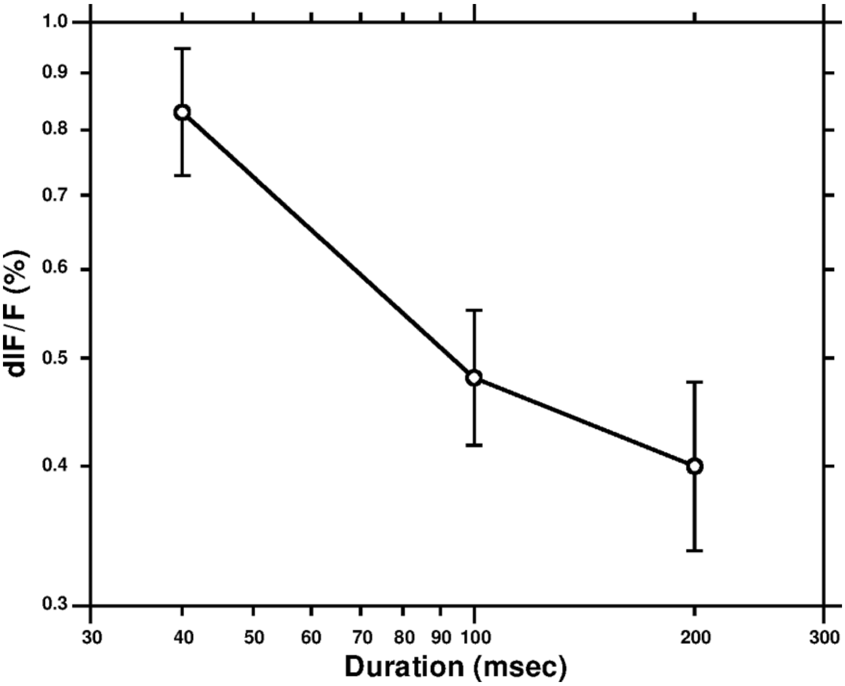

Figure 1. Pretraining frequency-discrimination thresholds (FDTs) as a function of stimulus duration in the right ear. The thresholds are expressed as a percentage of the test frequency. Each datapoint corresponds to a geometric grand average computed across the 10 listeners and the three runs per condition measured for each listener. The error bars represent the geometric standard errors across these geometric mean FDTs; the geometric standard errors were computed as 10 raised to the power of the standard error of the log-transformed FDTs.

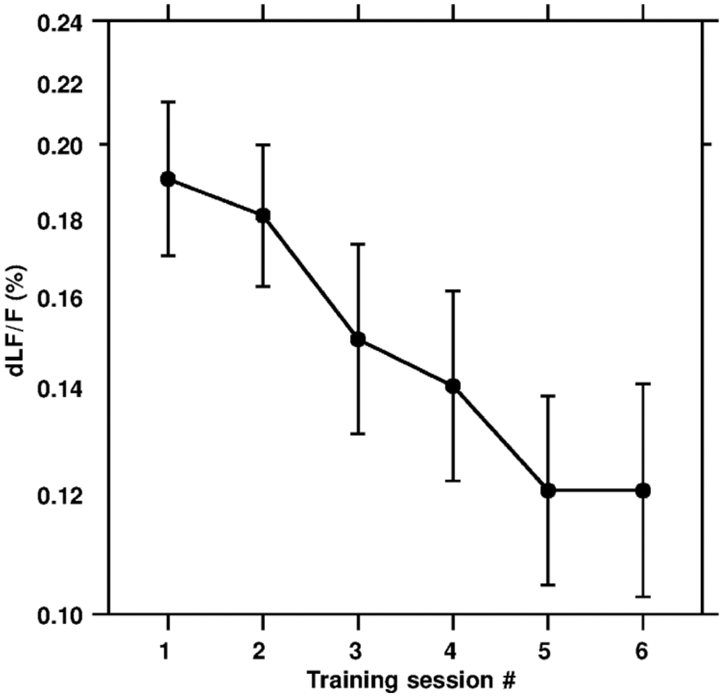

Figure 2. Frequency-discrimination thresholds (FDTs) as a function of the training session. The thresholds are expressed as a percentage of the test frequency. Each datapoint corresponds to a geometric grand average computed across the 10 listeners and the 15 runs obtained for each listener on each training session. The error bars represent the geometric standard errors across these geometric mean FDTs.

all amount of improvement between the first and last training sessions.

Figure 4 shows the relative variations in the FDTs measured in the right ear between the first and the last test sessions at the different stimulus durations. Overall, the log-transformed FDTs proved to be significantly different between the two sessions, as reflected by a very significant session effect [$F(1,9) = 65.42$, $p = .00002$]. An HSD Tukey test revealed that the FDTs measured using tones of 200 msec—the duration used for training—were significantly smaller in the post- than in the pretraining session ($p = .00015$); at this duration, FDTs decreased by about 68% between the two sessions. Moreover, a significant difference was found for the two stimulus durations that were not used in training, with a decrease reaching 51% at 40 msec ($p = .0002$) and 66% at 100 msec ($p = .00016$). As indicated by a significant interaction between duration and session [$F(2,18) = 4.14$, $p = .033$], the variations in FDTs induced by training were not similar at all stimulus durations. As reflected in the results of planned comparisons, the FDT improvement was smaller for short- than for long-duration tones [$F(1,9) = 7.05$, $p = .026$], but not different between the two longest durations [$F(1,9) = 0.10$, $p = .75$].

Figure 5 shows the FDTs obtained in the right and left ears on the posttraining session. A three-way repeated measures ANOVA with the log-transformed FDTs as the dependent variable and the ear tested, the duration, and the repetition as factors revealed a difference between the FDTs obtained in the trained and the contralateral ears [$F(1,9) = 5.33$, $p = .046$]. The ear × duration interaction just failed to reach the statistical significance threshold [$F(2,18) = 3.30$, $p = .059$]. Post hoc comparisons revealed no significant difference in FDTs between the two ears in the two untrained duration conditions—namely, 40 msec ($p = .99$) and 100 msec ($p = .96$); in contrast, FDTs measured at the duration used for training (200 msec) proved to be significantly smaller in the trained than in the untrained ear ($p = .014$).

Discussion

Several previous studies have shown that the ability to detect small differences in frequency between successive tones improves markedly with practice over several hours, days, or even months, depending on the intensity of the training (Campbell & Small, 1963; Demany, 1985; Harris, 1952; Moore, 1973; Turner & Nelson, 1982; Wyatt, 1945). The results obtained by Campbell and Small indicated that FDTs measured for 800-msec long tones at 2 kHz using a 2AFC procedure were divided by a factor of about 2, on average after 6 consecutive days of training, corresponding to about 3,900 trials. In their study,

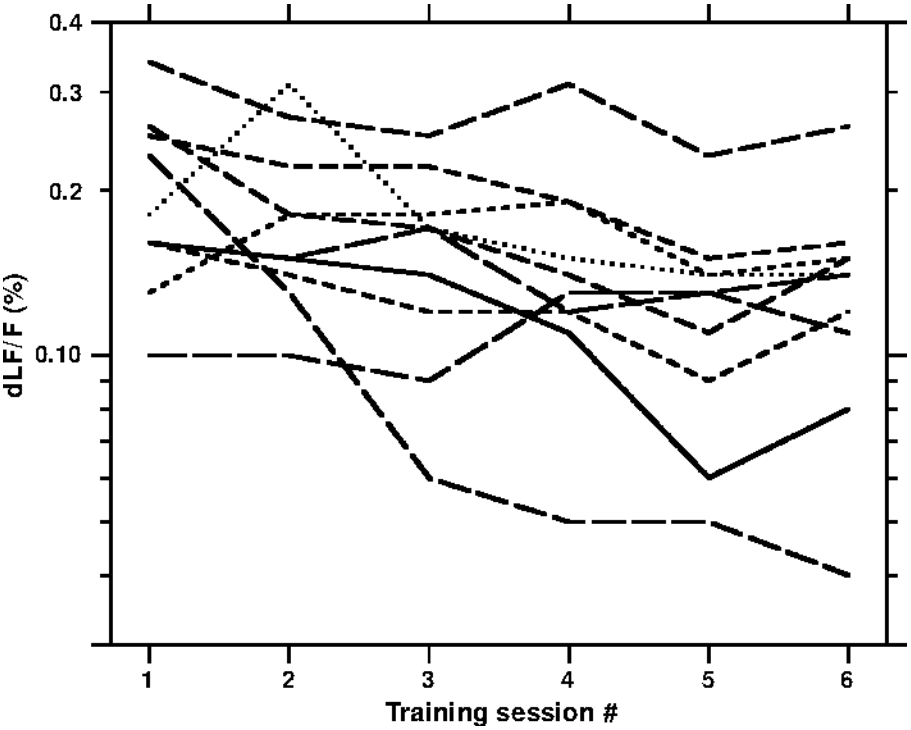

Figure 3. Individual learning curves. The different line types correspond to different subjects. For each subject, the line segments connect the geometric mean frequency-discrimination thresholds obtained on successive training sessions, from the first to the sixth.

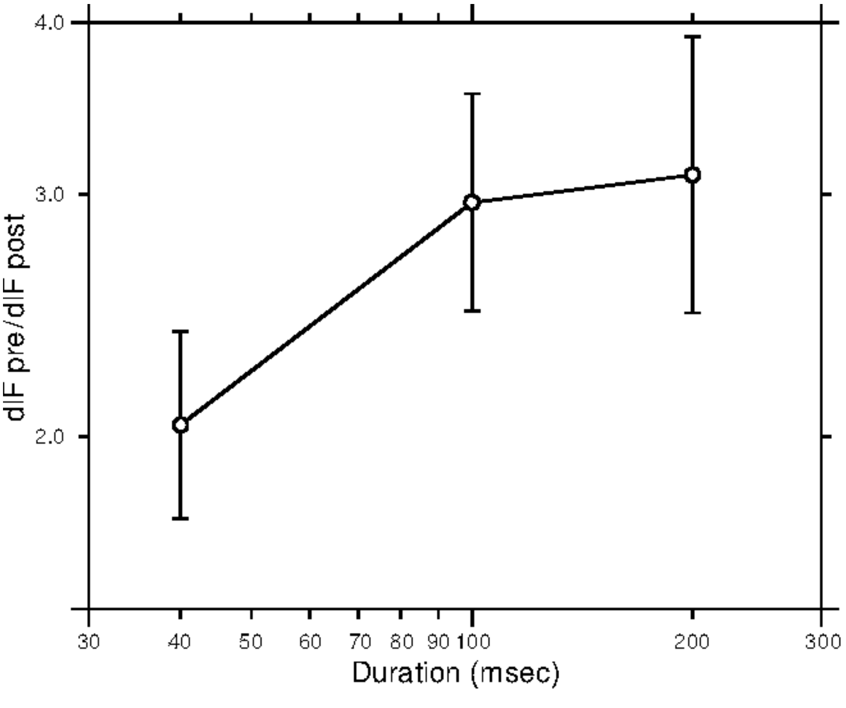

Figure 4. Variations in frequency-discrimination thresholds (FDTs) between the pre- and the posttraining sessions. Each datapoint was obtained by dividing the relative FDTs obtained in a given condition on the pretraining session by the FDTs obtained in the same condition on the posttraining session. As in previous figures, FDTs were expressed as a percentage of the test frequency and geometrically averaged across listeners and runs within conditions. The error bars represent the geometric standard errors across the computed FDT ratios.

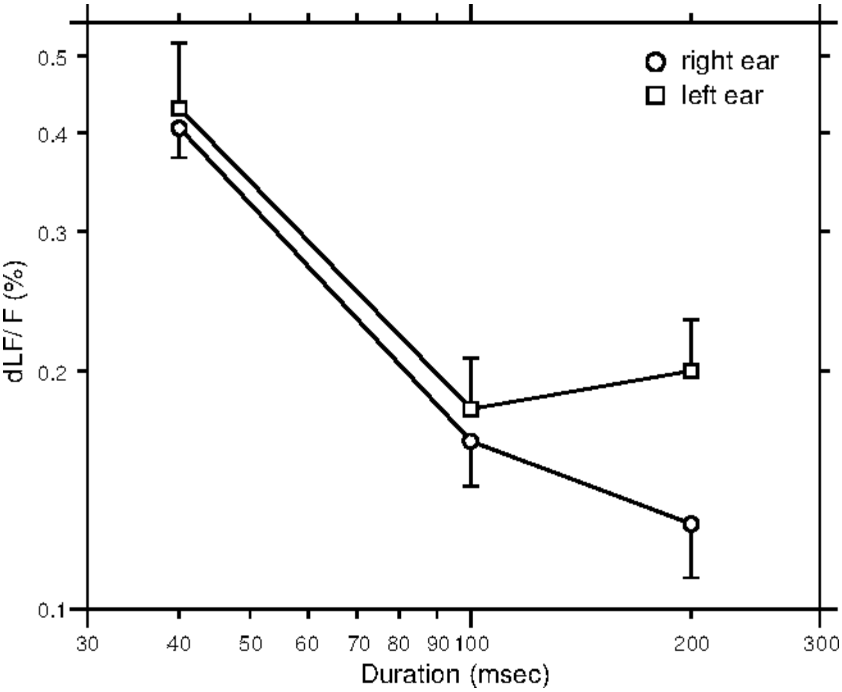

Figure 5. Posttraining frequency-discrimination thresholds (FDTs) in the right and left ears. The thresholds are expressed as a percentage of the test frequency. Each datapoint corresponds to a geometric grand average computed across the 10 listeners and the three runs per condition measured for each listener. The error bars represent the geometric standard errors across the geometric mean FDTs; the geometric standard errors were computed as 10 raised to the power of the standard error of the log-transformed FDTs.

an asymptote was reached after about 4 h of training, which corresponded to approximately 2,600 trials. Watson (1980) later reported that between 1,600 and 4,200 trials were necessary for frequency-discrimination performance to reach an asymptote. Demany found FDTs for tones at 360 and 2500 Hz—the test frequencies closest to the 1-kHz frequency used here—to be roughly halved over 10 blocks of 70 trials corresponding to two 75-min sessions separated on average by 2 days. In the present study, FDTs were monitored over more than six sessions of approximately 2 h each, spanning 3 weeks. Over this period, they were found to decrease by 68% on average. Overall, when plotted on a logarithmic scale, FDTs were found to follow a grossly linear decreasing trend. Only toward the very end of the training period (i.e., over the last two sessions) did they appear to reach a plateau. Assuming that the listeners performed an average of 50 trials per run, including the pretraining session, it can be estimated that performance stabilized on average after about 3,150 trials with stimuli presented in the trained ear at the trained duration.

Transfer of learning across durations. An important outcome of the present study is that although listeners were trained using only one ear and one stimulus duration, FDTs measured at other durations and/or in the other ear were significantly smaller in the post- than in the pretraining session. This finding indicates that learning in frequency discrimination generalizes across stimulus durations and between the two ears. An important question concerns whether the observed transfer of learning across durations and ears was complete or partial. In order to prove unequivocally that the transfer was complete, one would have to demonstrate that the improvement observed in the untrained conditions (or ear) was as large as if the listeners had been trained in these conditions (or this ear). Because this information cannot be obtained within the same subjects, one would have to resort to comparisons between different groups of subjects trained in different conditions. This was not done in this study. However, some indication as to whether frequency-discrimination learning transferred completely or not across durations can be inferred from a comparison between the present results and data in the literature. The results from a previous study by Moore (1973) indicate that in trained listeners, the FDTs for 1-kHz tone pips are on average equal to about 0.15% of the center frequency for 100- and 200-msec long tones, which compares well with the FDTs obtained in the present study—0.13% at 100-msec and 0.16% at 200-msec tones. At 50 msec, the average FDT was about 0.20% in the Moore study, substantially smaller than the 0.40% average in our study. This suggests that the smaller improvement observed in the 40-

msec condition in the present study does not simply reflect an inherent limitation in frequency-discrimination learning at this short duration—as would be the case if learning effects were overall smaller or slower for short than for long tones. Rather, it appears that in the trained ear, frequency-discrimination learning transferred entirely from the 200- to the 100-msec condition, but only partially to the 40-msec condition.

A first possible interpretation of this duration dependence of learning transfer is that frequency discrimination involves qualitatively different underlying neural mechanisms, depending on whether the tones are short or long. Traditionally, two mechanisms have been hypothesized to be involved in the coding of frequency in the auditory system: a place-based encoding mechanism that relies on the fact that stimuli with different frequencies elicit different spatial patterns of responses in the peripheral auditory system and a temporal encoding mechanism that is related to the fact that up to about 4–5 kHz, auditory nerve fiber discharges are phase locked to the input waveform, so that the time intervals between successive spikes are integer multiples of the stimulus period (Rose, Brugge, Anderson, & Hind, 1968). Physiological data and models (see Geisler & Sinex, 1982; Goldstein & Srulovicz, 1977; Siebert, 1968) indicate that at frequencies lower than about 4–5 kHz, the temporal encoding of stimulus frequency is generally more accurate than the place code and can account for the very small FDTs measured in human subjects (Moore, 1973), whereas the place code cannot. However, the accuracy of statistical estimates of stimulus frequency derived from temporal information decreases rapidly at short durations, since only a few cycles are present in the stimulus waveform. If temporal encoding is effectively more accurate than place encoding at long durations, but less accurate at short durations, it is conceivable that in order to achieve optimal discrimination performance in all circumstances, the central nervous system relies on the former mechanism with long stimuli and on the latter with short stimuli. The finding of limited transfer of frequency-discrimination learning between long and short tones might thus be explained by the fact that practice in frequency discrimination with long-duration tones produced a selective improvement in the functioning of the temporal encoding mechanism, which had little effect at short durations because at these durations, frequency discrimination primarily relies on a different encoding mechanism.

The hypothesis that frequency-discrimination training can differentially affect place-based and temporal encoding mechanisms is supported by results from Demany (1985), which showed that training in frequency discrimination at 6000 Hz did not generalize to 200 Hz, whereas training at frequencies below 4–5 kHz did generalize widely to 200 Hz. Demany interpreted this finding as a possible result of the fact that, as suggested by psychophysical (Moore, 1973) and electrophysiological (Rose et al., 1968) data, frequency discrimination is subtended by a temporal mechanism at low (<5 kHz) frequencies and a place mechanism at high (>5 kHz) frequencies. To the extent that frequency discrimination relies on a temporal mechanism at long (100- and 200-msec) durations and on a place mechanism at short (40-msec) durations, the present results can be viewed as another argument for the notion that frequency-discrimination training can affect, selectively, the underlying mechanisms of frequency encoding in the auditory system.

Although the interpretation above is appealing, it relies entirely on the hypothesis that frequency discrimination involves different mechanisms for short and long tones. However, there exist psychoacoustical data and physiologically plausible model results that indicate that FDTs measured at short and long durations can be accounted for by the operation of a unique mechanism, be it placed based (Freyman & Nelson, 1986, 1987) or temporal (Hanekom & Krüger, 2001; Micheyl, Moore, & Carlyon, 1998). Therefore, it is worth considering alternative interpretations. Another possible cause for the different transfer effect at 100 and 40 msec is that frequency discrimination involves the same kind of mechanism at all durations, but that tones having different durations excite different, yet overlapping, neural populations and that the neural population activated by 200-msec tones overlaps more with that activated by 100-msec tones than with that activated by 40-msec tones. Then, to the extent that training at 200 msec selectively affected the neural population activated by 200-msec tones, one could predict a larger learning transfer for 100-msec tones than for 40-msec tones, without having to assume different underlying mechanisms. A possible reason for greater overlap between the neural populations activated by 100- and 200-msec long tones than between those excited by 100- and 40-msec long tones might reside in the fact that the physical power spectrum of a pure tone broadens as duration decreases. At relatively long durations such as 100 and 200 msec, where the spectrum slopes are much steeper than that of peripheral auditory filters in the considered frequency range (i.e., around 1000 Hz), differences in duration are not reflected by dramatic changes in peripheral excitation patterns. However, as duration decreases further, the spectrum slope eventually becomes shallower than that of auditory filters, and the pattern of excitation elicited in the peripheral auditory system becomes substantially different from that obtained at longer durations. However, simulated peripheral excitation patterns computed by using the equations described in Glasberg and Moore (1990) for tone durations of 40, 100, and 200 msec prove to be very similar; only at shorter durations, like 10 msec, does the excitation pattern shape become widely different from that evoked by the 200-msec duration tone. Therefore, it appears unlikely that the failure of frequency-discrimination learning to generalize entirely between 200- and 40-msec tones can be explained by the differences in the patterns of excitation evoked by these tones in the peripheral auditory system.

Nevertheless, the auditory periphery system is only the first stage of a long chain of processes, and it may well be the case that more central responses to such short and long tones do differ substantially. The results of the present study do not allow us to distinguish between the two interpretations above or to decide whether frequency discrimination is subtended by qualitatively different neural mechanisms for short and long durations, or whether short- and long-duration tones, although being discriminated in frequency through a unique mechanism, mainly excite different neural populations.

Transfer of learning across ears. In regard to the transfer of learning between ears, the results of Experiment 1 showed that following training, FDTs were overall as small in the left, untrained ear as in the right, trained ear. This finding of learning transfer between ears for auditory frequency discrimination can be paralleled with the findings of learning transfer between eyes for various visual tasks (Ball & Sekuler, 1987; Berardi & Fiorentini, 1987; Schoups & Orban, 1996) and between hands for tactile discrimination (Sathian & Zangaladze, 1997; Spengler et al., 1997).

A first possible interpretation for the existence of across-ear learning transfer is that the improvements observed in the untrained ear simply reflect learning of the task and/or test procedure, which does not depend on the stimulus presentation side. Accordingly, the finding that the posttraining FDTs were as small in the untrained as in the trained ear at the two untrained durations suggests that, at these untrained durations, the improvements seen in the two ears resulted entirely from procedural learning. On the other hand, the fact that, at the trained duration, the posttraining FDTs remained significantly larger in the untrained ear supports the notion that some of the improvement obtained at the training duration in the trained ear was caused by genuine sensory learning processes that are ear specific. These conclusions are not consistent with that reached above, on the basis of the results shown in Figure 5 and the comparison of the posttraining FDTs with data in the literature, according to which part of the improvement at 100 msec in the trained ear reflects the transfer of true sensory learning.

An alternative interpretation of the observed transfer of frequency-discrimination learning across ears is that the neural units that process frequency differences are not different for the right and left ears, which requires that these units be located at a stage of the auditory system that receives binaural inputs—thus, above the level of the cochlear nucleus—and be insensitive to the ear in which the stimuli are presented. If one assumes once again that the frequency-discrimination abilities of the two ears are normally similar, the finding that posttraining FDTs were significantly smaller in the right (trained) ear than in the left (untrained) ear for the 200-msec (trained) duration indicates that although practice in frequency discrimination transferred widely to the opposite ear, part of the improvement in frequency-discrimination performance was specific to the trained ear.

Whichever of the two interpretations above is considered, the conclusion reached on the basis of the present results is that frequency-discrimination learning transfers widely, but not entirely, across ears. In a recent study, Demany and colleagues (Demany & Semal, in press; Demany et al., 2000) also showed a large generalization of frequency-discrimination learning across the ears but failed to show any significant improvement in the ear-specific component of the performance. Thus, although these authors did not reject the possibility that some weak ear specificity existed, their results left open the possibility of complete transfer of learning across ears.

One problem with our interpretation of the left/right differences in posttraining FDTs at 200 msec as reflecting incomplete transfer of frequency-discrimination learning between ears comes from the fact that it relies entirely on the assumption of normally identical FDTs in the left and right ears. This assumption sounds reasonable given, first, that the posttraining FDTs were indeed not different between the two ears at the two untrained durations and, second, that in the extensive psychoacoustical literature devoted to frequency discrimination, there is to our knowledge no report of significant ear differences in frequency discrimination for monaurally presented pure tones in normal-hearing subjects. However, absence of demonstration is not demonstration of absence, and the possibility remains that the right-ear advantage for frequency discrimination with 200-msec tones observed on the posttraining session reflects an intrinsic superiority of the right ear for the processing of long-duration tones. If it is the case that the right ear is intrinsically superior to the left ear for the frequency discrimination of long-duration tones, FDTs measured with 200-msec tones should already be smaller in the right than in the left ear before training. Unfortunately, comparison of pretraining performance between the two ears was obscured by our choice in Experiment 1 in order to systematically test the right ear before the left—based on the fact that our primary aim was to investigate transfer of frequency-discrimination learning across durations rather than across ears in this study. Therefore, we carried out a control experiment consisting of the measurement of pretraining FDTs for 10 additional subjects who went through the same pretraining measurements as the 10 subjects from Experiment 1, except for the fact that their left rather than their right ears were systematically tested first. We reasoned that if, after collapsing the data of these two subject groups, FDTs measured using the 200-msec tones proved not to be different between the two ears, we would have gone some way toward disproving the *intrinsic ear asymmetry* hypothesis.

EXPERIMENT 2

Subjects

This second, control experiment involved 10 new subjects (4 male and 6 female, between the ages of 18 and 22 years; $M = 19.9$, $SD = 1.59$). Like those in Experiment 1, these subjects were all right handed (means score = 79.3 and $SD = 16.36$ on the Edinburgh hand-

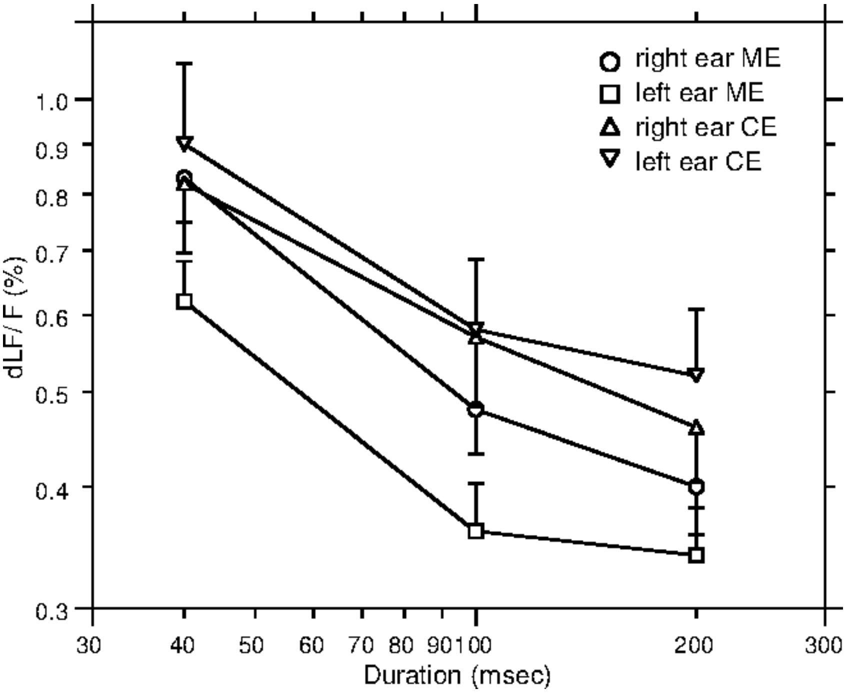

Figure 6. Pretraining frequency-discrimination thresholds (FDTs) as a function of stimulus duration in the right and left ears for the main experiment subjects (ME) and the control experiment subjects (CE). The thresholds are expressed as a percentage of the test frequency. Each datapoint corresponds to a geometric grand average computed across the 10 listeners of each group and the three runs per condition measured for each listener. The error bars represent the geometric standard errors across these geometric mean FDTs, computed as 10 raised to the power of the standard error of the log-transformed FDTs.

edness questionnaire) and had no prior experience in psychoacoustic testing. They were paid an hourly wage for their services.

Procedure

The 10 additional subjects who were involved in this control experiment took part in a single test session that was similar to the pretraining session of Experiment 1, except for the order of testing of the two ears: In contrast to what was done in Experiment 1, in this experiment, the left ear was systematically tested before the right ear.

Results

Figure 6 shows the mean FDTs measured for the different stimulus durations in the right and left ears of the subjects who were tested at all durations in the right ear first and of the subjects who were tested at all durations in the left ear first. The FDTs generally appeared to be smaller, if only slightly, in the ear that was tested second than in the ear that was tested first. This difference between the first- and second-tested ears appeared at first sight to be larger in the subjects from the first experiment who were tested in the right ear first than in subjects from the second experiment who were tested in the left ear first.

Overall (i.e., with the data of all subjects pooled together), no statistically significant difference was noted between the two ears [$F(1,18) = 1.87, p = .19$]. No influence of the order of testing of the two ears was observed either [$F(1,18) = 0.95, p = .34$]. Nevertheless, a significant interaction was obtained between ear and ear-testing order (i.e., group) [$F(1,18) = 6.33, p = .021$], indicating that the order in which the two ears was tested had an influence on the differences between the two ears. In fact, a significant difference between the two ears was observed in the first group only [$F(1,9) = 6.06, p = .036$]. In the second group, it failed to reach the 0.5% statistical threshold [$F(1,9) = 0.87, p = .37$].

In order to get further insight into this interaction, planned comparisons between the ear differences in FDTs obtained in the two subject groups were carried out at each of the different durations. These comparisons just failed to reveal a statistically significant difference for the ear differences in FDTs between the two groups for the 40-msec duration [$F(1,18) = 4.21, p = .055$] and showed no significant difference at the two longer durations [$F(1,18) = 1.76, p = .20$ at 100 msec, and $F(1,18) = 1.43, p = .25$ at 200 msec].

Discussion

When one considers the data of the subjects tested in the right ear first and of the subjects tested in the left ear first overall, no significant difference in FDTs between the two ears was observed. The observation of significantly smaller FDTs in the left ear in the pretest session for the subjects who took part in the first experiment appears to be due, not to an intrinsic difference in the frequency-discrimination performance between the two ears—since this effect was not observed in the control group—but to the fact that this ear was systematically tested after the right ear. It is likely that the observed left-ear superiority observed in Experiment 1 resulted from the fact that the left ear benefited from the prior training in the right ear during the course of the first session. This beneficial effect might have resulted either from a genuine transfer of learning between the two ears or, more simply, from procedural learning, which is unlikely to depend on the test ear.

The rather surprising finding, in the control experiment, that the subjects who were tested in the left ear first did not show such a transfer of learning to the opposite ear during this initial session can be interpreted in several ways. A first interpretation is that this simply stems from intersubject differences in the time course of procedural learning effects. Namely, the subjects involved in Experiment 2 did perhaps require on average more practice than the subjects in Experiment 1 to become familiar with the task, so that they had not improved as much during the training in the first ear before testing in the other ear began. On the other hand, they were perhaps fully familiar with the test procedure well before testing in the first ear ended, so that the average FDTs measured in this first-tested ear had already benefited from the procedural learning effect. The observation that the FDTs measured for the subjects in Experiment 2 were generally above those measured for the subjects in Experiment 1 favors the preceding scenario. Another possible interpretation of the observed difference in the influence of ear testing order is that the transfer of frequency-discrimination learning across ears depends on which ear is tested first. However, at present, there are no data in the literature to support this interpretation.

Finally, it is important to acknowledge the fact that although we have gone some way toward testing for intrinsic differences in frequency-discrimination abilities between the left and right ears in Experiment 2, we have certainly not fully explored this possibility. It is indeed possible that intrinsic differences between the two ears do not show up at the level of pretraining performance but would be apparent in posttraining performance. The only way to fully explore this possibility would be to redo the present study, having the subjects be trained in the left ear, collapsing the data of all subjects, including those trained in the right ear, and then comparing posttraining FDTs in the left and right ears. We chose not to do so in the present study for two main reasons: First, as explained in the introduction, the primary aim of this study was to test for transfer of frequency-discrimination learning across durations. Second, systematic differences in pure-tone frequency-discrimination performance or frequency-discrimination learning between the right and left ears seemed very unlikely a priori. Nevertheless, on the basis of the results of the present study, we decided to run another long-term study, which, by involving a larger number of subjects, half of which to be trained in one ear and the other half in the opposite ear, should help to provide more definitive answers to the question of whether frequency-discrimination learning transfers partially or completely from the right to the left ear, and vice versa.

CONCLUSION

The results obtained in this study indicate that training in frequency discrimination in the right ear with 200-msec long tones leads to improved performance for tones of other durations—namely, 100 and 40 msec—in the same ear, as well as in the opposite ear. These results indicate that frequency-discrimination learning transfers across durations and ears. However, further examination of the data suggests that although the benefit of learning obtained with 200-msec long stimuli transferred totally to the 100-msec long stimuli, it transferred only partially to the shortest, 40-msec long stimuli. Moreover, posttraining performances were found to be significantly better in the trained than in the untrained ear for the trained duration only. When comparing the pretraining FDTs obtained for the 10 subjects in Experiment 1 who were systematically tested in the right ear first and those measured for the 10 additional subjects tested in the left ear first, no significant difference was observed between the right and left ears; this indicates that there are no intrinsic differences between right- and left-ear frequency-discrimination performance for pure tones. Altogether, these findings indicate that although practice in frequency discrimination generalizes across stimulus durations and ears, part of the improvement is specific to the range of durations and to the ear that is used for training.

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NOTES

1. The choice of this rather large interstimulus interval was motivated primarily by the fact that this study forms part of a bigger, long-term project wherein comparisons between psychophysical and electrophysiological estimates of frequency-discrimination performance in humans are intended and the experimental setup for electrophysiological response measurements requires long interstimulus delays. As discussed later in the article, the frequency-discrimination thresholds that were obtained in the present study by using this unusually long delay proved quite comparable with those obtained in earlier studies in which shorter interstimulus intervals were generally used.

2. The use of geometric instead of arithmetic means, of log-transformed instead of raw frequency-discrimination thresholds (FDTs) for statistical analyses, and of logarithmic rather than linear axes for representing FDTs, was justified by the fact that the underlying perceptual frequency scale is known to be logarithmic like.

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